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What are the 100 most cited fungal genera?

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CONTENTS

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Studies in Mycology 108: 1–411 (2024).

Studies in Mycology

What are the 100 most cited fungal genera?

C.S. Bhunjun[1,2], Y.J. Chen[2], C. Phukhamsakda[2], T. Boekhout[3,4], J.Z. Groenewald[3], E.H.C. McKenzie[5], E.C. Francisco[3,6], J.C. Frisvad[7], M. Groenewald[4], V.G. Hurdeal[1,2], J. Luangsa-ard[8], G. Perrone[9], C.M. Visagie[10], F.Y. Bai[11,12], J. Błaszkowski[13], U. Braun[14], F.A. de Souza[15], M.B. de Queiroz[16], A.K. Dutta[17], D. Gonkhom[1,2], B.T. Goto[16], V. Guarnaccia[18], F. Hagen[3,19], J. Houbraken[3], M.A. Lachance[20], J.J. Li[21], K.Y. Luo[21], F. Magurno[22], S. Mongkolsamrit[8], V. Robert[3], N. Roy[17], S. Tibpromma[23], D.N. Wanasinghe[24], D.Q. Wang[21], D.P. Wei[2,25,26], C.L. Zhao[21], W. Aiphuk[2], O. Ajayi-Oyetunde[27], T.D. Arantes[28], J.C. Araujo[29,30], D. Begerow[31], M. Bakhshi[32], R.N. Barbosa[33], F.H. Behrens[34], K. Bensch[3], J.D.P. Bezerra[28], P. Bilański[35], C.A. Bradley[36], B. Bubner[37], T.I. Burgess[38], B. Buyck[39], N. Čadež[40], L. Cai[11], F.J.S. Calaça[29,30,41], L.J. Campbell[42], P. Chaverri[43,44], Y.Y. Chen[45], K.W.T. Chethana[1,2], B. Coetzee[46,47], M.M. Costa[3], Q. Chen[11], F.A. Custódio[48], Y.C. Dai[49], U. Damm[50], A.L.C.M.A. Santiago[51], R.M. De Miccolis Angelini[52], J. Dijksterhuis[3], A.J. Dissanayake[53], M. Doilom[54], W. Dong[54], E. Álvarez-Duarte[55], M. Fischer[34], A.J. Gajanayake[1,2], J. Gené[56], D. Gomdola[1,2,57], A.A.M. Gomes[58], G. Hausner[59], M.Q. He[11], L. Hou[11,60], I. Iturrieta-González[56,61], F. Jami[62], R. Jankowiak[35], R.S. Jayawardena[1,2,63], H. Kandemir[3], L. Kiss[64,65], N. Kobmoo[8], T. Kowalski[35], L. Landi[66], C.G. Lin[2,53], J.K. Liu[53], X.B. Liu[67,26,68], M. Loizides[69], T. Luangharn[2], S.S.N. Maharachchikumbura[53], G.J. Makhathini Mkhwanazi[46], I.S. Manawasinghe[54], Y. Marin-Felix[70,71], A.R. McTaggart[72], P.A. Moreau[73], O.V. Morozova[74,75], L. Mostert[46], H.D. Osiewacz[76], D. Pem[1,2,57], R. Phookamsak[24], S. Pollastro[52], A. Pordel[77], C. Poyntner[78], A.J.L. Phillips[79], M. Phonemany[1,2,57], I. Promputtha[80], A.R. Rathnayaka[1,2,57], A.M. Rodrigues[81], G. Romanazzi[66], L. Rothmann[82], C. Salgado-Salazar[83], M. Sandoval-Denis[3], S.J. Saupe[84], M. Scholler[85], P. Scott[38,86], R.G. Shivas[64], P. Silar[87], A.G.S. Silva-Filho[88], C.M. Souza-Motta[33], C.F.J. Spies[89], A.M. Stchigel[56], K. Sterflinger[90], R.C. Summerbell[91,92], T.Y. Svetasheva[75], S. Takamatsu[93], B. Theelen[3], R.C. Theodoro[94], M. Thines[95], N. Thongklang[1,2], R. Torres[96], B. Turchetti[97], T. van den Brule[3,98], X.W. Wang[11], F. Wartchow[99], S. Welti[71], S.N. Wijesinghe[1,2,57], F. Wu[49], R. Xu[100,101], Z.L. Yang[27,68], N. Yilmaz[10], A. Yurkov[102], L. Zhao[3], R.L. Zhao[11,12], N. Zhou[103], K.D. Hyde[1,2,54,104*], P.W. Crous[3,10,105*]

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Abstract: The global diversity of fungi has been estimated between 2 to 11 million species, of which only about 155 000 have been named. Most fungi are invisible to the unaided eye, but they represent a major component of biodiversity on our planet, and play essential ecological roles, supporting life as we know it. Although approximately 20 000 fungal genera are presently recognised, the ecology of most remains undetermined. Despite all this diversity, the mycological community actively researches some fungal genera more commonly than others. This poses an interesting question: why have some fungal genera impacted mycology and related fields more than others? To address this issue, we conducted a bibliometric analysis to identify the top 100 most cited fungal genera. A thorough database search of the Web of Science, Google Scholar, and PubMed was performed to establish which genera are most cited. The most cited 10 genera are *Saccharomyces*, *Candida*, *Aspergillus*, *Fusarium*, *Penicillium*, *Trichoderma*, *Botrytis*, *Pichia*, *Cryptococcus* and *Alternaria*. Case studies are presented for the 100 most cited genera with general background, notes on their ecology and economic significance and important research advances. This paper provides a historic overview of scientific research of these genera and the prospect for further research.

Key words: Bibliometric analysis, fungi, highly-cited, Web of Science.

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AJ, Gené J, Gomdola D, Gomes AAM, Hausner G, He MQ, Hou L, Iturrieta-González I, Jami F, Jankowiak R, Jayawardena RS, Kandemir H, Kiss L, Kobmoo N, Kowalski T, Landi L, Lin CG, Liu JK, Liu XB, Loizides M, Luangharn T, Maharachchikumbura SSN, Makhathini Mkhwanazi GJ, Manawasinghe IS, Marin-Felix Y, McTaggart AR, Moreau PA, Morozova OV, Mostert L, Osiewacz HD, Pem D, Phookamsak R, Pollastro S, Pordel A, Poyntner C, Phillips AJL, Phonemany M, Promputtha I, Rathnayaka AR, Rodrigues AM, Romanazzi G, Rothmann L, Salgado-Salazar C, Sandoval-Denis M, Saupe SJ, Scholler M, Scott P, Shivas RG, Silar P, Souza-Motta CM, Silva-Filho AGS, Spies CFJ, Stchigel AM, Sterflinger K, Summerbell RC, Svetasheva TY, Takamatsu S, Theelen B, Theodoro RC, Thines M, Thongklang N, Torres R, Turchetti B, van den Brule T, Wang XW, Wartchow F, Welti S, Wijesinghe SN, Wu F, Xu R, Yang ZL, Yilmaz N, Yurkov A, Zhao L, Zhao RL, Zhou N, Hyde KD, Crous PW (2024). What are the 100 most cited fungal genera? *Studies in Mycology* **108**: 1–411. doi: 10.3114/sim.2024.108.01

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INTRODUCTION

Fungi are a diverse group of eukaryotic organisms that play important roles in numerous biological processes (Pawlowski *et al.* 2012, Antonelli *et al.* 2020). Fungi can be found in a wide range of habitats (Hyde *et al.* 2020c, Apurillo *et al.* 2023, Asghari *et al.* 2023, Gunarathne *et al.* 2024, Thakshila *et al.* 2024), but their actual number is poorly understood. There are estimated to exist between 2 to 11 million species (Tedersoo *et al.* 2010b, Hawksworth & Lücking 2017, Baldrian *et al.* 2021, Lücking *et al.* 2021), but only about 155 000 species have been formally described (Bánki *et al.* 2023). There are approximately 20 000 fungal genera that have been described since the 1690s (Phukhamsakda *et al.* 2022) and about 2 000 new species have been described each year in the past two decades (Cheek *et al.* 2020, Bhunjun *et al.* 2022). Over the years several genera have emerged as being more commonly researched than others, with numerous studies on their biology, ecology, and pathogenicity. This raises the question why some genera have impacted mycology and related fields more than others. Are these genera important pathogens with a large number of studies aiming to better understand the underlying mechanisms of pathogenicity? Are these genera used in the production of various foods and beverages and a better understanding of their physiology and ecology can be vital in the development of new products? Or are these genera more commonly studied as they are a rich source of bioactive compounds with numerous biotechnological applications? Or are they simply occurring on many substrates across the globe? Therefore, there is a need to determine the most researched genera as well as provide insights into various aspects of their biology, ecology, and pathogenicity with prospects for future research.

In this study, the Web of Science database was used to establish which genera are most cited as of December 2021 (Table 1). The 100 most cited genera are presented as case studies with general background, notes on their ecology and economic significance and important research advances. This study provides a valuable resource by highlighting the importance and research trends associated with these genera.

METHODS

The list of fungal genera was selected from Wijayawardene *et al.* (2022) and the 100 most cited genera were determined by searching the Web of Science Core Collection database (http://apps.webofknowledge.com/). The taxon name was used as a query under "Topic" on Web of Science and the genera were ranked according to the summary of citation numbers obtained from the citation report of Web of Science. There were no restrictions on publication type or language, but the period of 2011 to 2021 was selected. All the searches were performed in December 2021. The number of publications and summary of times cited of each genus were retrieved from the citation report. When compiling the list of the top 10 cited articles, publications that only refer to the coincidental use of the name of the genus or species epithet were excluded as well as publications that refer to fungi now placed in other genera. The publication titles, number of publications and number of citations were retrieved and analysed by Excel (2016) and VOSviewer v. 1.6.15 software. The VOSviewer software was also used to retrieve high-frequency words or terms to map the network of keywords for the 25 most cited genera.

CASE STUDIES

In this section, we provide a review of the 100 most cited genera with a general background, ecology, economic significance and important research advances. The genera are listed according to the number of citations, starting from the highest cited genus.

1. *Saccharomyces* Meyen, Arch. Naturgesch. 4 (2): 100. 1838.

Type species: *Saccharomyces cerevisiae* Meyen

Classification: *Ascomycota*, *Saccharomycotina*, *Saccharomycetes*, *Saccharomycetales*, *Saccharomycetaceae.*

Background

Saccharomyces was introduced in 1838 by F.J.F. Meyen for T. Schwann's "*Zuckerpilz*", which was a sugar fungus responsible for fermentation as demonstrated by the fermentation experiments Schwann performed in 1837 (Barnett 1998). Three species, *S. cerevisiae*, *S. pomorum* and *S. vini* were initially proposed by Meyen, with the specific epithets indicating their sources of beer, fermenting apple juice and wine, respectively (Barnett 2004). Reess (1870) described the morphology of *S. cerevisiae* with accurate drawings of the cells, asci and ascospores. Hansen (1883) described the formation and germination of ascospores of *S. cerevisiae* based on the study of pure cultures that he developed in the early 1880s (Barnett 2004).

At present, eight natural species, *S. arboricola*, *S. cerevisiae*, *S. eubayanus*, *S. jurei*, *S. kudriavzevii*, *S. mikatae*, *S. paradoxus*, and *S. uvarum*; and two natural hybrids, *S. pastorianus* (syn. *S. carlsbergensis*) and *S. bayanus*, are included in the genus *Saccharomyces* (Alsammar & Delneri 2020) (Fig. 1). *Saccharomyces pastorianus* is an alloploid hybrid formed by *S. cerevisiae* and *S. eubayanus*, while *S. bayanus* is a triple-hybrid with a genome composed of mainly *S. uvarum* and *S. eubayanus* sequences with introgressions from *S. cerevisiae* (Libkind *et al.* 2011). The hybrid species are sexually infertile and their ascospores are mostly inviable, while the natural species

Table 1. Top 100 cited genera starting with the most cited genus and the number of citations from the Web of Science (WoS) from the period of 2011 to 2021.

Rank	Genera	WoS Citation	Rank	Genera	WoS Citation
1	*Saccharomyces*	>1 000 000	51	*Microsporum*	11 474
2	*Candida*	>500 000	52	*Curvularia*	11 008
3	*Aspergillus*	>400 000	53	*Rhizomucor*	10 915
4	*Fusarium*	363 128	54	*Pyricularia*	10 856
5	*Penicillium*	130 850	55	*Parastagonospora*	10 146
6	*Trichoderma*	117 855	56	*Monascus*	10 083
7	*Botrytis*	103 497	57	*Hanseniaspora*	9 891
8	*Pichia*	102 697	58	*Paracoccidioides*	9 763
9	*Cryptococcus*	95 586	59	*Schizophyllum*	9 725
10	*Alternaria*	73 134	60	*Plasmopara*	9 535
11	*Phytophthora*	69 739	61	*Auricularia*	9 237
12	*Rhizopus*	51 691	62	*Russula*	9 156
13	*Phanerochaete*	50 545	63	*Zygosaccharomyces*	9 140
14	*Colletotrichum*	46 970	64	*Torulaspora*	9 132
15	*Trametes*	46 427	65	*Boletus*	9 078
16	*Rhizoctonia*	46 317	66	*Botryosphaeria*	9 058
17	*Pleurotus*	45 475	67	*Cunninghamella*	8 997
18	*Ganoderma*	44 643	68	*Diaporthe*	8 987
19	*Neurospora*	44 091	69	*Bipolaris*	8 933
20	*Cladosporium*	38 580	70	*Lentinula*	8 733
21	*Yarrowia*	37 460	71	*Erysiphe*	8 683
22	*Agaricus*	34 079	72	*Scedosporium*	8 662
23	*Kluyveromyces*	33 194	73	*Zymoseptoria*	8 661
24	*Mucor*	30 923	74	*Phellinus*	8 392
25	*Verticillium*	30 674	75	*Sporothrix*	8 267
26	*Sclerotinia*	27 698	76	*Macrophomina*	8 240
27	*Rhodotorula*	26 581	77	*Flammulina*	8 218
28	*Beauveria*	26 077	78	*Pseudogymnoascus*	7 988
29	*Puccinia*	25 970	79	*Podospora*	7 890
30	*Cordyceps*	23 831	80	*Amanita*	7 672
31	*Trichophyton*	21 756	81	*Cercospora*	7 493
32	*Metarhizium*	21 615	82	*Lactarius*	7 481
33	*Pythium*	20 902	83	*Lasiodiplodia*	7 394
34	*Funneliformis*	20 832	84	*Exophiala*	7 344
35	*Ustilago*	20 809	85	*Monilinia*	7 268
36	*Rhizoglomus*	17 651	86	*Coccidioides*	6 936
37	*Acremonium*	17 481	87	*Melampsora*	6 915
38	*Chaetomium*	16 519	88	*Antrodia*	6 910
39	*Paecilomyces*	16 324	89	*Brettanomyces*	6 693
40	*Trichosporon*	15 922	90	*Ascochyta*	6 690
41	*Malassezia*	15 632	91	*Epichloe*	6 496
42	*Phoma*	15 402	92	*Pyrenophora*	6 439
43	*Thermomyces*	15 013	93	*Hymenoscyphus*	6 420
44	*Lentinus*	13 964	94	*Diplodia*	6 337
45	*Mortierella*	12 787	95	*Inonotus*	6 331
46	*Debaryomyces*	12 476	96	*Ophiostoma*	5 912
47	*Metschnikowia*	11 995	97	*Neofusicoccum*	5 591
48	*Talaromyces*	11 976	98	*Hericium*	5 458
49	*Geotrichum*	11 900	99	*Phakopsora*	5 143
50	*Pestalotiopsis*	11 758	100	*Leptosphaeria*	5 133

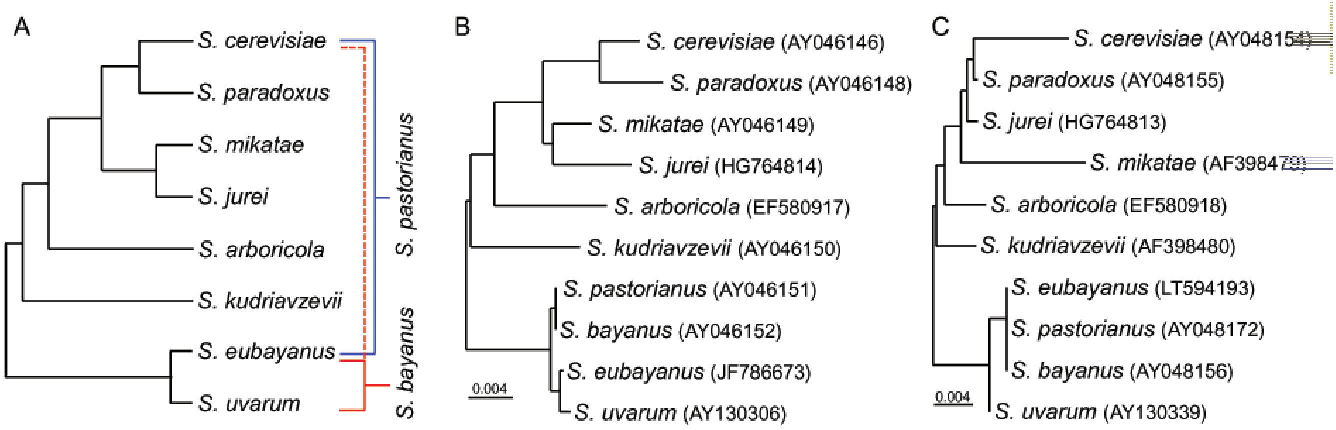

Fig. 1. Phylogenetic relationships of the currently recognised *Saccharomyces* species inferred from the **A.** maximum likelihood of whole genome, **B.** neighbour joining tree of internal transcribed spacer (ITS) region of the rRNA gene, and **C.** neighbour joining tree of D1/D2 domain of the large subunit (LSU) of the rRNA gene sequences. The parents of the two hybrid species are marked in A. and the parent that donates only minor genome sequences is marked by a dashed line. GenBank accession numbers for the ITS and D1/D2 sequences of type strains are shown in parentheses.

can mate with each other (Naumov 1996). Thus, the species exhibit post-zygotic isolation and the biological species concept combined with consideration of genome sequence divergence is used to define species in the genus (Liti *et al.* 2006). The species are morphologically and physiologically similar (Vaughan-Martini & Martini 2011), but the eight natural species can be identified using ITS and D1/D2 sequence analyses (Fig. 1B, C). The two hybrid species, which usually occur in fermentation associated environments, can be differentiated further using specific markers targeting the genome sequences of the parental species of the hybrids (Bing & Bai 2018).

Ecologically, *Saccharomyces* species occur broadly in nature associated with bark, rotten wood of broad-leaved trees, especially *Fagales*, and nearby soil (Sampaio & Gonçalves 2008, Wang *et al.* 2012d, Hittinger 2013, Alsammar & Delneri 2020, Bai *et al.* 2022). In contrast to the expectation that these yeasts may distribute commonly in sugar-rich environments, as implied by the etymology of the genus name (sugar fungus), they have rarely been isolated from fruit and orchards, except for *S. cerevisiae*. Though *S. cerevisiae* exists on fruit, the success rate of *S. cerevisiae* isolation from fruit is generally lower than that from broad-leaved tree bark (Wang *et al.* 2012d, Bai *et al.* 2022). Geographically, some *Saccharomyces* species are cosmopolitan while others occur in only limited regions (Table 2). *Saccharomyces cerevisiae* and *S. paradoxus* usually coexist in nature globally, but the former distributes ubiquitously from tropical to temperate climate zones, while the latter has rarely been found in tropical areas (He *et al.* 2022b). *Saccharomyces eubayanus*, *S. uvarum* and *S. kudriavzevii* are usually cryophilic or cryotolerant species since they are more easily isolated at low temperatures (Sampaio & Gonçalves 2008) or occur more commonly at high altitudes. The hybrid species *S. pastorianus* and *S. bayanus* are also considered cryophilic because they are usually associated with low-temperature fermentation processes.

Saccharomyces species usually grow as diploids in nature. Their life cycles are illustrated using *S. cerevisiae* as an example (Fig. 2), which has been well documented in the laboratory (Herskowitz 1988). The diploid cells usually reproduce asexually by budding and undergo meiosis and sporulation in response to nutrition depletion, especially nitrogen starvation. Four haploid spores are usually formed in an ascus with two of the spores having mating type a (*MAT*a) and the other two *MATα*. Intratetrad mating can occur between a pair of spores with opposite mating types within the ascus upon germination and form a diploid cell. Ascospores can also germinate and reproduce asexually by budding to form *MAT*a and *MATα* haploid cell lines. A haploid cell can mate with another haploid with an opposite mating type either from an ascospore of the same strain (selfing) or from an ascospore of a different strain (outcrossing). Haploid cells can also restore the diploid state through a haplo-selfing or autodiploidisation process regulated by a mating-type switch mechanism (Lee & Haber 2015).

Table 2. Ecological and geographical distributions of the wild *Saccharomyces* species.

Species	Observed habitats in nature	Geographical distribution
S. arboricola	Bark and exudates of *Quercus*, *Cyclobalanopsis*, *Juglans*, and *Castanea*; soil; insects; mushrooms; fruit	Asia (China), Oceania (New Zealand)
S. cerevisiae	Bark, rotten wood, and nearby soil of broad-leaved trees, fruit	Cosmopolitan in tropical to temperate climate zones
S. eubayanus	Bark, leaves, exudates and seeds of *Quercus*, *Nothofagus*, *Araucaria*; rotten wood; sporocarps of *Cyttaria*; soil	Asia (China), North America, South America (Argentina, Chile), Oceania (New Zealand)
S. jurei	Bark of *Quercus*	Europe
S. kudriavzevii	Bark of *Quercus*, *Cyclobalanopsis*, and *Castanea*; soil; decayed leaves	Asia, Europe
S. mikatae	Bark of *Quercus*, *Ulmus*, *Juglans*, *Diospyros*, *Betula*; soil; fruit	Asia
S. paradoxus	Bark, rotten wood, and nearby soil of broad-leaved trees, mostly *Fagales*	Cosmopolitan in subtropical (rare) to temperate climate zones
S. uvarum	Bark or seed of *Nothofagus*, *Quercus*, *Fagus*, *Araucaria*; sporocarps of *Cyttaria*; soil; wine; beer; fruit; juice	Asia, Europe, North America, South America, Oceania

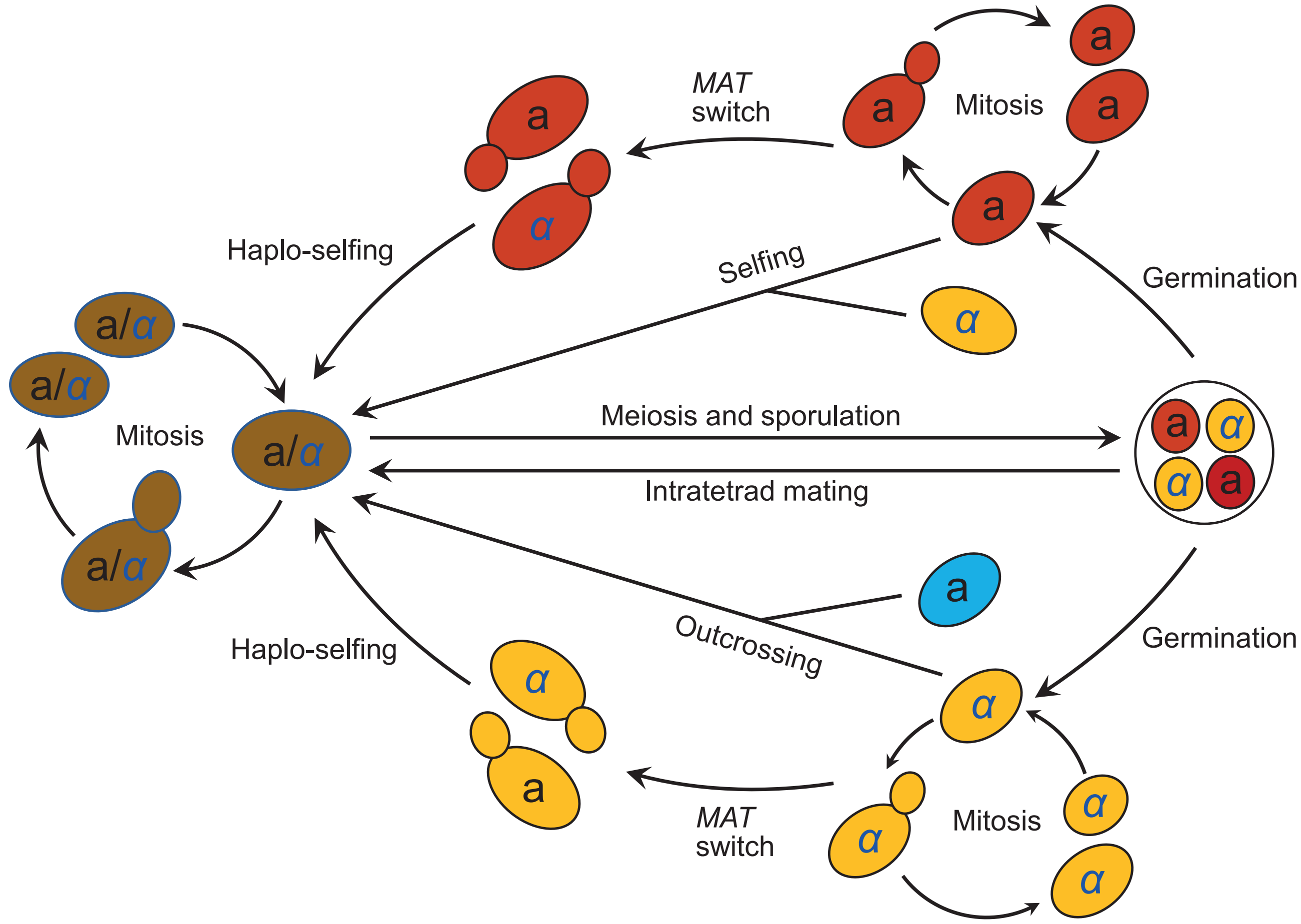

Fig. 2. Life cycle of *S. cerevisiae*. *Saccharomyces cerevisiae* usually grows in nature as a diploid microbe. Diploid cells (a/α) either reproduce asexually by budding (mitosis) or undergo meiosis and sporulation in response to nutrition depletion, resulting in the formation of tetrads with four ascospores each. Ascospores either undergo intratetrad mating to form a diploid cell or germinate to form haploid cells (a or α). A haploid cell either reproduces by budding or mates with a sibling (selfing) or non-sibling (outcrossing) haploid with an opposite mating type to form a diploid cell or undergoes haplo-selfing or autodiploidization through a process known as mating-type (*MAT*) switch to restore the diploid phase.

Economic and scientific significance

A unique trait of *Saccharomyces* species is that they preferentially metabolise sugars through an anaerobic fermentation pathway to produce ethanol and CO_2, even in the presence of oxygen for aerobic respiration. This aerobic fermentative trait is known as the Crabtree effect (Dedeken 1966), which shares several features with the Warburg effect (enhanced glycolytic activity and reduced oxidative phosphorylation) of tumour cells (Diaz-Ruiz *et al.* 2009). This trait is usually thought of as an outcome of adaptative evolution which endows *Saccharomyces* species with an enhanced ability of fast sugar consumption and ethanol production and thus a strong ability to outcompete other microbes in sugar-rich niches (Piškur *et al.* 2006). The fast and strong CO_2 and ethanol production abilities of the yeasts have been explored by humans for bread and alcoholic beverage production worldwide for thousands of years. The earliest archaeological evidence for wine-like beverage production in about 7 000 BC was found in a Neolithic village in China (McGovern *et al.* 2004).

The role of yeast as the agent of fermentation was revealed 150 years ago by pioneering scientists, including Theodor Schwann and Louis Pasteur (Barnett 1998, 2000). In the early 1880s, Emil Christian Hansen developed an effective technique for isolating pure yeast cultures and paved the way for their use in standardised industrial fermentation (Barnett & Lichtenthaler 2001). Although ancient practices employing spontaneous fermentation by natural microbial communities dominated by *Saccharomyces* yeasts are still used in traditional fermented food production worldwide, elaborately selected or bred *S. cerevisiae* or *S. pastorianus* strains are usually used in large-scale industrial production of bread, beer, wine, and spirits. The current worldwide market of alcoholic drinks is estimated to be over 1 600 billion US dollars. Beer contributes the largest market segment at nearly 640 billion US dollars, while spirits and wine amount to approximately 520 and 360 billion US dollars, respectively (data from https://www.statista.com/outlook/cmo/alcoholic-drinks/worldwide).

Saccharomyces cerevisiae is also used for bioethanol production (Eliodório *et al.* 2019). There is an increasing demand for clean renewable biofuels to cope with climate change (Liu *et al.* 2021a). Among such biofuels, bioethanol is currently the largest product from crops and other feedstock biomass (Eliodório *et al.* 2019). *Saccharomyces cerevisiae* is the dominant species in industrial bioethanol production due to its ability to efficiently and completely ferment sugars from hydrolysates of feedstock biomass into ethanol (Walker & Walker 2018). The annual world bioethanol production from 2016 to 2021 ranged from 26 to 29 billion gallons (Renewable Fuels Association 2022).

With the advantages of easy cultivation, a fast growth rate, a simple single-celled life cycle with clear vegetative and sexual reproduction states, sharing with multicellular eukaryotes many fundamental cellular structures and biological properties, and a relatively small eukaryotic genome, *S. cerevisiae* has become one of the most powerful eukaryotic models in virtually every discipline of biology (Botstein & Fink 1988, 2011, Duina *et al.* 2014). The first evidence of enzymatic activities outside of a living cell was obtained using yeast extracts by Edward Buchner in the early 1900s, which founded the groundwork for biochemistry and metabolism research (Barnett & Lichtenthaler 2001). In the 1930s, Øjvind Winge and Carl Lindegren began to use yeast as an experimental organism in genetic studies (Mortimer 2000). The genetic and biochemical experiments performed by Fred Sherman in the 1960s and 1970s attracted broad attention to the yeast system from the scientific community (Liebman & Haber 2013). Then, the successful transformation of yeast with a plasmid replicable in *Escherichia coli* in 1978 (Hinnen *et al.* 1978) established the central role of *S. cerevisiae* as a model in molecular biology.

A milestone in the history of biology is the sequencing of the first eukaryotic genome of *S. cerevisiae* in 1996, which was the outcome of a worldwide collaboration of hundreds of researchers (Goffeau *et al.* 1996). Approximately 6 000 genes were recognised in the genome of the yeast strain S288C with a total size of 12 000 kb and 16 chromosomes. The high-quality genome sequence of *S. cerevisiae*, which is comprehensively annotated in the *Saccharomyces* Genome Database (SGD, http://www.yeastgenome.org/) has provided a wealth of information for intensive studies on genomics and many other disciplines of biology (Cherry *et al.* 2012, Engel *et al.* 2014). Based on the genomic sequence and efficient tools for homologous recombination in yeast, a budding yeast deletion library has been generated through a cooperative effort of the international yeast community (Winzeler *et al.* 1999, Giaever *et al.* 2002). These resources together with the Gene Ontology Consortium (GO) database (Ashburner *et al.* 2000; http://www.geneontology.org/) and a series of other resources available to the scientific community (Botstein & Fink 2011, Duina *et al.* 2014) have greatly improved the studies on the functions of genes and proteins and laid the groundwork for the fields of functional genomics and systems biology, which focus on how genes and proteins interact and work together to determine the traits of organisms.

The budding yeast system has facilitated many landmark discoveries in biology. Since the beginning of the 21st century, at least five Nobel Prizes have been awarded to scientists for their breakthrough work mainly using *S. cerevisiae* as a model organism. Lee Hartwell revealed the foundations of regulated cell division in budding yeast and was awarded a Nobel Prize in Physiology or Medicine in 2001. Roger Kornberg deciphered the structure of the components critical for transcription using the budding yeast toolkit and was awarded a Nobel Prize in Chemistry in 2006. Jack Szostak, Elizabeth Blackburn, and Carol Greider were awarded the 2009 Nobel Prize in Physiology or Medicine for their work in eukaryotic telomere structure involving budding yeast. Two other excellent discoveries that took advantage of the yeast system are Randy Schekman's work on eukaryotic vesicle trafficking (2013 Nobel Prize in Physiology or Medicine) and Yoshinori Ohsumi's work on mechanisms of autophagy (2016 Nobel Prize in Physiology or Medicine). These examples highlight the far-reaching impact that the yeast system has had on our understanding of basic biological processes relevant to all eukaryotes, including humans.

Research interests

There are over 50 000 publications and over 1 000 000 citations from 2011–2021 in the Web of Science (Fig. 3), with numerous publications involving *S. cerevisiae* every year. It is not easy to figure out the exact number because of the extremely broad application of the model organism as an experimental tool and the use of the huge amount of genomic, proteomic and metabolomic data generated from yeast in biological research, as shown by the top cited articles in the Web of Science (Table 3). Several notable hotspots of research directly on *Saccharomyces* species or exclusively using the species as a model or tool are discussed here based on highly cited publications in the past decade (Fig. 4).

Speciation and evolution

Saccharomyces species usually exhibit post-zygotic reproductive isolation and it is easy to test the degree of isolation by examining

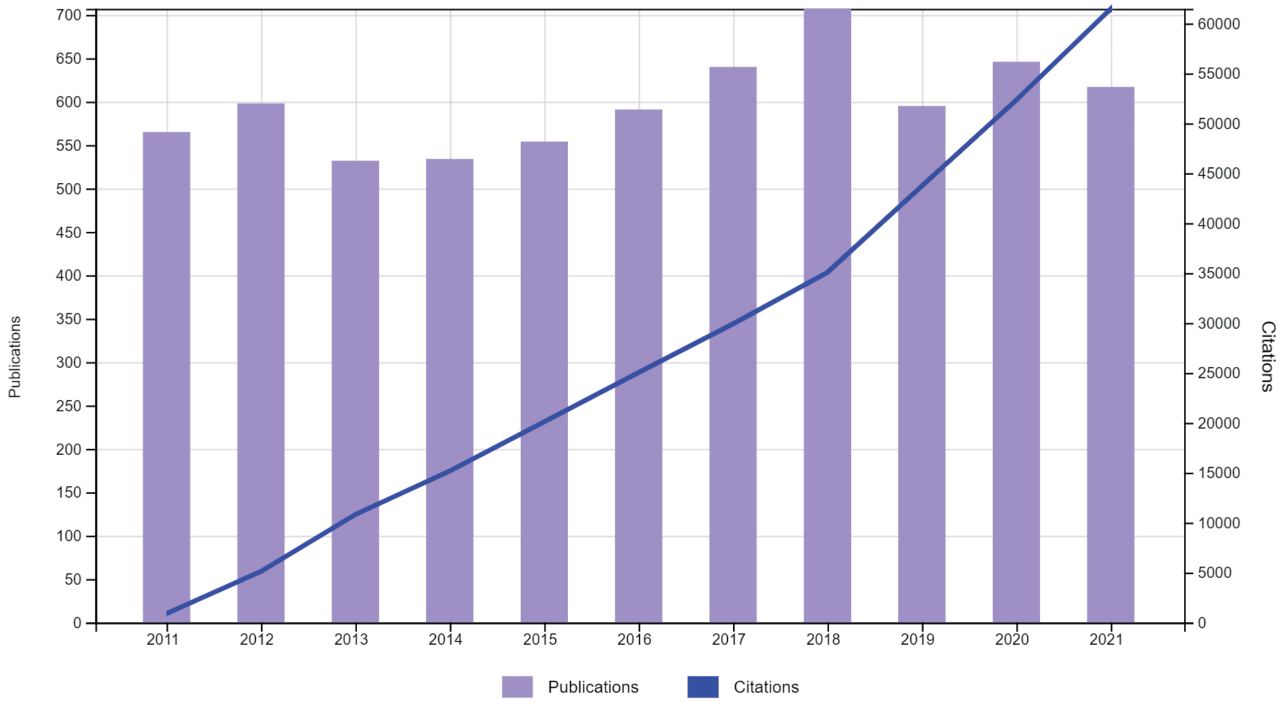

Fig. 3. Trends in research of *Saccharomyces* in the period 2011–2021. The figure shows citations for only 10 000 records.

Table 3. Top 10 cited articles related to *Saccharomyces* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	*Saccharomyces* genome database: the genomics resource of budding yeast	1 044	Cherry *et al.* (2012)
2	Search-and-replace genome editing without double-strand breaks or donor DNA	985	Anzalone *et al.* (2019)
3	Genome engineering in *Saccharomyces cerevisiae* using CRISPR-Cas systems	939	DiCarlo *et al.* (2013)
4	A global genetic interaction network maps a wiring diagram of cellular function	617	Costanzo *et al.* (2016)
5	Production of amorphadiene in yeast, and its conversion to dihydroartemisinic acid, precursor to the antimalarial agent artemisinin	454	Westfall *et al.* (2012)
6	Genome evolution across 1,011 *Saccharomyces cerevisiae* isolates	435	Peter *et al.* (2018)
7	High-resolution mapping reveals a conserved, widespread, dynamic mRNA methylation program in yeast meiosis	415	Schwartz *et al.* (2013)
8	Structure of the yeast mitochondrial large ribosomal subunit	397	Amunts *et al.* (2014)
9	The one hour yeast proteome	386	Hebert *et al.* (2014)
10	The reference genome sequence of *Saccharomyces cerevisiae*: Then and now	202	Engel *et al.* (2014)

spore viability of the crosses between strains from the same or different species. Thus, the genus has become a powerful model in research on the mechanism of speciation (Chou & Leu 2010, Ono *et al.* 2020). Typically, intra- and inter-specific crosses usually result in ~1 % or less and above 50 % spore viability, respectively (Liti *et al.* 2006, Dujon & Louis 2017). Several mechanisms underlying post-zygotic reproductive isolation between *Saccharomyces* species have been identified. Chromosomal translocations or rearrangements can lead to unbalanced chromosomal segments and lethality in the meiotic spores lacking the translocated segments harbouring essential genes (Liti *et al.* 2006, 2009, Hou *et al.* 2014, 2015, Dujon & Louis 2017). Genetic incompatibility or Bateson-Dobshansky-Muller incompatibility is another mechanism, which leads to improper interactions of genes from different parents in an offspring of a hybrid and thus causes sterility of the hybrid. Such incompatible genes causing reproductive isolation are usually

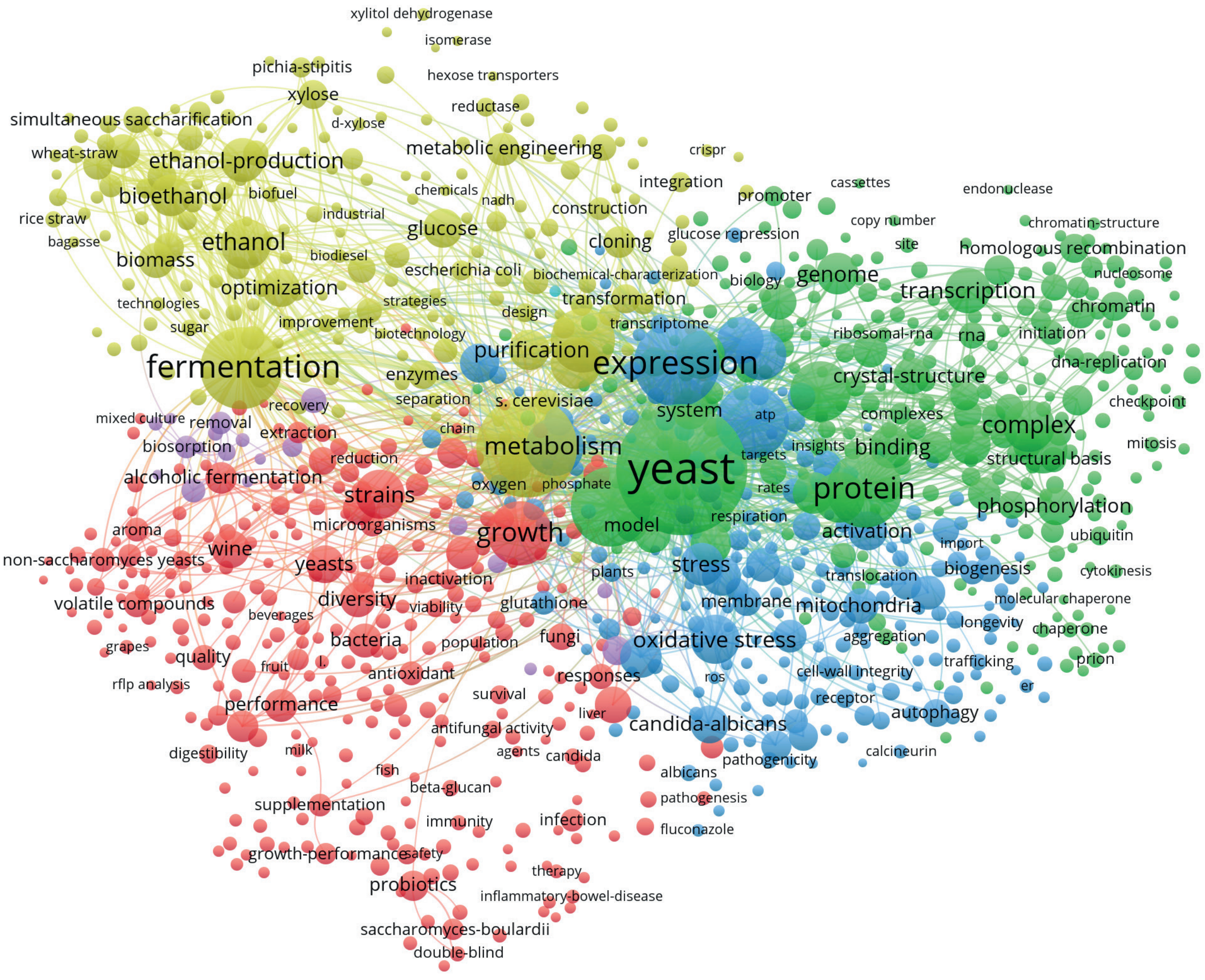

Fig. 4. Network visualisation of keywords of the publications related to *Saccharomyces*. The larger the text and the circle the more often the subject has been cited.

called "speciation genes". A few examples of genetic incompatibility, particularly between nuclear and mitochondrial genes, have been characterised in *Saccharomyces* species (Lee *et al.* 2008, Chou & Leu 2010, Chou *et al.* 2010). However, it is not clear whether the incompatibility occurred prior to or after speciation (Louis 2009, 2011). The third mechanism is anti-recombination due to sequence divergence, which acts to prevent recombination between nonidentical sequences mediated by the mismatch repair system during meiosis, resulting in the failure of meiotic crossovers required for proper chromosome segregation (Ono *et al.* 2020).

Saccharomyces has also become a model genus in evolutionary genetics and genomics (Hittinger 2013). The genomes of 2 478 *S. cerevisiae*, 409 *S. paradoxus*, 303 *S. eubayanus*, 82 *S. uvarum*, 30 *S. kudriavzevii*, 10 *S. arboricola*, two *S. jurei*, and two *S. mikatae* strains have been sequenced and released in GenBank. Population genetics and genomic studies have shown that the wild and domesticated populations of *S. cerevisiae* are separated in phylogeny and show hallmark differences in heterozygosity and sexuality (Fay & Benavides 2005, Liti *et al.* 2009, Duan *et al.* 2018, Peter *et al.* 2018). The global genetic diversity of *S. cerevisiae* is mainly contributed by strains from Far East Asia, and the ancient basal lineages of the species have been found only in primeval forests in China, supporting an "out-of-China" origin hypothesis of the species (Wang *et al*. 2012d, Liti 2015, Duan *et al.* 2018, Peter *et al.* 2018, Bai *et al.* 2022). In addition to *S. cerevisiae*, the wild species *S. paradoxus* is a promising alternative model in ecology and evolutionary biology (Boynton & Greig 2014, Leducq *et al.* 2016). The genetic diversity of *S. paradoxus* is much higher than that of *S. cerevisiae* and the population structure of the former is well delineated along with geographical boundaries (Liti *et al.* 2009, Xia *et al.* 2017). A highly diverged ancient lineage of *S. paradoxus* has been identified in China (He *et al.* 2022b).

Another interesting progress in the evolution of *Saccharomyces* species is the identification of *S. eubayanus* as the wild ancestor of lager beer yeast *S. pastorianus* (Libkind *et al.* 2011, Bing *et al.* 2014). *Saccharomyces eubayanus*, contributing to the non-ale subgenome of the hybrid *S. pastorianus*, was first discovered from native forests in Patagonia, Argentina (Libkind *et al.* 2011) and was then isolated from the Tibetan Plateau (Bing *et al.* 2014). Population genetics and genomics analyses have shown that the genetic diversity of *S. eubayanus* is much higher in Far East Asia than in America, suggesting that *S. eubayanus* is native to Far East Asia. One of the Tibetan lineages of the species exhibited closer affinity with lager yeast than the Patagonian lineage (Bing *et al.* 2014, Okuno *et al.* 2016). Thus, a Tibetan origin hypothesis of lager yeast has been proposed (Bing *et al.* 2014), which is supported by the finding that the mitochondrial genome of *S. pastorianus* originates exclusively from the Tibetan lineage of *S. eubayanus* (Okuno *et al.* 2016).

Synthetic biology

A post-genomic global collaboration of the yeast community is the synthetic yeast genome project Sc2.0, aiming to build a functional synthetic genome of an eukaryote and to answer fundamental biological questions relating to properties of chromosomes, genome structure and evolution, gene content, function of RNA splicing, and the distinction between prokaryotes and eukaryotes, and to establish a platform for the development of biotechnology (Dymond *et al.* 2011, Richardson *et al.* 2017). Six chromosomes (synII, synIII, synV, synVI, synX, and synXII) and the right arm of chromosome IX (synIXR) have been successfully synthesised (Richardson *et al.* 2017, Pretorius & Boeke 2018). Then, a functional single-chromosome yeast from a haploid cell of *S. cerevisiae* containing 16 linear chromosomes has been created by successive end-to-end chromosome fusions and centromere deletions (Shao *et al.* 2018).

Benefiting from the rapid developments of synthetic biology and genome editing tools, especially the CRISPR-Cas9 system (DiCarlo *et al.* 2013), *S. cerevisiae* has been developed as a cell factory to produce many chemicals, bioactive secondary metabolites, and pharmaceuticals (Nielsen *et al.* 2019). For example, amorphadiene, which is the precursor to the antimalarial agent artemisinin, was produced by fermentation from engineered *S. cerevisiae* (Westfall *et al.* 2012). *Saccharomyces cerevisiae* was also engineered to produce opioid compounds thebaine and hydrocodone starting from sugar by reconstructing the full biosynthesis pathway required for the expression of 21 (thebaine) and 23 (hydrocodone) enzymes from plants, mammals, bacteria, and yeast itself (Galanie *et al.* 2015). Through metabolic rewiring, directed evolution, and bioprocess optimisation, *S. cerevisiae* was reprogrammed from ethanol fermentation to a pure lipogenesis metabolism for high-level production of free fatty acids (Yu *et al.* 2018).

Structural biology

Because of the high-level conservation between yeast and human in protein sequences and cell organelle structures and their functions, *S. cerevisiae* has been used as a powerful model in structural biology. Due to the application of yeast as a model system in the study of human mitochondrial disorders (Barrientos 2003), the structure of yeast mitochondrial ribosomal large subunit was solved using single-particle cryo-electron microscopy. A nearly complete atomic model with a resolution of 3.2 angstroms was built *de novo*, including 39 proteins and expansion segments of mitoribosomal RNA (Amunts *et al.* 2014). The structure of the intact spliceosome of *S. cerevisiae*, which mediates splicing of the precursor messenger RNA (pre-mRNA) involving intron removal and exon ligation, was resolved at atomic resolution through a series of structural studies since 2016 (Wan *et al.* 2020). The molecular mechanism of pre-mRNA splicing was elucidated based on structural studies together with biochemical and genetic investigations (Wan *et al.* 2020). The structural studies on human spliceosomes performed simultaneously revealed strict conservation between humans and yeast in the overall organisation of the spliceosome and the configuration of the splicing active site (Wan *et al.* 2020).

Epigenetics

Post-synthesis modifications of DNA, RNA, and proteins all potentially impact their function and are the main targets of epigenetics, which focuses on heritable changes in gene function that are not attributed to alterations of the DNA sequence. Previous studies have shown that DNA methylation and RNA interference (RNAi) machinery are absent from *S. cerevisiae* (O'Kane & Hyland 2019). The lack of these processes simplifies the examination of the remaining epigenetic marks. The lack of potential complications caused by the cross-talk between the DNA methylation and histone modification pathways as observed in animal cells (Cedar & Bergman 2009) and the limited functionally redundant copies of the genes encoding core histone proteins make *S. cerevisiae* one of the best models available for studying the inheritance of histone modification-dependent chromatin states. Epigenetic mechanisms involving heritable silent chromatin in *S. cerevisiae*, including telomere silencing, mating type silencing, and rDNA silencing, have been extensively studied (Rusche *et al.* 2003, Grunstein & Gasser 2013, Gartenberg & Smith 2016, O'Kane & Hyland 2019).

Messenger RNA (mRNA) methylation has been revealed as a key player in eukaryotic gene expression regulation, and N^6-methyladenosine (m^6A) is among the most abundant internal mRNA modification known in eukaryotic mRNA (Covelo-Molares *et al.* 2018). In *S. cerevisiae* mRNA methylation occurs only during meiosis. Deletion of the core RNA methyltransferase components delays meiotic entry but is not lethal to yeast. Therefore, *S. cerevisiae* is a promising tool in the study of mRNA methylation (Schwartz *et al.* 2013). Genomic maps of m^6A sites in meiotic yeast transcripts at nearly single-nucleotide resolution were generated using a high-resolution assay coupled with mutants defective in methylation, resulting in the identification of 1 308 putatively methylated sites within 1 183 transcripts (Schwartz *et al.* 2013). The study also showed a striking similarity in methylation profiles and components between yeast and mammals, enhancing the value of yeast as a compelling model system for studying the role of methylations (Schwartz *et al.* 2013).

Proteomics

Expression and interactions of proteins are essential for understanding biological phenomena. Technologies for large-scale quantitative measurement of proteins have been developed and improved substantially in recent decades. With its unmatched resources in genomics and transcriptomics, *S. cerevisiae* has been a preferred platform for proteomic studies. The first large-scale yeast proteome study using two-dimensional chromatography coupled with tandem mass spectrometry identified 1 483 proteins (Washburn *et al.* 2001). Ghaemmaghami *et al.* (2003) created a *S. cerevisiae* fusion library where each annotated ORF was fused to a TAP tag. They measured approximate expression levels of the tagged ORFs and found that about 4 500 proteins (80 % of the proteome) were expressed during normal growth conditions. Huh *et al.* (2003) fused more than 4 100 proteins to GFP and identified their subcellular locations, providing information about what their function might be.

Picotti *et al.* (2013) generated an almost complete reference map (97 % of the genome-predicted proteins) of the *S. cerevisiae* proteome using a strategy based on high-throughput peptide synthesis and mass spectrometry and applied the maps to a protein quantitative trait locus (QTL) analysis. Hebert *et al.* (2014) developed a protocol for comprehensive analysis of the yeast proteome in just over one hour with improved sample preparation and chromatographic separations, and by using a new Orbitrap hybrid mass spectrometer. On average, each 1 h analysis achieved the detection of 3 977 proteins (1 % false discovery rate). Ho *et al.* (2018) generated a unified protein abundance data set, covering about 5 400 proteins by combining 21 quantitative yeast proteome data sets, including MS-, GFP-, and western blotting-based methods. Recently, Gao *et al.* (2021b) generated the largest yeast proteome data set, including 5 610 identified proteins, using a strategy based on optimised sample preparation and high-resolution mass spectrometry. These yeast proteome data sets are important resources for further systematic studies.

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2. **Candida** Berkhout, Schimmelgesl. Monilia: 41. 1923.

Type species: *Candida vulgaris* Berkhout [(syn. *Candida tropicalis* (Castellani) Berkhout]

Classification: *Ascomycota*, *Saccharomycotina*, *Pichiomycetes, Serinales, Debaryomycetaceae.*

Background

Candida was introduced by C.M. Berkhout (1923) in her PhD thesis to accommodate asexually reproducing yeasts that form hyphae that may disarticulate and form blastoconidia by budding from the hyphae or each other. Berkhout's translated diagnosis of the genus reads as "Few hyphae, sessile, disarticulating into shorter or longer fragments. Conidia formed budding from hypha or each other; they are small and colourless (hyaline)". *Candida vulgaris*, currently a synonym under *C. tropicalis* (Lachance *et al*. 2011), was selected by Berkhout as the generic type. The expansion of the genus *Candida* over the years is clearly illustrated by the number of species listed in the first monograph on asexual yeasts (Diddens & Lodder 1942) and all subsequent five editions of "*The Yeasts, a Taxonomic study*" (TYTS, Lodder & Kreger-van Rij 1952, Lodder 1970, Kreger-van Rij 1984, Kurtzman & Fell 1998, Kurtzman *et al.* 2011) that contained 26, 30, 81, 196, 163, and 314 species, respectively. *Candida* contains asexually reproducing *Saccharomycotina* budding yeasts with white, moist colonies that may or may not form pseudohyphae or true hyphae, and produces yeast cells by blastoconidiogenesis. For a long time, morphologically similar yeasts belonging to both *Basidiomycota* and *Ascomycota* were included in the genus. Yarrow & Meyer (1978) changed the generic concept by including yeasts that do not form hyphae. Thus, they merged *Torulopsis* (with no hyphae) with *Candida* (with hyphae) giving nomenclatural priority. *Torulopsis* was described by Berlese (1895) with *T. rosea* as the type species. However, the taxonomic concept of *Torulopsis* remained doubtful as its true identity could not be verified because no strain was available. Yarrow and Meyer recombined *Torulopsis glabrata*, originally described as *Cryptococcus glabratus* Anderson, in *Candida* as *C. glabrata* (Anderson) Yarrow & Meyer (1978). This merging of *Candida* and *Torulopsis* has contributed to the present highly polyphyletic nature of the genus (see below).

This expansion of *Candida* was followed by a taxonomic clean-up by the removal of yeasts with basidiomycetous affinity (Weijman *et al*. 1988), thus restricting *Candida* to ascomycetous yeasts with the following characteristics: *Candida* Berkhout char. *emend*. Weijman, Rodrigues de Miranda & Van der Walt: Cells globose, ellipsoid, ovoid, cylindrical, elongate, rarely ogival, triangular, apiculate or ampulliform. Cell wall by TEM ascomycetous, two-layered. Vegetative reproduction is holoblastic and as a rule multilateral budding. Pseudohyphae and as a rule non-disarticulating hyphae may occur, the latter if septate, non-porate or with closure lines or disjunctives (micropores plasmodesmata). Chlamydospores may occur. Pigmentation, when manifest, due to non-carotenoids. Amyloid compounds giving a positive starch reaction absent. Xylose, rhamnose and fucose are absent in cell wall hydrolysates. The presence of disarticulating hyphae is considered by these authors a key feature.

With the advent of molecular phylogeny, it became clear that *Candida*, as defined above, belongs to many phylogenetic lineages within *Saccharomycotina* (Kurtzman 1987, 1990, 1993a, 1993b, 1993c, Kuramae *et al.* 2006, Lachance *et al*. 2011, Gabaldón *et al*. 2013, Daniel *et al*. 2014, Hittinger *et al.* 2015, Shen *et al*. 2018). Barns *et al*. (1991) using sequence analysis of the small subunit (SSU or 18S) ribosomal RNA (rRNA) gene had already noticed that *C. glabrata* clustered distinctly from *C. albicans* and *C. tropicalis*, and was more closely related to *Saccharomyces cerevisiae*. This was confirmed by Kurtzman & Robnett (1997, 1998) who in several studies using partial sequence (D1/D2 regions) of LSU showed that *C. glabrata* belongs to a different lineage than *C. tropicalis*, but also from *C. albicans* (Kurtzman &

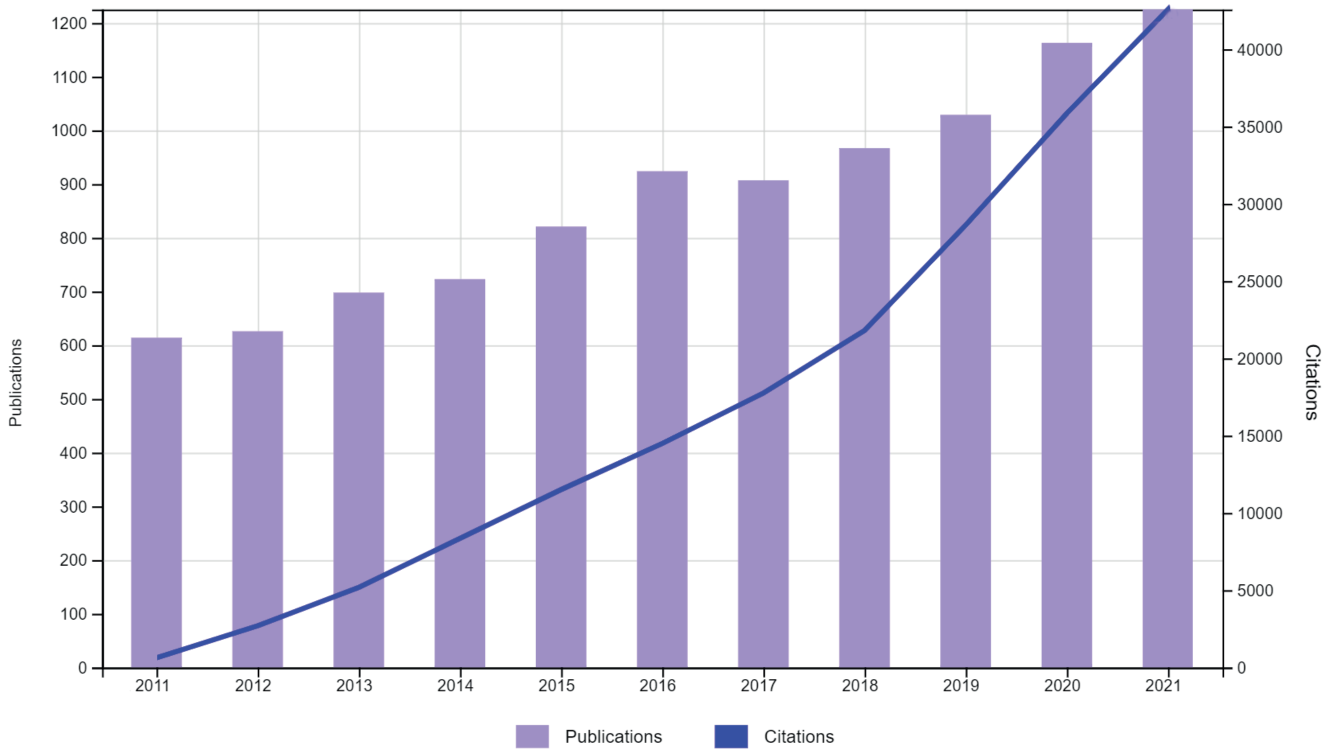

Fig. 5. Trends in research of *Candida* in the period 2011–2021. The figure shows citations for only 10 000 records.

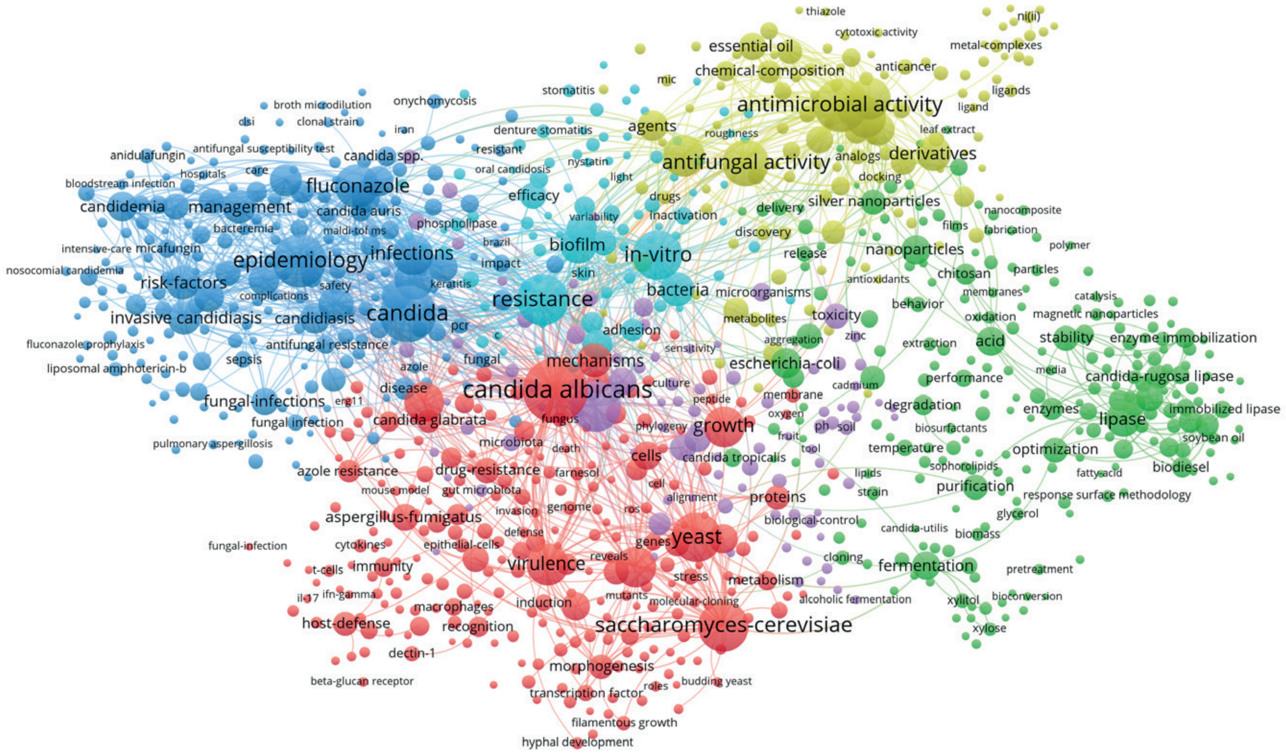

Fig. 6. Network visualisation of keywords of the publications related to *Candida*. The larger the text and the circle the more often the subject has been cited.

Robnett 1998). This was later confirmed by phylogenetic analyses using whole genome-based data (Fitzpatrick *et al.* 2006, Kuramae *et al.* 2006, Robbertse *et al*. 2006, Gabaldón 2013, Pryszcz *et al*. 2014, 2015, Hittinger *et al*. 2015). All these studies confirmed the large phylogenetic distances between various lineages of ascomycetous budding yeasts (Kurtzman & Robnett 1998, Dujon 2006). As a result, the 314 described species, plus the 51 species that were not yet included in the 5th edition of TYTS, belonged to at least 28 clades (Lachance *et al*. 2011). Daniel *et al*. (2014) listed 12 sexually defined ascomycetous genera that contain *Candida* species. *Candida glabrata* clustered in *Saccharomycetaceae* and *C. albicans* and *C. tropicalis* in the so-called Lodderomyces clade of *Debaryomycetaceae*. The website "theyeasts.org", the electronic successor of TYTS, still lists 288 species in *Candida*, while the remaining species have been reclassified in a large number of genera: *Ambrosiozyma*, *Blastobotrys*, *Clavispora*, *Danielozyma*, *Diddensiella*, *Diutina*, *Groenewaldozyma*, *Hemisphaericaspora*, *Hyphopichia*, *Kazachstania*, *Kuraishia*, *Kurtzmaniella*, *Martiniozyma*, *Metschnikowia*, *Metahyphopichia*, *Meyerozyma*, *Middelhovenomyces*, *Nakazawaea*, *Ogataea*, *Priceomyces*,

Table 4. Top 10 cited articles related to *Candida* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Tryptophan catabolites from microbiota engage aryl hydrocarbon receptor and balance mucosal reactivity via interleukin-22	1 134	Zelante *et al.* (2013)
2	*Candida albicans* pathogenicity mechanisms	973	Mayer *et al.* (2013)
3	Fate mapping of IL-17-producing T cells in inflammatory responses	799	Hirota *et al.* (2011)
4	ESCMID* guideline for the diagnosis and management of *Candida* diseases 2012: non-neutropenic adult patients	791	Cornely *et al.* (2012)
5	Chronic mucocutaneous candidiasis in humans with inborn errors of interleukin-17 immunity	708	Puel *et al.* (2011)
6	*Candida* species: current epidemiology, pathogenicity, biofilm formation, natural antifungal products and new therapeutic options	686	Sardi *et al.* (2013)
7	Growth of *Candida albicans* hyphae	665	Sudbery (2011)
8	Invasive candidiasis	650	Kullberg & Arendrup (2015)
9	Type I interferon inhibits interleukin-1 production and inflammasome activation	648	Guarda *et al.* (2011)
10	Antifungal drug resistance: mechanisms, epidemiology, and consequences for treatment	624	Pfaller (2012)

Saccharomycopsis, *Saturnispora*, *Scheffersomyces*, *Spathaspora*, *Spencermartinsiella*, *Starmerella*, *Sugiyamaella*, *Suhomyces*, *Teunomyces*, *Tortispora*, *Wickerhamiella*, *Yamadazyma*, and *Zygoascus*. To further complicate the current polyphyly of the genus, the 288 species retained in *Candida* are distributed into at least 25 clades or families: namely clades Ambrosiozyma, Barnettozyma, Candida glaeboa, Cyberlindnera, Dipodascaceae, Kazachstania, Kodamaea, Kurtzmaniella, Lodderomyces/Spathaspora, Metschnikowia/Clavispora, Meyerozyma, Nakaseomyces, Nakazawaea, Ogataea, Phaffia/Komagataella, Phaffozyma, Pichia, Priceomyces, Scheffersomyces, Starmera, Sugiyamaella, Suhomyces, Wickerhamomyces, Yamadazyma, Yarrowia, Zygoascus, and, in addition, 13 unaffiliated clades. As the generic type *C. vulgaris*, a current synonym under *C. tropicalis* belongs to the Lodderomyces clade, it is clear that this clade will form the core of the *s. str.* circumscription of the genus *Candida* after this has been fully revised. Even the Lodderomyces clade might host a number of genera. To link the name *Candida* to that of the infectious disease candidiasis, the most common fungal infection in man/animals, and *C. albicans* its main causative agent, it might be needed to reconsider the typification of the genus and select *C. albicans* as a neotype. Proper actions to realise this have to be taken by yeast taxonomists and nomenclatural experts. With the global emergence of *Candida auris* as a human pathogen (Rhodes & Fisher 2019, Chow *et al*. 2020, Chakrabarti & Sood 2021), a species that belongs to the Metschnikowia clade, such typification issues should be convincing for the nomenclature purists, and also for the broader community of clinicians. Clinical arguments for such restriction of the genus *Candida* can be found in the extensive differences in antifungal susceptibility patterns and clinical aspects by species belonging to the various clades (Schmalreck *et al.* 2014, Stavrou *et al.* 2019, 2020). Restriction of *Candida* to the clade that contains *C. albicans* will also be beneficial for the acceptance of other species that are currently classified in the polyphyletic genus *Candida*, for use in biotechnology, fermentation and biocontrol.

Ecological and economic significance

Candida ranks number two in the list of most cited fungal genera, which is mainly due to the large number of opportunistic infections caused by species hitherto classified in the genus. Candidiasis occurs globally with an estimated > 400 000 cases per year (Brown *et al*. 2012). Fifty to 75 percent of fertile women suffer from at least one episode of vulvovaginal candidiasis and five to eight percent suffer from four episodes annually (Brown *et al*. 2012). Among the top five clinically most important yeasts are *C. albicans*, *C. tropicalis*, *C. glabrata* and *C. parapsilosis* (*s. lat.*), whereas others, such as *Pichia kudriavzevii* (Boidin *et al*. 1965) and *Meyerozyma* (*Pichia*) *guilliermondii* are in medical literature commonly referred as *C. krusei* and *C. guilliermondii*, respectively (Cleveland *et al.* 2012, Guinea 2014, Pfaller *et al.* 2014, Schmalreck *et al*. 2014, Da Matta *et al*. 2017, Stavrou *et al.* 2019, Kmeid *et al.* 2020).

Invasive candidiasis comprises bloodstream infections or candidemia, and also deep-seated infections (Kullberg & Arendrup 2015). The latter have a mortality of 40 % even when treated with antifungals (Kullberg & Arendrup 2015). Another ongoing process, with an increased risk for patients, is the shift from infections caused by *C. albicans* to those caused by non-albicans *Candida* species (Kullberg & Arendrup 2015, Stavrou *et al*. 2019). Recently, *Candida auris*, has emerged as a global threat in human invasive infection exhibiting mortality rates ranging from 30 to 60 % (Calvo *et al*. 2016, Chowdhary *et al*. 2016, De Almeida *et al*. 2021, Chakrabarti & Sood 2021). Since its description in 2009, the species is associated with hospital-acquired infection causing outbreaks worldwide. *Candida auris* infections are challenging to treat as the species exhibits a resistant profile to fluconazole and variable susceptibility to other triazoles, echinocandins, and polyenes drug classes (Satoh *et al*. 2009, Chowdhary *et al*. 2014b, 2018, Chow *et al*. 2018, 2020). *Candida auris* is commonly misidentified as *C. haemulonii*, *C. famata*, *C. sake*, and even *Saccharomyces cerevisiae* by phenotypical identification methods, and accurate species characterisation requires molecular sequencing (ITS region) or MALDI-TOF MS (Kathuria *et al*. 2015, Girard *et al*. 2016, Ruiz Gaitán *et al*. 2017, Das *et al*. 2019, Ding *et al*. 2019). Due to the clinical challenges posed by *C. auris*, several public health authorities have released clinical guidelines for use in healthcare facilities on infection prevention in order to control this emerging pathogen, also highlighting the importance of notifying the cases to health authorities. As species belonging to the various *Candida* clades show differences in their susceptibility to antifungals, species identity may give a clue for the treatment of patients suffering from infections by such non-conventional *Candida* species (Schmalreck *et al.* 2014, Stavrou *et al.* 2019).

Virulence factors, such as differences in adhesion to epithelial cells, secretion of hydrolytic enzymes, yeast-hyphal dimorphism, the extent of biofilm formation, and phenotypic switching determine the pathogenic potential of *Candida* species and their isolates (Mayer *et al*. 2013, Sardi *et al*. 2013, Nobile & Johnson 2015, Ramos *et al*. 2015, Wakade *et al.* 2020). Risk factors for invasive candidiasis include a long stay at intensive care units/critical illness, abdominal surgery, pancreatitis, hematologic malignant diseases, solid organ transplantation, solid organ tumours, use of broad-spectrum antibiotics, use of catheters, use of chemotherapy, and neonatal state or being colonised by *Candida* yeasts (Nucci *et al*. 1998, Pasqualotto *et al*. 2007, Pfaller *et al.* 2014, Kullberg & Arendrup 2015, Da Matta *et al.* 2017, Warris *et al*. 2020). The secretion of candidalysin, a recently found cytolytic peptide (Moyes *et al*. 2016), modulates innate immunity thus impacting immune regulation (Ho *et al*. 2020). For instance, candidalysin induces early and robust early and innate Th17 cell-derived interleukin 17A (IL-17A) (Verma *et al*. 2017, Ho *et al*. 2020). Complex immunomodulatory mechanisms increase or decrease the susceptibility of the host to *C. albicans*, *e.g.*, mechanisms that enhance colonisation resistance of the gut and reduce colonisation by *C. albicans* relate to the effect of tryptophan metabolites that expand lactobacilli via aryl hydrocarbon receptor-dependent transcription of interleukin 22 (IL-22). The resulting IL22-dependent mucosal balance enhances the survival of microbial communities, and also reduced colonisation by *C. albicans* and protection against inflammation (Zelante *et al*. 2013). Other immune active molecules, such as interleukin-17 (IL-17), relate to mucocutaneous immunity against *C. albicans* (Hirota *et al.* 2011, Puel *et al.* 2011), whereas Type I interferon inhibited the production of interleukin-1 (IL-1) also impacts susceptibility of the host to the yeast (Guarda *et al*. 2011).

Clinically relevant is the observation that many *Candida* species or strains show reduced susceptibility to one or several of the major classes of antifungals (Pfaller 2012, Schmalreck *et al*. 2014, Arendrup & Patterson 2017, Cortegiani *et al*. 2019, Stavrou *et al*. 2019). Treatment options are presented in a large series of clinical guidelines, *e.g*., dealing with neonates, non-neutropenic patients, patients suffering from haematological malignancies, HIV infections and AIDS, patients at intensive care units, *etc*. (Papas *et al*. 2004, Cornely *et al*. 2012, Hope *et al*. 2012a, Lortholary *et al*. 2012, Ullmann *et al*. 2012a, b, Chaves *et al*. 2018), and also for infections caused by non-albicans *Candida* species (Mermel *et al*. 2011, Arendrup *et al*. 2014).

Genetic processes, such as hybridisation, either or not followed by processes of post-hybridisation genetic diversification resulting in (massive) loss of heterozygosity are considered to have played a role in the evolution of virulence of human opportunists in species (complexes), such as the *C. albicans*, *C. inconspicua*, and *C. parapsilosis* complex (Pryszcz *et al*. 2015, 2014, Mixão & Gabaldón 2018, Mixão *et al*. 2021).

Beyond the clinical importance of *Candida* species, others are also biotechnologically important. For example, *C. rugosa* produces lipases and sterol esterases that are important for application in the food industry, production of pharmaceuticals, biosurfactants, biofuels, bio-sensor, cosmetics, *etc*. (Benjamin & Pandye 1998, Barriuso *et al*. 2016). *Candida tropicalis* and *C. maltosa* are utilised for the production of xylitol (Guo *et al.* 2006, Kumar *et al*. 2022). Several species that were previously classified in *Candida* and that are now in genera like *Kluyveromyces*, *Scheffersomyces* and *Yarrowia* are also highly important from fermentation and biotechnological perspectives, but outside the scope of this text. *Candida parapsilosis* has been used as a biocatalyst for organic transformations, *i.e*., deracemisation, enantioselective reductions, and kinetic resolutions (Chadha *et al*. 2016). *Candida tropicalis* has been associated as a relevant metaboliser of hydrophobic substrates, such as fatty acids or alkanes, to produce long-chain dicarboxylic acid, and modulation in the copy number of the *ctfat1p* gene plays an important role to improve the production of this compound (Lebeault *et al*. 1970, Zhang *et al*. 2021c). The species can successfully decontaminate phenol wastewater and soil under salt or no-salt conditions within pH and temperatures ranging from 3.0 to 9.0, and to 20 °C, respectively (Wang *et al*. 2011a, Basak *et al*. 2014, Gong *et al*. 2021). *Meyerozyma* (*Candida*) *guilliermondii* is an effective yeast for bioconversion of xylose into xylitol, a promising productor of ethanol and aromas which is able to reduce the content of patulin in culture medium, and use hydrocarbons as a sole carbon source on minimal salts medium (Schirmer-Michel *et al*. 2008, Guo *et al*. 2009, Wah *et al*. 2013, Chen *et al*. 2017e, Hashem *et al*. 2018).

Research interests

There are over 40 000 publications and over 500 000 citations from 2011–2021 in the Web of Science (Fig. 5). The research interests of *Candida* yeasts focus on improving the taxonomy, epidemiology and diagnostics of *Candida*-related infections, understanding the regulation of virulence, interaction with the host immune system, fundamental cell biology and biochemistry, comparative and functional genomics, and role in human (and animal) microbiomes (Fig. 6). This is clearly reflected in the highly cited papers (Table 4). Beyond this, the use of specific *Candida* species and strains for use in biotechnology, fermentations, and biocontrol is also important. Immune response mediated by interferons and interleukins in *C. albicans* infections is also a highly cited topic. The main aspects addressed in the top-cited papers include conservative cytokines production of T_H17 cells in an acute cutaneous infection caused by *C. albicans*; the role of interleukin-17A and interleukin-17F in the mucocutaneous immunity against chronic mucocutaneous candidiasis; pro-interleukin-1β induced by aluminium salts, and *C. albicans* suppressed by type I interferon role to develop *Candida* infections.

In the top-cited review papers, aspects include data regarding epidemiology, antifungal susceptibility profile by the manufacturer, and natural options of *Candida* species added to the integrative analysis of classical and novel pathogenic mechanisms of *C. albicans* involved in host infection highlighting molecules related to adhesion and invasion of tissues, enzymes profiles, fitness attributes, and yeast morphology switching; consensus recommendations to the diagnosis and management options for non-neutropenic adult patients with *Candida* infections intended to provide practical assistance in the laboratory and clinical decisions in different hospitalised populations, as critically ill individuals under risk factors for invasive candidemia, surgical intensive care units patients, and others; transduction pathways and the molecular processes to activate a program of hypha-specific gene transcription; and trends and strategies in invasive candidiasis.

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3. ***Aspergillus*** P. Micheli ex Haller, Hist. stirp. Helv. (Bernae) 3: 113. 1768.

Type species: *Aspergillus glaucus* (L.) Link

Classification: *Ascomycota*, *Pezizomycotina*, *Eurotiomycetes*, *Eurotiales*, *Aspergillaceae.*

Background

Aspergillus was introduced by Micheli (1729) who considered the characteristic vesiculated conidiophores to resemble an aspergillum, also called a holy water sprinkler. The name was later validated by Von Haller (1768) and sanctioned in Fries (1832). The genus is typified by *A. glaucus* [IMI 211383 (neotype); CBS 516.65 = NRRL 116 = ATCC 16469 = IMI 211383 (ex-neotype)]. Several sexual morphs (teleomorphs) like *Eurotium*, *Emericella*, *Neosartorya*, *etc*. are associated with *Aspergillus*, with phylogenetic analyses resolving these in a large clade, within which sexual morphs typically also resolved as distinct subclades (Houbraken & Samson 2011). Following the concept of single nomenclature (One Fungus = One Name) (McNeill *et al.* 2012), a debate followed on whether to use a broad concept of *Aspergillus* or split the genus based on the smaller clades typically represented by sexual generic names (Pitt & Samson 2007, Houbraken & Samson 2011, Pitt & Taylor 2014, 2016, Samson *et al.* 2014, 2017, Kocsube *et al.* 2016, Taylor *et al.* 2016, Houbraken *et al.* 2020). *Aspergillus* was eventually chosen by the community with several sexual and asexual genera synonymised with the former (Samson *et al.* 2014). A review of the genus resulted in Samson *et al.* (2014) publishing an accepted species list, providing guidelines to work with and identify *Aspergillus* strains, and proposing calmodulin as an alternative identification marker. Many new species were subsequently described which necessitated a review by Houbraken *et al.* (2020) who accepted 446 species (currently 454) and classified them into 6 subgenera, 27 sections and 75 series. More recently, Visagie *et al.* (2024) provided an update on taxonomic revisions and new species published since Houbraken *et al.* (2020), which brought the number of accepted species in *Aspergillus* to 453 (currently 467).

Ecological and economic significance

Food mycology and ecology

Aspergillus represents one of the most economically important fungal genera (Samson *et al.* 2014). *Aspergillus* spp. are widespread geographically and can be either beneficial or harmful microorganisms, however, they mainly have a saprophytic lifestyle and predominantly grow on decaying plant material (Perrone & Gallo 2017). They are among the most successful groups of moulds with important roles in natural ecosystems and the human economy.

Aspergilli are important in fermented food of Asian cuisines by enhancing nutrients, textures, and flavours (Bennett 2010). In particular, important in food mycology as beneficial are the three koji moulds *A. oryzae*, *A. sojae*, and *A. luchuensis,* the Koku-kin (national fungi) that are certified by the Brewing Society of Japan (Ichishima 2016). These koji moulds can be classified as yellow-, black-, and white-koji moulds (Hong *et al.* 2014). For example, *A. oryzae* is used for the production of sake, shochu (distilled sake), amazake (a sweet beverage), and mirin (sweet alcoholic seasoning) in Japan and for Huang-chiu (yellow wine) in China (Kitagaki & Kitamoto 2013, Ashu *et al.* 2016). The Black-koji moulds are used in Japan to produce shochu (*A. kawachii* = *A. luchuensis*) and awamori (*A. luchuensis*) (Hong *et al.* 2014). Many additional uses in food mycology are also known for *Aspergillus*: *i.e.*, *A. chevalieri* and *A. pseudoglaucus* in traditional fermentation and ripening of katsuobushi (Takenaka *et al.* 2020); various species of sections *Aspergillus*, *Flavi* and *Nigri* are commonly isolated from meju, a brick of dried fermented soybeans popular in Korean cuisine (Hong *et al.* 2015); and also, from fermented tea including Pu-erh tea and Fuzhuan Cha (Fu brick tea) (Park *et al.* 2017).

Unfortunately, Aspergilli are one of the major causes of degradation of agricultural products, as they can contaminate foods and feeds at different stages including pre- and postharvest, processing and handling (Perrone & Gallo 2017). So, although important in fermented foods, they can cause undesirable changes of sensorial, nutritional and qualitative nature like pigmentation, discoloration, rotting, and development of off-odours and off-flavours, but most importantly they can produce dangerous mycotoxins that contaminate food, agricultural and food products (Perrone *et al.* 2007, Bennet 2010, Taniwaki *et al.* 2018). However, only a handful of species are significant mycotoxin producers in agricultural products and food and mainly belong within the subgenus *Circumdati.* In particular, three species groups are represented: *A. flavus* - *A. parasiticus* and their close relatives; *A. westerdijkiae* - *A. steynii* and their close relatives; *A. carbonarius* and the closely related species in series (Visagie *et al.* 2014b, Frisvad *et al.* 2019, Houbraken *et al.* 2020). Most *Aspergillus* species are saprophytic, but in some cases can be pathogenic like in the *Flavi* group producing aflatoxins on peanuts and maize. These species can grow in these plants under unfavourable growth conditions for the plants, such as drought stress, which permits infection of developing nuts or grains, and hence the production of aflatoxins before harvest (Saori & Keller 2011). Subgenera *Circumdati* and *Nigri* species occur mainly as postharvest infections having no affinity with crop plants, with some exceptions like *A. carbonarius* and closely related species on grapes (Perrone *et al.* 2008, Perrone & Gallo 2017). *Aspergillus* species can grow at a very wide range of temperatures, water activities and pH, so its species are cosmopolitan and prevalent components of different ecosystems in a wide range of environmental and climatic zones (Klich 2002, Abdel-Azeem *et al.* 2016). They are widely present in soils (Klich 2002, Jaime-Garcia & Cotty 2010), salt marshes (Butinar *et al.* 2011), agricultural ecosystems (Perrone *et al.* 2007, Taniwaki *et al.* 2018), arctic (Arenz *et al.* 2014), stones, fossils, water, animal and humans, *etc*. (Abdel-Azeem *et al.* 2019). They are very important in decomposition processes driving the natural cycling of chemical elements, particularly in the carbon cycle; they are part of a consortia of organisms from different kingdoms that recycle starches, hemicelluloses, celluloses, pectins and other sugar polymers. Some aspergilli are capable of degrading more refractory compounds such as fats, oils, chitin, and keratin (Bennet 2007). Recently the beneficial impact of *Aspergillus* species in soil and environment has been reviewed (Nayak *et al.* 2020), and also, its protective role as plant growth-promoting fungi has been evidenced (Daigham *et al.* 2023).

Their ability to disperse spores globally in air, to survive and grow in different environmental and geographical habitats, together with high reproductive and competitive capabilities means that “ubiquitous” is among the most common adjectives used to describe these moulds (Horn & Dorner 2002, Bennet 2007, Mehl & Cotty 2013).

Research interests

There are over 35 000 publications and over 400 000 citations from 2011–2021 in the Web of Science (Fig. 7) with the top 10 most cited articles listed in Table 5. Most publications focused on secondary metabolites and diseases associated with *Aspergillus* (Fig. 8).

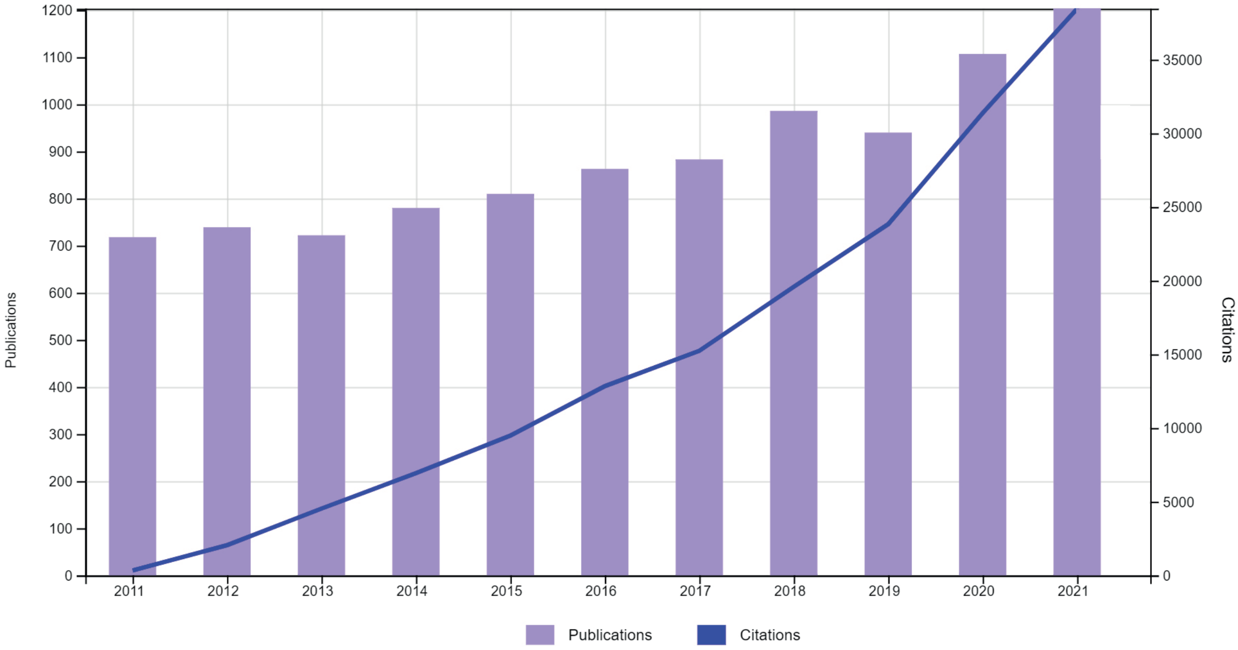

Fig. 7. Trends in research of *Aspergillus* in the period 2011–2021. The figure shows citations for only 10 000 records.

Table 5. Top 10 cited articles related to *Aspergillus* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Hidden killers: human fungal infections	2 175	Brown *et al*. (2012)
2	Practice guidelines for the diagnosis and management of Aspergillosis: 2016 update by the infectious diseases society of America	1 079	Patterson *et al*. (2016)
3	Immunity to fungal infections	729	Romani (2011)
4	A comprehensive evaluation of normalization methods for Illumina high-throughput RNA sequencing data analysis	655	Dillies *et al*. (2011)
5	Antifungal drug resistance: mechanisms, epidemiology, and consequences for treatment	624	Pfaller (2012)
6	Impact of mycotoxins on humans and animals	608	Zain (2011)
7	Epidemiology and clinical manifestations of mucormycosis	604	Petrikkos *et al*. (2012)
8	Regulation of fungal secondary metabolism	569	Brakhage (2013)
9	Phylogeny, identification and nomenclature of the genus *Aspergillus*	557	Samson *et al*. (2014)
10	Diagnosis and management of Aspergillus diseases: executive summary of the 2017 ESCMID-ECMM-ERS guideline	529	Ullmann *et al*. (2018)

Extrolites

The 467 species described and accepted in *Aspergillus* can produce a very large number of small molecule extrolites, also called secondary metabolites, specialised metabolites or natural products (Samson *et al*. 2014, Frisvad 2015, Frisvad & Larsen 2015, Houbraken *et al*. 2020). While *Aspergillus* spp. share many secondary metabolites (SMs) with *Penicillium* spp., these two genera share many secondary metabolites with *Talaromyces* spp. (Yilmaz *et al*. 2014). Like in other filamentous fungi, the SMs produced by *Aspergillus* species are produced in species specific profiles (Frisvad 2015), and recently it has been shown that profiles of carbohydrate active enzymes (CAZymes) are also species specific in *Aspergillus* and *Penicillium* (Barrett *et al*. 2020).

Important drugs or promising drugs in clinical trials produced by isolates of *Aspergillus* species include lovastatin (= mevinolin = monacolin K) produced by *A. terreus* (Huang *et al*. 2021d), fumagillin produced by *A. fumigatus* (Kornienko *et al*. 2015, Frisvad & Larsen 2016), and the anticancer halimide (= phenylahistin) produced by *A. calidoustus* (Kornieno *et al*. 2015, Aldholmi *et al*. 2020). Many other bioactive potential drug candidates have been found in species of *Aspergillus* (Lee *et al*. 2013).

The most important mycotoxin from *Aspergillus* is the most carcinogenic secondary metabolite known, aflatoxin B_1, and this toxin is produced foremost by species in section *Flavi*: *A. aflatoxiformans*, *A. austwickii*, *A. cerealis*, *A. flavus*, *A. minisclerotigenes*, *A. luteovirescens* (syn. *A. bombycis*), *A. mottae*, *A. nomiae*, *A. novoparasiticus*, *A. parasiticus*, *A. pipericola*, *A. pseudocaelatus*, *A. pseudonomiae*, *A. pseudotamariit*, *A. togoensis* and *A. transmontanensis*, and aflatoxin is of serious consequence for food safety (Varga *et al*. 2011, Frisvad *et al*. 2019, Kjærbølling *et al*. 2020). Aflatoxins and sterigmatocystins are also produced by *Aspergillus* species from other sections that rarely occur in foods, feeds or the built environment (Rank *et al*. 2011). In addition to aflatoxins, many species in section *Flavi* also produce the mycotoxins 3-nitropropionic acid and cyclopiazonic acid, adding to the high toxicity of *A. flavus* and similar species. Many species

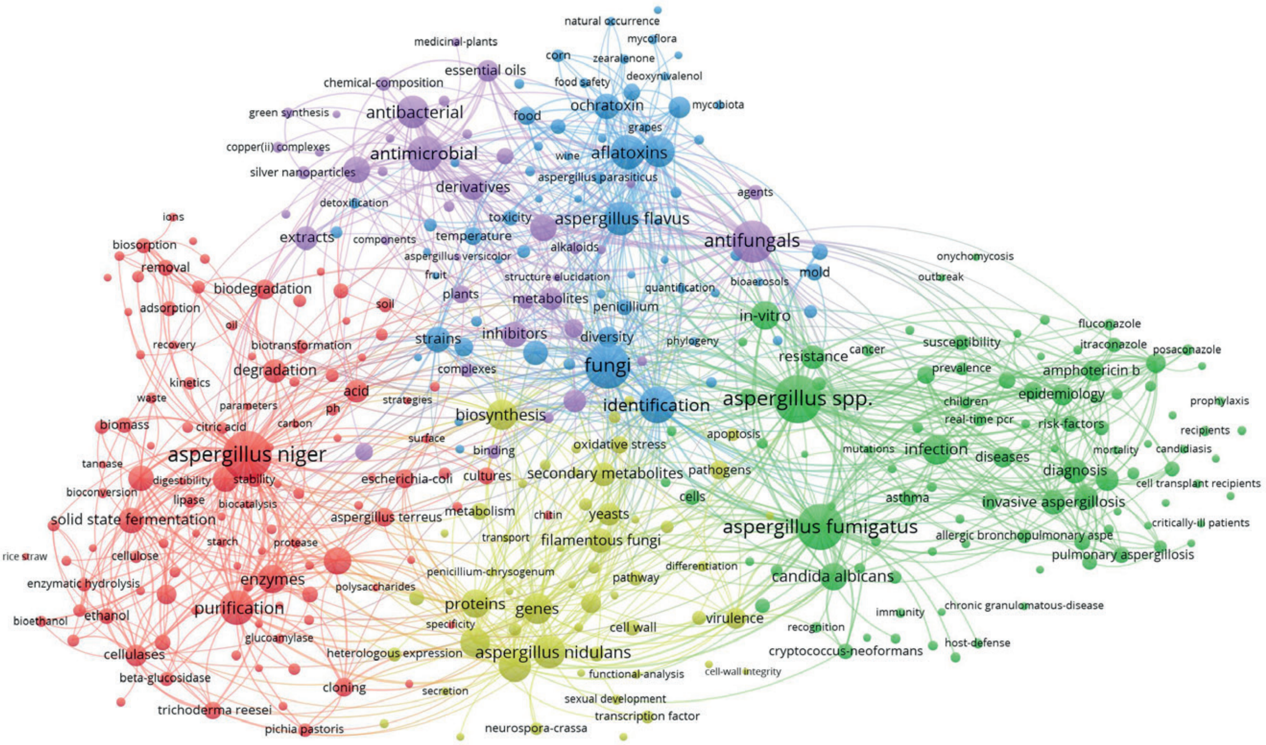

Fig. 8. Network visualisation of keywords of the publications related to *Aspergillus*. The larger the text and the circle the more often the subject has been cited.

in *Aspergillus* subgenus *Nidulantes*, section *Nidulantes* series *Versicolores* can produce sterigmatocystin and these species are common in the built environment. Other important mycotoxins from *Aspergillus* species include ochratoxin A, produced by *A. westerdijkiae*, *A. steynii, A. ochraceus* and other species in section *Circumdati* (Visagie *et al*. 2014c), by *A. alliaceus* in section *Flavi* and *A. niger*, *A. welwitschiae* and *A. carbonarius* in section *Nigri* (Abarca *et al*. 1994, Samson *et al*. 2004). *Aspergillus niger* and the closely related *A. welwitschiae*, can in addition, produce fumonisin B_2, B_4 and B_6 (Frisvad *et al*. 2007, 2011, Logrieco *et al*. 2014). The mycotoxin patulin is produced by members of section *Clavati*, most importantly *A. clavatus* (Bergel *et al*. 1943) that can occur in breweries and produce both patulin and cytochalasin E in the barley (LopezDiaz & Flannigan 1997). In addition to ochratoxins, species in *Aspergillus* section *Circumdati* can also produce the mycotoxins penicillic acid, xanthomegnin, viomellein, vioxanthin, avrainvillamide and stephacidin A (Visagie *et al*. 2014c, Mikkola *et al*. 2015).

Authors: G. Perrone, C.M. Visagie and J.C. Frisvad

4. **Fusarium** Link, Mag. Ges. Naturf. Freunde Berlin 3: 10. 1809.

Synonyms: *Fusisporium* Link, Mag. Ges. Naturf. Freunde Berlin 3: 19. 1809.
Selenosporium Corda, Icon. Fung. 1: 7. 1837.
Gibberella Sacc., Michelia 1: 43. 1877.
Lisea Sacc., Michelia 1: 43. 1877.
Sporotrichella P. Karst., Meddel. Soc. Fauna Fl. Fenn. 14: 96. 1887.
Gibberella subgen. *Lisiella* Cooke & Massee, Grevillea 16: 5. 1887.
Lisiella (Cooke & Massee) Sacc., Syll. Fung. 9: 945. 1891.
Septorella Allesch., Hedwigia 36: 241. 1897.
Ustilaginoidella Essed, Ann. Bot. 25: 351. 1911.
Rachisia Linder, Deutsche Essigind. 17: 467. 1913.
Stagonostroma Died., Krypt.-Fl. Mark Brandenb. 9: 561. 1914.
Fusidomus Grove, J. Bot. 67: 201. 1929.
Pseudofusarium Matsush., Microfungi Solomon Isl. Papua-New Guinea: 46. 1971.

Type species: *Fusarium sambucinum* Fuckel

Classification: *Ascomycota*, *Pezizomycotina*, *Sordariomycetes*, *Hypocreales*, *Nectriaceae.*

Background

For decades the genus *Fusarium* has attracted significant attention from researchers from different disciplines, resulting in a long and rather conflictive taxonomic history. Its high relevance derives from its diverse ecology, worldwide distribution, and species richness. It includes some of the most important plant pathogens (Dean *et al*. 2012), common endophytes and occasionally saprobes (Zhang *et al.* 2023a), opportunistic animal and human pathogens (Al-Hatmi *et al.* 2019, Lombard *et al.* 2019b, Song *et al.* 2023), and producers of bioactive secondary metabolites, including mycotoxins (Ibrahim *et al.* 2021).

Fusarium was first described by Link (1809), and characterised by forming elongated, fusoid, multiseptate conidia. Currently, 18 species complexes are recognised in *Fusarium s. str.* using multigenic genealogy, morphology, secondary metabolite data, sexual reproduction and host diversity. Among these, the *Fu. fujikuroi* species complex (SC) (FFSC), *Fu. chlamydosporum* SC (FCSC), *Fu. incarnatum-equiseti* SC (FIESC), *Fu. oxysporum* SC (FOSC), and *Fu. sambucinum* SC (FSAMSC, including the internal *Fu. graminearum* clade) encompass the most relevant species for agriculture, animal and human health, and biotechnology (Crous *et al*. 2021a, 2022).

Laboratory identification of *Fusarium s. lat.* (including the genera *Albonectria*, *Bisifusarium*, *Cyanonectria*, *Fusarium s. str.*, *Geejayessia*, *Luteonectria*, *Neocosmospora*, *Nothofusarium*, and *Setofusarium*), mostly rely on molecular characterisation using translation elongation factor (*tef1*) and RNA polymerase II second largest subunit (*rpb2*) markers. Morphological data, such as culture features (colony texture, pigmentation, type of aerial mycelium, presence of sporodochia), sexual morph (ascomata colour, wall thickness, ornamentation, presence and nature of basal stroma), and asexual morph (nature of conidiophores, conidiogenous cells, conidia and chlamydospores), as well as host preference, can be used for species identification (Leslie & Summerell 2006, Crous *et al*. 2021b). Mycotoxin profiling may also be helpful to separate *Fusarium s. str.* from other closely related fusarioid genera as, for instance, trichothecenes, known to be produced by species of *Fusarium s. str.* are generally not detected from other fusarioid genera; while cyclosporins, dihydrofusarin, polyketides neovasipyrones and vasinfectin A have been reported only from *Neocosmospora* species but not from *Fusarium s. str.* (Crous *et al*. 2021a).

Ecological and economic significance

Species of *Fusarium s. lat.* can cause diseases in numerous economically important crops (Afroz *et al*. 2020, Paul *et al.* 2020, Lombard *et al.* 2022), in forests (Hyde *et al.* 2023b), and also infect animals and humans (Chang *et al*. 2006, O'Donnell *et al*. 2009). Plant diseases cause significant economic losses and threaten global food security. They are difficult to eradicate due to elevated resistance or tolerance to fungicides. Similarly, most of the clinically relevant *Fusarium* species are also resistant to currently available antifungal agents and such diseases can be fatal (Al-Hatmi *et al*. 2016). Some of these diseases and infections are summarised below.

Plant diseases

Two main plant diseases, wilt and root rot caused by *Fusarium s. lat.*, result from fungal spores that can remain dormant in the soil or an alternative host for a prolonged period (Dita *et al*. 2018). When a suitable host is introduced to the environment, spores germinate and penetrate the roots. The mycelium invades the plant vascular system by growing through the cortex to the epidermis. Constant production of fungal spores occurs in vascular tissues from where they spread throughout the plant. As a result of vascular tissue blockage, leaves may turn yellow (Dita *et al*. 2018, Arie 2019). In the case of pitch canker and malformation, air-borne spores enter the host through a fresh wound, or the fungus can be transmitted via insects (Fox *et al*. 1991, Dwinell *et al*. 2001). Stress factors such as drought might increase the incidence and severity of diseases as shown in the crown and root rot diseases in asparagus and citrus species (Nigh 1990, Sandoval-Denis *et al.* 2018).

Crown rot is a disease caused mainly by *Fu. culmorum* and *Fu. pseudograminearum*. These species can infect barley, oats, rye and wheat (Kazan & Gardiner 2018, Hagerty *et al*. 2021). Fusarium crown rot (and root rot) disease in *Asparagus officinalis* (Elmer 2001) is caused by *Fu. oxysporum s. lat.* and *Fu. annulatum*.

Ear rot disease affects maize ears and kernels, and is one of the most important maize diseases, due to yield decrease and mycotoxin contamination of the grain. It is mainly associated with *Fu. annulatum*, *Fu. subglutinans*, *Fu. verticillioides,* and less frequently with *Fu. culmorum* and *Fu. graminearum* (Duncan & Howard 2010, Oldenburg & Ellner 2015, Lanubile *et al*. 2017).

Wilt disease affects tomato and sweet potato (caused by *Fu. oxysporum s. lat.*), cabbage (*Fu. equiseti* and *Fu. oxysporum s. lat.*), date palms (by *Fu. oxysporum f. sp. canariensis* and *Fu. oxysporum s. lat.*), oil palms (by *Fu. oxysporum f. sp. elaidis*), and banana (also called Panama disease, by *Fu. odoratissimum*), the latter is considered one of the most destructive banana diseases (Ploetz 2001, Song *et al*. 2004, Liu *et al*. 2017e, Dita *et al*. 2018, Maryani *et al*. 2019, Afroz *et al*. 2020, Paul *et al.* 2020).

Stalk rot and grain mould in sorghum are mainly induced by *Fu. andiyazi*, *Fu. annulatum*, *Fu. beomiforme*, *Fu. nygamai*, *Fu. sacchari*, *Fu. thapsinum* and *Fu. verticillioides*. In stalk rot, *Fusarium* mainly colonises the plant stem, causing tipping and breaking, but it can also interfere with grain formation. In grain mould, *Fusarium* species infect and colonise the grains, causing a reduction in grain size and weight (Leslie *et al*. 2005, Petrovic *et al*. 2009, Mohamed Nor *et al*. 2019).

Bakanae disease is the most important disease of rice caused by *Fusarium* species. *Fusarium fujikuroi* is the main causal agent, but other species of the FFSC, such as *Fu. andiyazi*, *Fu. annulatum*, *Fu. sacchari*, *Fu. subglutinans* and *Fu. verticillioides* have also been reported to be associated with Bakanae symptoms (Ploetz 2001, Amatulli *et al*. 2010, Wulff *et al*. 2010, Hsuan *et al.* 2011, Kim *et al*. 2014). The disease causes abnormal plant development and infected plants either eventually die or lose the ability to produce grain (Kim *et al*. 2014).

Head blight disease, scab or tombstone occurs in wheat and barley heads, and is induced predominantly by *Fu. graminearum*. The disease disrupts the development of kernels and causes discolouration and grain weight loss (McMullen *et al*. 2012).

Pitch canker affects *Pinus* species and is caused by *Fu. circinatum* (Steenkamp *et al*. 2012, Pfenning *et al*. 2014). The fungus can infect the vegetative and reproductive parts of plants. Disease symptoms include wilting and discolouration of leaves, branch dieback, mortality of female flowers and mature cones, damping-off of seedlings and seed deterioration (Wingfield *et al*. 2008).

Malformation of mango refers to abnormal growth of vegetative and reproductive parts of the mango plant caused by *Fu. mangiferae*, *Fu. mexicanum*, *Fu. sterilihyphosum* and *Fu. tupiense* (Britz *et al*. 2002, Otero-Colina *et al*. 2010, Lima *et al*. 2012).

Pokkah boeng occurs in sugarcane and is caused by species of the FFSC, such as *Fu. sacchari*, *Fu. proliferatum* and *Fu. madaense*. Disease symptoms include chlorosis and necrosis of leaves, death of the top of the plant and stalk rot (Costa *et al.* 2019).

Human and animal infections

Fusarium s. lat. contains highly relevant species in human and veterinary medicine, mostly opportunistic agents affecting immunocompromised hosts, commonly involved in keratitis, skin infections, and onychomycosis, and also associated with deep-seated and disseminated, often fatal infections. Clinically relevant fusarioid fungi are distributed in several *Fusarium* species complexes *i.e*., FCSC, FFSC, FIESC, FOSC, FSAMSC, and also in the closely related genera *Bisifusarium* and *Neocosmospora* (Dignani & Anaissie 2004, Chang *et al*. 2006, O'Donnell *et al*. 2009, 2010).

Mycotic keratitis can be caused by *Fu. fujikuroi*, *Fu. oxysporum s. lat.*, and several species of *Neocosmospora* (*N. falciformis*, *N. gamsii*, *N. keratoplastica*, *N. lichenicola*, *N. metavorans*, *N. petroliphila*, *N. solani*, *N. suttoniana* and *N. tonkinensis*) (Chang *et al*. 2006, Walther *et al*. 2021, Boral *et al*. 2018, Oliveira dos Santos *et al*. 2020). A history of ocular trauma is the major predisposing factor for mycotic keratitis caused by these fungi. However, contact lens usage and the presence of primary viral or bacterial eye infections are also linked to mycotic keratitis (Oliveira Dos Santos *et al*. 2020, Harbiyeli *et al*. 2021, Walther *et al*. 2021). Successful treatment of mycotic keratitis depends on timely diagnosis and appropriate initial therapy. However, in the case of mycotic keratitis and endophthalmitis caused by filamentous fungi, diagnosis may be prolonged and keratoplasty or even enucleation of the infected eye is required (Erdem *et al*. 2018, Hof 2020).

Disseminated fusariosis is mainly caused by species of *Neocosmospora* and *Fu. oxysporum s. lat.* (Hoenigl *et al*. 2021). Immunocompromised individuals are mostly infected through physical trauma or by inhalation of microconidia. The fungi disseminate hematogenously and affect different parts of the body, especially the lungs and sinuses (Nucci *et al*. 2018). These infections are often fatal (Guarro 2013).

Skin infections caused by species of *Bisifusarium*, *Fusarium s. str.*, and *Neocosmospora*, can be seen as subcutaneous nodules or necrotic, ulcerated lesions (Gupta *et al*. 2000b). Immunosuppression and traumatic injury are the main predisposing factors for these infections (Tram *et al*. 2020, Khalid *et al*. 2021). Even though these infections can be resolved by applying appropriate antifungal therapy, surgical debridement, skin transplantation and even amputation may be required to prevent further dissemination (Goussous *et al*. 2019). In some cases, patients do not survive due to septicemia or secondary infections (Tram *et al*. 2020, Khalid *et al*. 2021).

Onychomycosis is rarely caused by species of *Bisifusarium*, *Fusarium s. str.* or *Neocosmospora* (Uemura *et al*. 2022). Risk factors for onychomycosis can include climate, age, chronic skin illness, footwear, history of peripheral vascular diseases, diabetes and immunosuppression. Onychomycosis caused by non-dermatophyte species might make systemic dissemination of the fungus easier in case of immunosuppression (Girmenia *et al*. 1992, Gupta *et al*. 2000a).

Species of *Fusarium s. lat.* occasionally cause infections in animals. They can cause opportunistic infections in aquatic animals (Smyth *et al*. 2019, Cafarchia *et al*. 2020, Mallik *et al*. 2020), and insects (O'Donnell *et al.* 2012), keratitis in horses (O'Donnell *et al.* 2016), meningoencephalitis, invasive sinusitis and facial mycetoma in dogs (Evans *et al*. 2004, O'Donnell *et al*. 2010). Animal diseases associated with toxigenic *Fusarium* species were summarised by Nelson *et al*. (1994). Soil and sand are thought to be the main sources of infections as well as mycotoxins obtained from animal feed (Wu 2007, Sáenz *et al*. 2020).

Research interests

There are 25 152 publications and 363 128 citations from 2011–2021 related to *Fusarium s. lat.* in the Web of Science (Fig. 9) with the top 10 most cited articles listed in Table 6. Most of the publications focused on the impact of mycotoxins on plants, humans and animals, as well as epidemiology, diagnosis and management of infections caused by *Fusarium* species (Fig. 10).

Disease management

Species of *Fusarium s. lat.* that are involved in plant diseases are mostly resistant to fungicides and fumigants. Additionally, many *Fusarium* species are facultative pathogens with a saprobic phase and can survive for long periods in soil and plant debris. Therefore, the main approach to preventing diseases is to increase host resistance. Breeding programs to obtain resistant cultivars, eradication of infected plants and local quarantine procedures to prevent the spread of the disease to unaffected areas are recommended. Farm hygiene procedures such as using disease-free planting materials, and improving soil health to suppress fungal growth and reduce the intensity of the disease are recommended for disease control (Moore *et al*. 2001, Dita *et al*. 2018).

Clinical aspects

Treatment of mycotic keratitis caused by *Fusarium s. lat.* mainly relies on the use of natamycin (5 %) and voriconazole (1 %) (Jiang *et al*. 2020). In the case of unavailability of natamycin, a combination of liposomal amphotericin B and voriconazole has also been shown to be effective (Boral *et al*. 2018). Alternative treatments such as chlorhexidine (0.02 %) eye drops, and collagen cross-linking gave promising results (Zhu *et al*. 2018, Kunt *et al*. 2020, Oliveira Dos Santos *et al*. 2021). High-dose intravenous

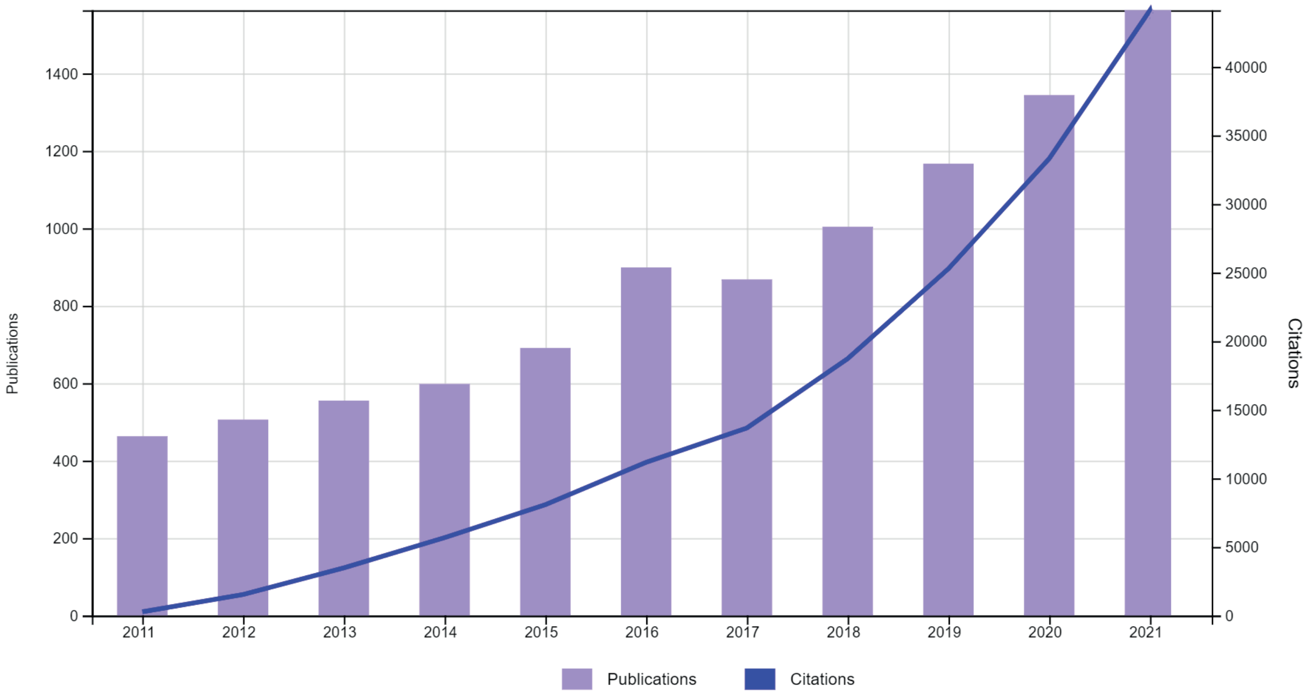

Fig. 9. Trends in research of *Fusarium* in the period 2011–2021. The figure shows citations for only 10 000 records.

Table 6. Top 10 cited articles related to *Fusarium* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	The top 10 fungal pathogens in molecular plant pathology	1 769	Dean *et al.* (2012)
2	Mycotoxins: Occurrence, toxicology, and exposure assessment	785	Marin *et al.* (2013)
3	Impact of mycotoxins on humans and animals	608	Zain (2011)
4	A polycationic antimicrobial and biocompatible hydrogel with microbe membrane suctioning ability	552	Li *et al.* (2011c)
5	Masked mycotoxins: A review	512	Berthiller *et al.* (2013)
6	Climate change, plant diseases and food security: an overview	420	Chakraborty & Newton (2011)
7	A unified effort to fight an enemy of wheat and barley: *Fusarium* head blight	399	McMullen *et al.* (2012)
8	Occurrence, toxicity, and analysis of major mycotoxins in food	392	Alshannaq & Yu (2017)
9	Current situation of mycotoxin contamination and co-occurrence in animal feed-focus on Europe	392	Streit *et al.* (2012)
10	Production and characterization of antifungal compounds produced by *Lactobacillus plantarum* IMAU10014	365	Wang *et al.* (2012b)

amphotericin B, voriconazole or posaconazole are recommended for the treatment of invasive fusariosis (Pound *et al*. 2011, Hoenigl *et al*. 2021, Khalid *et al*. 2021). Combined therapy is widely used primarily because of the severe nature of infections (Hoenigl *et al*. 2021). Onychomycosis by *Fusarium s. lat.* can be treated with terbinafine and itraconazole, however, recurrence may happen (Tosti *et al*. 2003). The wide range of antifungal drug resistance among *Fusarium s. str.* and *Neocosmospora* species is one of the main difficulties to control infections by these agents. To overcome this problem, the efficiency of novel antifungal agents, host-pathogen interactions, as well as drug-drug interactions remain relevant for future investigations.

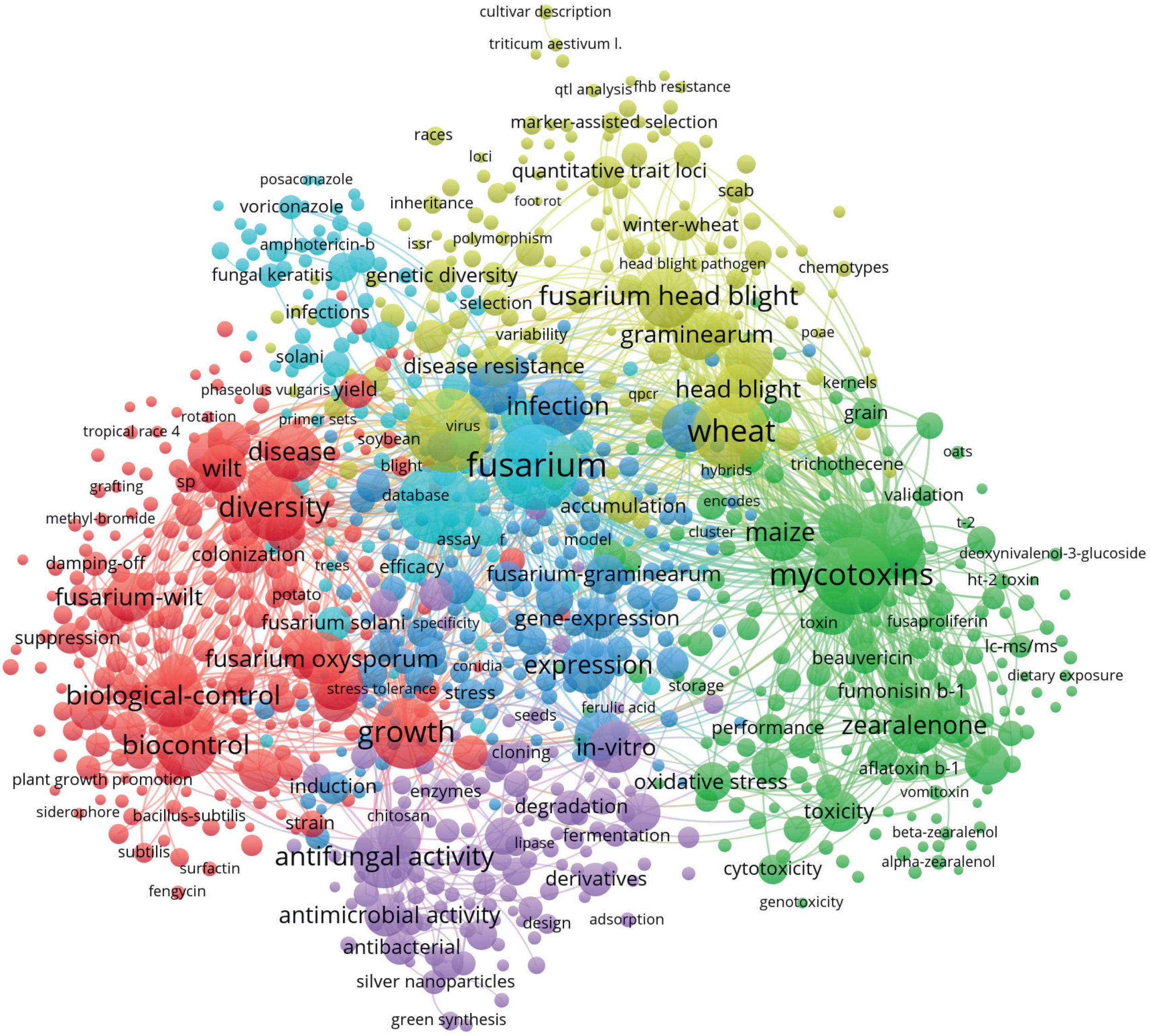

Fig. 10. Network visualisation of keywords of the publications related to *Fusarium*. The larger the text and the circle the more often the subject has been cited.

Toxins

Secondary metabolites of fungi can play a role in fungal pathogenesis, but in the case of mycotoxins, they might also contaminate food and feed produced by these plants. A variety of mycotoxins *i.e*., trichothecenes, fumonisins, beauvericin, enniatin, fusaric acid, fusarin and moniliformin are known to be produced by species of different *Fusarium* complexes, mainly species from the FFSC, FSAMSC and FIESC (Desjardins 2006, Sy-Cordero *et al*. 2012, Wang & Xu 2012, Proctor *et al*. 2020). Among these mycotoxins, trichothecenes can be produced by many species of the FSAMSC and FIESC. This mycotoxin class includes diacetoxyscirpenol (DAS), T-2 toxin, deoxynivalenol (DON), 3-acetyl-deoxynivalenol (3- ADON), 15-acetyl-deoxynivalenol (15-ADON), and nivalenol (NIV). Trichothecenes were shown to be toxic to animals and humans (Bertero *et al*. 2018, Ji *et al*. 2019, Proctor *et al*. 2020), and can act as virulence factors in the development of plant diseases, such as wheat head blight by *Fu. graminearum* (Proctor *et al*. 1997). The trichothecenes NIV and T-2 have an immunosuppressive effect on humans and animals (Zain 2011, Ji *et al*. 2019). A correlation was found between DON and Fusarium head blight disease caused by *Fu*. *pseudograminearum* (Kazan & Gardiner 2017). Nivalenol is produced mainly by *Fu*. *graminearum* and *Fu*. *cerealis* (syn. *Fu*. *crookwellense*). It can be detected in barley, maize, rice, wheat, and cereal products (Ji *et al*. 2019). Several types of grains have been found to contain T-2 toxin, one of the most acutely toxic trichothecenes. Major producers of the T-2 toxin are *Fu*. *langsethiae* followed by *Fu*. *poae* and *Fu*. *sporotrichioides* (Ji *et al*. 2019). Another important group of mycotoxins are the fumonisins, mainly produced by species of the FFSC, such as *Fu. annulatum* (as *Fu. proliferatum*) and *Fu. verticillioides* (Pitt 2014). Fumonisins have often been isolated from corn and its products and they have severe effects both in humans and animals (Summerell & Leslie 2011). Zearalenone is produced by *Fu*. *culmorum*, *Fu*. *graminearum*, and *Fu*. *sporotrichioides* and can cause estrogenic effects in farm animals (Zain *et al*. 2011). For further reading about the effects of other mycotoxins produced by fusarioid taxa (*e.g.*, fusarins, fusaric acid, moniliformin, enniatins, beauvericins, cyclosporins, vasinfectin-A) see Zain (2011), Bertero *et al*. (2018) and Ji *et al*. (2019).

Taxonomy and phylogeny

As in many other fungal groups, *Fusarium* taxonomy has not been exempted from conflicts and disputes, and also required revision, especially after the wide use of molecular techniques and the One Fungus = One Name declaration (Hawksworth *et al*. 2011, Taylor 2011). Currently, two opposing systems exist, one that argues for a purely cladistic, comprehensive generic definition, without acknowledging any synapomorphies for morphological recognition (Geiser *et al*. 2013, 2021, O'Donnell *et al*. 2020); and a second alternative (as applied here) based on the combination of available genetic, morphological and physiological data to define narrower, morphologically recognisable taxonomic units (Lombard *et al.* 2015, Crous *et al.* 2021a). According to the latter treatment, species previously described in the *Fu*. *dimerum* SC, *Fu*. *buxicola* SC, *Fu*. *staphyleae* SC, *Fu solani* SC and *Fu*. *ventricosum* SC were reclassified in the genera *Bisifusarium*, *Cyanonectria*, *Geejayessia*, *Neocosmospora*, and *Rectifusarium*, respectively. Furthermore, three additional genera were recognised within *Fusarium s. lat.*, namely *Luteonectria*, *Nothofusarium*, and *Setofusarium*. Further studies using whole genome data and typifying the described taxa will further improve the delimitation of genera in *Fusarium s. lat.* and provide a more stable nomenclature for taxonomists, plant pathologists, medical mycologists, students, and regulatory authorities.

Despite the divergent and conflicting generic taxonomic approaches, species-level taxonomy has remained more or less stable, with several novelties proposed in later years, mostly helped by the proliferation of molecular phylogenetic studies and recent monographic treatments (O'Donnell *et al.* 2004, 2009, 2010, Lombard *et al.* 2019a, b, Sandoval-Denis *et al.* 2019, Xia *et al.* 2019, Yilmaz *et al.* 2021).

Authors: H. Kandemir, M.M. Costa and M. Sandoval-Denis

5. ***Penicillium*** Link, Mag. Gesell. naturf. Freunde, Berlin 3(1–2): 16. 1809.

Type species: *Penicillium expansum* Link

Classification: *Ascomycota*, *Pezizomycotina*, *Eurotiomycetes*, *Eurotiales*, *Aspergillaceae.*

Background

Penicillium was introduced by Link (1809) with three species, *P. expansum*, *P. glaucum* and *P. candidum*. *Penicillium expansum* [CBS H-7082 (neotype); CBS 325.48 = ATCC 7861 = ATHUM 2891 = CCRC 30566 = FRR 976 = IBT 3486 = IBT 5101 = IMI 039761 = IMI 039761ii = MUCL 29192 = NRRL 976 = VKMF-275 (ex-neotype)] For much of its history, classification and identifications were based on morphology, which is notoriously difficult to interpret. Monographic treatments on the genus and its associated sexual morph (teleomorphic) genera *Eupenicillium* and *Talaromyces* included Thom (1930), Raper & Thom (1949), Pitt (1980) and Ramírez (1982). These works typically emphasised the need for standard working methods to delineate and classify species more accurately.

The early days of DNA sequencing and phylogenetic analyses revealed that *Penicillium* was polyphyletic, segregating into two clades defined by *Eupenicillium* and *Talaromyces* (LoBuglio *et al.* 1993, Berbee *et al.* 1995). Peterson (2000) noted that subgeneric classifications based on conidiophore branching patterns were not consistent with phylogenetic clades. Frisvad & Samson (2004) stabilised the taxonomy of *Penicillium* subgenus *Penicillium* in their revision where they introduced the polyphasic species concept characterising species based on morphological, extrolite and DNA sequence data.

The move to single-name nomenclature in the International Code of Nomenclature for algae, fungi, and plants (ICNafp; McNeill *et al.* 2012) allowed the opportunity for Houbraken & Samson (2011) to redefine *Penicillium*. Based on a four-gene phylogeny, they reviewed generic concepts in *Trichocomaceae,* redefined *Penicillium* to include several other genera like *Chromocleista*, *Eupenicillium*, *Eladia*, *Hemicarpenteles*, *Torulomyces*, and *Thysanophora*, adding to already synonymised genera *Aspergillopsis*, *Carpenteles*, *Citromyces*, *Coremium*, *Floccaria*, *Pritzeliella*, *Hormodendrum* and *Walzia*, and introduced the family *Aspergillaceae* to accommodate for example *Aspergillus* and *Penicillium*. In addition, they showed that *Talaromyces* formed a monophyletic clade with most *Penicillium* subgenus *Biverticillium* species in *Trichocomaceae*. These *Penicillium* names were subsequently transferred to *Talaromyces* by Samson *et al.* (2011). Finally, Houbraken & Samson (2011) introduced a new subgeneric classification dividing *Penicillium* into two subgenera and 25 sections. Visagie *et al*. (2014b) updated the "accepted species

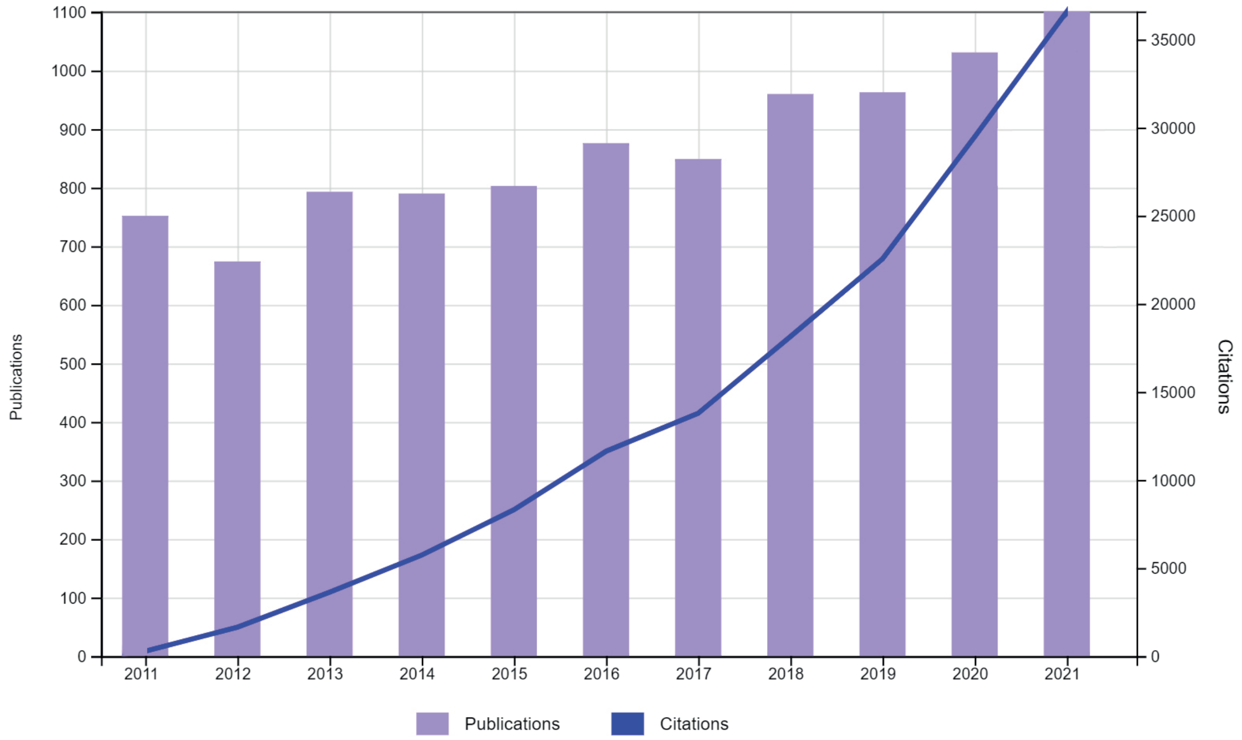

Fig. 11. Trends in research of *Penicillium* in the period 2011–2021.

Table 7. Top 10 cited articles related to *Penicillium* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Thoughts and facts about antibiotics: where we are now and where we are heading	555	Bérdy *et al.* (2012)
2	Curcumin nanoparticles: preparation, characterization, and antimicrobial study	467	Basniwal *et al.* (2011)
3	Antifungal activity of zinc oxide nanoparticles against *Botrytis cinerea* and *Penicillium expansum*	420	He *et al.* (2011)
4	Identification and nomenclature of the genus *Penicillium*	393	Visagie *et al.* (2014b)
5	Occurrence, toxicity, and analysis of major mycotoxins in food	392	Alshannaq & Yu (2017)
6	Current situation of mycotoxin contamination and co-occurrence in animal feed-focus on Europe	392	Streit *et al.* (2012)
7	Food fermentations: microorganisms with technological beneficial use	377	Bourdichon *et al.* (2012)
8	Production and characterization of antifungal compounds produced by *Lactobacillus plantarum* IMAU10014	365	Wang *et al.* (2012b)
9	Phylogeny of *Penicillium* and the segregation of *Trichocomaceae* into three families	316	Houbraken & Samson (2011)
10	50-plus years of fungal viruses	312	Ghabrial *et al.* (2015)

list", becoming the first of its kind that incorporated DNA reference sequences. It followed on from previous lists published by Pitt & Samson (1993) and Pitt *et al.* (2000), but in principle, the 354 species accepted all had reference sequences available needed for their identification. This review also proposed standardised working methods specifying growth medium formulations, incubation conditions, PCR and sequencing protocols and suggested the use of *tub* as a secondary identification marker for species identifications. In the following years, many new species were introduced and necessitated an update to the species list in which Houbraken *et al.* (2020) accepted 483 *Penicillium* species (501 accepted on 14 April 2022). A large sequencing effort also means that an almost complete dataset for ITS, *tub*, *cal* and *rpb2* is available for at least the ex-type strain of each species. Building on the proposed subgeneric and sectional classification (Houbraken & Samson 2011), a new series classification was proposed resulting in *Penicillium* now containing two subgenera, 32 sections and 89 series. More recently, Visagie *et al.* (2024) provided an update on taxonomic revisions and new species published since Houbraken *et al.* (2020), which brought the number of accepted species in *Penicillium* to 535 until 31 December 2022 (currently 598)..

Ecological and economic significance

Food mycology and ecology

Penicillium is one of the most common fungal genera occurring worldwide in a diverse range of habitats, from soil to vegetation, air, indoor environments and various food products. Its species play important and various roles, such as the production of speciality cheeses, Camembert or Roquefort (Thom 1906, Nelson 1970, Giraud *et al.* 2010), and fermented sausages (Ludeman *et al.* 2010, Magistà *et al.* 2017), decomposition of organic materials, causing devastating

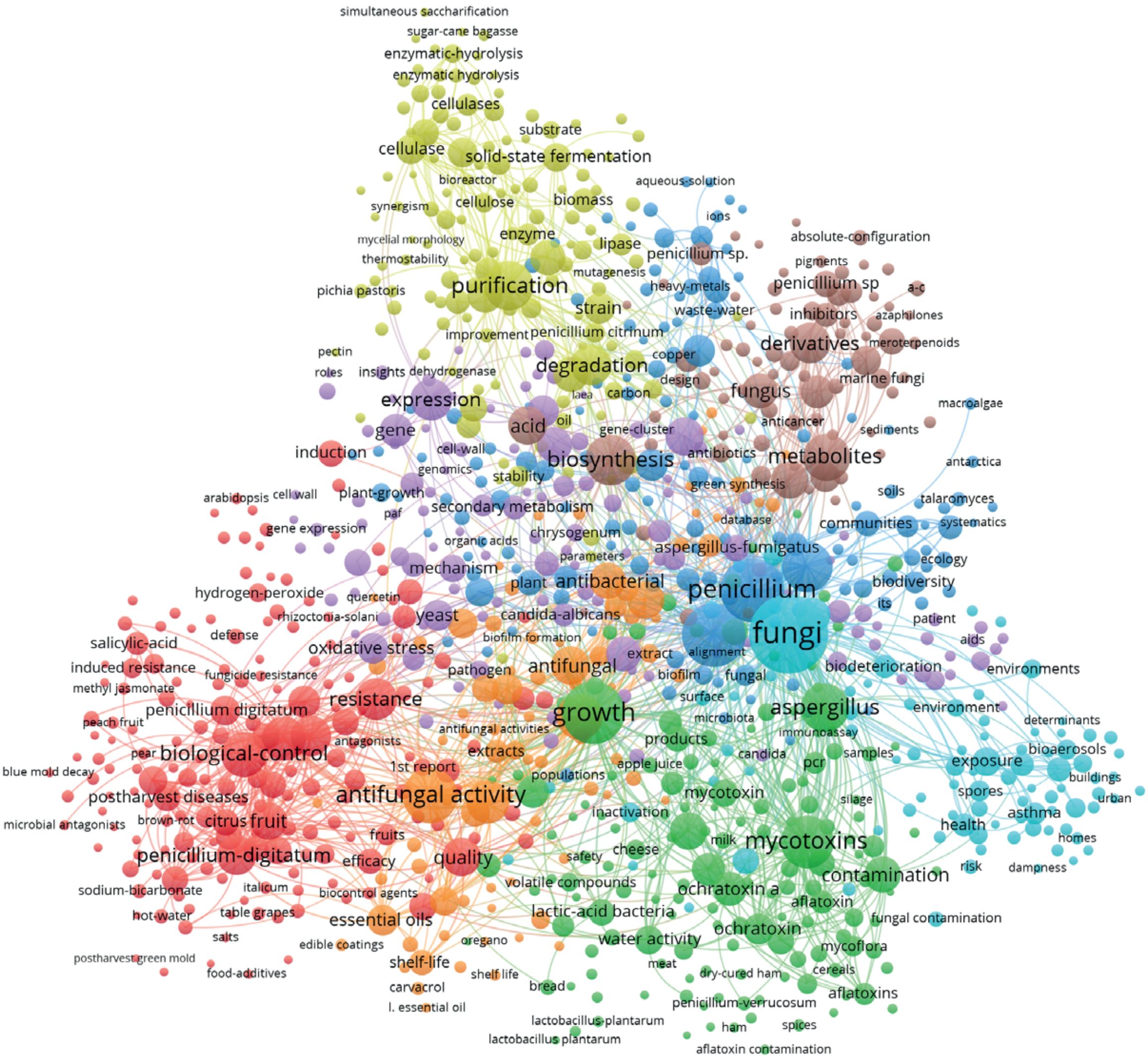

Fig. 12. Network visualisation of keywords of the publications related to *Penicillium*. The larger the text and the circle the more often the subject has been cited.

rots as pre- and postharvest pathogens on food crops (Samson *et al.* 2010), production of a diverse range of mycotoxins (Frisvad *et al.* 2004). The biggest claim for the genus is the production of penicillin, which revolutionised medical approaches to treating bacterial diseases (Fleming 1929, Thom 1945).

In general, *Penicillium* species are strictly aerobic, nutritionally undemanding, mostly saprobes and able to grow in a wide range of physicochemical environments. A few are capable of invading plants or animals, but none is obligately parasitic. Some examples are fruit pathogens (*P. expansum* on apples and mainly responsible for patulin contamination in fruit juices (Yu *et al.* 2020)); *P. digitatum* and *P. italicum* on citrus fruits (Papoutsis *et al.* 2019), species able to grow at very low water activity and low temperatures (*P. brevicompactum*, *P. chrysogenum*, and *P. olsonii*), and at low oxygen tension (*P. roqueforti*). They are fast-growing fungi, producing a high number of exogenous dry-walled spores that are easily disseminated by air. Most species show optimal growth at moderate to low temperatures and are capable of growth at water activities (a^w) below 0.9. Additional species important in food mycology are *P. paneum*, and *P. carneum*. These two species are peculiar for their rapid growth and formation of velutinous colonies and they are unique for their high tolerance to propionic acetic and lactic acid (Perrone & Susca 2017). Although *P. roqueforti* is well known for cheese production like Roquefort, Stilton and Gorgonzola, it is an important spoilage microorganism of airtight-stored grain and relevant accumulation of roquefortine C in grains (Petersson & Shnürer 1999). Recently five different domesticated populations have been identified by genomic studies in *P. roqueforti* (Dumas *et al.* 2020, Crequer *et al.* 2023). The emblematic species *P. camemberti,* used as a starter species in the production of many cheeses, is regarded as a domesticated species derived from the contaminant species *P. commune* (Giraud *et al.* 2010, Panelli *et al.* 2012). Penicillia represents 50 to 90 % of fungal species occurring on dry-cured meat, especially on the surface of ripening products, such as dry-fermented traditional sausages, with the prevalence of *P. nalgiovense*, followed by *P. olsonii*, *P. chrysogenum*, *P. commune*, *P. solitum* and a recently described species *P. salamii* (Perrone et al. 2015, Magistà *et al.* 2017). The halotolerant *P. chrysogenum* was shown in some studies to improve the quality of ham by promoting proteolysis and contributing to the development of the typical ham flavour (Comi & Iacumin 2013), while *P. commune* has been cited as responsible for the phenol acid defect (off-odour). Although most moulds found on cured meat products are non-toxigenic, strains of *P. nordicum* and *P. verrucosum* are reported for ochratoxin A (OTA) risk in these products, especially *P. nordicum* as a well-adapted species of NaCl-rich and protein-rich food, and represent the most commonly occurring ochratoxigenic species on dry-cured meat products (Iacumin *et al.* 2009, Scaramuzza *et al.* 2015). In addition, *Penicillium* species with interesting technological properties were also observed in the fermentation of various table olives products (Bavaro *et al.* 2017). Although the detected level of toxic metabolites of fungi in table olives was very low, they are a potential source of fungal toxic metabolites due to *Penicillium* spoilage (Medina-Pradas & Arroyo-López 2015). Recently, a new species *P. gravinicasei* in sect. *Cinnamopurpurea*, has been reported as being involved in the seasoning of cheese in caves (Anelli *et al.* 2018). Recently *P. brevicompactum* was studied for the first time as a potential pigment producer using submerged fermentation, and it was demonstrated to be a safe source of natural pigments with interesting properties for the food industry (Fonseca *et al.* 2022a).

Research interests

There are 9 592 publications and 130 850 citations from 2011–2021 in the Web of Science (Fig. 11), with the top 10 most cited articles included in Table 7. Most publications focused on taxonomy and secondary metabolites from *Penicillium* (Fig. 12).

Extrolites

Penicillium can produce many small molecule extrolites (Frisvad 2015). Despite this, genome sequencing has shown that it is only 10–20 % of the SMs that can potentially be produced on common laboratory media (Grijseels *et al*. 2016, Nielsen *et al*. 2017).

Important drugs produced by *Penicillium* species include the cholesterol-lowering compactin (= mevistatin) produced primarily by *P. solitum* (Frisvad & Filtenborg 1989, Chakravari & Sahal 2004; under the incorrect producer-name *P. citrinum*), the antifungal griseofulvin produced by *P. janczewskii* and *P. griseofulvum* (Petersen *et al*. 2014), the immunosuppressive mycophenolic acid produced industrially by *P. brevicompactum* (Wu *et al.* 2020b), adenophostin produced by *P. brevicompactum* (Takahashi *et al.* 1993), the antibiotic penicillin produced industrially by *P. rubens* (Houbraken *et al*. 2011a), and the immunosuppressive bredinin produced by *P. brefeldianum* (Iwata *et al*. 1977, Ishikawa *et al*. 1980). Many other bioactive compounds have been isolated from *Penicillium* species (Frisvad & Samson 2004, Frisvad *et al*. 2004, Nicoletti & Trincone 2016) and some may be important future drugs.

Important mycotoxins produced by *Penicillium* species include the nephrotoxin ochratoxin A produced by *P. verrucosum* (Frisvad 1985, Pitt 1987) and *P. nordicum* (Larsen et *al*. 2001), the nephrotoxin citrinin produced by *P. verrucosum*, *P. expansum* and *P. citrinum* (and many other species) (Hetherington & Raistrick 1931, Harwig *et al*. 1973, Houbraken *et al*. 2011b), penicillic acid produced primarily in cereals by species in series *Viridicata* (Frisvad 2018), and patulin produced primarily by *P. expansum* in pomaceous fruits but also by many other species (Frisvad 2018).

Authors: G. Perrone, C.M. Visagie and J.C. Frisvad

6. **Trichoderma** Pers., Neues Mag. Bot. 1: 92. 1794.

Type species: *Trichoderma viride* Pers.

Classification: *Ascomycota*, *Pezizomycotina*, *Sordariomycetes*, *Hypocreales*, *Hypocreaceae.*

Background

Trichoderma is a hyperdiverse and cosmopolitan genus with the number of species exponentially increasing since it was first described in 1794, from one species in 1930, five in 1960, 25 in 1990, 120 in 2010, to *ca*. 460 in 2022 (Index Fungorum and MycoBank). *Trichoderma* species are most known for biological control properties against phytopathogens and used in biotechnology (*e.g.*, enzyme production) (Fig. 13). In agriculture, *Trichoderma* has also been utilised to promote plant growth, protect and alleviate plants from abiotic stressors (*e.g.*, drought or extreme salinity), and even bioremediate or remove contaminants from soils (Harman *et al.* 2004, Hermosa *et al.* 2012, Khan & Mohiddin 2018). In biotechnology, its applications range from biofuel/bioethanol production, animal feed and textile manufacturing, to nanotechnology (Bhat 2000, Polizeli *et al.* 2005, Dhawan & Kaur 2007, Gajbhiye *et al.* 2009, Fayaz *et al.* 2010, Elamawi *et al.* 2018). The efficacy of this genus comes from the diversity of enzymes and secondary metabolites that it produces. For example, more than 600 enzymes are in BRENDA, The Comprehensive Enzyme Information System (as of April 2022), compared to *ca*. 1 500 in *Aspergillus*, *ca*. 900 in *Fusarium*, and 80 in *Cercospora*. In addition, more than 1 000 compounds, including secondary metabolites, have been identified in *Trichoderma* (Zeilinger *et al.* 2016, Zhang *et al.* 2021b).

The number of enzymes and secondary metabolites produced by *Trichoderma* is possibly a result of its ability to colonise different types of substrata and compete against other microorganisms in a variety of natural habitats and ecosystems (Samuels 1996, 2006, Druzhinina *et al.* 2011, Chaverri & Samuels 2013, Contreras-Cornejo *et al.* 2016). For example, *Trichoderma* has been found inhabiting terrestrial and marine/aquatic soils, travelling in air, decomposing plant material, parasitising nematodes and other fungi, growing endophytically in living plant tissues, and, less commonly, causing infections in immunocompromised humans (Garo *et al.* 2003, Rubini *et al.* 2005, Andersen *et al.* 2011, Gazis & Chaverri 2015, Hatvani *et al.* 2019, Ogaki *et al.* 2020, Nafady *et al.* 2022). In addition, *Trichoderma* species have been found in most parts of the world, even in extreme northern and southern latitudes, and from moist tropical or subtropical forests to arid, temperate or boreal ecosystems (Samuels 2006, Kubicek *et al.* 2008, Gazis & Chaverri 2015, Cummings *et al.* 2016, Ogaki *et al.* 2020).

Until recently, it was thought that the majority of *Trichoderma* spp. were saprobes because they were typically found in soils or decaying plant material. However, it is now accepted that its main nutritional mode is mycotrophy, cryptically parasitising or antagonising *e.g.*, fungi in the soil or immersed in decomposing wood, in addition to growing directly on other fungal sporocarps (Kubicek *et al.* 2011, Atanasova *et al.* 2013, Chaverri & Samuels 2013). It has been hypothesised that endophytically, *Trichoderma* acts with similar mechanisms, providing potential benefits to the plant (*e.g.*, abiotic and biotic stress protection and alleviation) (Bailey *et al.* 2006, Qin *et al.* 2016, De Silva *et al.* 2019b) or waiting as latent saprobes for the plant to die (Parfitt *et al.* 2010).

Morphologically, the asexual morph of *Trichoderma* is characterised by complex conidiophores that generally branch in a pyramidal fashion (*i.e.*, the basal branches are longer than those at the tips), with hyaline phialides formed on the exposed fertile branches, and conidia that are usually smooth, rarely ornamented, typically ellipsoidal to nearly oblong, rarely globose, and mostly green or hyaline, rarely yellow. If chlamydospores are formed, they are typically globose to subglobose and are terminal or intercalary. There are some exceptions where the morphology of the conidiophores is much simpler, *i.e.*, acremonium-, gliocladium-, or verticillium-like (*e.g.*, *T. pulvinatum*, *T. virens*, or *T. citrinum*, respectively).

Relatively few species of *Trichoderma* have a known sexual morph (previously known as *Hypocrea*). When known, they form cushion-shaped, brightly or lightly coloured (*e.g.*, whitish, yellowish, ochre to reddish brown, dark green to almost black), fleshy stromata composed of pseudoparenchymatous tissue or highly compacted hyphae, generally up to 5 mm diam, although stromata of some species may be several centimetres wide. Perithecia are fully immersed in the stroma and paraphyses are absent. Asci are cylindrical, normally containing eight, 1-septate ascospores that disarticulate at the septum early in their development, producing 16 part-ascospores. Part-ascospores may be smooth to ornamented (spinulose or warted), generally dimorphic, green or hyaline, and rarely yellowish.

Persoon (1794) originally described *Trichoderma* as a "gasteromycete" and Fries erected *Hypocrea* in 1825. It was several years later that Tulasne & Tulasne (1860) and Brefeld (1891) proved the link between *Trichoderma* and *Hypocrea* by following *Trichoderma* hyphae to the stroma and by isolating ascospores into pure cultures, respectively. Bisby (1939) recognised only one species, *T. viride*. Rifai (1969) was one of the first to suggest the complex taxonomy of the genus, dividing it into nine "species aggregates," *i.e.*, *T. aureoviride*, *T. hamatum*, *T. harzianum*, *T. koningii*, *T. longibrachiatum*, *T. piluliferum*, *T. polysporum*, *T. pseudokoningii*, and *T. viride*. He regarded each species aggregate as comprising more than one morphologically cryptic species. Rifai also concluded that asexual characters alone might not be useful in its taxonomy.

Before Rifai's critical taxonomic revision, Dingley (1952, 1957) had already published the first "modern" treatments of *Hypocrea* when she described, characterised, and illustrated several species including their asexual morphs. Dingley identified all the *Hypocrea* asexual morphs as being typical of *T. viride,* despite their differences which were evident in her illustrations. Some years later, Doi produced substantial *Hypocrea* monographs, and described many more species from Japan, Papua New Guinea, and South America (*e.g.*, Doi 1966, 1969, 1972, 1975, 1976). In his works, Doi described and illustrated sexual and asexual morphs. By the early 1990s, Bissett was discussing the implications of basing a *Trichoderma* classification on Rifai's species aggregates (Bissett 1991a) because some were narrowly defined species, whereas others could be interpreted as having relatively large numbers of species. For example, he suggested that more than 20 distinct species could be assigned to each of the morphological species *T. hamatum*, *T. koningii*, and *T. viride* (Bissett 1984, 1991a, b, c, 1992). He then revised the taxonomy and recognised five sections: sect. *Hypocreanum*, sect. *Longibrachiatum*, and sect. *Pachybasium*; sect. *Saturnisporium*, and sect. *Trichoderma* (Bissett 1984, 1991a, b, c, 1992). These sections are still used (*e.g.*, Vizcaino *et al.* 2005, Samuels *et al.* 2012, Qin & Zhuang 2016, Zhang *et al.* 2022). More recent significant *Trichoderma* taxonomic treatments include Samuels *et al.* (1998, 2012), Chaverri & Samuels (2003), Chaverri *et al.* (2003a), Lu *et al.* (2004), Overton *et al.* (2006), Jaklitsch *et al.* (2006, 2008), Jaklitsch (2009, 2011) and Jaklitsch & Voglmayr (2015). In addition, smaller studies added many new species (*e.g.*, Chaverri *et al.* 2002, 2003a, 2011, 2015, Chaverri & Samuels 2003, Zhu & Zhuang 2015, Qin & Zhuang 2016b, c, Zhang & Zhuang 2017).

The introduction of DNA sequencing and phylogenetics revolutionised the study of *Trichoderma* systematics. The ITS nrDNA region was the first marker to be used in the late 1990s (Kuhls *et al.* 1997, Ospina-Giraldo *et al.* 1998, 1999, Lieckfeldt *et al.* 1999, Dodd *et al.* 2000, Lieckfeldt & Seifert 2000, Lee & Hseu 2002). Then, in the mid to late 2000s, additional markers/genes were added (*e.g.*, endochitinase, ECH42; translation elongation factor 1-alpha, *tef1*; mitochondrial small subunit rDNA; actin, *act*; DNA-directed RNA polymerase second largest subunit, *rpb2*; and calmodulin, *cal*) (Kullnig *et al.* 2001, Kullnig-Gradinger *et al.* 2002, Chaverri & Samuels 2003, Chaverri *et al.* 2003b). This decade was the beginning of the exponential growth in the number of new species described. Still today, the suggested secondary barcodes for *Trichoderma* taxonomy are *tef1* and *rpb2* (Chaverri *et al.* 2015, Cai & Druzhinina 2021), as it is well-accepted among *Trichoderma* taxonomists that the ITS region is not able to distinguish species. In general, *tef1* gives support to terminal clades and *rpb2* to the backbone of the genus phylogeny (Chaverri & Samuels 2013, Chaverri *et al.* 2015, Robbertse *et al.* 2017, Cai & Druzhinina 2021). However, *Trichoderma* systematists still recommend the use of several genes (Chaverri *et al.* 2015, Cai & Druzhinina 2021). GenBank's database of DNA sequences from *Trichoderma* types is well curated, containing most of the described species (Robbertse *et al.* 2017, Cai & Druzhinina 2021). A decrease in the cost of genome sequencing has made it possible to produce many *Trichoderma* genomes, with about 85 genomes on the Joint Genome Institute's MycoCosm website (https://mycocosm.jgi.doe.gov) and 32 on GenBank. This new genomic data pave the way to discover novel and improved markers for taxonomy and species circumscription. For additional information on taxonomic history and resources for *Trichoderma*, see reviews in Samuels (1996, 2006), Samuels & Hebbar (2015), and Cai & Druzhinina (2021).

Ecological and economic significance

Trichoderma is ubiquitous and was thought to only inhabit the soil and decomposing plant material (Kubicek *et al.* 2011, Atanasova *et al.* 2013, Chaverri & Samuels 2013). In the soil, species of *Trichoderma* may be found as chlamydospores or may be actively parasitising nematodes, oomycetes, or other fungi (Samuels *et al.* 2002, Rubini *et al.* 2005, Samuels 2006, Gazis & Chaverri 2015, Nafady *et al.* 2022). In rotting wood, they may be saprobic or mycotrophic on other fungi immersed in the wood. However, *Trichoderma* spp. have also been found as endophytes in roots, and more recently in stems of some tropical trees in natural forests such as *Coffea*, *Hevea*, *Micrandra*, and *Theobroma* (Samuels *et al.* 2006, Gazis & Chaverri 2010, Yu *et al.* 2015c, Kwasna *et al.* 2016, Skaltsas *et al.* 2019, Rodriguez *et al.* 2021). In most cases, the nutritional mode is cryptic because the species are not obviously growing on other fungal sporocarps, and thus, it is challenging to determine if they are mycotrophs or saprotrophs. The ability of some *Trichoderma* species to colonise almost systemically in plant tissues has been demonstrated experimentally *in planta*. For example, Bailey *et al.* (2006, 2008) and Pujade-Renaud *et al.* (2019) inoculated planting soil and seeds with endophytic *Trichoderma* spp., *i.e.*, *T. lentiforme*, *T. hamatum*, *T. neotropicale*, and *T. koningiopsis*, and demonstrated that the fungi were able to colonise seedling roots, stems and, in some cases, leaves.

The mycotrophic ability of many *Trichoderma* spp. has made this group one of the most used in the biological control of phytopathogens. The *T. harzianum* complex possibly contains most species used as bio fungicides (Chaverri *et al.* 2015). Members of this complex have been used to control fungi, *e.g.*, *Alternaria*, *Botrytis*, *Corynespora*, *Curvularia*, *Fusarium*, *Moniliophthora*, *Phyllosticta*, *Rhizoctonia*, *Sclerotinia*, *Sclerotium*, and *Zymoseptoria* (Sempere & Santamarina 2007, John *et al.* 2010, Crozier *et al.* 2015, You *et al.* 2016, Soto *et al.* 2018, Baiyee *et al.* 2019, Kerdraon *et al.* 2019, Silva *et al.* 2021, Navarro *et al.* 2022, Yadav & Ghasolia 2022); oomycetes, *e.g.*, *Pythium* and *Phytophthora* (Benhamou & Chet 1997, Ahmed *et al.* 1999, Chowdappa *et al.* 2013); *Spongospora* (O'Brien & Milroy 2017); and nematodes, *e.g.*, *Meloidogyne* (Sharon *et al.* 2007). The antifungal mechanisms in *Trichoderma* can be divided mainly into direct parasitism, where *e.g.*, fungal cell-wall degrading enzymes are produced; and antibiosis due to the secretion of secondary metabolites (SMs), including volatile organic compounds (VOCs) (Ghorbanpour *et al.* 2018, Köhl *et al.* 2019). Examples of wall-degrading enzymes are proteases, endochitinases, β-1,3-glucanases, polygalacturonases, xylanases, and cellulases (Hermosa *et al.* 2013, Ghorbanpour *et al.* 2018). Secondary metabolites include polyketides, pyrones, terpenes, metabolites derived from amino acids, and polypeptides (Schuster & Schmoll 2010), while volatile compounds are acids, alcohols, aldehydes, esters, ethers, hydrocarbons, ketones and different classes of terpenes (Cruz-Magalhaes *et al.* 2019, Rajani *et al.* 2021).

The benefits of *Trichoderma* are not restricted to mycotrophy but also expand to other plant-beneficial effects such as induced systemic resistance (ISR), plant growth promotion, and abiotic stress protection and alleviation. For example, jasmonic acid, ethylene, hydrophobin-like SSCP orthologues, and higher expression of pathogenesis-related enzymes, such as chitinases, β-1,3-glucanase, and peroxidases, among others, are associated with ISR (Hermosa *et al.* 2012). Additional information on *Trichoderma* and ISR can be found in reviews by Harman *et al.* (2004), Shoresh *et al.* (2010), Hermosa *et al.* (2012), and Mendoza-Mendoza *et al.* (2018). Some mechanisms involved in plant growth promotion by *Trichoderma* are auxin signalling (Contreras-Cornejo *et al.* 2009) and production and activity of indole acetic acid and ACC deaminase which then manipulate the phytohormone regulatory network (Gravel *et al.* 2007, Hermosa *et al.* 2013). Reviews by Harman *et al.* (2004), Hermosa *et al.* (2012) and Mendoza-Mendoza *et al.* (2018) contain additional information. Involvement of *Trichoderma* in plant resistance to heat, salinity, and drought has been attributed to the production of heat-shock proteins, n-acetyl-β-hexosaminidase, Kelch-repeat domain protein related to protein-protein interactions, and alleviation of damage by reactive oxygen species (ROS), water-use efficiency and secretion of phytohormonal analogues (Hermosa *et al.* 2013, Kashyap *et al.* 2017, Mona *et al.* 2017). There is also evidence that secondary metabolites play an important role in plant stress tolerance by coordinately working to bring growth regulation and protecting membranes from ROS (Mona *et al.* 2017, Phukhamsakda *et al.* 2018b, 2019, Macabeo *et al.* 2020, Garcia *et al.* 2022).

Fungal cellulases currently dominate the industrial applications of cellulases, and *T. reesei* is the main industrial source of cellulases and hemicellulases that depolymerise biomass into simple sugars that are then used in biofuels, including ethanol (Lynd *et al.* 2002, Himmel *et al.* 2007, Bischof *et al.* 2016). Cellulases from *Trichoderma* spp. have also been applied in the pulp and paper, textile, and food industries (Schuster & Schmoll 2010). Transformation techniques facilitating the genetic engineering of *T. reesei* became available in the early 1990s (see review in Bischof *et al.* 2016), making this species among the first hosts for the expression of mammalian proteins (Harkki *et al.* 1989). Currently, about 11 % of all enzyme formulations registered by the Association of Manufacturers and Formulators of Enzyme Products are produced using *T. reesei* as the expression host (see review and fig. 1 in Bischof *et al.* 2016). Additional enzymes produced by *Trichoderma* spp. are pectinases, xylanases, chitinases, lipases, proteases, amylases, manganese peroxidases, and laccases, which are used in various industries such as animal feed, antimicrobial purposes, biorefineries, detergents, detoxification of pollutants, fruit juice clarification, leather, medicine, and waste management (Gautam & Naraian 2020).

Research interests

The number of publications and citations linked to *Trichoderma* is on an upward trend (Fig. 13). The research interests continue to be related to their plant beneficial abilities and industrial enzyme production. There are 9 380 publications and 117 855 citations from 2011–2021 in the Web of Science (Fig. 14), with the top 10 most cited articles included in Table 8. The highest cited article "Induced systemic resistance by beneficial microbes" (Pieterse *et al.* 2014) reviews the beneficial interactions between microbiomes and plants, with a focus on roots. In this review, the roles of *Trichoderma* in induced systemic resistance, modulation of root immunity, and disease-suppressive soils are discussed. The next six articles in the ranking are related to enzyme production for the biofuel and biorefinery industries (Table 8).

Future perspectives

With advances in the sequencing and availability of more than 80 *Trichoderma* genomes, it will now be possible to mine efficiently for bioactive natural products (*e.g.*, secondary metabolites and proteins) and to better understand the ecology of *Trichoderma* (Katz & Baltz 2016, Ziemert *et al.* 2016). For example, genome mining of *T. afroharzianum* T-22 (labelled as *T. harzianum* in the publication of Chen *et al*. 2019a) identified and characterised a cryptic iterative polyketide synthases (IPKS)-containing cluster that synthesises tricholignan A, which has been shown to reduce iron (III) and promote plant growth under iron-deficient conditions (Chen *et al.* 2019a). Chen *et al.* (2019a) used heterologous reconstitution and biochemical studies to unravel the biosynthetic pathway. In addition, genome mining could be used to explore how, why, or what *Trichoderma* is using to become a successful plant symbiont. For example, the detection of sets of genes encoding proteins involved in phytohormone biosynthesis and signalling (Guzmán-Guzmán *et al.* 2019).

Trichoderma could also be an important component in a strategy to produce crops more resilient to the effects of climate change, declining soil fertility, pollutants in soils, fungicide resistance, and phytopathogens (Harman *et al.* 2004, Hermosa *et al.* 2012, Kashyap *et al.* 2017, Mohapatra *et al.* 2022). Innovative research on plant-beneficial *Trichoderma* should also be geared to understand interactions with other inhabitants in the microbiome, including endophytes. For example, there is increasing evidence that *Trichoderma* is a core component in healthy endophytobiomes of some tropical trees in their natural habitats (Gazis & Chaverri 2015, Skaltsas *et al.* 2019, Aldrich-Wolfe *et al.* 2020, Rodriguez *et al.* 2021, Fonseca *et al.* 2022b). However, little is known about how *Trichoderma* artificially inoculated in plants may interact with other fungi in the plant endo- or rhizosphere. There is evidence of non-target effects (*e.g.*, toxicity and competitive displacement) by several biocontrol species or isolates. For example, Naseby *et al.* (2000) found that the fungistatic VOCs produced by *Trichoderma* cf. *harzianum* also had a negative impact on plant growth at high doses. Szczepaniak *et al.* (2015) inoculated soils with *T.* cf. *viride* together with a bacterial consortium of 195 species. After one year, only 73 bacterial species were recovered from the consortium,

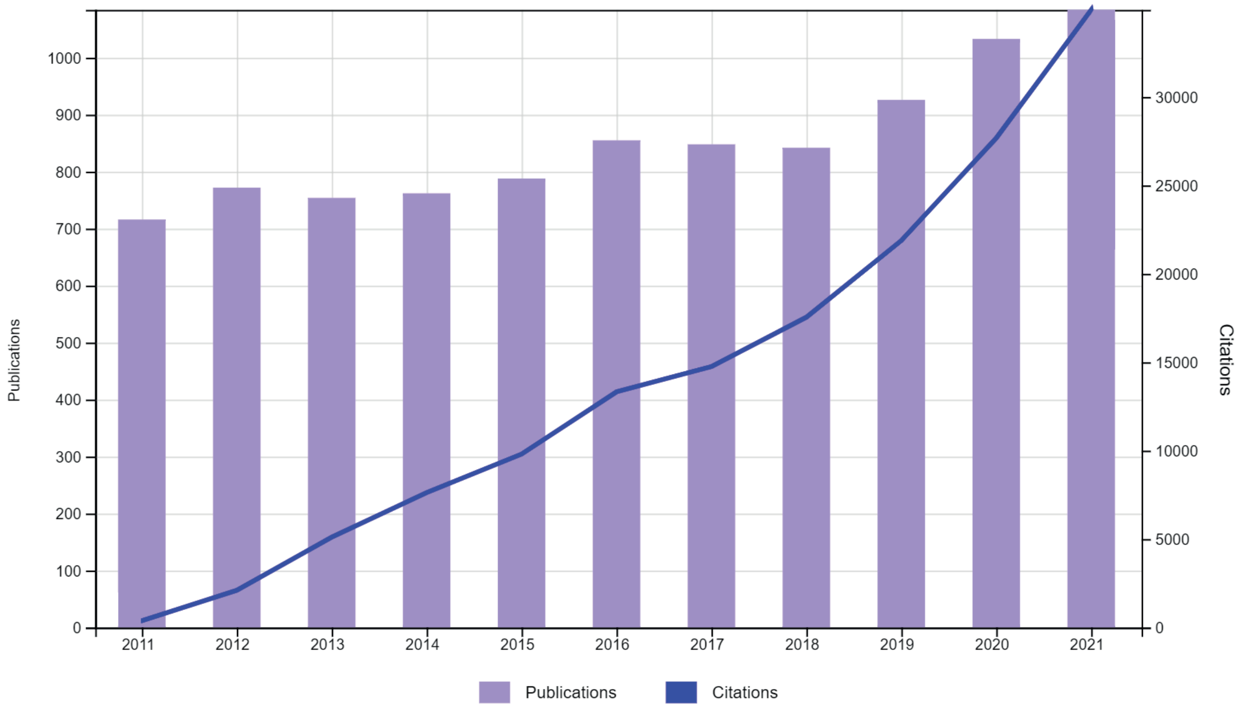

Fig. 13. Trends in research of *Trichoderma* in the period 2011–2021.

suggesting an antagonistic effect. Similarly, other species of *Trichoderma* may reduce the germination of arbuscular mycorrhizal fungal spores (McAllister *et al.* 1994, Brimner & Boland 2003). In contrast, the inoculation of *Trichoderma* spp. in natural soils significantly increased the fungal rhizospheric community (Naseby *et al.* 2000, Cordier & Alabouvette 2009). For more on this topic, see the review by Jangir *et al.* (2019).

The correct identification of *Trichoderma* continues to be problematic. In the Web of Science, more than 4 000 publications identified the species used as *T. harzianum*. It is now accepted among *Trichoderma* systematists that *T. harzianum s. str.* is mostly found in temperate regions, especially Europe, and with limited biocontrol potential. Those used in biocontrol studies belong to others in the *T. harzianum* species complex, *e.g.*, *T. afroharzianum*, *T. guizhouense*, *T. lentiforme*, and *T. simmonsii* (Chaverri *et al.* 2015). This problem is aggravated by the fact that many sequences in GenBank are incorrectly identified (pers. obs.), even though the tools for a correct identification by doing BLAST with type sequences and relatively informative secondary barcodes (*tef1* and *rpb2*) are available (Robbertse *et al.* 2017, Cai & Druzhinina 2021). Additionally, even

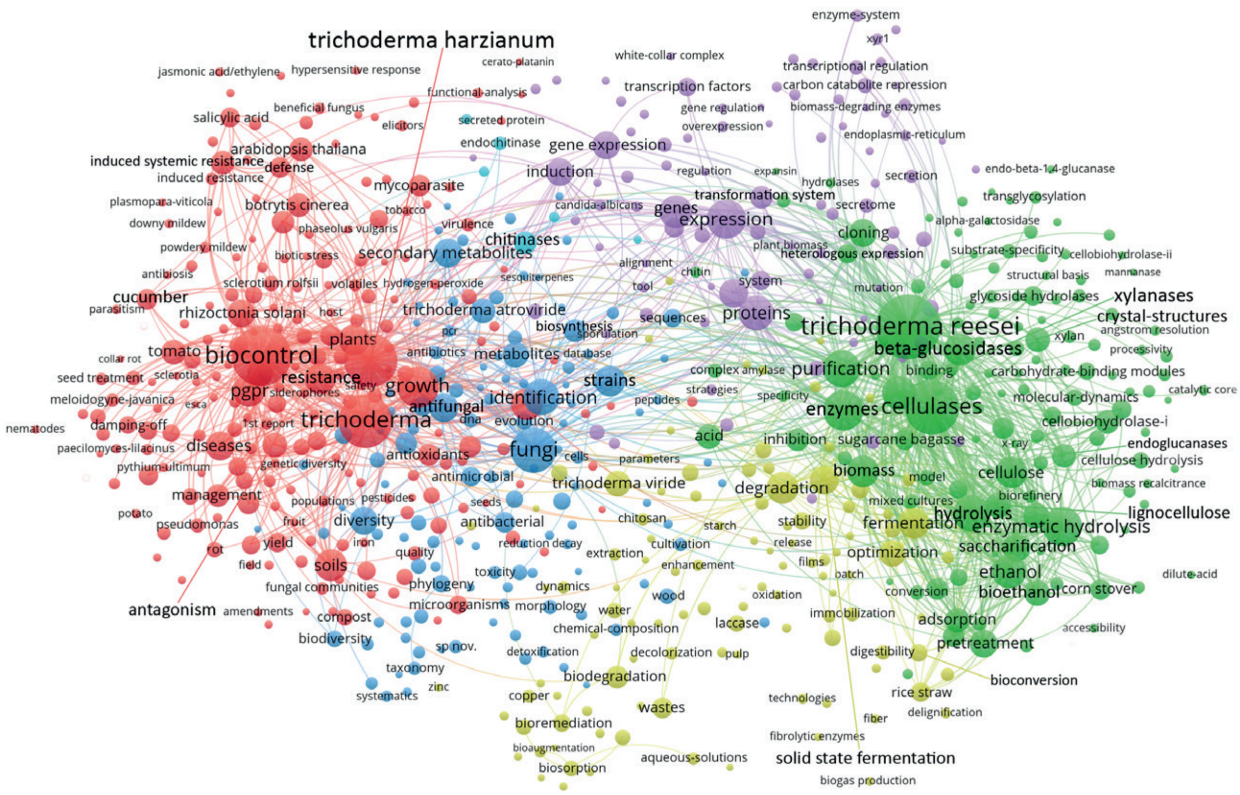

Fig. 14. Network visualisation of keywords of the publications related to *Trichoderma*. The larger the text and the circle the more often the subject has been cited.

Table 8. Top 10 cited articles related to *Trichoderma* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Induced systemic resistance by beneficial microbes	1 089	Pieterse *et al.* (2014)
2	Bioethanol production from agricultural wastes: an overview	901	Sarkar *et al.* (2012)
3	Expansion of the enzymatic repertoire of the CAZy database to integrate auxiliary redox enzymes	681	Levasseur *et al.* (2013)
4	The challenge of enzyme cost in the production of lignocellulosic biofuels	607	Klein-Marcuschamer *et al.* (2012)
5	Novel enzymes for the degradation of cellulose	601	Horn *et al.* (2012)
6	A review of lignocellulose bioconversion using enzymatic hydrolysis and synergistic cooperation between enzymes – Factors affecting enzymes, conversion and synergy	571	Van Dyk & Pletschke (2012)
7	How does plant cell wall nanoscale architecture correlate with enzymatic digestibility?	515	Ding *et al.* (2012)
8	Mycorrhiza-induced resistance and priming of plant defenses	439	Jung *et al.* (2012)
9	Plant-beneficial effects of *Trichoderma* and of its genes	432	Hermosa *et al.* (2012a)
10	Fungal cellulases	416	Payne *et al.* (2015)

deposited whole genomes are incorrectly identified. For example, the genome of *Trichoderma* isolate T6776 was deposited with the name "*T. harzianum*" (Baroncelli *et al.* 2015). When extracting the *rpb2* and *tef1* regions from that genome, the correct identification is *T. afroharzianum* (pers. obs.). More studies on the genomics, ecology, biological control, or biotechnology of *Trichoderma* should include a robust identification. This could be advanced by, for example, increasing the number of *Trichoderma* systematists that can advocate for better taxonomy and provide more solid journal article peer reviews (see review in Cai & Druzhinina 2021, which includes a section on the taxonomy impediment facing *Trichoderma*).

Author: P. Chaverri

7. ***Botrytis*** P. Micheli ex Pers., Neues Mag. Bot. 1: 120. 1794.

Type species: *Botrytis cinerea* Pers.

Classification: *Ascomycota*, *Pezizomycotina*, *Leotiomycetes*, *Helotiales*, *Sclerotiniaceae.*

Background

Botrytis is a large genus of plant pathogenic hyphomycetes infecting numerous host plants (Holz *et al.* 2007). *Botrytis* species have been reported to attack 596 genera of vascular plants representing over 1 400 plant species (Elad *et al.* 2016). *Botrytis* species are found ranging from tropical and subtropical to cold temperate zones or even deserts (Elad *et al.* 2007, 2016). Diseases by *Botrytis* species cause 10 to 100 billion USD in annual losses worldwide (Boddy 2015). The estimated average cost to control disease is around 18 USD/acre while management costs, depending on the importance of *Botrytis* diseases, can be up to approximately 57 USD/acre (Steiger 2007).

Botrytis was introduced in Von Haller (1768) and *Botrytis cinerea* is the type species. There are species of *Botrytis* that cause significant losses in agriculture, floriculture and horticulture but the most common and most important species is *Botr. cinerea* (Droby & Lichter 2004). *Botrytis cinerea* is responsible for considerable losses in crops, notably bulbous crops, grape vines and legume crops and it causes post-harvest spoilage of many fruits (Droby & Lichter 2004, Jackson 2014). *Botrytis cinerea* was voted by researchers and the scientific community to be the second most important plant pathogen infecting over 200 plant species (Anderson 1924, Beever & Weeds 2004, Capieau *et al.* 2004, Choquer *et al.* 2007, Mirzaei *et al.* 2007, Dean *et al.* 2012). However, *Botrytis cinerea* is also used for the production of sweet dessert wines (Sauternes) (Magyar 2011).

Botrytis species can produce both sexual and asexual morphs. The asexual morph produces copious amounts of conidia, although the survival time of conidia is normally short and depends on environmental conditions (Kerssies *et al.* 1995, Beever & Weeds 2004, Blanco *et al.* 2006, Carisse *et al.* 2012, Nassr & Bakarat 2013, Hahn 2014). The sexual morph of *Botr. cinerea* was first induced under laboratory conditions by Faretra & Antonacci (1987). Sexual morph compatibility is controlled by a single mating-type locus with *mat*-1 and *mat*-2 alleles (Faretra *et al.* 1988). Sclerotia, large melanised hyphal aggregates, occur with sexual reproduction and they are long-term survival structures (Hahn 2014). In addition, *Botrytis* can produce chlamydospores that can survive periods of up to 3 mo during drought (Urbasch 1983).

Intensive research on *Botrytis* has been carried out by Elad *et al.* (2004) with a combination of genome sequences. A comprehensive review of *Botrytis* species diversity was published by Walker (2016) and additional information was provided by Fillinger & Elad (2016). They recognised 74 species records in Species Fungorum (2022). The type species (*Botr. cinerea*) is also an important model organism that has been used for understanding the development of fungicide resistance and plant-pathogen interactions (Staats *et al.* 2005, Amselem *et al.* 2011, Hahn 2014, Valero-Jiménez *et al.* 2019).

Ecological and economic significance

Botrytis species on bulb crops

Several *Botrytis* species are pathogens in bulb crops. *Botrytis squamosa* and *Botr. allii* are the most important fungal diseases pathogenic to onions and are causal agents of botrytis neck rot (Lorbeer 1992, 1997, Lacy & Lorbeer 1995).

Botrytis species in legume crops

Grey mould caused by *Botr. cinerea* is ubiquitously distributed and results in significant production losses. It is also a severe problem for lentils in Australia, India, Syria, and Morocco (Beniwal *et al.*

1993). When conditions are conducive *Botr. cinerea* causes grey mould that can infect the entire crop which is a serious concern in Australia, Argentina, Bangladesh, India, Nepal and Pakistan (Karki *et al.* 1993, Haware 1998, Pande *et al.* 2002). The disease occurs worldwide (Nene *et al.* 1984, Pande *et al.* 2002).

Botrytis on major crops

Botrytis cinerea is a major pathogen causing post-harvest fruit decay in table grapes with infection leading to grape decay during storage (Coertze & Holz 1999, 2002). *Botrytis cinerea* is also present at the harvest stage of tomatoes (Chastagner *et al.* 1978). *Botrytis* species cause post-harvest rots on kiwifruit, which develop mainly during cold storage (Brook 1992). Fruit rot in strawberries is a worldwide problem (Blacharski *et al.* 2001).

Research interests

There are 6 968 publications and 103 497 citations from 2011–2021 in the Web of Science (Fig. 15), with the top 10 most cited articles included in Table 9. Most publications focused on fungal disease caused by *Botrytis cinerea* and disease management (Fig. 16).

Disease management

Rapid conidial germination and infection, with mycelium growth able to occur under a wide range of microclimate conditions, leads to severe disease management problems all around the world (Elad *et al.* 2007). Disease management can use physical technologies to control *Botr. cinerea* modifying several parameters such as absolute and relative gas pressure, sonication, temperature, and UV irradiation (Crisosto *et al.* 2002, De Simone *et al.* 2020). The main physical methods investigated against grey mould decay in table grapes are listed in De Simone *et al.* (2020). Chemical technologies to control *Botr. cinerea* have been widely used but for long-term storage, there may be negative developmental effects in humans and animals (Youssef *et al.* 2015, Carter *et al*. 2015). Sulphur dioxide (SO_2) is the main method used to control the *Botr. cinerea* spoilage of post-harvest fruit commodities (De Simone *et al.* 2020). Several succinate dehydrogenase inhibitors (SDHIs) have been introduced as chemical alternatives with inhibition rates of 80.1–94.4 % for *Botr. cinerea* in table grapes (Avenot & Michailides 2010, Vitale *et al.* 2016). Levels of CO_2 from 5–10 % failed to prevent the development of *Botr. cinerea* (Uota 1957, Laszlo 1985). The main chemical methods in both liquid and gas forms investigated against grey mould decay in table grapes are listed in De Simone *et al.* (2020). Leroux *et al.* (2002a, b) and Walker *et al.* (2013) have shown effective resistance management of *Botrytis cinerea* (grey mould) by using anti-*Botrytis* fungicides and Hahn (2014) listed major fungicides for use against *Botr. cinerea*. Multisite inhibitors have been used for long-term control but these methods now have low effectiveness when compared to active site-specific compounds (Edgington 1984). The control of *Botr. cinerea* by using microbial resources or antimicrobial compounds of biological origin has been widely accepted as an eco-friendly approach free of synthetic chemicals (Russo *et al.* 2017, Linares-Morales *et al.* 2018, Raveau *et al.* 2020). Research has proved that some raspberry cultivars can be inhibitory to *Botr. cinerea* thereby avoiding latent infections (Williamson & Jennings 1992). These findings suggest that cultivar selection will play a major role in future *Botrytis* management strategies. In addition, *Trichoderma harzianum* and *T. viride* are known for their antifungal effects and have controlled grey mould in field experiments (Mukherjee & Haware 1993, Haware 1998).

Toxins

Culture filtrates of *Botr. cinerea* can be phytotoxic when applied to plant tissue (Rebordinos *et al.* 1996). The toxic compounds were identified as botcinolide (a highly substituted lactone) and botrydial types (a tricyclic sesquiterpene) (Cutler *et al.* 1993, Colmenares *et al.* 2002).

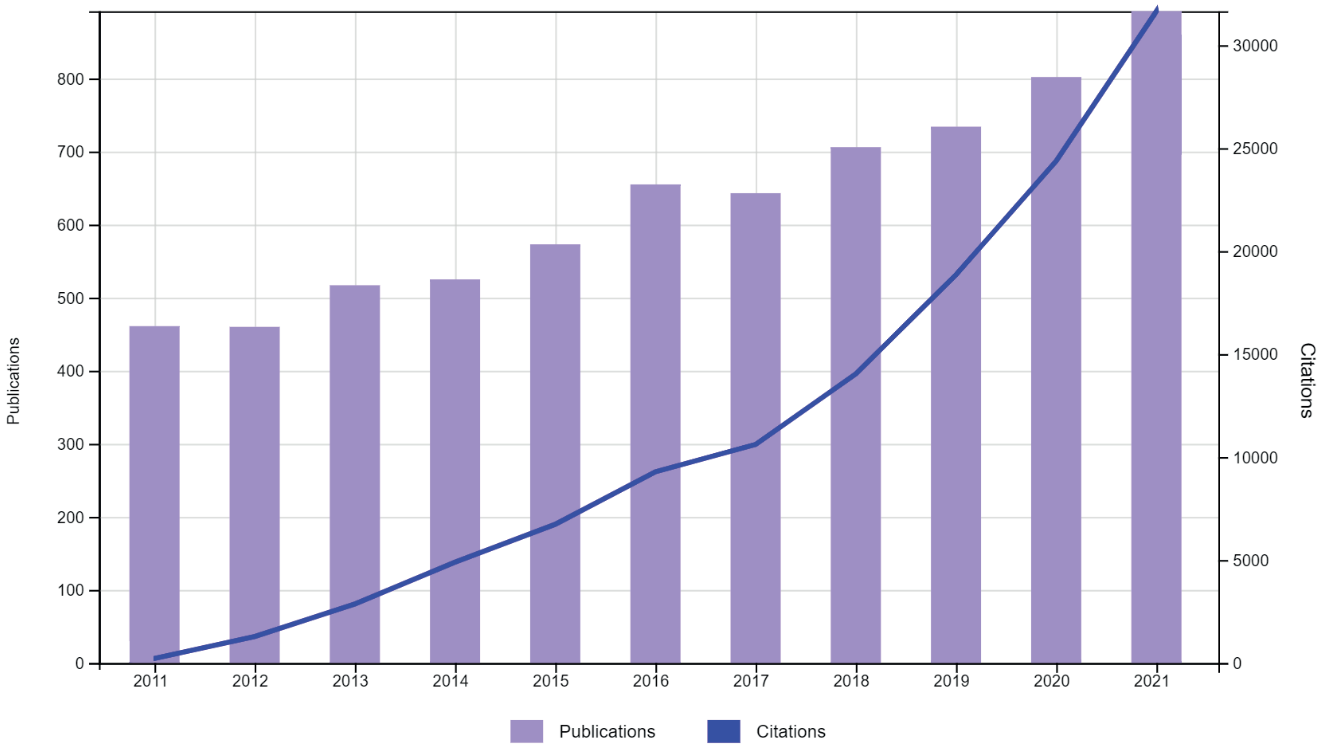

Fig. 15. Trends in research of *Botrytis* in the period 2011–2021.

Table 9. Top 10 cited articles related to *Botrytis* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	The top 10 fungal pathogens in molecular plant pathology	1 769	Dean *et al.* (2012)
2	Genomic analysis of the necrotrophic fungal pathogens *Sclerotinia sclerotiorum* and *Botrytis cinerea*	603	Amselem *et al.* (2011)
3	Fungal small RNAs suppress plant immunity by hijacking host RNA interference pathways	594	Weiberg *et al.* (2013)
4	Phosphorylation of a WRKY transcription factor by two pathogen-responsive MAPKs drives phytoalexin biosynthesis in *Arabidopsis*	444	Mao *et al.* (2011)
5	Antifungal activity of zinc oxide nanoparticles against *Botrytis cinerea* and *Penicillium expansum*	420	He *et al.* (2011)
6	Derepression of ethylene-stabilized transcription factors (EIN3/EIL1) mediates jasmonate and ethylene signaling synergy in *Arabidopsis*	404	Zhu *et al.* (2011b)
7	Production and characterization of antifungal compounds produced by *Lactobacillus plantarum* IMAU10014	365	Wang *et al.* (2012b)
8	The microbial ecology of wine grape berries	360	Barata *et al.* (2012)
9	Plants send small RNAs in extracellular vesicles to fungal pathogen to silence virulence genes	333	Cai *et al.* (2018)
10	*Arabidopsis* WRKY33 is a key transcriptional regulator of hormonal and metabolic responses toward *Botrytis cinerea* infection	291	Birkenbihl *et al.* (2012)

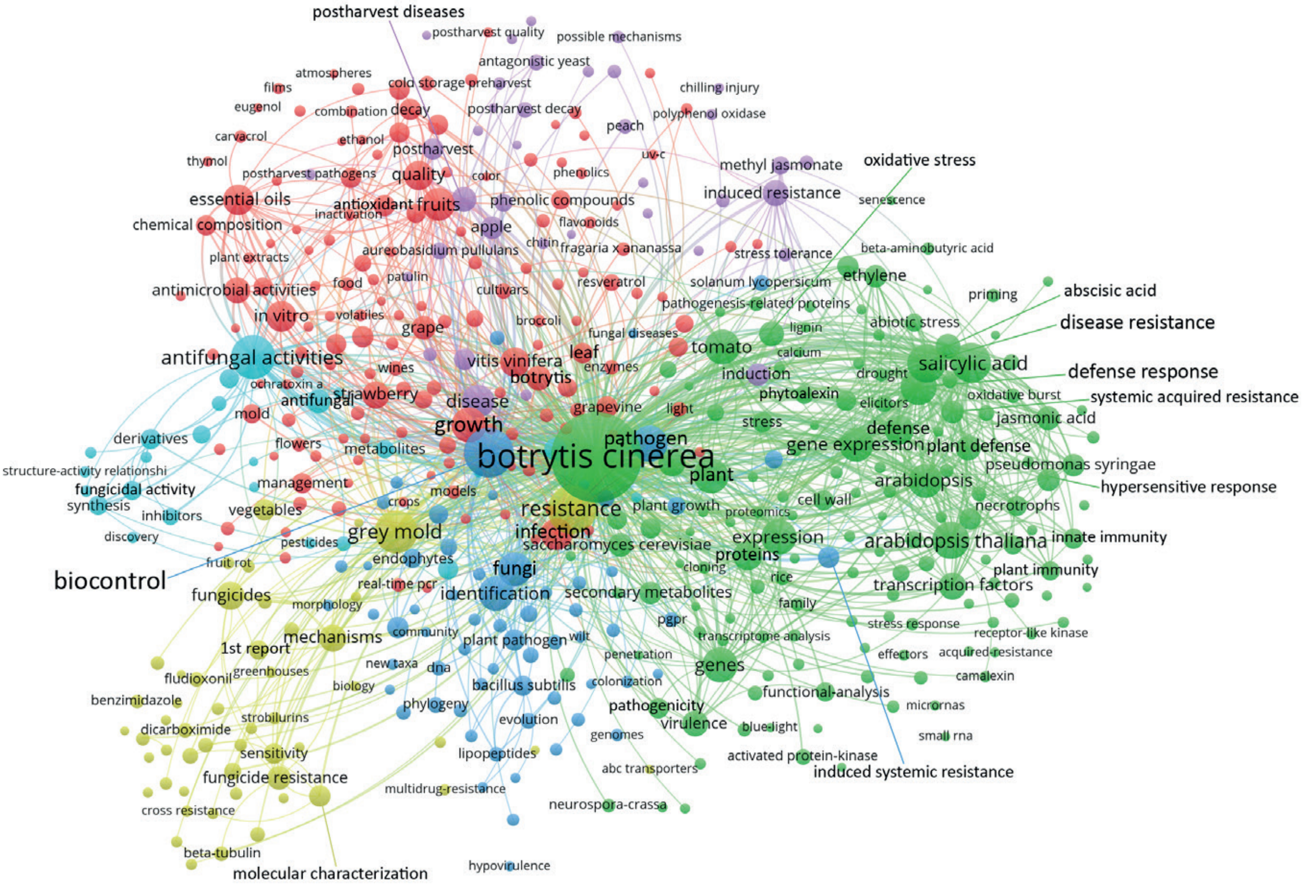

Fig. 16. Network visualisation of keywords of the publications related to *Botrytis*. The larger the text and the circle the more often the subject has been cited.

Taxonomy and phylogeny

Initially, ITS sequences were used for *Botrytis* but showed limited phylogenetic information and could not resolve relationships between species (Holst-Jensen *et al.* 1998). Staats *et al.* (2005) used glyceraldehyde-3-phosphate dehydrogenase (*gapdh*), heat shock protein 60 (*hsp*60) and *rpb*2 to build a phylogenetic tree and to test congruence between different phylogenetic trees. Staats *et al.* (2007) used ethylene-inducing proteins 1 and 2 (*nep1* and *nep2*) as phylogenetically informative markers and O'Gorman *et al.* (2008) mentioned that *gapdh* and β-tubulin (*tub*) genes helped lead to the revival of a long-lost species while *hsp*60 was used for uncharacterised endophytic isolates. Khan *et al.* (2013a) used ITS, ribosomal intergenic spacer (IGS), and *gapdh* to identify *Botrytis* species infecting onions. Garfinkel (2021) stated that sequence data for the *gapdh*, *hsp*60, *rpb*2, *nep1* and *nep2* genes are necessary for identifying new species of *Botrytis*.

Author: S. Tibpromma

8. ***Pichia*** E.C. Hansen, Centbl. Bakt. ParasitKde, Abt. I 12(19): 538. 1904.

Type species: *Pichia membranifaciens* (E.C. Hansen) E.C. Hansen

Classification: *Ascomycota*, *Saccharomycotina*, *Pichiomycetes, Pichiales, Pichiaceae.*

Background

The genus *Pichia* is one of the oldest yeast genera described and studied by pioneers of yeast research. This genus was described by Hansen (1904) for a non-sugar-fermenting yeast, which he had isolated from gelatinous material on the roots of an elm tree attacked by a fungus. Hansen originally described the yeast as *Saccharomyces membranifaciens* in 1888 and later in 1904 transferred it to a newly established genus as *Pi. membranifaciens* (reviewed in Kurtzman 1998). Hansen developed techniques for obtaining and maintaining pure yeast cultures (reviewed in Barnett & Lichtenthaler 2001). The development of these techniques made studies and descriptions of new species possible because isolated pure cultures could be maintained and re-investigated (compared with potential new species). Some strains from the period of the pioneering research 1880–1900 are still available, including Hansen's strain of *Pi. membranifaciens*, which was preserved in several culture collections. In the following years, the number of species described in the genus has increased to 12 in the work by Guilliermond (1920). The authors usually examined characteristics of colony growth (colour, size and shape), growth in liquid culture and the microscopic appearance of vegetative cells and filaments, including ascospores. One peculiar micromorphological characteristic of the genus *Pichia* is the shape of ascospores with a ring or ledge, which is also visible in the light microscope. This shape of spores was called hat-shaped or galeate. The size and position of the ledge varies between species.

Since Hansen established the genus *Pichia*, the definition of this taxon has changed considerably to accommodate the ever-increasing number of new species assigned to the genus. Lodder (1972) listed 35 *Pichia* species in the second edition of the compendium "*The Yeasts, a Taxonomic Study*", whereas Kreger-van Rij (1984) included 56 species in the third edition. Physiological tests, electron microscopy, biochemical comparisons and characteristics of DNA were used to redefine *Pichia*. This resulted in a series of merging and splitting of species with members of *Debaryomyces*, *Hansenula*, *Issatchenkia*, *Komagataella*, *Williopsis*, and *Yamadazyma* (reviewed in Kurtzman 1998). For example, *Hansenula* and *Pichia* were separated from each other primarily based on a single physiological test, the ability to assimilate nitrate as a sole source of nitrogen (reviewed in Kurtzman 1998). The shape of ascospores and the position of the ledge was the characteristic of *Issatchenkia*. *Williopsis*, which was characterised by Saturn-shaped ascospores (spherical with an equatorial ring), was merged with *Hansenula* and later reinstated (reviewed in Kurtzman 1998). The type of coenzyme Q separated *Debaryomyces*, *Issatchenkia* and *Yamadazyma*. Early application of partial rRNA sequences separated several former *Hansenula* species, and new genera *Komagataella*, *Kurashia*, *Nakazawaea*, and *Ogataea* were proposed to accommodate them. Using the percentage of DNA relatedness (DNA-DNA re-association) as a taxonomic marker, Kurtzman (1984) transferred nearly all *Hansenula* species to *Pichia* and separated species with hat-shaped and Saturn-shaped spores between *Pichia* and *Williopsis*, respectively. The concept of the large genus *Pichia* was retained until broad sequencing of the D1/D2 domains of the large subunit nrRNA gene (LSU) and subsequent analyses convincingly demonstrated that *Pichia* was polyphyletic (Kurtzman & Robnett 1998).

Subsequent multi-gene (Kurtzman *et al.* 2008) and whole-genome (Shen *et al.* 2019) phylogenetic analyses demonstrated that the core of *Pichia* (where the type species *Pi. membranifaciens* is placed) is distantly related to most of the aforementioned genera, except for *Issatchenkia*. Several biotechnologically important species were renamed following the reclassification of *Pichia*. *Hansenula* was abandoned, and the yeast known as *Hansenula anomala* was transferred to a new genus *Wickerhamomyces* (Kurtzman 2011b); *Wickerhamomyces anomalus* was conserved against older nomenclatural synonyms (Daniel *et al.* 2012). *Pichia pastoris* was renamed as *Komagataella pastoris* (Kurtzman *et al.* 2008, Kurtzman 2009, 2011a). Another biotechnologically important species *Candida utilis* appeared to be conspecific to *Pichia jadinii* and the latter was transferred to *Cyberlindnera* as *Cyberlindnera jadinii* (Kurtzman 1998, Kurtzman *et al.* 2008). Yeast genera that include former species of *Pichia* are *Ambrosiozyma*, *Barnettozyma*, *Cyberlindnera* (formerly also *Lindnera*), *Hyphopichia*, *Komagataella*, *Kregervanrija*, *Kurashia*, *Meyerozyma*, *Millerozyma*, *Nakazawaea*, *Ogataea*, *Peterozyma*, *Phaffomyces*, *Priceomyces*, *Saturnispora*, *Scheffersomyces*, *Starmera*, *Wickerhamomyces*, *Yamadazyma*, and *Zygoascus* (Kurtzman *et al.* 2008, Kurtzman 2011a). A few phylogenetically related to the genus *Pichia* (*Pichi*a clade, Kurtzman *et al.* 2008) asexual yeasts are still classified in *Candida* (Daniel *et al.* 2014).

Ecological and economic significance

Yeasts within *Pichia* have a few remarkable phenotypic traits. Many species are thermotolerant, growing at and above 37 °C (Kurtzman 2011c). *Pichia cecembensis* and *Pi. kudriavzevii* can grow above 40 °C (Kurtzman 2011a). *Pichia kluyveri*, *Pi. kudriavzevii*, and *Pi. membranifaciens* can grow at or below pH 2 and resist high osmotic pressure (Peter *et al.* 2017, Vicente *et al.* 2021). An overview of yeasts in natural habitats is provided in the chapters of the book series *Yeasts in Natural Ecosystems* cited below (Buzzini *et al.* 2017a, b).

Like with many other ascomycetous yeasts, species of *Pichia* can be found on substrates visited or modified by insects. Many *Pichia* species have been reported to be associated with slime fluxes of trees (Phaff & Starmer 1987, Peter *et al.* 2017). However, most of these species were reclassified and transferred to other genera *Barnettozyma*, *Cyberlindnera*, *Kodamaea*, *Komagataella*, *Meyerozyma*, *Millerozyma*, *Ogataea*, and *Wickerhamomyces* (Peter *et al.* 2017), and only two species, *Pi. exigua* and *Pi. scutulata* remained in the genus (Kurtzman 2011c). Rotting tissues of cacti and fruits harbour a diverse community of yeasts (Ganter *et al.* 2017, Peter *et al.* 2017). *Pichia cactophila* is a ubiquitous cactophilic yeast, whereas several other species, *Pi. barkeri*, *Pi. cephalocereana*, *Pi. deserticola*, *Pi. eremophila*, *Pi. heedii*, and *Pi. insulana* have a narrow geographic (and host) distribution range (Ganter *et al.* 2017, Yurkov 2017). Several former *Pichia* species, presently classified in *Starmera* and *Yamadazyma*, also inhabit decaying cactus tissues (Ganter *et al.* 2017). Ripe and decaying fruits attract many insects that vector yeasts, including *Pi. cecembensis*, *Pi. nakasei*, *Pi. membranifaciens*, *Pi. kudriavzevii*, and *Pi. occidentalis* (Kurtzman 2011c, Ganter *et al.* 2017). Some species were also found in rotting wood (Cadete *et al.* 2017). Several previously reported insect-associated *Pichia* spp. are now classified in the genera *Cyberlindnera*, *Kuraishia*, *Meyerozyma*, *Millerozyma*, *Ogataea*, *Scheffersomyces*, *Starmera*, and *Wickerhamomyces* (Blackwell 2017). A few species, including *Candida californica*, *C. pseudolambica*, *Pi. kluyveri*, *Pi. membranifaciens*, and *Pi. occidentalis* are associated with insect larvae (Scheidler *et al.* 2015, Steyn *et al.* 2016, Becher *et al.* 2018, Dmitrieva *et al.* 2021, Cho & Rohlfs 2023). Though ascomycetous yeasts are not abundant on plant surfaces, *Pi. kudriavzevii* and *Pi. manshurica* were reported as inhabitants of this substrate (Limtong & Kaewwichian 2015, Limtong & Nasanit 2017, Opulente *et al.* 2019). Aquatic habitats, marine and freshwater, including tap water, house appliances and wastewater, harbour the following species: *Pi. fermentans*, *Pi. kluyveri*, *Pi. kudriavzevii*, and *Pi. occidentalis* (Babič *et al.* 2017, Hagler *et al.* 2017, Libkind *et al.* 2017). Two species *Pi. kudriavzevii* and *Pi. terricola* were isolated from migratory birds (Moschetti *et al.* 2017), but this is not the primary substrate for the two species. Most soil-borne yeasts are basidiomycetes (Yurkov 2018) but the ascomycetous *Pi. fermentans*, *Pi. kluyveri*, *Pi. membranifaciens*, and *Pi. terricola* were reported from soils, particularly agricultural, like orchards (Vadkertiová *et al.* 2017). Other common soil species belong to genera where former *Pichia* species have been placed, namely *Barnettozyma*, *Cyberlindnera*, *Meyerozyma*, and *Wickerhamomyces* (Yurkov 2018).

Surfaces of berries and fruits harbour ascomycetous yeasts that multiply with fruit ripening following the increasing availability of sugars coming through the cuticle. Some of these yeasts later end up in fruit juice or wine. Yeast proliferation may have a negative impact on the quality of grapes. For instance, sour rot of grapes (leaking juice from grape berries and distinctive vinegar smell) is caused by several filamentous fungi and yeasts that are transmitted to berries by insects, *e.g.*, wasps and drosophila flies. In addition to *Metschnikowia* species that are commonly associated with sour rot, *Pi. kudriavzevii*, *Pi. membranifaciens*, and *Pi. kluyveri*, are believed to contribute to this fruit disorder (Barata *et al.* 2012).

Pichia fermentans (syn. *Candida lambica*), *Pi. kluyveri*, *Pi. manshurica*, *Pi. membranifaciens* (syn. *C. valida*), *Pi. occidentalis* (syn. *C. sorbosa*), *Pi. terricola*, and *Candida californica*, which is phylogenetically placed in the *Pichia* clade, were named among largely aerobic non-*Saccharomyces* yeasts in grape must and wine fermentations (Jolly *et al.* 2014). Formerly classified in the genus *Pichia*, *Meyerozyma guilliermondii* and *Wickerhamomyces anomalus* also occur on grapes and in wine. These yeasts are present in grape must and the initial stages of spontaneous wine fermentations. Some of these yeasts may survive in later stages of fermentation thanks to higher ethanol and acid tolerance. Because of predominantly aerobic growth and poor fermentation capabilities, these yeasts can be used in the production of low-alcoholic wines (Jolly *et al.* 2014, Vicente *et al.* 2021). *Pichia kluyveri* is one of the most frequently used species to produce beverages with reduced alcohol concentration (Vicente *et al.* 2021). This yeast has also been successfully employed in beer, cider, durian, and tequila fermentations (Gibson *et al.* 2017, Capece *et al.* 2018, Sannino *et al.* 2019, Vicente *et al.* 2021). Owing to the limited ability to ferment glucose, this yeast produces a number of flavour compounds (*e.g.*, fruity esters and higher alcohols) through modification of hop compounds (Capece *et al.* 2018).

Yeast metabolites largely affect wine properties such as taste, aroma and colour. Co-fermentation of wine with *Saccharomyces cerevisiae* and *Meyerozyma guilliermondii* may improve colour stability (reviewed in Jolly *et al.* 2014). Ferments produced by yeasts, *e.g.*, beta-glucosidases from *Pichia terricola* and *Wickerhamomyces anomalus*, can release bound volatile compounds and have a positive effect on wine quality. Esters, higher alcohols, glycerol and acids produced by yeasts during wine fermentation also influence its sensory quality, either positively or negatively (off-flavour). *Pichia kluyveri* can produce substantial amounts of higher alcohols, esters (Méndez-Zamora *et al.* 2020) and volatile thiols, compounds that give a typical character to some grape varieties, like Sauvignon Blanc (reviewed in Jolly *et al.* 2014). Mixed fermentations with *Saccharomyces cerevisiae* and *Pichia fermentans* produced wines with increased concentrations of some volatile compounds and polysaccharides, improving both wine taste and body (reviewed in Jolly *et al.* 2014). Wine spoilage through the production of compounds negatively changing the taste or aroma (off-flavour) is a major concern for winemakers. Yeasts of the genus *Pichia* were reported to have both positive and negative impacts on wine spoilage. *Pichia manshurica* and *Pi. membranaefaciens* release compounds which could produce off-flavours and odours (Perpetuini *et al.* 2020).

Yeasts of the genus *Pichia* do not belong to prominent spoilage yeasts in the wine industry. On the contrary, these yeasts were used for biological control of spoilage yeasts. Several species such as *Pi. cactophila*, *Pi. eremophila*, *Pi. fermentans*, *Pi. kluyveri*, *Pi. kudriavzevii*, *Pi. manshurica*, *Pi. membranifaciens*, *Pi. occidentalis*, *Pi. scutulata*, and *Pi. terricola* produce antimicrobial compounds known as killer toxins, small proteins encoded by selfish extrachromosomal DNA or RNA virus-like particles (Klassen *et al.* 2017). The ability to secrete killer toxins is strain-specific. Not only yeasts are sensitive to killer toxins. Other target organisms include filamentous fungi, bacteria and protozoa that may compete in certain natural habitats with the killer yeast (Klassen *et al.* 2017). Toxins of *Pi. kluyveri* and *Pi. membranifaciens* have been demonstrated to be active against a wide variety of food and beverage spoilage yeasts, including *Brettanomyces bruxellensis*, but also to occasionally inhibit some *Saccharomyces* strains in wine (Klassen *et al.* 2017, Vicente *et al.* 2021). Formerly classified in *Pichia*, *Babjeviella inositovora*, *Millerozyma acaciae*, *Millerozyma farinosa*, and *Wickerhamomyces anomalus* possess well-characterised killer toxins. Other frequently mentioned in the literature as *Pichia* spp. killer yeasts include *Cyberlindnera jadinii*, *Kodamaea ohmeri* and *Komagataella pastoris* (Klassen *et al.* 2017).

Among opportunistic human pathogens, *Pichia kudriavzevii* is the fifth most common cause of candidemia (Cooper 2011) and responsible for about 1–6 % of yeast infections in humans (Stavrou *et al.* 2019). This yeast is also known under the names *Issatchenkia orientalis* and the former asexual morph name, *Candida krusei*. Treatment of infections caused by this yeast can be problematic due to the species showing intrinsic resistance to fluconazole, the most used antifungal drug (Stavrou *et al.* 2019, Jaimu *et al.* 2021). Although this dimorphic ascomycetous yeast is widespread in natural and anthropogenic sources (see above) and is found in healthy individuals (Inacio & Daniel 2017), *Pi. kudriavzevii* can cause life-threatening infections in immunocompromised patients, including persons with traumatic injuries and in surgical care (Jaimu *et al.* 2021). Genome sequences of 30 *Pi. kudriavzevii* strains were highly similar, suggesting that environmental, industrial, and clinical strains are not genetically distinct (Douglass *et al.* 2018). Another clinically relevant *Pichia* species are *Pi. norvegensis* and *Candida inconspicua*, which are phylogenetically placed in the genus *Pichia* and closely related to *Pi. cactophila* (Kurtzman 2011a, Lachance *et al.* 2011). The two species are difficult to differentiate using conventional biochemical markers and *C. inconspicua* was probably mistaken for *Pi. norvegensis* (Mixão *et al.* 2019). Although infections caused by these fluconazole-resistant yeasts are rare

(Stavrou *et al.* 2019), a 10-fold increase of *C. inconspicua* cases in HIV patients has been reported (Mixão *et al.* 2019).

Research interests

There are 7 969 publications and 102 697 citations from 2011–2021 in the Web of Science (Fig. 17), with the top 10 most cited articles included in Table 10. Fermentation (natural, industrial) and research on yeast physiology (*e.g*., pathways and their regulations) received substantial attention from researchers during the last decade. Yeast biotechnology remains the focus of many studies on enzymes, accumulation of lipids for biofuel production and growing yeast biomass on a variety of agricultural and industrial waste substrates (Fig. 18). The composition, dynamics and interactions of yeast communities in natural and artificial environments is an important topic for the food industry and winemaking, as reflected in the network visualisation of keywords (Fig. 18). The range of applications includes biocontrol of spoilage using antagonistic interactions of yeasts using killer toxins and co-fermentation with mixed starter cultures, and the effects on the final product.

Pichia fermentans (also known as *Candida lambica*) has been isolated from a variety of foods and fruit juices. This yeast is a spoilage organism of orange juice and brined green olives (reviewed in Kurtzman 2011c). The species has been successfully used for biocontrol of brown rot of apples. Only a few human infections caused by *Pi. fermentans* are known (Pfaller *et al.* 2004, Vervaeke *et al.* 2008).

Pichia kluyveri is common in natural fermentations of agricultural products such as coffee beans (Kurtzman 2011c). This yeast is used to produce low-alcoholic beer, wine and other beverages (see above). Some strains of the species can grow at 37 °C, but the species is not considered to be clinically relevant. A single strain of *Pi. kluyveri* was isolated from an oral lesion of a cancer patient (Aslani *et al.* 2018).

Pichia kudriavzevii (also known as *Candida krusei* and *Issatchenkia orientalis*) is widely distributed in nature (see above). This yeast is also frequently encountered in natural fermentations, like cocoa and cassava starch (*e.g*., Daniel *et al.* 2009). The species was reported among biotechnology-relevant oleaginous yeasts for biodiesel production from cheap substrates. As noted above, *Pi. kudriavzevii* is also a common clinical isolate.

Pichia manshurica is common in natural fermentations, including rotting plant material (Kurtzman 2011c). Kurtzman (2011b) indicated that past ecological studies that reported the occurrence of *Pi. membanifaciens* may have also included *Pi. manshurica*, due to high phenotypic similarity of the two species. The species was reported among biotechnology-relevant oleaginous yeasts for biodiesel production from cheap substrates. The clinical importance of *Pi. manshurica* is unknown but the species can grow at 37 °C. *Pichia membranifaciens* is widespread in nature (see above) but shows a limited spectrum of assimilated carbon sources (Kurtzman 2011c). This yeast is commonly found in rotted fruits and fermented beverages (*e.g*., Kombucha), but is also regarded as a food and beverage spoilage organism (Kurtzman 2011c). Because this species does grow at 37 °C, its clinical importance is unlikely. This yeast is promising for the conversion of biodiesel-derived waste (Chatzifragkou *et al.* 2011). Several asexual species phylogenetically related to *Pichia* are still classified as *Candida* spp. (Lachance *et al.* 2011), *e.g*., *C. californica* (fruits and drosophila flies), *C. ethanolica* (fodder yeast grown on ethanol), *C. inconspicua* (Italian cheese), and *C. pseudolambica* (plants, insects).

In addition to the already mentioned applications and properties of species of *Pichia*, the below-mentioned yeasts significantly contributed to the citations to the genus *Pichia*. Many publications focused on the genetic manipulation and tools for the expression of proteins in *Komagataella pastoris* and related species, also known as the *Pichia pastoris* model. This model is widely used to produce proteins of medical interest, like antibodies and antimicrobial peptides.

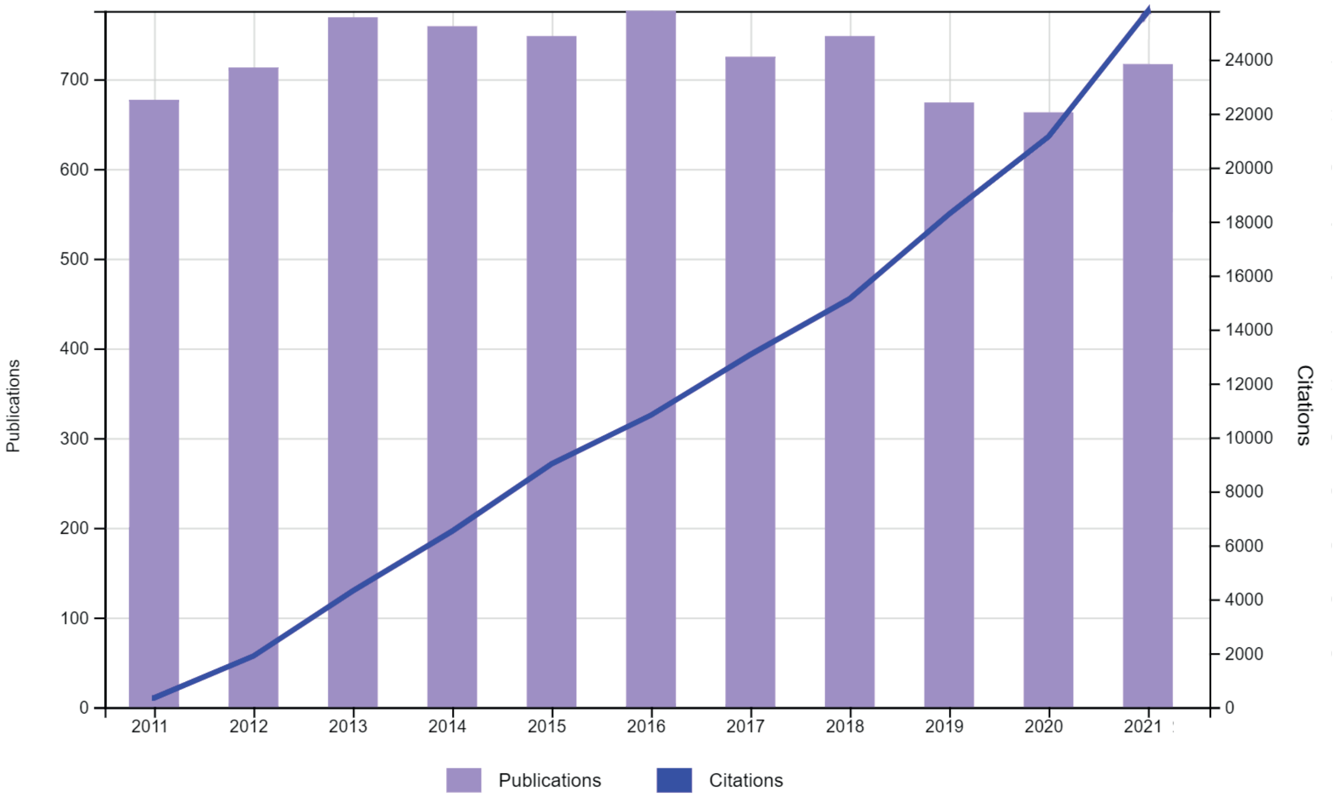

Fig. 17. Trends in research of *Pichia* in the period 2011–2021.

Table 10. Top 10 cited articles related to *Pichia* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Not your ordinary yeast: non-*Saccharomyces* yeasts in wine production uncovered	465	Jolly *et al.* (2014)
2	The microbial ecology of wine grape berries	360	Barata *et al.* (2012)
3	Microbial xylanases: engineering, production and industrial applications	268	Juturu & Wu (2012)
4	Oral mycobiome analysis of HIV-infected patients: identification of *Pichia* as an antagonist of opportunistic fungi	204	Mukherjee *et al.* (2014)
5	Biotechnological conversions of biodiesel derived waste glycerol by yeast and fungal species	203	Chatzifragkou *et al.* (2011)
6	Advances in recombinant antibody manufacturing	201	Kunert & Reinhart (2016)
7	Mechanistic insights into selective autophagy pathways: lessons from yeast	195	Farre & Subramani (2016)
8	Production of recombinant proteins by yeast cells	182	Çelik & Çalık (2012)
9	Antimicrobial and probiotic properties of yeasts: from fundamental to novel applications. Frontiers in microbiology	154	Hatoum *et al.* (2012)
10	A double WAP domain-containing protein Es-DWD1 from *Eriocheir sinensis* exhibits antimicrobial and proteinase inhibitory activities	153	Li *et al.* (2013b)

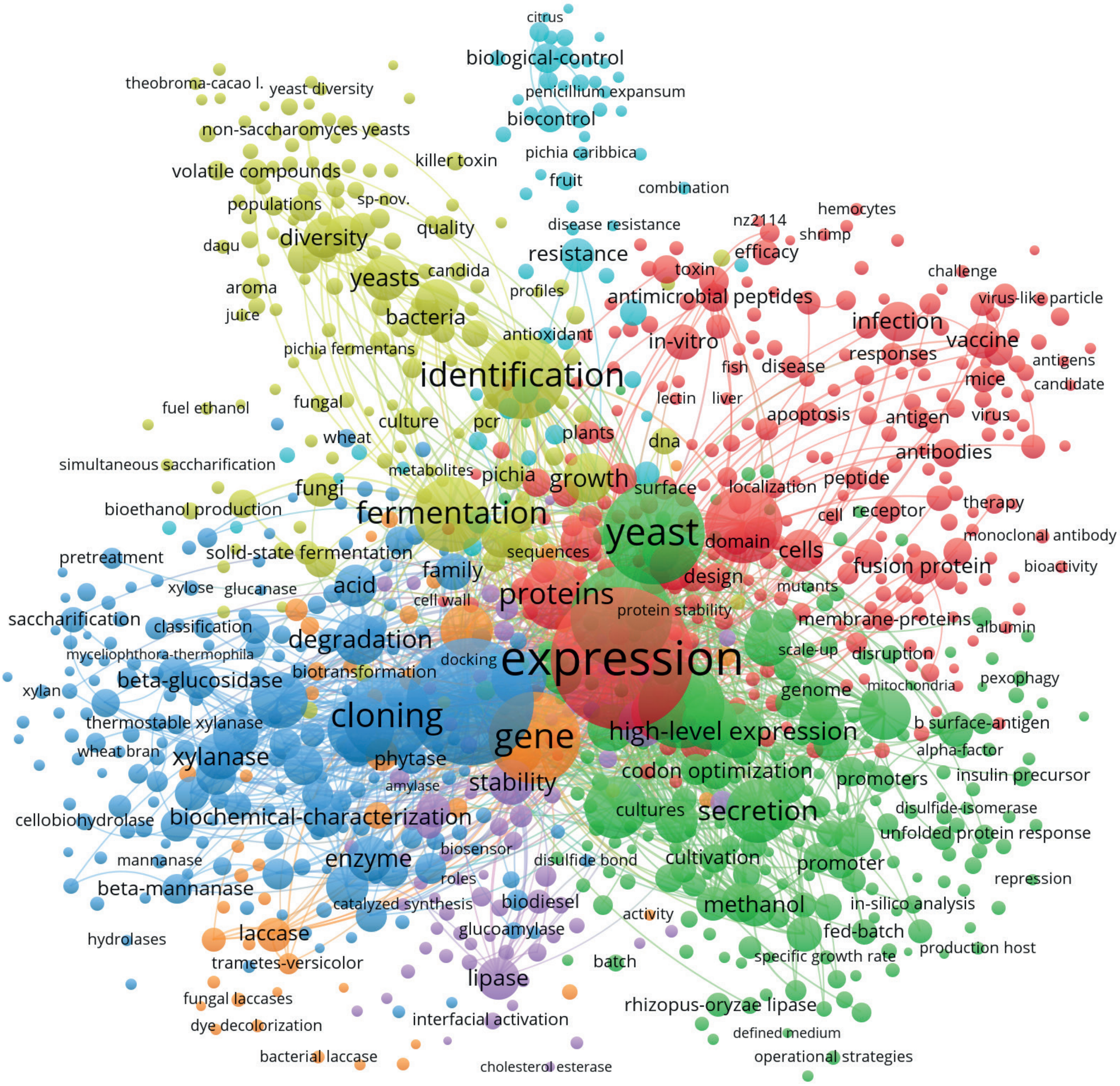

Fig. 18. Network visualisation of keywords of the publications related to *Pichia*. The larger the text and the circle the more often the subject has been cited.

Selected former Pichia species

Komagataella pastoris (formerly *Pichia pastoris*) has become a highly successful system for the expression of heterologous genes. A program to convert abundant methanol to a protein source for animal feed that started in the 1960s developed into what is today two important biological tools: a model eukaryote used in cell biology research and a recombinant protein production system (Cregg *et al.* 2000). To date well over 200 heterologous proteins have been expressed in *K. pastoris*. This yeast was developed as a source of single-cell proteins because it can reach high cell densities growing on either glucose or methanol under fermentation conditions. This ability was used to produce large quantities of medically and industrially important proteins (*e.g.*, antibodies, antimicrobial peptides) and enzymes. The species became a model organism for synthetic biology, studies on organelles and the metabolism of eukaryotic cells (Gasser & Mattanovich 2018). Most nodes in the network visualisation of keywords (red, blue, purple, and yellow) refer to research on *Komagataella* (Fig. 18).

Pichia pastoris was reassigned to *Komagataella* following the phylogenetic analysis of ribosomal gene sequences (Yamada *et al.* 1995a, Kurtzman *et al.* 2008, Kurtzman 2009). Discovery of two more species, *K. pseudopastoris* (Dlauchy *et al.* 2003) and *K. phaffi* (Kurtzman 2005), which were practically indistinguishable by reactions on the standard fermentation and assimilation tests commonly used in yeast taxonomy, raised the question of which yeast is being used in studies of gene expression (Kurtzman 2009). Multi-gene sequence analyses demonstrated that commercial *Pichia pastoris* strains commonly used in gene-expression research belong to a different species, namely *K. phaffii* (Kurtzman 2009). With the isolation of new strains and the re-analysis of old *Pi. pastoris* strains, seven species of *Komagataella* are known today (Naumov *et al.* 2018). *Komagataella* species are common in slime fluxes in Canada, the USA and Europe (Péter *et al.* 2017b, Naumov *et al.* 2018).

Wickerhamomyces anomalus (formerly *Pichia anomala*, *Hansenula anomala*) is frequently associated with food and feed products, either as a production organism or as a spoilage yeast (Passoth *et al.* 2006). Physiologically, this species has several extraordinary traits, namely the ability to grow under low pH, high osmotic pressure, and low oxygen tension (Passoth *et al.* 2006). This yeast contributes to the production of wine aroma. *Wickerhamomyces anomalus* was used as a biocontrol agent to inhibit the development of moulds in airtight stored grains and spoilage yeasts in wines. The ability to secrete killer toxins has been demonstrated in many strains and the known toxins differ considerably with respect to their activity spectrum, molecular characteristics, chemical properties, and stability (Passoth *et al.* 2006, Klassen *et al.* 2017). The physiological properties of these yeasts were extensively studied with respect to the regulation of aerobic and anaerobic growth and fermentation on different carbon sources (Passoth *et al.* 2006). *Wickerhamomyces anomalus* produces ethanol under oxygen limitation, while in completely aerobic cultures only a little ethanol is produced (the opposite of the Crabtree effect). This yeast was named among promising species for low-alcohol and non-alcoholic beers (Gibson *et al.* 2017). Most green nodes in the network visualisation of keywords may refer to research on *W. anomalus*.

The placement of *Pichia anomala* in *Wickerhamomyces* following multigene phylogenetic analysis (Kurtzman *et al.* 2008) has raised concern about whether these results argued for the placement of this yeast in a new genus or an earlier described genus *Hansenula* (Kurtzman 2011b, Daniel *et al.* 2012). The species was described by Hansen in 1891 as *Saccharomyces anomalus* and 45 more taxonomic synonyms exist for this yeast (Kurtzman 2011b). Because of the uncertain origin of old type material (two neotypes of *Hansenula anomala*) or the absence thereof for older names *Saccharomyces anomalus* and *S. sphaericus*, the genus *Hansenula* was considered invalid (Kurtzman 2011b). *Pichia* and *Hansenula* were phenotypically almost indistinguishable and polyphyletic in phylogenetic analyses (Kurtzman 1998, 2011a, b). Because type material of the type species of *Pichia* existed and that of *Hansenula* did not, it was unclear to which phylogenetic clade the name *Hansenula* should be attributed. Therefore, the genus where *Pichia anomala* was placed received a new name *Wickerhamomyces*, and that name was conserved against the name *Hansenula* (Daniel *et al.* 2012).

Scheffersomyces stipitis (formerly *Pichia stipitis*) and some other xylose-fermenting yeasts are particularly interesting for biotechnology because of their ability to convert lignocellulose to ethanol. Members of the genus *Scheffersomyces* formerly known as *Pi. segobiensis*, *Pi. stipitis* and *Candida shehatae* are the best-known species. The genetics of xylose utilisation pathways were extensively studied in *Scheffersomyces stipitis*. Natural habitats of xylose-fermenting yeasts include decaying wood and wood-inhabiting insects (Blackwell 2017, Péter *et al.* 2017b). Less known and distantly related to the genus *Pichia*, the genus *Spathaspora* shares the metabolic trait of xylose fermentation (Martinez-Jimenez *et al.* 2021).

Ogataea polymorpha (formerly *Pichia angusta*, *Hansenula polymorpha*) is an important yeast in industrial biotechnology. *Ogataea* species are methylotrophic yeasts that can grow on methanol as a sole source of energy. The growth on methanol involves the oxidation of methanol into formaldehyde and hydrogen peroxide by the peroxisomal enzyme alcohol oxidase (Saraya *et al.* 2012). The number of peroxisomes depends on the growth substrate. This feature made *O. polymorpha* a good model organism to study peroxisome biology (Saraya *et al.* 2012). Another interesting physiological trait is the ability to assimilate nitrate as the sole source of nitrogen. Molecular mechanisms and transport of nitrate were studied in this yeast. This species is attractive for biotechnology because of its thermotolerant nature (Peter *et al.* 2017, Buzzini *et al.* 2018) and the ability to grow at temperatures reaching (and exceeding for some strains) 50 °C. Together with *Komagataella pastoris* and *K. phaffi*, *Ogataea polymorpha* and *O. methanolica* are the most frequently used yeasts for heterologous protein production. Many species of *Ogataea* were isolated from plant exudates (slime fluxes), decaying plant material (rotting wood and cacti) or in association with insects (Peter *et al.* 2017, Stefanini 2018).

Cyberlindnera jadinii (formerly *Pichia jadinii*, *Candida utilis*, *Torulopsis utilis*, *Torula utilis*) is a well-known fodder yeast and industrial producer of single-cell protein (SCP). Yeast biomass is used as a nutrition and source of proteins and vitamins in animal husbandry and human foods. Industrial utilisation of *Cyberlindnera jadinii* started in Germany during World War I, when common protein sources became scarce (reviewed in Barnett 2004). The yeast efficiently assimilates pentoses (xylose and arabinose), organic acids alcohols, and can grow on hardwood hydrolysates from the pulp industry, agricultural waste, molasses and oils (Buerth *et al.* 2016). *Cyberlindnera jadinii* is rich in glutamic acid and for this reason, it has been used to replace the flavour enhancer monosodium glutamate, MSG (Ritala *et al.* 2017). There is an interest in using this species for the expression of heterologous genes, but the wide application of the yeast retarded due to polyploidy of *Candida utilis* strains (reviewed in Buerth *et al.* 2016). A common food or feed additive (with FDA GRAS status), *Cyberlindnera jadinii* is well suitable for medical uses as it can transit gastrointestinal tract without losing viability by virtue of acid and temperature tolerance. This edible yeast can be utilised as a probiotic or probably as an antagonist to *Candida albicans* (reviewed in Buerth *et al.* 2016).

The yeast presently known as *Cyberlindnera jadinii* was originally described as *Torula utilis*, though the name *Torula* was already used for some moulds (reviewed in Barnett 2004). The species was reclassified as *Torulopsis utilis* in 1934 and later in 1952 as *Candida utilis* (reviewed in Barnett 2004). Biochemical and physiological studies, and research using properties of DNA, including DNA relatedness, single- and multi-gene phylogenies, suggested that *Candida utilis* is conspecific to *Pichia jadinii* (reviewed in Barnett 2004, Kurtzman *et al.* 2008). The name *Candida utilis* was abandoned in favour of *Pi. jadinii*, which was later reclassified as *Cyberlindnera jadinii*. Astonishingly, the improper and obsolete name "*Torula* yeast" can still be found in the modern literature for *Cyberlindnera jadinii*.

Millerozyma farinosa (formerly *Pichia farinosa*) is a widely distributed halotolerant yeast (Peter *et al.* 2017, Buzzini *et al.* 2018). Strains have been isolated from such diverse substrates as agricultural products, food (*e.g.*, miso, soy mash), animal dung and petroleum, as well as from clinical samples (Kurtzman 1998). Strains of *M. farinosa* show killer properties.

Meyerozyma guilliermondii (formerly *Pichia guilliermondii*, *Candida guilliermondii*) and closely related *Meyerozyma caribbica* (formerly *Pichia caribbica*) are widespread species isolated from a variety of substrates that include soil, plants, food sources, industrial applications and clinical samples. *Meyerozyma caribbica* is utilised for biocontrol of post-harvest decay in fruits (Cao *et al.* 2013a). This yeast was reported to degrade mould toxin patulin and reduce its concentration in apples (Cao *et al.* 2013a, Zheng *et al.* 2018). *Meyerozyma guilliermondii* can produce the vitamin riboflavin (B2) as well as a sweetener xylitol (Kurtzman 2011c, Averianova *et al.* 2020). This yeast is also present in some traditional fermentations. *Meyerozyma guilliermondii* is considered an opportunistic human pathogen and has been reported to represent on average 2 % of clinical yeast isolates, a prevalence similar to that of *Pichia kudriavzevii* (Stavrou *et al.* 2019). Similar to several prominent human pathogens, *Meyerozyma guilliermondii* possesses genetic machinery to adapt and survive in the human host (Stavrou *et al.* 2019). The two *Meyerozyma* species also show resistance to azole drugs (Stavrou *et al.* 2019).

Author: A. Yurkov

9. **Cryptococcus** Vuill., Rev. Gén. Sci. Pures Appl. 12: 741. 1901.

Type species: *Cryptococcus neoformans* (San Felice) Vuill.

Classification: *Basidiomycota*, *Agaricomycotina*, *Tremellomycetes*, *Tremellales*, *Cryptococcaceae.*

Background

The first descriptions of *Cryptococcus* date to the 1890s when the German physicians Otto Busse and Abraham Buschke described a yeast infection of a woman's tibia. The obtained culture was described as *Saccharomyces hominis* (Busse 1894, Buschke 1895). Sanfelice, an Italian researcher, described in 1894 a similar yeast in fermenting peach juice and, subsequently, he observed that the cultured yeast behaved pathogenic when injected in mice (Sanfelice 1894). A few years later, the French mycologist Jean-Paul Vuillemin observed that the *S. hominis* isolates were unable to produce ascospores which led him to move the species to the genus *Cryptococcus* and renamed it *Cryptococcus hominis*. The yeast described by Sanfelice as *Saccharomyces neoformans* was transferred to *Cryptococcus* and the ex-type strain is preserved in the CBS culture collection as CBS 132. Unfortunately, the *Cr. hominis* ex-type strain was not preserved, hence *Cr. neoformans* became the valid species name. Until the late 1970s, *Cryptococcus* yeasts were a relatively rare encounter in medical clinics until the HIV pandemic started. In 1950, three serotypes were recognised based on the serological properties of the polysaccharide capsule and were named serotypes A, B and C (Evans 1950). The fourth serotype named D was described nearly two decades thereafter (Wilson *et al.* 1968). In 1970, an atypical *Cryptococcus* isolate from an infection, in what is now known as the Democratic Republic of Congo was described by Vanbreuseghem & Takashio (1970) as *Cr. neoformans* var. *gattii*. A few years thereafter, Kwon-Chung *et al.* (1982) described the sexual phase of *Cr. neoformans,* and with the dual nomenclature at that time, it was named *Filobasidiella neoformans* with two varieties, var. *neoformans* (for serotype A and D isolates) and var. *gattii* (for serotype B and C isolates). With the adoption of the "One Fungus = One Name" principle, all taxa were later placed in the genus *Cryptococcus*, with *Filobasidiella* becoming a synonym of *Cryptococcus* (Liu *et al.* 2015c, d). Presently, seven species are recognised in the *Cr. neoformans*/*Cr. gattii* complex (Hagen *et al.* 2015), namely *Cr. neoformans*, *Cr. deneoformans*, *Cr. bacillisporus*, *Cr. gattii*, *Cr. deuterogattii*, *Cr. decagattii* and *Cr. tetragattii*. Note that this taxonomy proposal has been fiercely debated (Hagen *et al.* 2017, Kwon-Chung *et al.* 2017). Recently, another lineage of *Cr. gattii* was discovered in Zambia (Farrer *et al.* 2019), but its taxonomic status is not yet settled. *Cryptococcus* species are phylogenetically more closely related to *Tremellomycetes* (*Basidiomycota*) than to the baker's yeast (Bahn *et al.* 2020).

Research interests

There are 6 909 publications and 95 586 citations from 2011–2021 in the Web of Science (Fig. 19), with the top 10 most cited articles included in Table 11. The research interests of *Cryptococcus* yeasts focus on improving the taxonomy, epidemiology, antifungal therapy, understanding the yeast interaction with the immune system of different host populations, cell wall characteristics, and the role of extracellular vesicles in the cryptococcal pathogenesis (Fig. 20). From the clinical perspective, the top-cited papers mainly include extensive reviews highlighting the human killer fungal pathogens, that include *Cryptococcus* yeasts, covering aspects from the microbiological characteristics to clinical aspects of cryptococcosis; molecular and cellular characteristics to the modulation of the immune response when faced with cryptococcosis; the role of sulphonamides and other carbonic anhydrase inhibitors as promising compounds in the treatment of infections caused by *Cryptococcus* and other microorganisms. Finally, a review of the biology and chemistry of the newest and conventional antifungals, highlighting particularities in the *Cryptococcus* infections is also a highly cited topic.

A recent study on the global incidence of cryptococcosis observed alarmingly high numbers of disease occurrences,

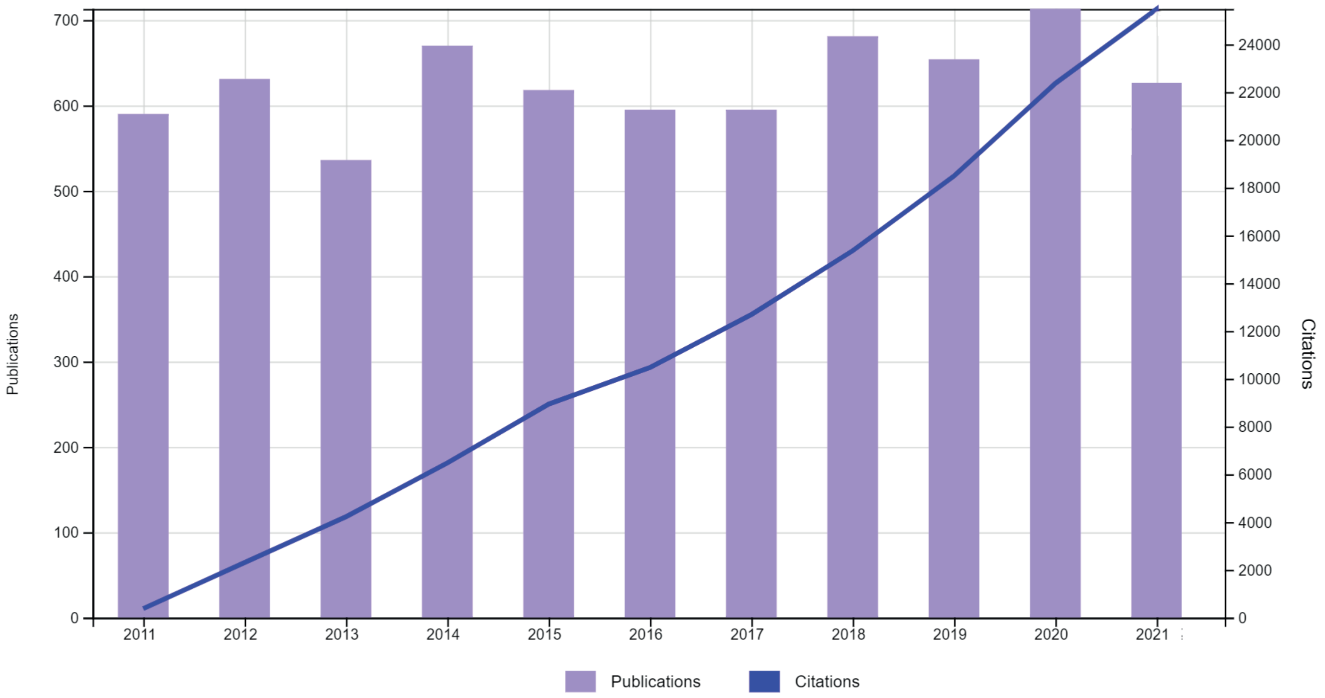

Fig. 19. Trends in research of *Cryptococcus* in the period 2011–2021.

Table 11. Top 10 cited articles related to *Cryptococcus* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Hidden killers: human fungal infections	2 175	Brown *et al.* (2012)
2	Emerging fungal threats to animal, plant and ecosystem health	1 678	Fisher *et al.* (2012)
3	Global burden of disease of HIV-associated cryptococcal meningitis: an updated analysis	863	Rajasingham *et al.* (2017)
4	Immunity to fungal infections	729	Romani (2011)
5	Through the wall: extracellular vesicles in Gram-positive bacteria, mycobacteria and fungi	520	Brown *et al.* (2015)
6	Structure-based drug discovery of carbonic anhydrase inhibitors	472	Supuran (2012)
7	The biology and chemistry of antifungal agents: A review	417	Kathiravan *et al.* (2012)
8	Recognition of seven species in the *Cryptococcus gattii*/*Cryptococcus neoformans* species complex	397	Hagen (2015)
9	Membrane vesicle release in bacteria, eukaryotes, and archaea: a conserved yet underappreciated aspect of microbial life	386	Deatherage & Cookon (2012)
10	The fungal cell wall: structure, biosynthesis, and function	365	Gow *et al.* (2017)

especially among immunocompromised humans in sub-Saharan Africa and parts of Asia and South America (Rajasingham *et al.* 2017). Using the global cryptococcal antigenaemia prevalence as a benchmark, 60 % of people with a CD4 cell count < 100 cells µL^{-1} were found to be positive, with 278 000 (range 195 500–340 600) people positive for cryptococcal antigen globally, and 223 100 (range 150 600–282 400) individuals with cryptococcal meningitis globally in 2014. Importantly, sub-Saharan Africa accounted for 73 % of the estimated cryptococcal meningitis cases in 2014 leading to 162 500 cases (range 113 600–193 900). Annual global deaths from cryptococcal meningitis were estimated at 181 100, with most (135 900) in sub-Saharan Africa. Cryptococcal meningitis was found to be responsible for 15 % of AIDS-related deaths (Rajasingham *et al.* 2017).

Other topics addressed in the top-cited papers include the biological mechanisms used by *Cryptococcus* to impact the extinction of wild animal hosts, the environmental changes and altered epidemiological dynamics of fungal emerging diseases; the physiological properties of the extracellular vesicles, testing current hypotheses on the mechanisms of vesiculogenesis, and their role in fungal pathogenesis; the reclassification of *Cryptococcus* species from an integrative analysis of molecular, biological and epidemiological data that led to the recognition of *Cr. gattii*/*Cr. neoformans* as a species complex; and the *Cryptococcus* cell wall and capsule, including details of its composition, synthesis, regulation, immune recognition, and therapy.

In the 5th edition of "*The Yeasts, a Taxonomic Study*" (TYTS, Kurtzman *et al.* 2011), 70 species were listed in the genus *Cryptococcus* (Fonseca *et al.* 2011), but it has been known for a long time that the genus in this context was highly polyphyletic (*e.g.*, Fell *et al.* 2000). In 2015, a taxonomic revision of the genus based on a multigene-based phylogeny limited the genus to species of

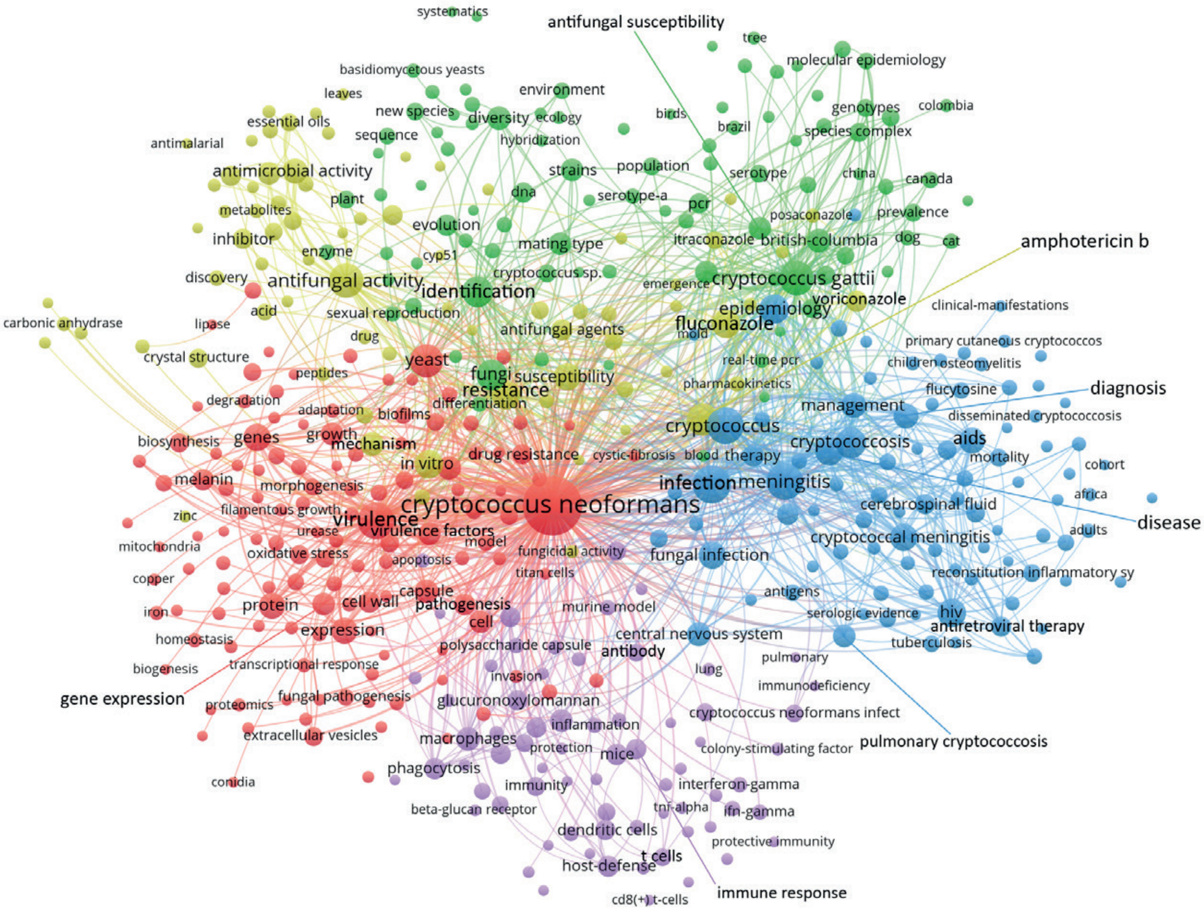

Fig. 20. Network visualisation of keywords of the publications related to *Cryptococcus*. The larger the text and the circle the more often the subject has been cited.

the *Cr. neoformans*/*Cr. gattii* complexes and some phylogenetically related species and, hence, the remainder were transferred to 29 other genera (Liu *et al.* 2015c, d; see also www.theyeasts.org). Species previously classified in the polyphyletic genus *Cryptococcus* are known for several biotechnological applications. Data from TYTS shows that several species formerly classified in *Cryptococcus* produce endoxylanases (*e.g.*, *Naganishia adeliensis*, *N. albidosimilis*, *N. albida*, *Saitozyma podzolica*), pectinases (*N. albida*), amylases (*S. flava*), epoxide hydrolases (*S. podzolica*), and are interesting as oleaginous yeasts that produce for example cacao butter equivalents (*Cutaneotrichosporon oleaginosus* also known as *Apiotrichum curvatum*), tolerate or accumulate heavy metals (*Vanrija humicola*, *S. podzolica*), degrade phenolic compounds (*Solicoccozyma terrea*), produce extracellular polysaccharides (*Papiliotrema flavescens*, *P. laurentii*) or might be used as biocontrol agents (*N. albida*) (Ykema *et al.* 1988, Fonseca *et al.* 2011, Smirnou *et al.* 2015, Bracharz *et al.* 2017a).

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10. ***Alternaria*** Nees, System der Pilze und Schwämme 72. 1816.

Type species: *Alternaria alternata* (Fr.) Keissl. (bas. *Torula alternata* Fr., syn. *Alternaria tenuis* Nees)

Classification: *Ascomycota*, *Pezizomycotina*, *Dothideomycetes*, *Pleosporales*, *Pleosporaceae.*

Background

Alternaria is a large genus of dematiaceous hyphomycetes with 837 species epithets listed in Index Fungorum (2023), of which 589 species epithets are legitimate (Hongsanan *et al.* 2020a, Wijayawardene *et al.* 2020). Presently, about 366 accepted species are mainly classified into 28 sections, but not all of them have been clarified based on molecular phylogeny (Woudenberg *et al.* 2014a, Lawrence *et al.* 2016, Jayawardena *et al.* 2019, Hongsanan *et al.* 2020a, Wijayawardene *et al.* 2020). *Alternaria* species are widely distributed in the environment and show a diverse ecological lifestyle that includes saprobic, endophytic, and pathogenic to plants and animals. Most species, however, are serious phytopathogens causing several severe diseases (*e.g.*, leaf and stem blight, leaf blotch, leaf spot, stem canker, and stem end rots) on a wide range of crop products often with significant economic losses (Thomma 2003, Polizzotto *et al.* 2012, Kustrzeba-Wójcicka *et al.* 2014, Woudenberg *et al.* 2014a, Ariyawansa *et al.* 2015a, Lawrence *et al.* 2016, Jayawardena *et al.* 2019, Marin-Felix *et al.* 2019a, Nishikawa & Nakashima 2020). Species in sections *Alternantherae*, *Alternaria*, *Brassicicola*, *Crivellia*, *Gypsophilae*, *Nimbya*, *Porri*, *Radicina* and *Sonchi* are usually causal agents of pre- and post-harvest diseases and may be both host and non-host specific (Mamgain *et al.* 2013, Woudenberg *et al.* 2014b, 2015, Zhu & Xiao 2015, Lawrence *et al.* 2016, Meena *et al.* 2016, Tralamazza *et al.* 2018).

Phytotoxins are produced during the plant infection process and, although they are not necessary for establishing diseases, they are essential virulence factors and participate in the intensity of disease symptoms (Thomma 2003, Meena *et al.* 2017). Some *Alternaria* species produce potential phytotoxins that can be used in biotechnological applications as efficient producers of active biological compounds, as biocontrol agents of pests and weeds against serious plant pathogens or as mycoherbicides (Sharma & Sharma 2014, Woudenberg *et al.* 2015, Lawrence *et al.* 2016, Kaur & Kumar 2019, Dalinova *et al*. 2020b).

Mycotoxins have also been described in *Alternaria* species which are a risk to human and animal health worldwide (Barkai-Golan 2008, Lopes *et al.* 2013, Mirhendi *et al.* 2013, Chowdhary *et al.* 2014a, Kustrzeba-Wójcicka *et al.* 2014, Woudenberg *et al.* 2014a, Lawrence *et al.* 2016, Lyskova *et al.* 2017, Cardona *et al.* 2020). *Alternaria* spores are commonly reported as airborne allergens causing mainly respiratory disorders and some species have also been reported to provoke infections, though usually in immunocompromised patients (Pastor & Guarro 2008, De Hoog *et al.* 2020). *Alternaria* species implicated in opportunistic human diseases (alternariosis) have always been identified as *Al. alternata* and *Al. infectoria* as causative agents of phaeohyphomycosis and infection of the cornea, nails, oral, sinus and skin in humans (Lawrence *et al*. 2016).

Alternaria was introduced as a monotypic genus by Nees von Esenbeck in 1816 to accommodate the dematiaceous hyphomycete forming chains of phaeodictyospores, with a beak of tapering apical cells, and was initially typified with *Al. tenuis*. Although years later, *Al. tenuis* was considered conspecific with *Torula alternata* (Fries 1832) and they were both synonymised with *Al. alternata,* which is currently recognised as the type of the genus (Keissler 1912). The genus is characterised mainly by its asexual morph, which shows inconspicuous conidiophores, mono- or polytretic conidiogenous cells, producing commonly large brown or dark dictyoconidia or phragmoconidia, with a terminal conical narrowing or "beak" at the apex, solitary or in chains; although species with meristematic growth are also known (Simmons 2007, Woudenberg *et al.* 2014a, Lawrence *et al.* 2016). Its sexual morph, only known for species of seven *Alternaria* sections, is characterised by small dark brown ascomata containing bitunicate asci and muriform ascospores (Woudenberg *et al.* 2014a, Ariyawansa *et al.* 2015a, Lawrence *et al.* 2016). The sexual morph of *Alternaria* has been linked to the genera *Lewia*, *Allewia* and *Crivellia* (Rossman *et al.* 2015). Phylogenetic results obtained by Woudenberg *et al*. (2014a) demonstrated that these genera formed internal clades within *Alternaria.* Thus, *Lewia*, *Allewia* and *Crivellia* were synonymised under *Alternaria* together with the genera *Brachycladium*, *Chalastospora*, *Chmelia*, *Embellisia*, *Nimbya*, *Sinomyces*, *Teretispora*, *Ulocladium*, *Undifilum* and *Ybotromyces* (Woudenberg *et al.* 2014a, Ariyawansa *et al*. 2015a). Based on taxonomic nomenclature (Article 57.2 of the International Code of Nomenclature for algae, fungi and plants; McNeill *et al.* 2012), Rossman *et al.* (2015) recommended to use *Alternaria* instead of *Lewia*, *Allewia* and *Crivellia* due to *Alternaria* being introduced earlier, widely used and the number of its species.

Taxonomic classification and revisions of *Alternaria* have been discussed by various authors (Elliott 1917, Simmons 1967, 1992, 2007, Joly 1964, Pryor & Gilbertson 2000, Pryor & Bigelow 2003, Hong *et al.* 2005, Lawrence *et al.* 2012, 2013, 2016, Woudenberg *et al.* 2014a, b, 2015). Extensive morphology-based taxonomic investigations on the genus were carried out by Emory G. Simmons (1920–2013), which were summarised in his monograph on *Alternaria* species identification (Simmons 2007). Based on the sporulation patterns and conidial morphology, Simmons (2007) recognised 275 species, which were divided into species-groups, each one typified by a representative species. However, handicaps to the correct identification of *Alternaria* species are the overlapping of morphological features among taxa and their plasticity, particularly when growing *in vitro.* Several molecular studies have been intended to establish relationships among morphological-based species and found that several species-groups described by Simmons were, in fact, representatives of monophyletic lineages that correlate with the currently established sections within the genus (Hong *et al.* 2005, Lawrence *et al.* 2012, 2013, Woudenberg *et al.* 2014a). Taxonomic traits and species composition of all *Alternaria* sections are summarised in Lawrence *et al.* (2016). However, molecular identification of *Alternaria* species is still a challenge because the conventional gene markers, such as the nrDNA barcodes and other functional genes (*act*, *tub*, *cal*, chitin synthetase, among many others), have failed to discriminate between species particularly belonging to the small-spored *Alternaria* sections, such as sect. *Alternaria* or sect. *Infectoriae* (Woudenberg *et al.* 2015, Lawrence *et al.* 2016, Poursafar *et al.* 2017, Patriarca *et al.* 2019). Consequently, whole-genome sequencing technologies have become essential tools to distinguish most of the described species (Lawrence *et al.* 2013, Woudenberg *et al.* 2015). The genomes of *Alternaria* spp. in sections *Alternaria* and *Brassicicola* are currently publicly available at the National Center for Biotechnology Information (NCBI) (Woudenberg *et al.* 2015).

Ecological and economic significance

Few fungal taxa can match the global impact that *Alternaria* has on natural ecosystems and its effects on human activities and health. *Alternaria* species are common saprobes on a wide range of substrates (*e.g.*, dead plants, paper, and foods) and more than 120 saprobic species have been restricted to the sections *Alternaria*, *Infectoriae*, and *Ulocladioides* (Thomma 2003, Lawrence *et al.* 2016). As saprobic fungi, along with other microorganisms, *Alternaria* species take part in the decomposition and mineralisation of plant residues through cellulolytic activity (Thomma 2003).

Alternaria has also been isolated from various asymptomatic plant tissues as endophytic fungi. Several studies have demonstrated the endophytic capability of *Alternaria* species living inside plant tissue without pathogenesis induction (Ma *et al.* 2010, Chen *et al.* 2011a, Polizzotto *et al.* 2012). However, it is still doubtful whether the fungus is living as an endophyte during the inactive latent period of weak pathogen or the influence of the host's health. Only saprobic species were revealed as endophytes (Ma *et al.* 2010, Lawrence *et al.* 2016). *Alternaria* stands out by the ability to cause diseases not only in plants but also in animals, including humans, and by the production of numerous secondary metabolites with a wide range of effects on different organisms.

Plant diseases

Alternaria species are reported to cause diseases in many economic plants from families such as *Apiaceae*, *Asteraceae*, *Brassicaceae*, *Cyperaceae*, *Fabaceae*, *Poaceae*, *Rosaceae*, *Rutaceae*, *Solanaceae*, *Vitaceae*, among others. They can infect more than 4 000 host plants, and *Al. alternata* can infect close to 100 plant species (Farr & Rossman 2022). Most *Alternaria* species are foliar pathogens, but they also attack flowers, stems, roots, and fruits, causing different kinds of lesions (Thomma 2003, Woudenberg *et al.* 2015, Lawrence *et al.* 2016, Marin-Felix *et al.* 2019a). The most common *Alternaria* diseases are detailed below.

Leaf spot: it is common on the surface of lower and older leaves on a variety of crops, including tomato, cabbage, fava bean, potato, cucumber and other vegetables, but also ornamental plants (Batta 2003, Michereff *et al.* 2012, Agamy *et al.* 2013, Behairy *et al.* 2014, Shoaib *et al.* 2014, Matić *et al.* 2020). Lesions are characterised by small dark circular spots with light brown centres, surrounded by dark concentric rings. Severely infected leaves turn yellow, wilt and fall, and can even show large necrotic areas (Batta 2003). It is a frequent disease in warm (20–32 °C) and moist (dew) weather regions. The main causal agents are *Alternaria alternata*, *Al. arborescens* species complex, *Al. brassicae*, *Al. brassicicola*, *Al. cinerariae*, and *Al. cucumerina* (Batta 2003, Reis & Boiteux 2010, Gannibal 2011, Blagojević *et al.* 2020, He *et al.* 2020a, Matić *et al.* 2020, Zhang *et al.* 2020d).

Leaf blight: the disease affects mature leaves near the crown of the plant and lesions first appear as small brown spots, often with a yellow halo, which progress to form large, irregular, brown spots. Severe infections can produce early defoliation, flower-bud abortion, premature ripening, and seed shrivelling, affecting yield and production (Akhtar *et al.* 1994, 2004). Temperatures between 15 and 25 °C and persistent leaf wetness by rain or dew promote infection (Shrestha *et al.* 2005b). Vegetables and cereals like wheat (Perelló *et al.* 1996), barley (Khudhair *et al.* 2014), tomato (Akhtar *et al.* 2004), onion (Karthikeyan *et al.* 2005) and mustard (Shrestha *et al.* 2005b) are only some of those most frequently affected. Species that are more frequently associated with this kind of lesion are *Alternaria alternata*, *Al. brassicae*, *Al. cucumerina*, *Al. dauci*, *Al. palandui*, *Al. triticina*, and *Al. triticimaculans*, among others (Perelló *et al.* 1996, Akhtar *et al.* 2004, Karthikeyan *et al.* 2005, Shrestha *et al.* 2005b, Khudhair *et al.* 2014).

Early blight: it is one of the most common diseases on tomatoes and potatoes, with *Al. solani*, *Al. tomatophila*, and *Al. alternata* being the main pathogens (Adhikari *et al.* 2017). Apart from the leaves, they can also affect fruits and seedling stems or stems of older plants, reducing crop yield by up to 79 % (Gwary & Nahunnaro 1998, Chaerani & Voorrips 2006, Adhikari *et al.* 2017). The infection is provoked in a wide range of environmental temperatures (8–32 °C), but with high levels of free moisture or near-saturation humidity (Adhikari *et al.* 2017). The most common symptoms include small dark spots that progress to larger spots with target-like concentric rings on leaves, sunken and dry brown areas on stems, and leathery and black spots on fruits. These are visible 2–3 d after infection, and spore production occurs 3–5 d later completing the cycle (Chaerani & Voorrips 2006).

Leaf blotch and fruit spot: *Alternaria alternata f. sp. mali* is commonly known as a causal agent of leaf blotch and fruit spot disease on apples worldwide (Harteveld *et al.* 2013, Woudenberg *et al.* 2015, Gur *et al*. 2017). However, multiple small-spored *Alternaria* species (*e.g.*, *Al. arborescens*, *Al. longipes* and *Al. tenuissima*) have also been implicated in alternaria leaf blotch on apples (Harteveld *et al.* 2013, 2014a). Alternaria leaf blotch is one of the most severe diseases on apples in Asia (*e.g.*, China, India, Israel, Iran, Japan, and South Korea), Australia and USA, causing defoliation of 15–25 %, or up to 80 % crop losses in some countries when conditions are conducive (Horlock 2006, Soleimani & Esmailzadeh 2007, Harteveld *et al.* 2013, 2014a, Sofi *et al.* 2013, Gur *et al.* 2017). The infection is provoked during winter and spring weather seasons and influenced by high relative humidity, the location of the orchards, mean temperature, cumulative amount of rain and mean rainfall (Harteveld *et al.* 2014b). The symptom of alternaria leaf blotch initially appears on leaves as circular to irregular brown spots that become larger in zonate circular or crescent-shaped rings and are lined with a dark brown to purple margin (Harteveld *et al.* 2013, 2014a, Gur *et al.* 2017). Fruit spot diseases are characterised by small, slightly sunken, light to medium brown spots (Persley & Horlock 2009, Harteveld *et al.* 2013).

Purple leaf blotch disease, caused by *Alternaria porri* on onions and leeks (*Allium* spp.), is a major foliar fungal disease in all *Allium* growing countries. This disease causes leaf damage and yield losses of up to 2.5–97 % during monsoon season (warm and humid environments) (Suheri & Price 2001, Gothandapani *et al.* 2015, Hahuly *et al*. 2018). The disease symptoms are difficult to distinguish from stemphylium leaf blight and are easily misidentified (Suheri & Price 2001, Hahuly *et al.* 2018). The symptoms appear on the older leaves and flower stalks as initially small whitish necrotic lesions, becoming larger elliptical, sunken purple lesions, subsequently turning brown and darker, with a yellow to pale brown margin (Suheri & Price 2001, Hahuly *et al.* 2018).

Stem canker: *Alternaria arborescens* (syn. *Al. alternata f. sp. lycopersici*) has been reported as the causal agent of stem canker on tomatoes worldwide, causing sustainable economic losses (Thomma 2003, Esmailzadeh *et al*. 2008, Woudenberg *et al*. 2015, Shao *et al*. 2020). *Alternaria arborescens* produced a host-specific AAL-mycotoxin and damages leaves and stems of tomatoes by forming necrotic spots on leaves and dark-brown concentric cankers on stems (Grogan *et al.* 1975, Witsenboer *et al.* 1992, Thomma 2003, Somma *et al.* 2011, Shao *et al.* 2020). The infection progresses rapidly in high humidity and temperatures (0.995 a_w at 30 °C) (Vaquera *et al.* 2014, Tomazonia *et al.* 2019).

Human and animal diseases

Alternaria has been associated with a wide range of human and animal syndromes. Although it is commonly known as an agent of allergic processes, it is currently considered an emerging pathogen able to cause infections in immunocompromised patients, although infections in immunocompetent individuals have been also reported (Sood *et al.* 2007, Pastor & Guarro 2008, Dessinioti *et al.* 2013, Hattab *et al.* 2019, De Hoog *et al*. 2020). Since *Alternaria* spores are one of the prevailing constituents in air, they are associated with respiratory disorders such as allergic sinusitis, bronchial asthma, pneumonitis or rhinitis (Pastor & Guarro 2008, Revankar & Sutton 2010, Klimek *et al.* 2015, Levetin *et al.* 2016). Immunosuppressed populations, particularly those who have undergone transplants, cancer treatments or have primary or acquired immunodeficiency, are especially susceptible to cutaneous and subcutaneous infections by *Alternaria* species (Kpodzo *et al.* 2011, González-Vela *et al.* 2014, Ferrándiz-Pulido *et al.* 2018, Iturrieta-González *et al.* 2019), but other types of infections have been also reported, such as ocular mycosis, cerebral and disseminated infections (Konidaris *et al.* 2013, Mirhendi *et al.* 2013, Cardona *et al.* 2020, McGirr *et al.* 2020). There are also documented cases of alternariosis, ranging from cutaneous to systemic infections, in cats, dogs, horses, and other animals (Dedola *et al.* 2010, Seyedmousavi *et al.* 2013, Avsever *et al.* 2017, Dworecka-Kaszak *et al.* 2020, De Hoog *et al*. 2020).

The most reported species are *Alternaria alternata*, *Al. infectoria*, *Al. tennuissima* and *Al. chartarum* (De Hoog *et al.* 2020). However, the real spectrum of pathogenic *Alternaria* species is still obscure because, in as many as 50 % of the cases of alternariosis reported, the identification of clinical isolates has not been carried out or was based only on morphological features or ITS barcode analysis (Pastor & Guarro 2008, Bajwa *et al.* 2017, Ferrándiz-Pulido *et al.* 2018).

Toxin production

Alternaria is one of the major mycotoxigenic fungi with about 70 described toxins (phytotoxins and mycotoxins) that play an important role in fungal pathogenicity and food safety (Escrivá *et al.* 2017, Pinto & Patriarca 2017).

Phytotoxins: They are formed during the infection and two categories have been recognised: (i) The "host-specific toxins", which affect a small group of specific plants, and their formation and activity are usually a prerequisite for successful colonisation of the plant host; examples of these toxins are produced by different *Alternaria alternata* pathotypes (Meena *et al.* 2019, Dalinova *et al.* 2020b). (ii) The "non-host specific toxins", to which a wider range of plants are sensitive, but they cause relatively mild phytotoxic effects and their formation is not necessary for successful colonisation of the host (Thomma 2003, Dalinova *et al.* 2020b). Many phytopathogenic *Alternaria* species produce nonspecific toxins that often target basic cellular processes, so they are regarded as potent mycotoxins, but may also exhibit other types of biological activities (*i.e.*, antimicrobial, insecticidal or cytotoxic activity) that enhance the survival of the fungus in competition with other (micro-)organisms for the substrate (Meena *et al.* 2017, Dalinova *et al.* 2020b).

Mycotoxins: Food contamination by mycotoxins occurs naturally, however, under certain environmental conditions, handling, transport and storage, and even refrigeration conditions mycotoxins may accumulate in vegetable foods and be harmful to humans and animals (Escrivá *et al.* 2017). Although *Alternaria alternata* is regarded as the major mycotoxin producer in the genus, others like *Al. citri*, *Al. solani*, *Al. longipes*, *Al. arborescens* and *Al. infectoria*, which are present in seeds, fruits, vegetables, and pet foods, are also relevant mycotoxin producers and all represent a serious threat to health worldwide (Barkai-Golan 2008, Jackson & Al-Taher 2008, Ostry 2008, Streit *et al.* 2013, Puntscher *et al.* 2018). *Alternaria* mycotoxins like alternariol, its methyl ether, as well as altertoxins seem to induce long-term toxicity effects (genotoxicity, carcinogenicity, mutagenicity, *etc.*), in contrast to tenuazonic acid, which is the only *Alternaria* mycotoxin that exhibits pronounced acute toxicity causing haematological disorders to oesophageal cancer (Escrivá *et al.* 2017, Pinto & Patriarca 2017, Dalinova *et al.* 2020b). Despite these harmful effects, *Alternaria* mycotoxin content in feed and food products is not currently regulated by any country. This is due not only to a lack of comprehensive toxicological information from different foodstuffs but also to a lack of research into their toxicity *in vivo* (Lee *et al.* 2015, Dalinova *et al.* 2020b).

Research interests

There are 6 446 publications and 73 134 citations from 2011–2021 in the Web of Science (Fig. 21), with the top 10 most cited articles included in Table 12. The majority of the publications focused on disease management (antifungals and resistances), parasite-host interactions of *Alternaria* species in plants and humans, bioactive compounds production, and taxonomy (Fig. 22).

Disease management

There are various strategies in the management of *Alternaria* diseases in plants, including the use of healthy and treated seed in hot water, 3–4-yr crop rotations, sanitation, weed control, shallow planting, use of balanced nutrients, proper plant density, proper drainage in the field, plant debris management and application of chemical treatments. Of note, however, is that no single method or approach in current use is feasible, viable, stable, or effective in dealing with any host-pathogen system (Saharan *et al.* 2016).

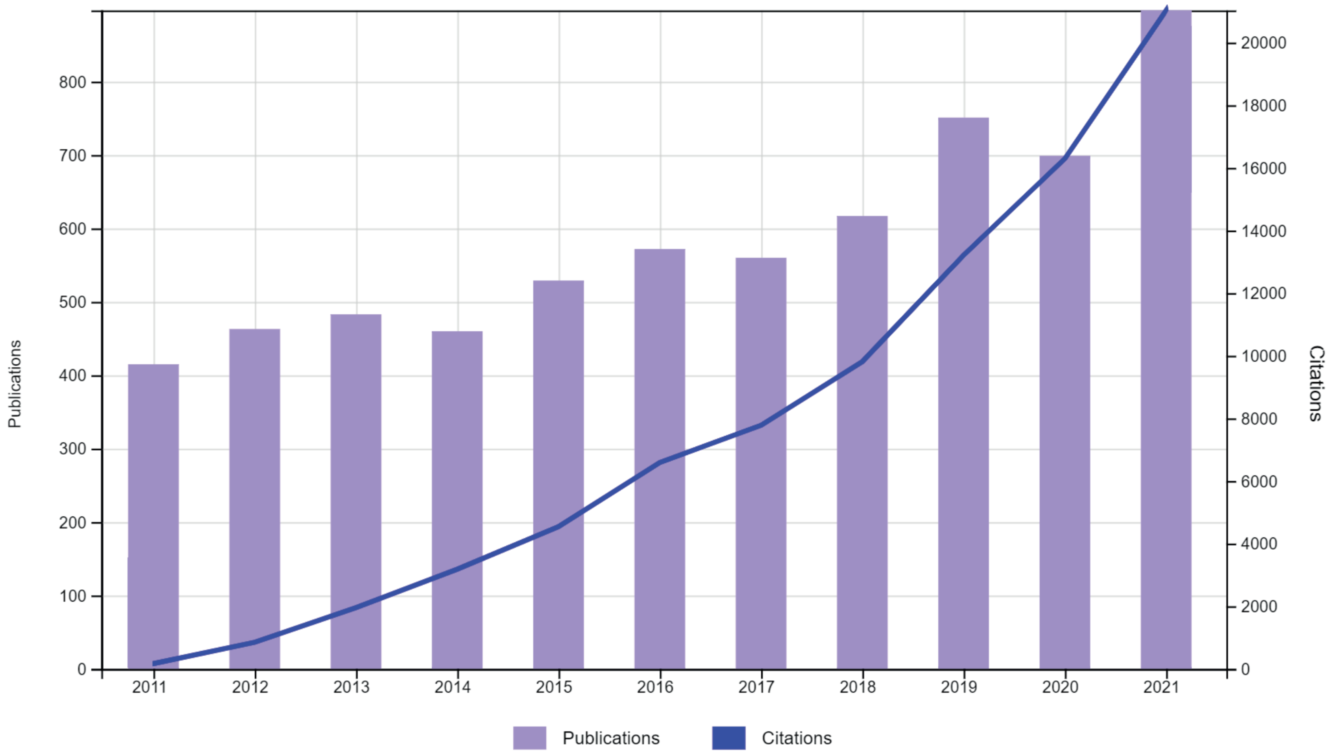

Fig. 21. Trends in research of *Alternaria* in the period 2011–2021.

Table 12. Top 10 cited articles related to *Alternaria* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Phytoalexins in defense against pathogens	533	Ahuja *et al.* (2012)
2	*Alternaria* redefined	441	Woudenberg *et al.* (2013)
3	Exosomes secreted by nematode parasites transfer small RNAs to mammalian cells and modulate innate immunity	410	Buck *et al.* (2014)
4	Next-generation systemic acquired resistance	379	Luna *et al.* (2011)
5	IL-33-responsive lineage$^-$CD25$^+$CD44^{hi} lymphoid cells mediate innate type 2 immunity and allergic inflammation in the lungs	372	Bartemes *et al.* (2012)
6	The danger signal, extracellular ATP, is a sensor for an airborne allergen and triggers IL-33 release and innate Th2-type responses	322	Kouzaki *et al.* (2011)
7	Fungi and allergic lower respiratory tract diseases	305	Knutsen *et al.* (2012)
8	Lung type 2 innate lymphoid cells express cysteinyl leukotriene receptor 1, which regulates Th2 cytokine production	275	Doherty *et al.* (2013)
9	Interferon and IL-27 antagonize the function of group 2 innate lymphoid cells and type 2 innate immune responses.	245	Moro *et al.* (2015)
10	Reference genes for accurate transcript normalization in citrus genotypes under different experimental conditions	228	Mafra *et al.* (2012)

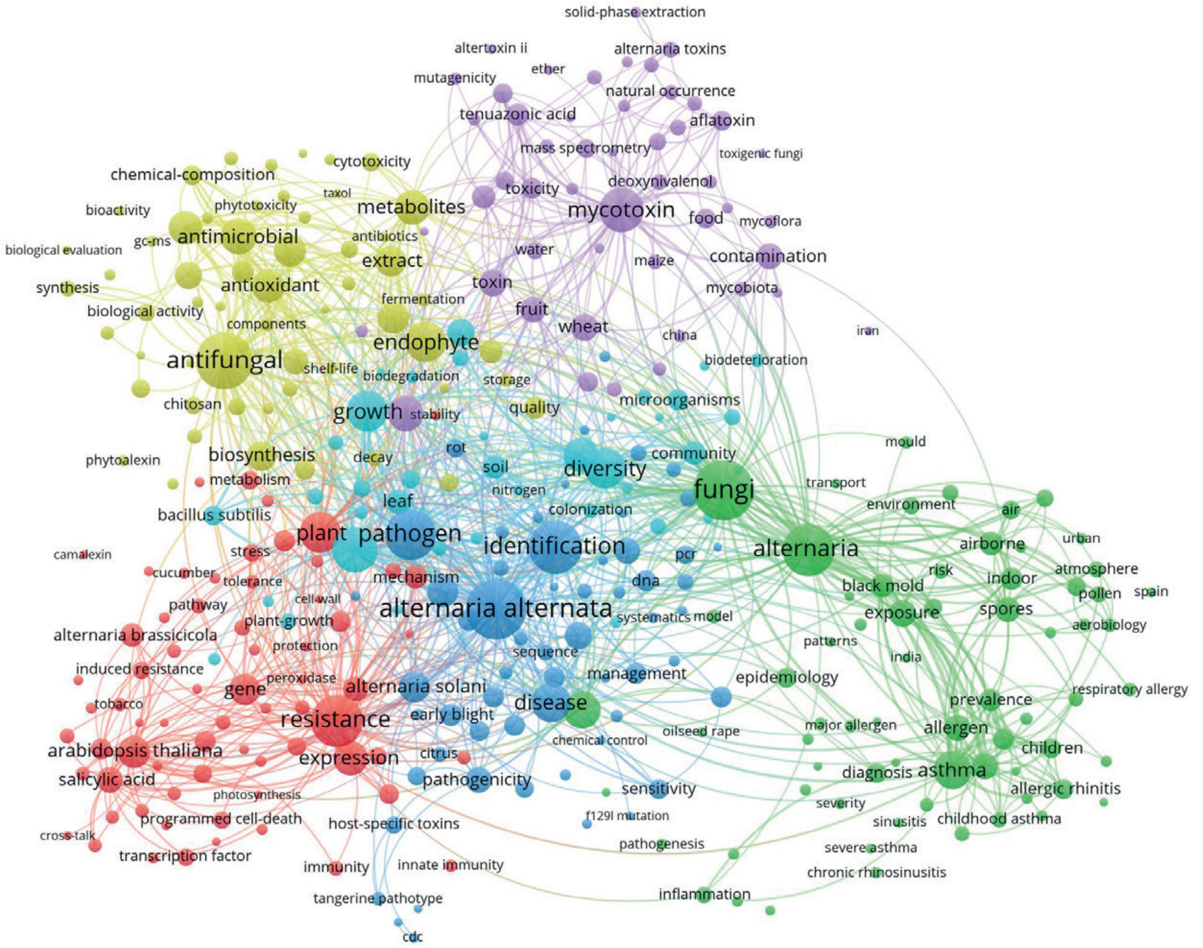

Fig. 22. Network visualisation of keywords of the publications related to *Alternaria*. The larger the text and the circle the more often the subject has been cited.

Common pathogenic fungal strains, including *Alternaria*, are often resistant to fungicides (Iacomi-Vasilescu *et al.* 2004, Fairchild *et al.* 2013, Mallik *et al.* 2014, Yang *et al.* 2019b). Different strategies have been proposed for reducing strain resistance, including mixing fungicides or using chemosensitisers (Brent & Hollomon 2007, Shcherbakova *et al.* 2020). However, with the focus on sustainable agriculture for the replacement of synthetic and toxic substances with environmentally friendly alternatives, research is currently in the direction of finding effective bioagents as antagonists against *Alternaria*, such as *Chaetomium globosum* or different *Trichoderma* species (Gveroska & Ziberoski 2011, Saharan *et al.* 2016, Ajayabhai *et al.* 2018, Ashwini 2019, Shafique *et al.* 2019); or looking for compounds with potent antifungal activity, such as plant extracts (Latif *et al.* 2006, Meena & Sharma 2012), ionic liquids (Karaman *et al.* 2020) or natural agents in nanoformulations like peppermint oil (Pandey *et al.* 2020) or silver nanoparticles plus a cyanobacterium (Mahawar *et al.* 2020). However, currently, the easiest, most financially viable, environmentally friendly, and safest way is the use of tolerant or resistant cultivars (Saharan *et al.* 2016), so that research is also focused on the development of *Alternaria* disease-resistant crops (Ceasar & Ignacimuthu 2012, Fatima *et al.* 2019, Meena & Samal 2019, Haque *et al.* 2020).

Because no optimal treatment has been defined for *Alternaria* human infections, multiple therapeutic options have been used, including thermotherapy with a successful outcome (Torres-Rodriguez *et al.* 2005). However, it always depends on the status of the patient concerned and the extent of the disease. Cutaneous and subcutaneous alternarioses commonly require surgical debridement in association with antifungal therapy (Pastor & Guarro 2008, Derber *et al.* 2010). The most used antifungal therapy includes itraconazole, voriconazole, and posaconazole (Chowdhary *et al.* 2014d, Bajwa *et al.* 2017, Ferrándiz-Pulido *et al.* 2018). However, due to hepatic impairment as a side effect reported for voriconazole (Schuermans *et al.* 2017) or significant drug interaction when using itraconazole (Mori *et al.* 2009), currently, posaconazole seems to be the treatment of choice for these infections (Bajwa *et al.* 2017, Schuermans *et al.* 2017). This correlates with the results of *in vitro* antifungal testing in several studies (Badali *et al.* 2009, Alastruey-Izquierdo *et al.* 2011, Gonzalez-Vela *et al.* 2014). Other drugs that show different degrees of effectiveness are amphothericin B, terbinafine or anidulafungin (De Hoog *et al.* 2020), but more *in vitro* and *in vivo* studies are required. Nevertheless, the lack of a standardised methodology for *in vitro* studies or for the correct identification of *Alternaria* species, and the difficulties in getting good sporulation of clinical isolates are handicaps in the advance of these studies.

Parasite-host interaction

The interaction between plants and pathogens induces stress response and, subsequently, the development of an intricate defence system associated with the activation of defence genes, synthesis and secretion of various molecules. In plant infections by *Alternaria*, the production of phytoalexins like camalexin, kauralexins, zealexins, brassinin, and scopoletin (Ahuja *et al.* 2012, Pedras *et al.* 2014, Sun *et al.* 2014, N'Guyen *et al.* 2021), or enzymes like chitinases and ß-1,3-glucanases (Fanta *et al.* 2003) have been extensively studied to elucidate their role in the host interaction and pathogenesis of these fungi (Thomma 2003, Meena & Samal 2019). In the same way, the interaction of *Alternaria* with human host cells induces an immune response and research is imperative to understand the fungal biology and details of mechanisms that may protect or drive diseases in humans (Bartemes & Kita 2018). The respiratory system is the most common entry for fungi, and thus several studies have focused on the characterisation of allergic immune responses against *Alternaria* through the study of innate and adaptive response, particularly lymphoid response involved in innate type 2 immunity, production of interleukins, toll-like receptors, among others (Bartemes *et al.* 2012, Kita 2015, Hayes *et al.* 2018). However, only the approaches of integrating genomic, proteomic and metabolomic insights will allow an understanding of the complex biology of host-pathogen interaction and allow the proposal of innovative strategies for mitigating or even eradicating *Alternaria* diseases.

Producers of active biological compounds

More than 300 secondary metabolites produced by *Alternaria* species have been isolated and structurally characterised (Lou *et al.* 2013, Song *et al.* 2019b, Dalinova *et al.* 2020a). In addition to their toxicogenic effects on plants and animals described previously, these molecules show other biological activities that attract the attention of scientists in various fields (biotechnologists, chemists, pharmacologists, plant pathologists, *etc.*), who investigate a wide range of applications. These molecules are used as prototypes of active chemical pesticides against bacteria (hydroxybostrycin, macrosporin, radicin, altenusin, porric acid, *etc.*), insects (tenuazoic acid and its synthetic derivatives, altenaene, destruxin B), downy mildews (compounds of diketopiperazine dipeptides), phytopathogenic moulds (helvolic acid, herbarin A, *etc.*), and weeds (cyclic tetrepeptide tentoxin, tenuazonic acid, radicinin, *etc.*). However, they are also the base for development of new drugs as anti-tumour agents (alterporriols, depudecin, destruxin B, *etc.*), anti-leukemic (α pyrone derivatives), anti-bacterial (altenusin, brassicicolin, *etc.*), antiparasitic (depudecin, altenusin) or antiviral (altertoxin V, tetrahydroalternasol C, *etc.*). A promising molecule produced by several *Alternaria* species and of medical interest is altenusin. It has been recently patented in China as a component of medicines for non-alcoholic fatty liver disease, obesity or type 2 diabetes; it is also able to inhibit tau-protein aggregation, a key compound associated with the development of Alzheimer's disease (Lou *et al.* 2013, Zheng *et al.* 2017, Dalinova *et al.* 2020b). Therefore, considering the number of *Alternaria* molecules still needing to be characterised and the large number of species for which secondary metabolite patterns have never been determined, the potential of this genus as a source of interesting compounds is high.

Taxonomy and phylogeny

The taxonomy of *Alternaria* continues to be a subject of debate. Based on several phylogenetic investigations carried out in the last decades, the genus has undergone important taxonomic changes and numerous, morphologically well-defined genera have been found to be congeneric with *Alternaria* (*i.e.*, *Allewia*, *Brachycladium*, *Chalastospora*, *Chmelia*, *Crivellia*, *Embellisia*, *Nimbya*, *Pseudoalternaria*, *Sinomyces*, *Teretispora*, *Ulocladium*, *Undiphilum* and *Ybotromyces*) (Pryor & Gilbertson 2000, Lawrence *et al.* 2012, 2013, Woudenberg *et al.* 2013, Ariyawansa *et al.* 2015a, Rossman *et al.* 2015). Based on the phylogeny of SSU, LSU, ITS, *gapdh*, *rpb2* and *tef1*, Woudenberg *et al.* (2013) emended the generic circumscription of *Alternaria*, and numerous well-supported internal clades were elevated to the taxonomic status of section, some of them correlated with the above-mentioned genera as well as some of Simmons' morphological species-groups. Therefore, in addition to six monophyletic lineages, the genus currently comprises 28 sections, each with a type specimen (Woudenberg *et al.* 2013, Lawrence *et al.* 2016, Al Ghafri *et al.* 2019, Jayawardena *et al.* 2019). However, because the phylogenetic relationships among closely related species could not be resolved by those markers, not even the ITS standard barcode for fungi, multi-gene analyses combining different loci have been used to resolve species boundaries in different sections; *i.e.,* ITS, *Alt a-1*, *endoPG*, *gapdh*, OPA10-2, *rpb2* and *tef1* for sect. *Alternaria* (Woudenberg *et al.* 2015); ITS, *ATPase* and *gapdh* for sect. *Chalastospora* (Marin-Felix *et al.* 2019a); combinations of three to five loci (ITS, *ATPase*, *gapdh rpb2* and *tef1*) for sections *Infectoriae* and *Pseudoalternaria*, depending on the authors (Deng *et al.* 2018, Poursafar *et al.* 2018, Iturrieta-González *et al.* 2019, Marin-Felix *et al.* 2019a); ITS, *Alt a-1*, *gapdh*, *rpb2* and *tef1* for sect. *Porri* (Woudenberg *et al.* 2014); ITS, *gapdh* and *rpb2* for sect. *Radicina* (Marin-Felix *et al.* 2019a); and ITS, *Alt a-1* and *gapdh* for sect. *Sonchi* (Lawrence *et al.* 2012, Deng *et al.* 2014). Unfortunately, there is no consensus on the molecular approach for identifying *Alternaria* species, especially those small-spored species involved in crop diseases, food contamination and human infections. To that end, polyphasic approaches have been carried out in recent investigations, integrating datasets on morphological features, molecular analyses, secondary metabolite profiling or experimental host range determination by inoculation tests (Ozkilinc *et al.* 2018, Patriarca *et al.* 2019, Nishikawa & Nakashima 2020). With this integrative approach, Somma *et al*. (2019) suggested that the sect. *Infectoriae* be defined as a separate genus from *Alternaria*. However, further efforts are needed to provide a more solid taxonomic system that allows correct species identification of these so relevant fungi.

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11. ***Phytophthora*** de Bary, J. Roy. Agric. Soc. England, ser. 2, 12: 240. 1876.

Type species: *Phytophthora infestans* (Mont.) de Bary

Classification: *Oomycota*, *Peronosporomycetes*, *Peronosporales*, *Peronosporaceae.*

Background

Phytophthora belongs to phylum *Oomycota*, related to other heterokonts like brown algae rather than in the fungal kingdom like most filamentous plant pathogens. Index Fungorum (2022) lists 352 species epithets, 223 of which are recognised species with an ex-type isolate and available sequence data (Abad *et al.* 2023b). Most species are plant pathogens with single to numerous hosts ranging from field crops, fruit trees, ornamentals and in natural ecosystems (Erwin & Ribeiro 1996, Hansen *et al.* 2012, Jung *et al.* 2015a, Burgess *et al.* 2021), causing a range of symptoms depending on the species, including root rot, stem and branch cankers, leaf blight and fruit rot (Erwin & Ribeiro 1996).

Sporangia, which can be caducous or persistent, produce zoospores, the infective propagule, that encysts and germinates to penetrate the host (Erwin & Ribeiro 1996). The majority of species are soil pathogens with persistent sporangia, while most *Phytophthora* causing diseases in aerial plant parts have caducous, air-borne sporangia. *Phytophthora* reproduces sexually by forming oospores; heterothallic species require two mating types while homothallic species are self-fertile. Oospores are often thick-walled and are thought to be a vital survival structure for over-wintering and/or surviving drought (González *et al.* 2019, Gyeltshen *et al.* 2021), although there is mounting evidence that many species persist within dead fragments of their hosts (Jung *et al.* 2013). Zoospores are motile and require free water to find and infect a host and are best suited to moist environments, especially those causing aerial diseases. However, some of the most significant impacts are in Mediterranean climates, where the relatively warm moist winter favours infection, and then plants cannot survive the long dry summer with compromised root systems (Dunstan *et al.* 2020, González *et al.* 2020).

De Bary introduced *Phytophthora* in 1876, with the type species, *Phytophthora infestans*, one of the first plant pathogens to be described. It was the causal agent of potato leaf blight and famine in the mid-19th century. Over the following 110 years, 60 more species were described, mainly causing diseases in plants of economic importance (Erwin & Ribeiro 1996). Most of these species have a global distribution associated with agriculture. Species were described based on the morphology of sporangia, their proliferation, oogonia, antheridia, oospores and the presence of chlamydospores and hyphal swellings or aggregations. Waterhouse (1963) classified species into six groups depending on whether the sporangia were papillate, semi-papillate or non-papillate and whether the antheridial attachment was amphigynous or paragynous. The seminal paper by Cooke *et al.* (2000) on the molecular phylogeny of *Phytophthora* based on ITS sequences divided the genus into 10 phylogenetic clades. These clades have been robust as additional nuclear and mitochondrial genes (Blair *et al.* 2008, Robideau *et al.* 2011, Martin *et al.* 2014, Yang *et al.* 2017b) have been added to the phylogenies and have laid the path for the description of numerous new taxa, many of which were morphologically indistinct but phylogenetically distant (Brasier *et al.* 2003, Burgess *et al.* 2009). While historically, new species recovery and descriptions were from agricultural settings, since 2000 most new species are from natural ecosystems.

Ecological and economic significance

Phytophthora species cause numerous economically significant plant diseases and also serious diseases within natural ecosystems; many species are cosmopolitan, while others are more host-specific. Below we consider the diseases caused by the most cited *Phytophthora* species.

Late blight of potatoes (and tomatoes) is caused by *Phytophthora infestans*, a predominantly aerial *Phytophthora* species infecting leaves and stems, favouring moist, cool environments (Grünwald & Flier 2005). Under ideal conditions, plants die within a few days. Rain washes sporangia into the soil where zoospores infect tubers. *Phytophthora infestans* is a poor saprophyte in the absence of a host and is killed off by frost and hot conditions. However, it can overwinter within infected tubers in a field. Globally, late blight causes around 10 % of crop loss annually and is especially severe in the Indo-Gangetic Plain (Savary *et al.* 2019).

Phytophthora root rot

Several species from the *Phytophthora megasperma* complex have been described, including *Phy. rosacearum* and *Phy. sansomeana* (Hansen *et al.* 2009). Following the description of a related species, *Phy. crassamura* (Scanu *et al.* 2015), many isolates of *Phy. megasperma* recovered from woody plants globally have been reassigned to *Phy. crassamura.* True *Phy. megasperma* is probably limited to *Fabaceae*. *Phytophthora medicaginis* (Phytophthora root rot of lucerne) and *Phy. trifolii* (Phytophthora root rot of clover) were considered subspecies of *Phy. megasperma* before being formally described (Hansen & Maxwell 1991). Interestingly, *Phy. megasperma* resides in clade 6 of the *Phytophthora* phylogeny, as does *Phy. crassamura* and *Phy. rosacearum*, while *Phy. sansomeana*, *Phy. medicaginis* and *Phy. trifolii* reside in clade 8 (Yang *et al.* 2017b). Phytophthora root rot of soybeans caused by *Phytophthora sojae* is one of the most studied *Phytophthora* diseases (Tyler 2007). The symptoms include damping-off of seedlings and then root rot of older seedlings. Management costs and annual crop losses amount to 1–2 billion US dollars. It has a very narrow host range and a global distribution.

Phytophthora stem rot of cowpea caused by *Phytophthora vignae* was first described in Australia and has a narrow distribution limited to Australia and Asia. It causes stem rot, leaf spots and may ultimately destroy root systems. Natural hosts predominantly include (*Fabaceae*) *Vigna unguiculata* and *V. sinensis*. In Queensland, Australia, it is associated with significant disease and can cause catastrophic loss and complete loss in susceptible commercial crops (Davis *et al.* 1994).

Red stele or red core root rot is the most important disease of garden strawberries (*Fragaria* × *ananassa*) (Ho & Jong 1988). It is caused by *Phytophthora fragariae* and has been reported in most regions except Africa and South America. The only other natural host of this pathogen is boysenberry (*Rubus ursinus* var. *longanobaccus*). Resistance has been uncovered in strawberries and used to breed resistant varieties (Al-Khayri & Islam 2018). Chemical control is usually used, but there is good evidence that integrated cultural and biological control could reduce the use of fungicides (Norman *et al.* 1996).

White tip is a significant disease of leeks (*Allium porrum*) caused by *Phytophthora porri*, with the most significant impacts during wet and cold periods (Smilde *et al.* 1996). The pathogen has a wide distribution, causing diseases in Africa, Asia, Oceania, Europe and North America (Declercq *et al.* 2010). The pathogen typically causes leaf blight and impacts the bulbs, collar and roots of *Allium* species, although also associated with *Campanula*, *Daucus*, *Dianthus*, *Gladiolus*, *Hyacinthus*, *Lactuca* and *Tulipa* species.

Lima Bean downy mildew is a destructive disease caused by *Phytophthora phaseoli*. At least six races have been identified, leading to severe disease outbreaks in the eastern United States (Evans *et al.* 2007). The impacts are most evident and destructive on pods, but the pathogen also infects shoots, leaves, and petioles. Symptoms include early irregularly shaped and purplish lesions on the leaves. The disease appears most commonly under humid conditions. This species has a wide distribution in the eastern United States and a limited distribution in Central America, Africa, Asia and Europe. Known natural hosts include *Phaseolus lunatus*, *Phaseolus limensis*, and *Phaseolus vulgaris*, although it has caused symptoms on a range of agricultural hosts following artificial inoculations (Erwin & Ribeiro 1996).

Black shank of tobacco, caused by *Phytophthora nicotianae* (syn. *Phy. parasitica*), mainly affects the roots and basal stem area; however, all parts of the plant can become infected (Panabieres *et al.* 2016). Roots become blackened and decayed, and in the final stages of the disease, the stem begins to turn black. The disease is predominantly managed with good hygiene, crop rotations and chemical control. Breeding new varieties of tobacco for resistance to the pathogen has had limited commercial success, although it is an area of ongoing research (Bao *et al.* 2019). *Phytophthora nicotianae* has been extensively researched as an important global pathogen; it has a wide distribution and host range including agriculture, horticulture and ornamental species, where it can affect the roots, stems, trunk, leaves, fruits and pods (Panabieres *et al.* 2016).

Pink rot of potatoes is caused by *Phytophthora erythroseptica*, a species with a global distribution but a very narrow host range. The tubers become infected while in the soil, but symptoms develop during storage. Avoiding the wounding of tubers during harvest and handling and rapid cooling and storage below 10 °C will reduce the impact (Salas *et al.* 2000). Management within the field is more difficult as the pathogen is resistant to common fungicides such as metalaxyl (Taylor *et al.* 2002). *Phytophthora cryptogea* is often also isolated alone or in association with *Phy. erythroseptica* from symptomatic tubers.

Root and stem rot is a common disease of numerous cultivated flowers, annual crops and ornamentals. Two of the pathogens often recovered in these situations are *Phytophthora cryptogea* and *Phy. drechsleri*; both are cosmopolitan species with numerous hosts (Erwin & Ribeiro 1996). These species are more often recovered from managed landscapes than from natural ecosystems. Several related species have now been described from the *Phy. cryptogea* species complex, including *Phy. pseudocryptogea,* which appears to be more common in natural ecosystems than *Phy. cryptogea* (Safaiefarahani *et al.* 2015). Isolates previously classified as *Phy. drechsleri* based on morphology have now been described as new species, many of which are not closely related to *Phy. drechsleri* (Burgess *et al.* 2009).

Phytophthora blight

Phytophthora capsici is a caducous species causing Phytophthora blight in vegetable crops, including capsicum and various other *Solanaceae* and *Cucurbitaceae*. The pathogen affects fruit and stems and causes root rot, stunted growth, and death of older plants (Hausbeck & Lamour 2004). Disease incidence and severity have increased significantly in recent decades, and very little natural resistance has been found in most crops. Disease management depends on cultivation, sanitation, and fungicides (Lamour *et al.* 2012). Many records of *Phy. capsici* in the tropics, especially those associated with woody hosts, are most likely records of a related species, *Phy. tropicalis* (Aragaki & Uchida 2001).

Diseases of fruits and pods

There are several *Phytophthora* diseases of fruits and pods, stem cankers, leaf diseases and root rot of important tropical crops such as cocoa, coconut, durian, rubber and taro (Erwin & Ribeiro 1996, Drenth & Guest 2004). Some species such as *Phy. palmivora* have a global distribution, while others have a more limited distribution; for example, *Phy. meadii* which is limited to Asia and the Pacific. While several species can cause the same symptoms on the same tree species, some of the best-known diseases include black stripe of rubber, bud rot and nut fall of coconut caused by *Phy. heveae*, taro leaf blight caused by *Phy. colocasiae*, bud rot of oil palm caused by *Phy. palmivora*, pod rot of rubber caused by *Phy. meadii* and black pod disease of cocoa caused by *Phy. megakarya* (Erwin & Ribeiro 1996, Drenth & Guest 2004).

Brown rot of citrus fruit caused by *Phytophthora hibernalis* was first described in Western Australia in 1926, although the disease had been known since 1916 (Carne 1926). It is now known to have an almost global distribution on *Citrus* species and other *Rutaceae*, and it is doubtful *Phy. hibernalis* originated in Australia. The most effective control is the use of fungicides in orchards (also to control other *Phytophthora* diseases of *Citrus*) and postharvest treatments (Adaskaveg & Förster 2014). *Phytophthora boehmeriae* also causes brown rot of citrus fruit and a variety of other diseases, including cotton boll blight. *Phytophthora boehmeriae* has a more limited distribution than *Phy. hibernalis*, and has not been reported in most of Europe or North America (Erwin & Ribeiro 1996).

Gummosis of citrus trees is the leading cause of stunted growth and mortality globally. The most common species associated with this disease is *Phytophthora citrophthora*, one of the first species described (Leonian 1925). This disease has been extensively studied, especially cultural and chemical control (Cacciola & di San Lio 2008). Resistant rootstocks (Matheron *et al.* 1998) and phosphite use (Matheron & Matejka 1988) are common control measures.

Sudden oak death

Phytophthora ramorum causes a significant disease of oak species on the west coast of North America known as sudden oak death. The pathogen spreads through aerial spores under moist conditions and causes significant bleeding cankers on trunks and branches, foliage dieback and death. In North America, there are sporulating hosts such as California bay laurels (*Umbellularia californica*), where the pathogen infects leaves and produces significant inoculum, and dead-end hosts such as tanoak (*Lithocarpus densiflorus*) and coast live oak (*Quercus agrifolia*), where infection often leads to death (Rizzo *et al.* 2002). Ramorum blight is common on numerous woody ornamentals, in particular *Rhododendron* (Grünwald *et al.* 2008). Within Europe, *Phy. ramorum* does not cause disease of oaks; however, it has been reported in commercial nurseries in over 20 countries (Grünwald *et al.* 2008), and it causes a significant decline of Japanese larch (*Larix kaempferi*) plantations (Brasier & Webber 2010) in the UK. *Phytophthora kernoviae* also causes significant disease in *Rhododendron* spp., *Fagus grandifolia* and *Vaccinium* spp. in the UK (Brasier *et al.* 2005). As *Phytophthora kernoviae* has limited impact on native species in New Zealand, it is hypothesised to be the species' origin (Gardner *et al.* 2015).

Port-Orford cedar root disease

Phytophthora lateralis is an invasive soilborne pathogen responsible for Port-Orford cedar root disease (*Chamaecyparis lawsoniana*) in the USA, first noted in Washington State in the 1920s. The disease causes distinct colour changes in the foliage and mass collapse. The pathogen is found throughout the natural range of Port-Orford cedar in the USA, in Europe and from old growth *C. obtusa* in Taiwan (Hansen 2015). The pathogen spreads readily through contaminated water, organic material, infected earth-moving equipment, and nursery stock. The disease is managed within the USA by mapping the pathogen distribution and controlling its spread and replanting with resistant cultivars identified within infected forests and from a breeding program (Hansen *et al.* 2000).

Phytophthora dieback

Phytophthora cinnamomi is one of the world's most devastating plant pathogens; it has a vast host range and a global distribution (Burgess *et al.* 2017). *Phytophthora cinnamomi* is the only oomycete and one of the only three plant pathogens listed as one of the 100 worst invasive alien species (Lowe *et al.* 2000). The pathogen was first described as the causal agent of stripe rust of *Cinnamomum burmannii* in Sumatra in 1922, and while the origin is unknown, most evidence points to a natural distribution in the uplands in south-east Asia (Arentz & Simpson 1986). While *Phy. cinnamomi* is a destructive plant pathogen of tree crops such as avocado and woody ornamentals, perhaps the most significant destruction is seen in Mediterranean climates where it causes Phytophthora dieback in susceptible *Proteaceae* communities in the Cape Floristic region of South Africa (Nagel *et al.* 2013) and the Southwest Botanical Province of Western Australia (Shearer *et al.* 2007). The most effective chemical control within managed landscapes is systemic fungicides (Coffey 1987) while preventing the spread into new areas is the primary control strategy for natural ecosystems (Cahill *et al.* 2008). As *Phy. cinnamomi* is a poor saprophyte, some success in eradication has been achieved using fallow periods (Dunstan *et al.* 2020).

Alder dieback is a serious root and collar rot disease of *Alnus* species throughout large regions of Europe and parts of North America. The disease is caused by *Phytophthora alni* (homoploid triploid hybrid) and the parental organisms *Phy. multiformis* (allotetraploid hybrid) and *Phy. uniformis* (diploid species) (Husson *et al.* 2015). *Phytophthora alni* is found throughout Europe and is associated with root and collar rot of riparian, nursery, and shelterbelt *Alnus glutinosa* and other *Alnus* species, including *A. incana* and *A. cordata. Phytophthora uniformis* occurs sporadically throughout parts of Europe in association with *Phy. alni* and is found in North America in Alaska and Oregon, where it is associated with declining *Alnus rubra* (Sims *et al.* 2015). *Phytophthora multiformis* has been found in fewer countries in Europe (Husson *et al.* 2015). The pathogens have significant impacts on riparian and forest ecosystems and are dispersed through water movement and flooding cycles, poor hygiene and infected plant material (Elegbede *et al.* 2010). Alders resistant to the disease have been identified, and screening and breeding have been proposed to help manage the disease (Chandelier *et al.* 2016).

Kauri dieback, caused by *Phytophthora agathidicida*, is a serious soil-borne disease of the keystone ecological species kauri (*Agathis australis*) in the rare podocarp forests of northern New Zealand. The pathogen has a devastating impact causing mass collapse and large bleeding cankers of the collar and trunk (Scott & Williams 2014). The disease has significant ecosystem impacts due to the loss of kauri, including large ancient trees and the subsequent loss of a range of rare understory species dependent upon the unique soil and ecological characteristics created by established kauri. Kauri has significant ecological and cultural roles for New Zealand's indigenous people. Maori groups have led a range of responses to manage kauri dieback, involving traditional knowledge (mātauranga Māori) and contemporary approaches (Lambert *et al.* 2018). The disease is managed using forest hygiene and chemical control, including injections of the systemic chemical control agent phosphite (Bradshaw *et al.* 2020c).

Red needle cast of radiata pine is an important disease of exotic forestry within New Zealand caused by *Phytophthora pluvialis*. The disease can cause needle banding and casting of radiata pine (*Pinus radiata*) and Douglas fir (*Pseudotsuga menziesii*) during seasons with conducive high rainfall environmental conditions, although it causes minimal symptoms during dry years (Dick *et al.* 2014). The pathogen does not infect or colonise woody tissue; however, the cumulative impact of needle casting can significantly impact wood development and commercial forestry (Hood *et al.* 2014, Scott & Williams 2014). Within New Zealand, the pathogen is effectively managed with chemical control using aerial copper application and screening and breeding for resistance (Rolando *et al.* 2017). *Phytophthora pluvialis* is also known to cause casting and productivity impacts in Douglas fir and *Pinus* species in North America (Oregon), although it is unknown to have severe impacts on natural forestry ecosystems in that region (Reeser *et al.* 2013).

Canker and root rot of woody trees

There are several cosmopolitan *Phytophthora* species with a broad host range and almost global distribution; *Phy. cambivora*, *Phy. niederhauseri*, *Phy. syringae*, *Phy. nicotianae*, *Phy. cinnamomi*, *Phy. mutivora* and *Phy. plurivora*. These are pathogens of trees and woody perennial shrubs in agriculture, ornamentals and natural ecosystems. *Phytophthora multivora* (Scott *et al.* 2009) and *Phy. plurivora* (Jung & Burgess 2009) are within the *Phy. citricola* species complex only recognised using molecular taxonomy. *Phytophthora citricola* was first recognised as a disease of *Citrus* spp. and many records from other hosts are incorrect. *Phytophthora cambivora* is commonly associated with cankers of chestnuts in Europe (Vettraino *et al.* 2005). *Phytophthora niederhauserii* was only recently described but already has an extensive host and geographic range and is common in orchards (Abad *et al.* 2014).

Research interests

There are 6 909 publications and 69 739 citations from 2011–2021 in the Web of Science (Fig. 23), with the top 10 most cited articles given in Table 13. The majority of the most cited publications focus on taxonomy, genomics, infection processes and molecular plant-microbe interactions and how these could be manipulated to aid disease management, the global movement of *Phytophthora* species and biological invasions, especially into natural ecosystems (Fig. 24). The highly cited papers are from the start of the decade, but similar themes remain essential today. *Phytophthora* species continue to be important pathogens in managed landscapes and natural ecosystems and are, in some cases, becoming tolerant of the fungicides used to control them (Hollomon 2015). The increasing impact of *Phytophthora* pathogens in natural ecosystems has led to increased emphasis on landscape-level management of disease and DNA metabarcoding to establish the diversity and distribution of *Phytophthora* within the landscape (Burgess *et al.* 2019).

Genomics and molecular plant-microbe interactions

Due to their impact on numerous crops, *Phytophthora* is a commonly studied plant pathogen. There are six species, *Phy. infestans*, *Phy. ramorum*, *Phy. sojae*, *Phy. capsici*, *Phy. cinnamomi* and *Phy. nicotianae*, among the top 10 oomycete pathogens in molecular plant pathology (Kamoun *et al.* 2015). Effectors and proteins expressed by plant pathogens aid in the infection process. Pathogenic *Phytophthora* species are known to have an extensive effector repertoire and are the topic of numerous studies. The most highly cited paper among these looked at effectors from *Phy. sojae* and found that different effectors play an important role at different stages of the infection process (Wang *et al.* 2011). If the expression of effectors from early in the infection process is disrupted, transformants lose their virulence. Mycorrhizal fungi have a demonstrated protective effect against colonisation by soilborne pathogens such as *Phytophthora*. It is through that a modulation of plant defences occurs due to mycorrhizal priming of the plant defences (generalised induced resistance) (Jung *et al.* 2012).

Many oomycetes have large genomes, and the genes involved in host interactions are often polymorphic. These genome regions are highly adaptable and plastic, enabling them to adapt to new hosts and new environments (Raffaele & Kamoun 2012). One excellent example of this is *Phy. infestans* which has undergone major population shifts over time due to successive emergence and migration of lineages usually involving the displacement of existing less fit lineages (Cooke *et al.* 2012). The genome of one lineage that emerged and dominated in Great Britain over three years had extensive changes to the effector genes, enabling it to overcome resistance in some common potato varieties (Cooke *et al.* 2012).

Biological invasions and climate change

Numerous *Phytophthora* species associated with food crops have a cosmopolitan distribution, and many species true origin remains unknown. More recently, the most common pathway for introduction, especially for species that invade natural ecosystems,

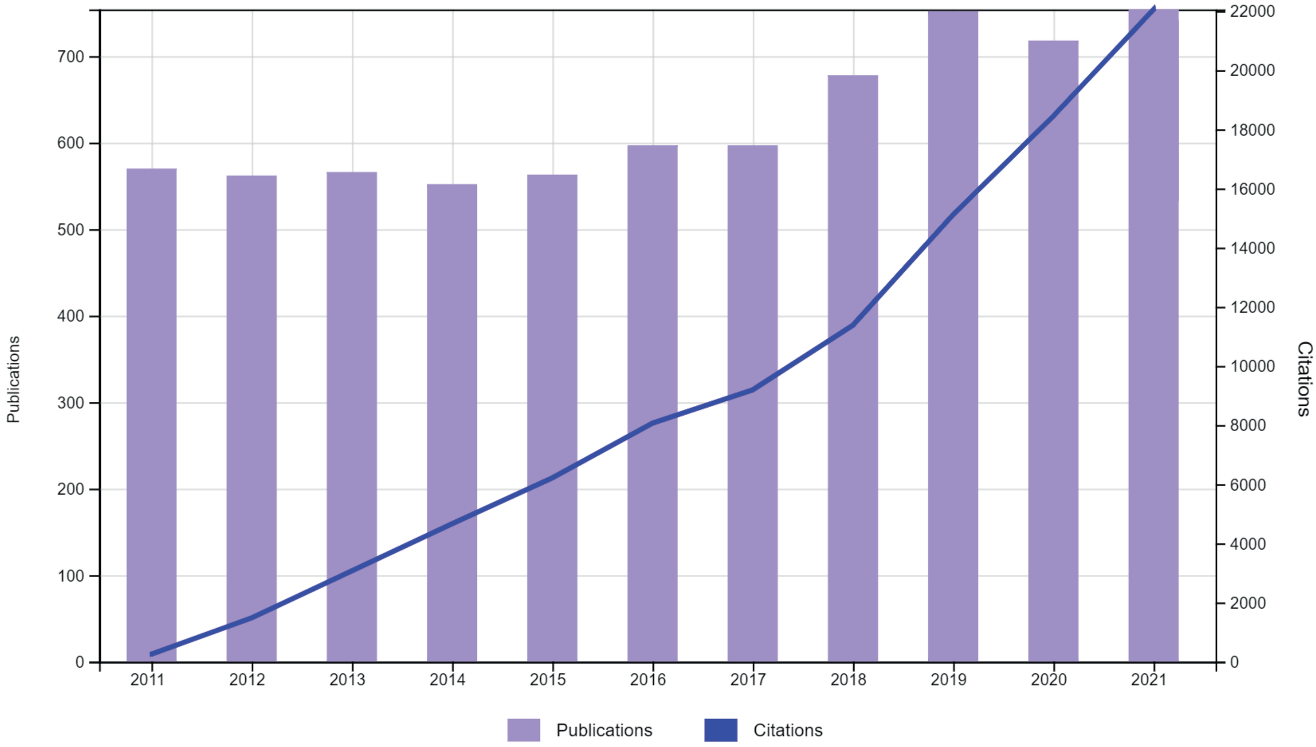

Fig. 23. Trends in research of *Phytophthora* in the period 2011–2021.

Table 13. Top 10 cited articles related to *Phytophthora* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Emerging fungal threats to animal, plant and ecosystem health	1 678	Fisher *et al.* (2012)
2	Mycorrhiza-induced resistance and priming of plant defenses	439	Jung *et al.* (2012)
3	The top 10 oomycete pathogens in molecular plant pathology	383	Kamoun *et al.* (2015)
4	DNA barcoding of oomycetes with cytochrome c oxidase subunit I and internal transcribed spacer	375	Robideau *et al.* (2011)
5	Genome evolution in filamentous plant pathogens: why bigger can be better	361	Raffaele & Kamoun (2012)
6	Climate change and forest diseases	359	Sturrock *et al.* (2011)
7	Live plant imports: the major pathway for forest insect and pathogen invasions of the US	347	Liebhold *et al.* (2012)
8	Biogeographical patterns and determinants of invasion by forest pathogens in Europe	323	Santini *et al.* (2013)
9	Transcriptional programming and functional interactions within the *Phytophthora sojae* RXLR effector repertoire	265	Wang *et al.* (2011b)
10	Genome analyses of an aggressive and invasive lineage of the Irish potato famine pathogen	237	Cooke *et al.* (2012)

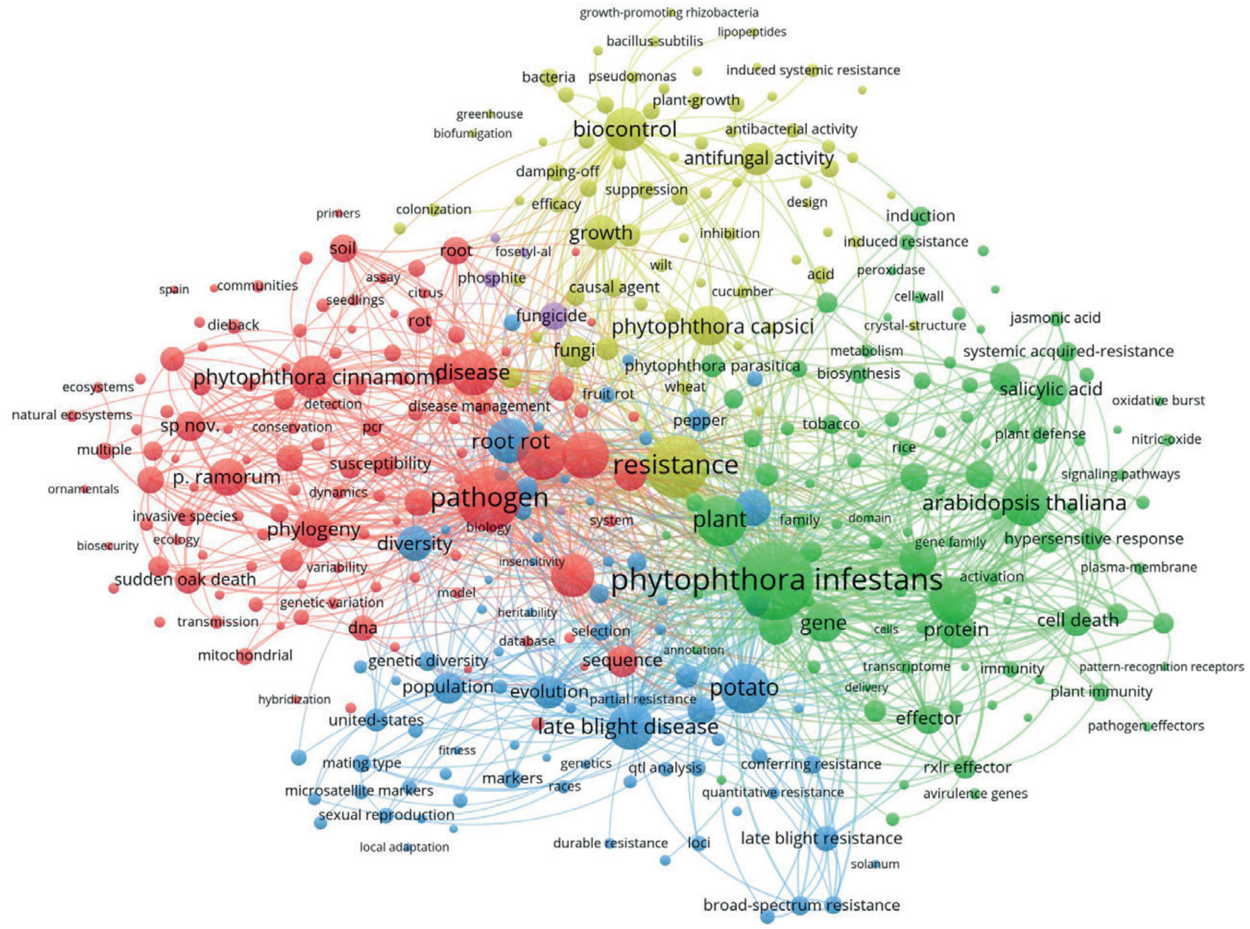

Fig. 24. Network visualisation of keywords of the publications related to *Phytophthora*. The larger the text and the circle the more often the subject has been cited.

has been through the nursery trade and live plant imports (Liebhold *et al.* 2012, Santini *et al.* 2013). While being significant agricultural pathogens, perhaps the greatest impact of introduced *Phytophthora* species has been in the natural environment (Sturrock *et al.* 2011, Fisher *et al.* 2012, Hansen *et al.* 2012). Sudden oak death caused by *Phy. ramorum* in the west coast USA (Rizzo & Garbelotto 2003), and Phytophthora dieback caused by *Phy. cinnamomi* in Australia (Cahill *et al.* 2008) have permanently changed the structure and function of impacted ecosystems. Sturrock *et al.* (2011) predicted that the impact of *Phytophthora* diseases would remain the same, or decrease, in warmer drier climates and increase in warmer wetter climates. These predictions have been supported by a species distribution model developed for *Phy. cinnamomi* using a global dataset of presence and absence records (Burgess *et al.* 2017).

Taxonomy and phylogeny

Until Cooke *et al.* (2000) published the first molecular phylogeny of *Phytophthora*, species descriptions had been based solely on morphological features, resulting in some species complexes that are now known to have been comprised of morphologically similar but phylogenetically unrelated species. There have been several phylogenetic studies including increasingly more *Phytophthora* species; Cooke *et al.* (2000) included 48 species from eight clades, this has increased to 82 species (Blair *et al.* 2008), then 109 species (Martin *et al.* 2014) and most recently 185 species representing 10 clades (Yang *et al.* 2017b). The ITS and *CO1* phylogenies of Robideau *et al.* (2011) are particularly cited as this publication included 1 205 isolates from 23 genera of oomycetes (not just *Phytophthora*), and it has thus been very useful for metabarcoding studies using environmental DNA. The most updated phylogeny based on type isolates and a complete revision of the genus has recently been published (Abad *et al.* 2023a).

Authors: T.I. Burgess and P. Scott

12. ***Rhizopus*** Ehrenb., Nova Acta Phys.-Med. Acad. Caes. Leop. -Carol. 10: 198. 1821.

Type species: *Rhizopus stolonifer* (Ehrenb.) Vuill.

Classification: *Mucoromycota*, *Mucoromycotina*, *Mucoromycetes*, *Mucorales*, *Rhizopodaceae.*

Background

Rhizopus constitutes an important genus within *Mucorales* with 11 accepted species (Walther *et al.* 2019, Jayawardena *et al.* 2020) and around 150 epithets listed in Index Fungorum (2022). They are common post-harvest pathogens, human pathogens, and saprobes. They pose a threat to agricultural products by damaging the taste and appearance of crops such as strawberries and sweet potatoes. They are also opportunistic pathogens causing mucormycosis in immunosuppressed humans and the cause of some animal diseases. Furthermore, endosymbiotic bacteria residing in the hyphae of some *Rhizopus* species produce the phytotoxin rhizoxin which can lead to human poisoning (Partida-Martinez *et al.* 2007, Gryganskyi *et al.* 2018). *Rhizopus* species have industrial and medical importance and occur worldwide. They are bio-industrial fermenters for food and are used in metabolite production. They are used to produce fermented products such as tempeh.

The conventional taxonomy of *Rhizopus* was primarily based on morphology and physiological characteristics. Similar to most *Mucorales*, the taxonomy of *Rhizopus* is based on asexual morphological characters and growth parameters. These characteristics included maximum growth temperature, sugar fermentation, and formation of acids. Organic acid patterns were used as a critical criterion for *Rhizopus* because it was shown that the ITS sequences had a clear relationship with acid production and that ITS was simple and effective for classification (Abe *et al.* 2003). Inui *et al.* (1965) concluded that 10 characters were important in the taxonomy of *Rhizopus* which includes the characteristics mentioned above. Other characteristics include the formation of sporangia, chlamydospores, rhizoids, and the shape and colour of the sporangia (Zheng *et al.* 2007). Karyological studies of isolated species from Korean soil showed that chromosome numbers can vary from a minimum of eight (*Rhiz. arrhizus*) to a maximum of 16 (*Rhiz. stolonifer*).

Even with the use of DNA sequence data, the classification of this genus remains contentious. Abe *et al.* (2006) provided the first molecular phylogenetic study of *Rhizopus* and separated the genus into three groupings which is congruent with the study of Schipper (1984); *Rhiz. microsporus*, *Rhiz. stolonifer*, and *Rhiz. arrhizus*. Later studies, based on ribosomal DNA (rDNA) and orotidine-5'-monophosphate decarboxylase gene (*pyrG*) sequences and morphology, either organised the genus into 10 species and seven varieties or into eight species (Liu *et al.* 2007, Zheng *et al.* 2007). In the phylogenetic reconstruction of the genus, several inconsistencies in topology have been noticed depending on which genes are used and the phylogenetic methods utilised. These have been demonstrated in Gryganskyi *et al.* (2018). Phylogenomic analysis based on 192 orthologous protein-coding genes from whole-genome sequencing supports the findings of Liu *et al.* (2007). It suggests that there may be a reduction in the number of accepted species in the future as these species may be phylogenetically nested within *Rhiz. delemar*, *Rhiz. stolonifer*, *Rhiz. arrhizus*, or *Rhiz. microsporus*.

Ecological and economic significance

Postharvest pathogens

Rhizopus species are known pathogens of several crops such as strawberries, tomatoes, and sweet potatoes. They cause diseases such as Rhizopus soft rot, head rot, and Rhizopus blight. The common causative species are *Rhiz. stolonifer*, *Rhiz. arrhizus*, and *Rhiz. microsporus*. Typically, a wound is necessary for infection to occur. Aerial spores land on these wounds or cracks and then produce enzymes that degrade the host cells (Jayawardena *et al.* 2020). Tomato which is highly consumed and is the second most important horticultural crop in the world (Alfaro-Sifuentes *et al.* 2019) is highly perishable and susceptible to mechanical damage during postharvest handling. It is estimated that 30 % of these fruits are lost due to postharvest disease of which 80 % are caused by *Rhiz. stolonifer* (Alfaro-Sifuentes *et al.* 2019). Soft rot by *Rhizopus* is also a devastating postharvest disease in sweet potatoes resulting in a 2 % loss in the stored roots (Scruggs *et al.* 2016).

***Rhizopus* soft rot** also affects peaches (Bautista-Baños *et al.* 2014). In Egypt and Brazil, postharvest diseases result in quality loss and rejection during sales (Bautista-Baños *et al.* 2014, Baggio *et al.* 2017). Notably, in Egypt, the frequency of isolating *Rhiz. stolonifer* from diseased peaches in markets was 56.5 % (Bautista-Baños *et al.* 2014). The presence of decayed fruits during postharvest handlings such as during transportation and storage can affect the quality and sale price of the fruit even if visible rotten fruits have been discarded and no apparent symptoms are seen. An increase of 1 % in the incidence of rots can reduce retail and wholesale prices by 1.24 % and 0.91 % respectively (Baggio *et al.* 2017).

Research interests

There are 3 353 publications and 51 691 citations from 2011–2021 in the Web of Science (Fig. 25), with the top 10 most cited articles listed in Table 14. Most publications are related to the application of *Rhizopus* to produce secondary metabolites, human pathogenicity (Mucormycosis), and taxonomy (Fig. 26).

Production of lactic acid through fermentation

Lactic acid, known as 2-hydroxypropanoic acid, is an organic acid that can be used as a preservative, acidulant, or as inhibitor

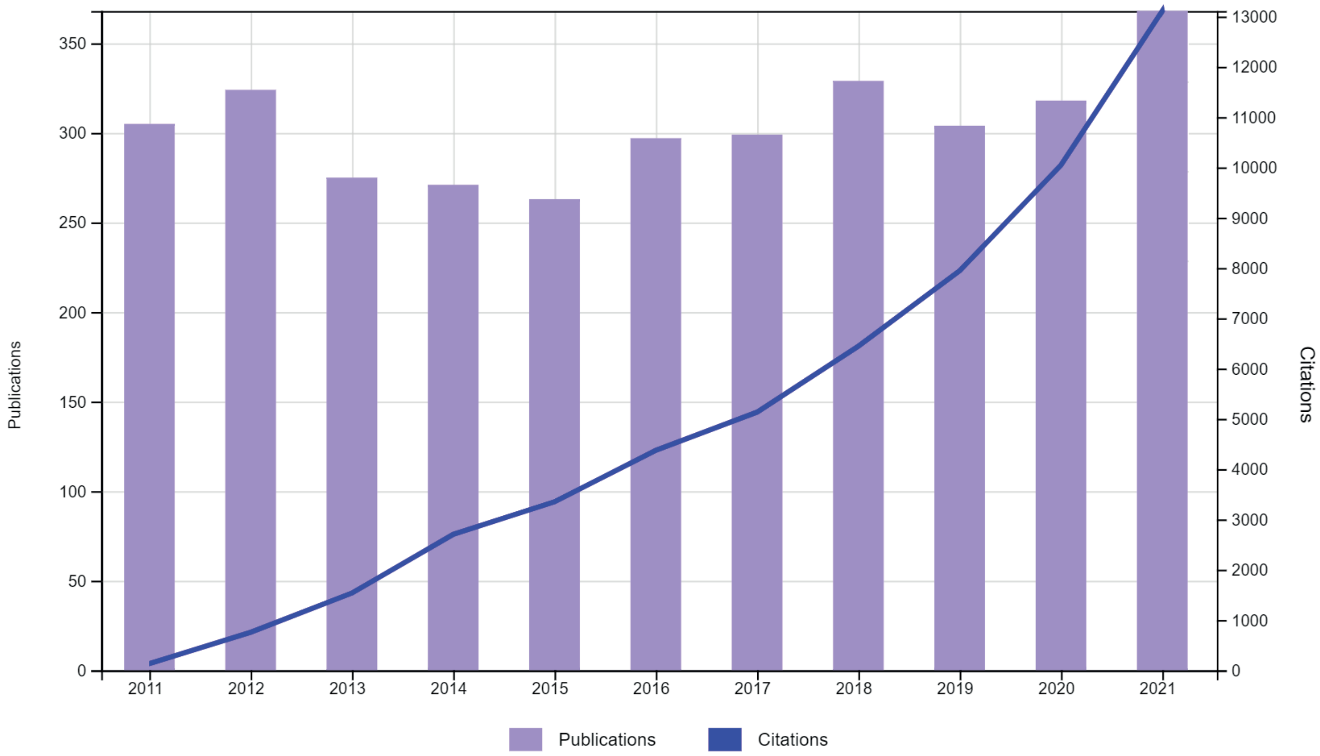

Fig. 25. Trends in research of *Rhizopus* in the period 2011–2021.

Table 14. Top 10 cited articles related to *Rhizopus* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Zygomycosis in Europe: analysis of 230 cases accrued by the registry of the European Confederation of Medical Mycology (ECMM) Working Group on zygomycosis between 2005 and 2007	380	Skiada *et al.* (2011)
2	Biological activities of α-pinene and β-pinene enantiomers	321	Da Silva Rivas *et al.* (2012)
3	Pathogenesis of mucormycosis	283	Ibrahim *et al.* (2012)
4	A global analysis of mucormycosis in France: The RetroZygo Study (2005–2007)	271	Lanternier *et al.* (2012)
5	Synthesis, characterization and catalytic activity of gold nanoparticles biosynthesized with *Rhizopus oryzae* protein extract	240	Das *et al.* (2012)
6	One stop shop: backbones trees for important phytopathogenic genera: I (2014)	235	Hyde *et al.* (2014)
7	Antibacterial effects of biosynthesized silver nanoparticles on surface ultrastructure and nanomechanical properties of gram-negative bacteria *viz. Escherichia coli* and *Pseudomonas aeruginosa*	223	Ramalingam *et al.* (2016)
8	Global epidemiology of mucormycosis	217	Prakash & Chakrabarti (2019)
9	The epidemiology and clinical manifestations of mucormycosis: a systematic review and meta-analysis of case reports	213	Jeong *et al.* (2019)
10	Daqu - A Traditional Chinese Liquor Fermentation Starter	173	Zheng *et al.* (2011b)

of bacterial spoilage in foods (Ajala *et al.* 2020, 2021). This acid can be produced using fermentation processes or chemical methods. Fermentative methods enable the use of renewable carbohydrates, which are cleaner and more ecological. However, the choice of substrate is key as it determines the efficiency and cost of production. *Rhizopus* species can be used for both surface and submerged fermentation to produce lactic acid. This species is also widely used as the cells have better resistance to a high concentration of lactic acid than commonly used bacterial producers (Ajala *et al.* 2021). However, homofermentative lactic acid bacteria are significantly more efficient than fungi in converting sugars to lactic acid because of the production of other by-products such as ethanol and fumaric acid by the *Rhiz. oryzae*-based process (Abedi & Hashemi 2020).

Mucormycosis

Mucormycosis (also known as zygomycosis) is a rare and lethal form of fungal infection (Rodríguez-Lobato *et al.* 2017). The disease is primarily caused by *Rhizopus* species, with 70 % of mucormycosis associated with this genus (Andrianaki *et al.* 2018). Over the past few decades, mucormycosis has become the third most common fungal infection in patients having haematological malignancies

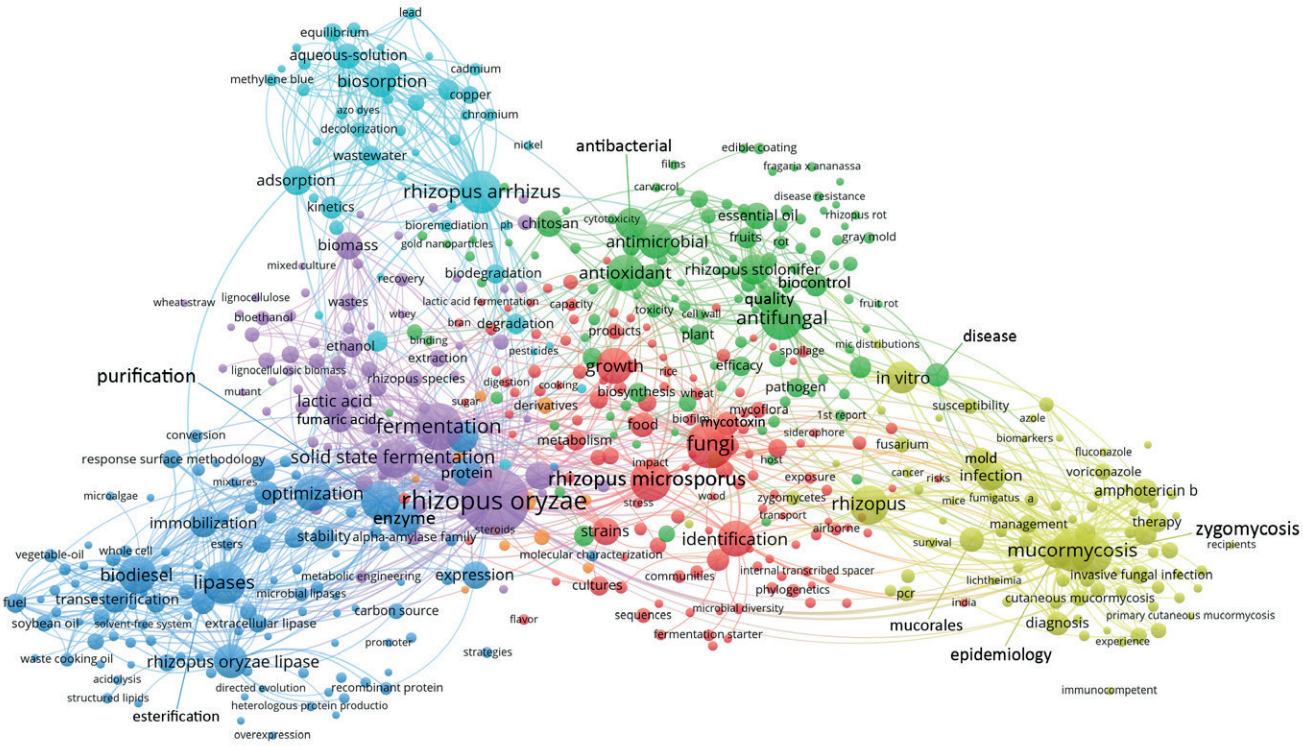

Fig. 26. Network visualisation of keywords of the publications related to *Rhizopus*. The larger the text and the circle the more often the subject has been cited.

or those having organ transplantation. The predominant species involved in this life-threatening disease are *Rhiz. delemar* and *Rhiz. arrhizus* (syn. *Rhiz. oryzae*). Other species are found in the genera *Mucor*, *Lichtheimia*, *Rhizomucor*, *Apophysomyces*, and *Cunninghamella* (Baldin & Ibrahim 2017). The main risk factors that make an individual prone to mucormycosis are neutropenia due to cancer treatment and diabetes mellitus especially those presenting with ketoacidosis, hematopoietic and organ transplantation (Baldin & Ibrahim 2017). The mortality rate of cutaneous mucormycosis is 31 % if a deep extension is present but primary cutaneous mucormycosis mortality is lower, especially in immunocompromised patients (Rodríguez-Lobato *et al.* 2017).

Disease management

Due to the devastating effect of *Rhizopus* species on postharvest crops, studies in controlling and managing the disease are crucial. Fungistatic mechanisms against Rhizopus rot such as antibiotics, antifungal activity, direct parasitism in pathogens, and induction of resistance of the host and competition by microbial antagonists have been suggested. Among these, the induction of disease resistance by other microbial agents of the host has been regarded as pivotal (Zhang *et al.* 2020). After treatment, resistance can be obtained through the production of antifungal substances, providing systemic and long-lasting resistance against the pathogenic organism. Chemical treatment methods are also used where the fruits are immersed in ethanol solutions and are effective in controlling decay by fungi. Other studies have tested several methods such as UV or β-aminobutyric acid (Özer Uyar & Uyar 2018).

Author: V.G. Hurdeal

13. ***Phanerochaete*** P. Karst., Bidr. Känn. Finl. Nat. Folk 48: 426. 1889.

Type species: *Phanerochaete alnea* (Fr.) P. Karst.

Classification: *Basidiomycota*, *Agaricomycotina*, *Agaricomycetes*, *Polyporales*, *Phanerochaetaceae.*

Background

Phanerochaete was introduced by Karsten (1889) with *Pha. alnea* as the type. This genus is a saprobic homobasidiomycete on woody debris and logs (De Koker *et al.* 2003). Most species of *Phanerochaete* are associated with white-rot of wood and are widely distributed on fallen branches and logs, branches attached to trees, twigs, and even wood buried in the soil (Eriksson *et al*. 1978, Burdsall 1985). It is a large genus of the family *Phanerochaetaceae*, with 204 records in Index Fungorum (2022). Infraspecific names in *Phanerochaete* and additional new species are anticipated (De Koker *et al*. 2000).

Phanerochaete is a member of the corticioid fungi, and it is characterised by resupinate, membranaceous basidiomata with or without rhizomorphs, a monomitic hyphal system with primarily simple-septate generative hyphae, clavate basidia with four sterigmata, and smooth, thin-walled, inamyloid basidiospores (Eriksson *et al.* 1978, Burdsall 1985, Bernicchia & Gorjón 2010). The simplicity of the morphological characters of *Phanerochaete* and the existence of species with sporocarps that fulfil only some of these morphological criteria renders the limits of the genus uncertain (Floudas & Hibbett 2015). Other authors have also discussed and approached the taxonomy of *Phanerochaete* in different ways (Parmasto 1968, Eriksson *et al*. 1978, Jülich & Stalpers 1980, Xu *et al*. 2020, Chen *et al*. 2021a, Wang *et al*. 2021).

Molecular studies involving *Phanerochaete* based on ribosomal DNA (rDNA) sequences, revealed the phylogenetic distribution of resupinate forms across the major clades of mushroom-forming fungi, in which *Pha. chrysosporium* nested into the phlebioid clade

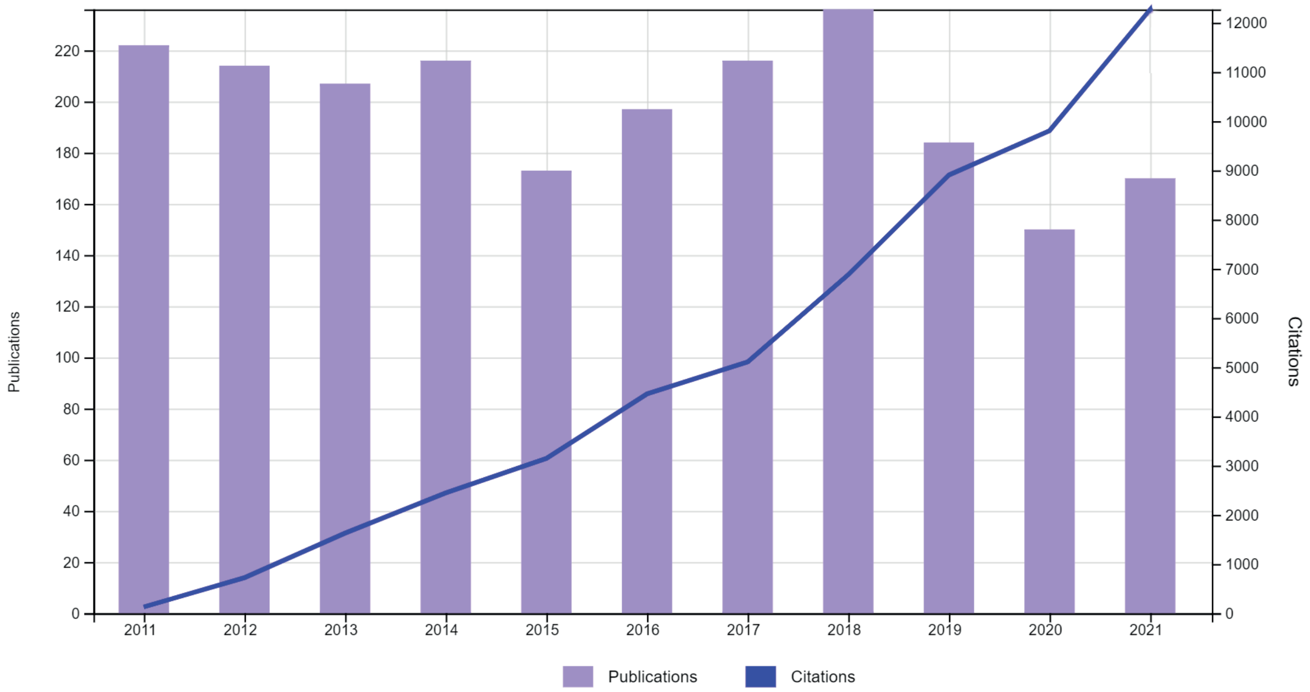

Fig. 27. Trends in research of *Phanerochaete* in the period 2011–2021.

Table 15. Top 10 cited articles related to *Phanerochaete* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Expansion of the enzymatic repertoire of the CAZy database to integrate auxiliary redox enzymes	681	Levasseur *et al.* (2013)
2	High-performance green flexible electronics based on biodegradable cellulose nanofibril paper	499	Jung *et al.* (2015b)
3	Untapped potential: exploiting fungi in bioremediation of hazardous chemicals	491	Harms *et al.* (2011)
4	Microbial decolouration of azo dyes: A review	480	Solis *et al.* (2012)
5	Extensive sampling of basidiomycete genomes demonstrates inadequacy of the white-rot/brown-rot paradigm for wood decay fungi	422	Riley *et al.* (2013)
6	Bioactive phenolic compounds: Production and extraction by solid-state fermentation. A review	367	Martins *et al.* (2011)
7	Lignocellulosic agriculture wastes as biomass feedstocks for second-generation bioethanol production: concepts and recent developments	316	Saini *et al.* (2015)
8	Fungal pretreatment of lignocellulosic biomass	257	Wan & Li (2012)
9	Lignin-degrading enzymes	230	Pollegioni *et al.* (2015)
10	Microbial decolorization and degradation of synthetic dyes: a review	206	Khan *et al.* (2013b)

in *Polyporales* (Binder *et al*. 2005). A DNA-phylogeny-based and morphology-based study to reconcile the polypores and genus concepts in the family *Phanerochaetaceae* (Miettinen *et al.* 2016), found the macromorphology of sporocarps and hymenophore construction did not reflect monophyletic groups, and *Ceriporia inflata* was combined into *Phanerochaete*. Amplifying nrLSU, nrITS, and *rpb*1 genes across the *Polyporales* revealed that eleven genera clustered into the family *Phanerochaetaceae*, and two families *Hapalopilaceae* and *Bjerkanderaceae* were placed as synonyms of *Phanerochaetaceae* (Justo *et al.* 2017). Recently, morphological studies and phylogenetic analyses found many new taxa of *Phanerochaete s. str.* and determined the taxonomic status of the new taxa within *Phanerochaete* (Wu *et al*. 2018c, Xu *et al*. 2020).

Ecological and economic significance

Phanerochaete is a genus that causes white rot on both softwood and hardwood and has attracted the attention of researchers for a long time (Floudas & Hibbett 2015). *Phanerochaete* are white-rot fungi that produce extracellular enzymes capable of completely degrading lignocellulose, the main component of wood and other plant cell walls (MacDonald *et al*. 2012) and the genus plays an important role in carbon cycling (Burdsall 1985). *Phanerochaete* species also have potential applications in the production of renewable chemicals and liquid fuel from wood, which is among the largest biomass resources that could be used to produce such chemicals (Lin & Tanaka 2006). The oxidative enzymes involved in wood degradation by *Phanerochaete* have also been shown to degrade a variety of persistent environmental pollutants, including chlorinated aromatic compounds, munitions, pesticides, and dyes (Cameron *et al*. 2000).

Ecology and distribution

Phanerochaete has been studied outside Europe (Burdsall 1985) in North America and Asia (Wu 1990). *Phanerochaete* is widely distributed from boreal to tropical forests (Burdsall 1985).

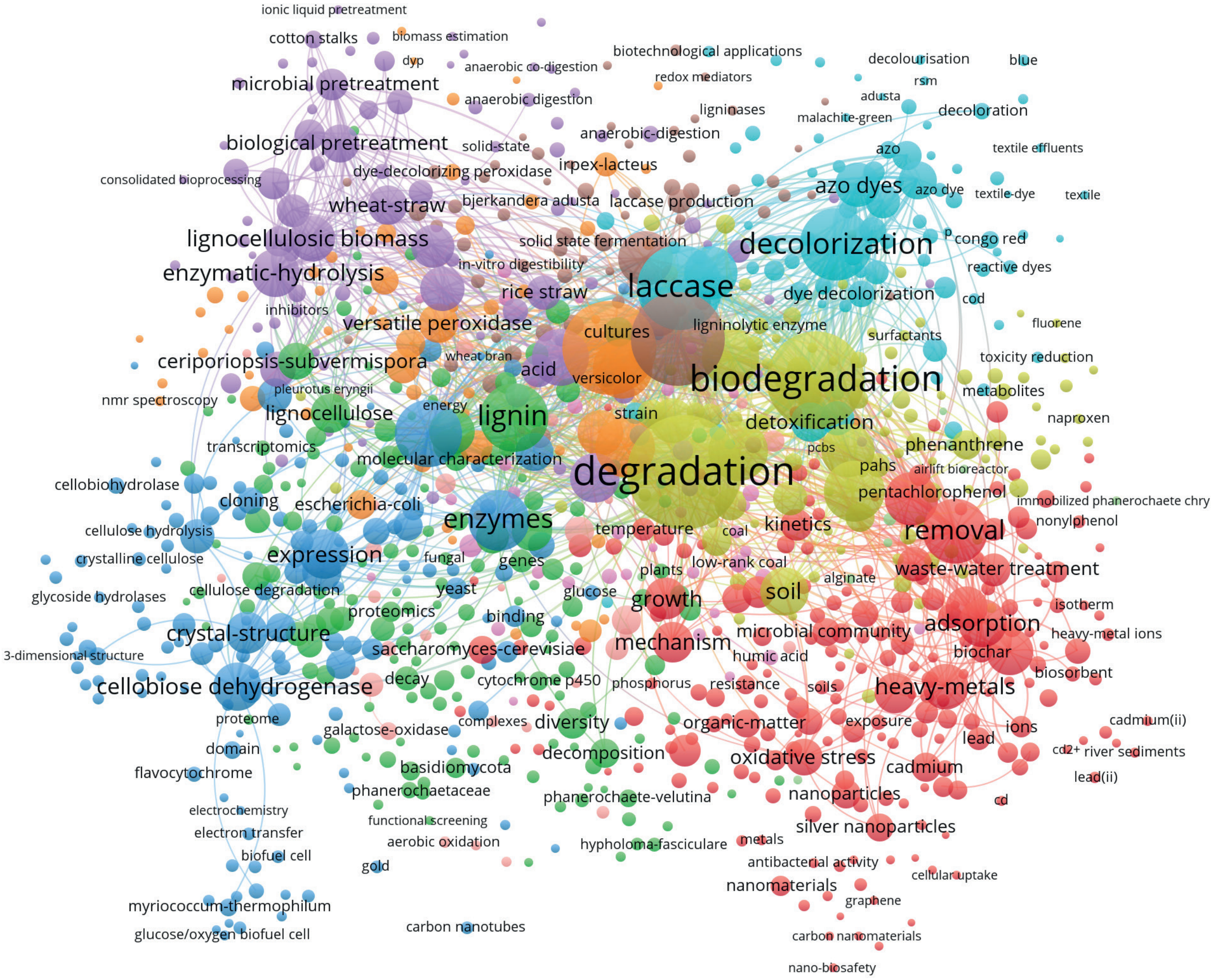

Fig. 28. Network visualisation of keywords of the publications related to *Phanerochaete*. The larger the text and the circle the more often the subject has been cited.

Phanerochaete species have been reported from America, Asia and Europe, New Zealand, and most of them are spreading in a limited region of Asia from the tropical southeast (Wu 1995, Dai 2011, Liu & He 2016, Xu *et al*. 2020, Chen *et al*. 2021a, Wang *et al*. 2021).

Important species and applications of *Phanerochaete*

Phanerochaete chrysosporium is the most intensively studied white-rot basidiomycete and is a model wood-decay organism due to its frequent discovery in wood chip storage piles in Europe and North America (MacDonald *et al*. 2012). *Phanerochaete chrysosporium* grows rapidly, has an optimum growth temperature of around 40 °C and produces numerous conidia (Burdsall & Eslyn 1974). Adding tourmaline to *Phanerochaete chrysosporium* can accelerate the effect to enhance the bioremediation process of contaminated soil with polycyclic aromatic hydrocarbons (PAHs) and organochlorine pesticides (OCPs) (Wang *et al.* 2014a). *Phanerochaete chrysosporium* may have potential use in industrial applications such as biopulping (Akhtar *et al.* 1998). Class II peroxidases and glyoxal oxidase, which are among the most important enzymes during lignin degradation, have been discovered in cultures of *Pha. chrysosporium* (Tien & Kirk 1983, Tien & Kirk 1984, Kersten & Kirk 1987). The use of white-rot fungi such as *Pha. chrysosporium* in decolourising textile wastewater has been widely reported (Lankinen *et al*. 1991, Cammarota & Sant Anna 1992, Bilgic *et al*. 1997, Young & Yu 1997, Tatarko & Bumpus 1998, Gomaa *et al*. 2008, Faraco *et al*. 2009, Sharma *et al*. 2009, Janusz *et al*. 2017).

Research interests

There are 2 185 publications and 50 545 citations from 2011–2021 in the Web of Science (Fig. 27), with the top 10 most cited articles listed in Table 15. Most of the publications focused on the use of lignin enzymes, and application in environmental pollution prevention and control, as well as taxonomy and diversity (Fig. 28).

Lignin enzymes

Lignin accounts for a large percentage of the energy that plants capture from the sun. It has been estimated that 25 % of the carbon fixed by photosynthesis is eventually transformed into lignin. This abundant polymer is a valuable potential resource and is the second most abundant renewable carbon source on earth. Lignin plays an important role in carbon recycling (Tien 1987). Lignin peroxidases were first discovered in *Pha. chrysosporium* (Tien & Kirk 1983, Paszczynski *et al.* 1986, Kirk & Farrell 1987, Janusz *et al.* 2017) The most obvious applications for ligninase are in the pulp and paper industry. The biological (or enzymatic) treatment of pulp can offer numerous advantages. Ligninase is potentially more selective in the removal of lignin than chemical processes. Studies with model compounds, and to a limited extent with pulps, indicate that the ligninase is highly selective for aromatic substrates. Carbohydrates have not been degraded by the ligninase (Tien 1987).

Environmental pollution prevention and control

The versatile lignin-degrading white-rot fungus, *Pha. chrysosporium*, is a strong degrader in nature and mineralises partially or completely a wide variety of recalcitrant organic pollutants such as chlorophenols, nitrotoluenes and polycyclic aromatic hydrocarbons (Barr & Aust 1994). Xenobiotics which are degraded by *Pha. chrysosporium* also include various azo, heterocyclic and polymeric dyes (Paszczynski *et al*. 1992, Spadaro *et al*. 1992, Ollikka *et al*. 1993). The quantities of contaminated sites with multi-elements have sharply increased (Cao *et al*. 2013b), due to anthropogenic activities such as rapid industrialisation and urbanisation (Sun *et al*. 2011b, Lee *et al*. 2012, Xu *et al*. 2013a). Heavy metals/metalloids and organic pollutants are carcinogenic and mutagenic (Xu *et al*. 2012c, Zeng *et al*. 2013a) and they may arouse amplification effects through the food chain in organisms, threatening human health and natural ecosystems (Zeng *et al*. 2013b, Dai *et al.* 2021).

Taxonomy and phylogeny

Recent molecular studies demonstrate that *Phanerochaete s. lat.* is polyphyletic and distributed across several lineages in the phlebioid clade of the *Polyporales* and also the *Hymenochaetales* (De Koker *et al*. 2003, Greslebin *et al*. 2004, Wu *et al*. 2010, Floudas & Hibbett 2015, Miettinen *et al*. 2016, Justo *et al*. 2017, Chen *et al*. 2018a). Revisiting the taxonomy of *Phanerochaete* based on a four gene dataset and extensive ITS sampling indicated that *Phanerochaete s. lat.* was polyphyletic and distributed across nine lineages in the phlebioid clade, in which six lineages could be assigned to described genera (Floudas & Hibbett 2015). Recent phylogenetic studies have also revealed morphologically cryptic taxa in *Phanerochaete s. str.* (*e.g*., Volobuev *et al.* 2015, Spirin *et al*. 2017, Phookamsak *et al.* 2019, Xu *et al*. 2020, Chen *et al*. 2021a, Wang *et al*. 2021).

Authors: C.L. Zhao, K.Y. Luo, D.Q. Wang and J.J. Li

14. ***Colletotrichum*** Corda, in Sturm, Deutschl. Fl., 3 Abt. (Pilze Deutschl.) 3(12): 41. 1831.

Type species: *Colletotrichum lineola* Corda

Classification: *Ascomycota*, *Pezizomycotina*, *Sordariomycetes*, *Glomerellales*, *Glomerellaceae.*

Background

Colletotrichum is one of the most common and most important genera of plant pathogenic fungi with currently 1 040 epithets listed in Index Fungorum (2024) and more than 300 accepted species; with both numbers constantly increasing (Jayawardena *et al.* 2021, Liu *et al*. 2022, Talhinhas & Baroncelli 2023).

Colletotrichum species cause diseases on fruits, leaves, stems and other aerial plant parts, commonly referred to as anthracnose (Udayanga *et al.* 2013). Other diseases caused by *Colletotrichum* species are for example leaf spot diseases, ripe rots and seedling blights (Yang *et al.* 2011, Cannon *et al.* 2012, Lima *et al.* 2013, Yan *et al.* 2015, Jayawardena *et al.* 2016). The symptoms caused are often dark sunken lesions or lesions with a dark margin (Than *et al.* 2008b). Germination and infection of *Colletotrichum* conidia require high relative humidity (≥ 95–98 %); pre-harvest disease is most serious in a warm environment (20–30 °C) (Khan & Hsiang 2003, Boddy 2016, Ansari *et al.* 2018, Hyde *et al.* 2020a). Species of *Colletotrichum* can be seed-borne and may survive in soil as saprobes on dead plants or as endophytes in non-host species (Freeman *et al.* 2002, Cannon *et al.* 2012, Ranathunge *et al.* 2016). A list of *Colletotrichum* species and host families and up-to-date trees are provided by Talhinhas & Baroncelli (2023).

The asexual morph of *Colletotrichum* species produces aseptate, hyaline, straight or curved conidia endogenously from hyaline conidiogenous cells, often intermingled with straight dark setae, in an acervulus that is formed under the epidermis or cuticle of the host plant that breaks due to increased tension and subsequently the acervulus is exposed to the environment (Sutton 1992, Khan & Hsiang 2003, Wharton & Diéguez-Uribeondo 2004, Than *et al.* 2008b, Huang *et al.* 2013a). Aseptate, hyaline ascospores formed in cylindrical to clavate asci in perithecia represent the sexual morph that was previously referred to as *Glomerella* and has only been observed in some of the species (Cannon *et al.* 2012, Damm *et al.* 2019). Conidia and ascospores may spread upon contact with water (dew, rain splash, irrigation) and via wind to new locations, new hosts or new plants or plant parts of the same host species (Ntahimpera *et al.* 1997). The plants are infected via appressoria that develop on the plant surface from the germinating spores and build up turgor pressure that enables infective hyphae to penetrate the cuticle or epidermis of the host (Chethana *et al.* 2021a). Further development depends on the production of host-induced virulence factors by the fungus (Kleemann *et al.* 2012, O'Connell *et al.* 2012).

Species of *Colletotrichum* are known to have different lifestyles and infection mechanisms, ranging from intracellular hemibiotrophy to subcuticular intramural necrotrophy (Perfect *et al.* 1999). Best studied is the hemibiotrophic lifestyle that is known from most of the species in the *Col. destructivum*, *Col. graminicola* and *Col. orbiculare* species complexes (Münch *et al.* 2008, O'Connell *et al.* 2012, Damm *et al.* 2013, 2014). These species have an initial biotrophic stage, in which host response is suppressed and the plants remain symptomless, and eventually switch to a necrotrophic stage, in which a significant number of plant cells are killed resulting in the development of symptoms (O'Connell *et al.* 2012).

Colletotrichum was introduced by Corda (1831), who observed rows of acervuli with curved conidia on dead stems of *Apiaceae* plants near Prague (today Czech Republic). Subsequently, hundreds of species were described from various host plants assuming *Colletotrichum* species to be strictly host-specific, until Von Arx (1957) reduced the number of species to 11 based on morphology. Von Arx (1957) regarded about 600 species that form straight cylindrical conidia as synonyms of *Col. gloeosporioides*. Since its description by Simmonds (1965), forms with straight conidia and acute ends were regarded as *Col. acutatum* and those with round ends as *Col. gloeosporioides*; both species being the most frequently reported and regarded as anthracnose pathogens of numerous host plants.

However, with the introduction of phylogenetic species recognition, species were circumscribed based on multi-locus sequence data in combination with informative morphological characters as well as data on physiology, pathogenicity, cultural characteristics and secondary metabolites as far as available, referred to as a polyphasic approach (Cai *et al.* 2009). As a result, host-specificity of individual species of the genus was revealed to be species-dependent and morphology to be unreliable (Damm *et al.* 2012a, Weir *et al.* 2012). Upon their epitypification, *Col. acutatum* and *Col. gloeosporioides* in a broad sense were identified as species complexes with more than 20 closely related species each and in a narrow sense revealed to be pathogens of a restricted host spectrum (Cannon *et al.* 2008, Phoulivong *et al.* 2010, Damm *et al.* 2012, Weir *et al.* 2012). Today, *Colletotrichum* species with more or less curved conidia are classified in the dematium, destructivum, graminicola/caudatum, spaethianum and truncatum species complexes (Crouch *et al.* 2009, Crouch 2014, Damm *et al.* 2009, 2014), and species with more or less straight conidia in the acutatum, agaves, boninense, dracaenophilum, gigasporum, gloeosporioides, magnum, orbiculare and orchidearum species complexes (Damm *et al.* 2012a, b, 2013, 2019, Weir *et al.* 2012, Liu *et al.* 2014, Bhunjun *et al.* 2021b). Further species complexes have recently been proposed (Liu *et al.* 2022, Talhinhas & Baroncelli 2023). Species that had previously been regarded as synonyms of *Col. gloeosporioides* or strains that were previously identified as this species were allocated to many of these complexes (*e.g.*, Damm *et al.* 2012a, 2014, 2019, Liu *et al.* 2014, 2016). Additionally, there are more than ten species that do not belong to any species complex and are referred to as singletons (Hyde *et al.* 2014, Jayawardena *et al.* 2021).

Ecological and economic significance

Colletotrichum is an important genus in both ecological and economic aspects. *Colletotrichum* species are widespread, especially in the tropics and subtropics, cause diseases of many different plant families and can infect every crop on earth, especially fruits, vegetables and ornamentals (Dean *et al.* 2012, Bhunjun *et al.* 2019, Jayawardena *et al.* 2020, Armand *et al.* 2023, Peng *et al.* 2023, Talhinhas & Baroncelli 2023, Zhang *et al.* 2023b, c); some of the most important diseases are discussed below.

Anthracnose of fruits and fruit rots

Colletotrichum species are of high economic importance for the fruit industry by causing diseases on fruits (*e.g.*, apple, citrus, grape and strawberry) like anthracnose and fruit rot that can cause yield losses of up to 100 % (Huang *et al.* 2013a, Leonberger *et al.* 2019, Dowling *et al.* 2020). Postharvest diseases of fruits are usually caused by several *Colletotrichum* species mainly belonging to the acutatum and gloeosporioides species complexes; most of these species are not host specific (Damm *et al.* 2012a, Weir *et al.* 2012, Jayawardena *et al.* 2021). For example, bitter rot of apples in the Southeastern USA is caused by 12 different *Colletotrichum* species; at least 22 species mostly belonging to the above-mentioned complexes are known from apples worldwide (Damm *et al.* 2012a, b, Weir *et al.* 2012, Bragança *et al.* 2016, Munir *et al.* 2016, Grammen *et al.* 2019, Moreira *et al.* 2019b). There are three important citrus diseases caused by *Colletotrichum*: post-bloom fruit drop (PFD), Key lime anthracnose (KLA) and postharvest anthracnose; the first two were almost exclusively reported from the Americas and are caused by *Col. abscissum*, *Col. gloeosporioides* and *Col. limetticola*, respectively (Damm *et al.* 2012a, Timmer & Peres 2015, Silva *et al.* 2017). *Colletotrichum abscissum* (often still referred to as *Col. acutatum*) is the main PFD pathogen and produces reddish-orange lesions with salmon-pink spore masses on citrus petals, which subsequently results in drop of fruitlets, while the calyces and floral buttons remain attached to the twigs, however, it does not cause postharvest anthracnose (Timmer & Peres 2015). *Colletotrichum gloeosporioides* is the most aggressive *Colletotrichum* species on citrus fruits in Europe and can be found on symptomatic leaves, fruits, petals and twigs of citrus species (Guarnaccia *et al.* 2017). At least 16 species belonging to the acutatum, boninense, dracaenophilum, gloeosporioides and truncatum species complexes have been reported associated with symptomatic citrus (Damm *et al.* 2012a, b, 2019, 2020, Crous *et al.* 2015, Liu *et al.* 2016a, Guarnaccia *et al.* 2017). Grape ripe rot is also caused by 16 *Colletotrichum* species in the acutatum, boninense and truncatum species complexes (Jayawardena *et al.* 2018b, Echeverrigaray *et al.* 2020), while over 20 *Colletotrichum* species in various species complexes are known from strawberry (Farr & Rossman 2022).

Anthracnose of chili pepper

Chili (*Capsicum annum*) is the fourth most important cultivated crop in the world (Saxena *et al.* 2016) and one of the most important ingredients and spices of tropical and subtropical cuisines. Anthracnose is one of the major constraints in chili production throughout Asia, as well as in Australia and Brazil, causing 10–80 % yield loss and reducing the marketability of the fruit (Than *et al.* 2008a, De Silva *et al.* 2019a). About 30 species are known from chili, belonging to the acutatum, boninense, gloeosporioides, spaethianum, truncatum, orchidearum and magnum species complexes (Diao *et al.* 2017, Mongkolporn & Taylor 2018, Damm *et al.* 2019, De Silva *et al.* 2017, 2019). *Colletotrichum truncatum* (syn. *Col. capsici*) was the most frequently isolated species from infected chili fruit in a survey in Asia (Indonesia, Malaysia, Sri Lanka, Thailand, Taiwan), followed by *Col. scovillei* and *Col. siamense* (De Silva *et al.* 2017). In a study from Korea, only *Col. scovillei* was found, which is absent in Australia (De Silva *et al.* 2017, Oo *et al.* 2017). Pathogenicity tests on chili fruit showed that *Col. scovillei* and *Col. javanense* are highly aggressive (De Silva *et al.* 2019a).

Anthracnose of legumes

Legumes like common beans (*Phaseolus vulgaris*), soybeans (*Glycine max*) and lentils (*Lens culinaris*) are important sources of protein for human and animal nutrition. Anthracnose diseases can devastate up to 50 % of grain production (Boufleur *et al.* 2021). Typical symptoms, for example of soybean anthracnose, are damping-off, dark spots on cotyledons, stems, petioles and pods and necrotic veins on leaves resulting in premature defoliation and grain germination, and pod rot (Boufleur *et al.* 2021). *Colletotrichum truncatum* is the main anthracnose pathogen of many legumes (Damm *et al.* 2009), while *Col. lindemuthianum* (orbiculare complex), although reported from 28 plant genera (Farr & Rossman 2022), within the legumes is restricted to *Phaseolus vulgaris* and *Phaseolus coccineus* (Damm *et al.* 2013, Liu *et al.* 2013a). Additional species are associated with beans, *e.g.*, *Col. spaethianum* with common beans and *Col. chlorophyti* and *Col. incanum* with soybeans, while *Col. musicola*, *Col. plurivorum* and *Col. sojae* were reported from both hosts (Damm *et al.* 2019, Yang *et al.* 2012c, 2014, Bofleur *et al.* 2020). Based on sequence data, Boufleur *et al.* (2021) revealed 13 species belonging to at least nine species complexes to be associated with soybeans with different global distribution and different roles in disease incidence, as some had been predominantly isolated from either symptomatic or asymptomatic tissue. In contrast, the main pathogen of lentil anthracnose is *Col. lentis* which belongs to the destructivum complex; the only other species from lentils identified using sequence data is *Col. nigrum* (Liu et al. 2013a).

Several *Colletotrichum* species are also known as endophytes of plants (Cannon *et al.* 2012, Damm *et al.* 2012b, Liu *et al.* 2015a, Jayawardena *et al.* 2020, 2021, Bhunjun *et al.* 2024). Many of them can switch their lifestyle from endophytic to pathogenic based on the physiological condition and genotype of the host plant and environmental factors (Photita *et al.* 2004, Promputtha *et al.* 2007, Hardoim *et al.* 2015, Da Silva *et al.* 2020b). Apart from being plant pathogens or endophytes, *Colletotrichum* species can also be pathogens of animals *e.g.*, insects and humans. Several species, including *Col. dematium*, *Col. fructicola*, *Col. gloeosporioides*, *Col. tropicale* and *Col. truncatum* were reported to cause keratitis in humans (Buchta *et al.* 2019, Hung *et al.* 2020). *Colletotrichum gloeosporioides* (*s. lat.*) was reported to cause a deep tissue mycosis in a person in Australia (Figtree *et al.* 2013), a severe corneal infection (Rodriguez 2014) and a cutaneous infection (Lin *et al.* 2015).

Research interests

Colletotrichum was listed as one of the top 10 fungal pathogens in molecular plant pathology based on their scientific and economic importance (Dean *et al.* 2012), which is also reflected in the high number of publications and high citation rate. The Web of Science lists 4 767 publications and 46 970 citations from 2011–2021 (Fig. 29). The 10 most cited articles are listed in Table 16. Most of the publications focused on certain species or species complexes, their identification and pathogenicity to specific plant hosts, molecular studies of the plant-pathogen interactions and diseases and their control (Fig. 30).

Taxonomy, phylogeny and identification

An accurate circumscription of the causal agent of a disease is the key to unambiguously identify it, understanding plant-pathogen interactions, host range and distribution and thus providing the basis for effective disease control and prevention. After many decades of uncertainty in *Colletotrichum* systematics, an international initiative started in 2009 with the epitypification of the type species *Col. lineola* and several other important species with curved conidia, multi-locus phylogenetic studies especially of species from *Amaryllidaceae* and *Poaceae*, a critical revision of the current application of species names and recommendations for studying and identifying *Colletotrichum* species (Cai *et al.* 2009, Crouch *et al.* 2009, Damm *et al.* 2009, Hyde *et al.* 2009, Yang *et al.* 2009). In the following years, a robust framework of more than 15 species complexes was established and many new species were revealed (Cannon *et al.* 2012, Crouch 2014, Damm *et al.* 2012a, 2012b, 2013, 2014, 2019, Weir *et al.* 2012, Liu *et al.* 2014, Bhunjun *et al.* 2021b, Liu *et al.* 2022); the data on the new species are regularly fed in a multi-locus online identification tool (qbank.eppo.int/fungi/). This facilitated the accurate identification of known and the allocation of previously unknown pathogens and endophytes and resulted in numerous surveys on specific hosts, disease studies and first reports that often include new species discoveries and pathogenicity tests (*e.g.*, Tao *et al.* 2013, Vieira *et al.* 2014, Sun *et al.* 2019, Damm *et al.* 2020, Alizadeh *et al.* 2022, Yang *et al.* 2023a). This process is progressing and a transition to genome-based systematics is foreseeable (O'Connell *et al.* 2012, Li *et al.* 2021b, Liu *et al.* 2022).

Colletotrichum species as model organisms to study plant-pathogen interactions

Colletotrichum species have been successfully used as model organisms to study plant-pathogen interactions because they can easily be manipulated in the laboratory and of the hemibiotrophic lifestyle of many species (Perfect *et al.* 1999, O'Connell *et al.* 2012, Baroncelli *et al.* 2017).

Initially, studies were based on morphological observations of hemibiotrophic growth of *Colletotrichum* species inside plants (O'Connell *et al.* 2012). The genetic basis of pathogenicity was investigated by manipulating individual genes, *e.g.*, of *Col. magnum* (Freeman & Rodriguez 1993, Rodriguez & Redman 2008). Now whole or partial genomes and transcriptomes are sequenced encircling the molecular origins of pathogenicity, host susceptibility,

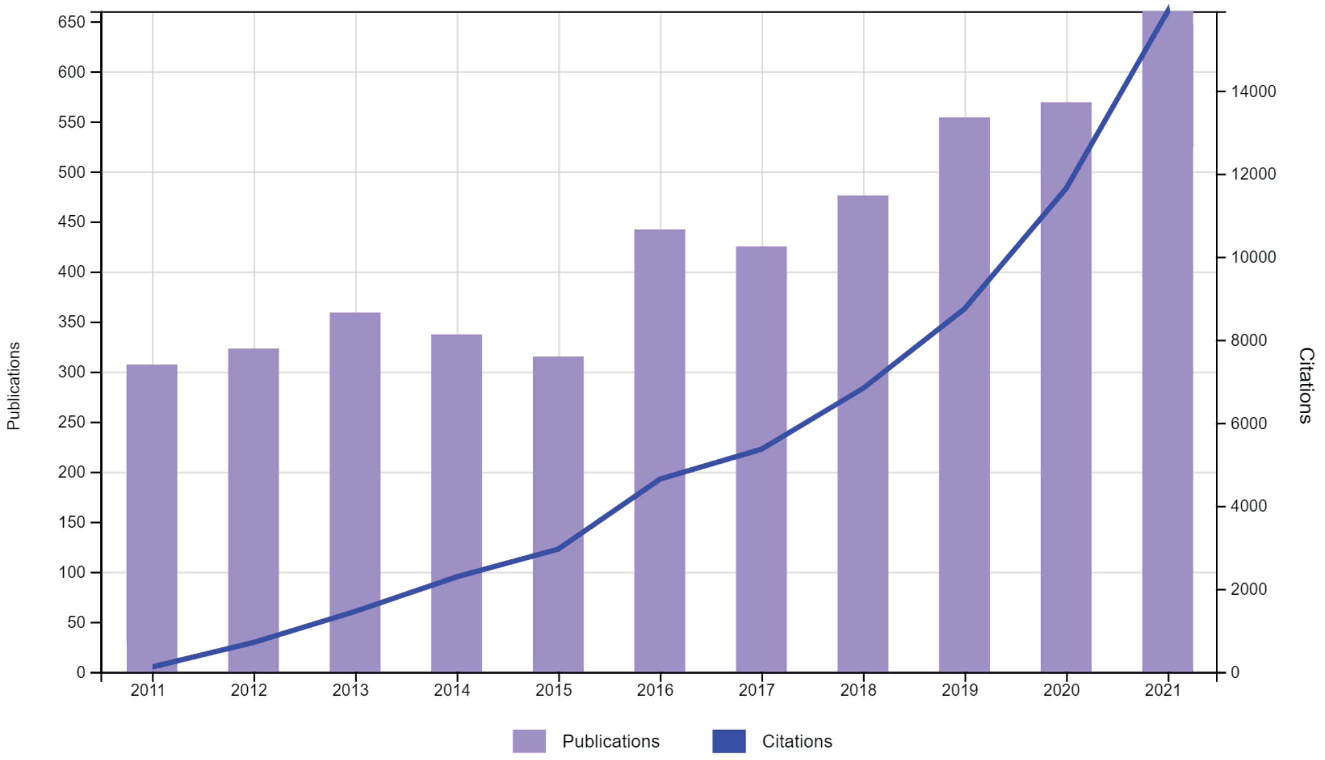

Fig. 29. Trends in research of *Colletotrichum* in the period 2011–2021.

Table 16. Top 10 cited articles related to *Colletotrichum* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	The top 10 fungal pathogens in molecular plant pathology	1 769	Dean *et al.* (2012)
2	The *Colletotrichum gloeosporioides* species complex	717	Weir *et al.* (2012)
3	Lifestyle transitions in plant pathogenic *Colletotrichum* fungi deciphered by genome and transcriptome analyses	536	O'Connell *et al.* (2012)
4	*Colletotrichum* – current status and future directions	500	Cannon *et al.* (2012)
5	The *Colletotrichum acutatum* species complex	479	Damm *et al.* (2012a)
6	Root endophyte *Colletotrichum tofieldiae* confers plant fitness benefits that are phosphate status dependent	273	Hiruma *et al.* (2016)
7	One stop shop: backbones trees for important phytopathogenic genera: I (2014)	235	Hyde *et al.* (2014)
8	The *Colletotrichum boninense* species complex	231	Damm *et al.* (2012b)
9	Sequential delivery of host-induced virulence effectors by appressoria and intracellular hyphae of the phytopathogen *Colletotrichum higginsianum*	213	Kleemann *et al.* (2012)
10	Comparative genomic and transcriptomic analyses reveal the hemibiotrophic stage shift of *Colletotrichum* fungi	209	Gan *et al.* (2013)

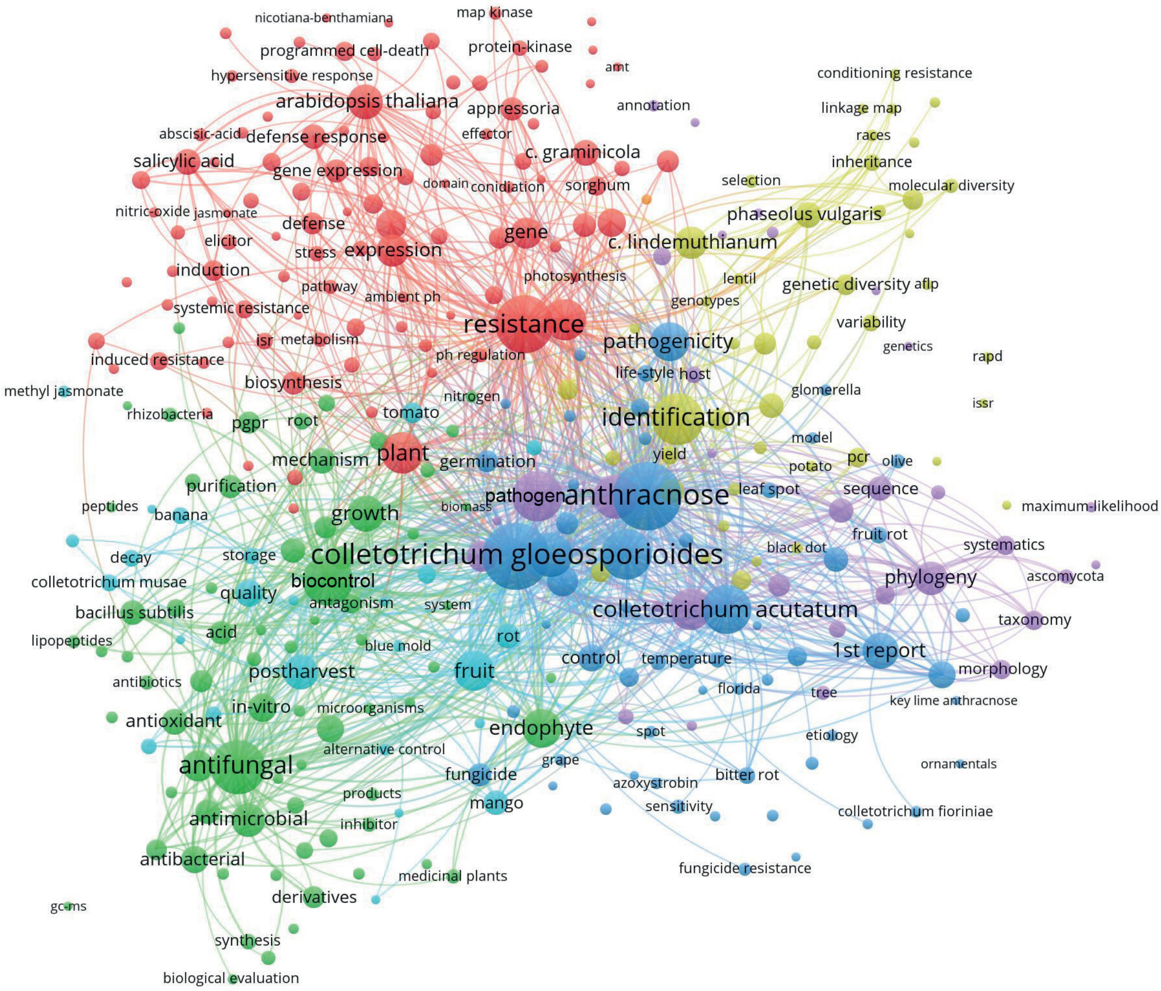

Fig. 30. Network visualisation of keywords of the publications related to *Colletotrichum*. The larger the text and the circle the more often the subject has been cited.

individual responses, drawbacks and benefits on both sides increasingly tighter. Comparative genomics and transcriptomics demonstrate for example the shift from biotrophic to necrotrophic lifestyle of hemibiotrophic species like *Col. graminicola*, *Col. higginsianum* and *Col. orbiculare* on gene level (Kleemann *et al.* 2012, O'Connell *et al.* 2012, Gan *et al.* 2013) and the thin line between pathogenic and beneficial interactions of closely related *Colletotrichum* species to *Arabidopsis thaliana* under phosphate deprivation (Hacquard *et al.* 2016, Hiruma *et al.* 2016).

The results of these studies also include the genome sequences of an increasing number of species, especially of those belonging to the acutatum, destructivum, graminicola and orbiculare complexes (O'Connell *et al.* 2012, Baroncelli *et al.* 2014a, b, Viswanathan *et al.* 2016, Gan *et al.* 2019a, b) that can be used to link different research and applied fields like evolutionary plant pathology, epidemiology and resistance breeding (www.colletotrichum.org/genomics/). Studies of plant-pathogen interactions, for example, focusing on genes involved in pathogenicity or fungicide resistance are the basis for disease management.

Disease management

Colletotrichum species cause anthracnose and other diseases of numerous hosts, including important crops and cause high yield losses and quality reductions of economic importance. Diseases caused by *Colletotrichum* species are currently controlled by fungicides like azoxystrobin, mancozep, cabendazim, thiophanate methyl and triazoles (Dias *et al.* 2016, Nataraj *et al.* 2020, Damm *et al.* 2020, Poti *et al.* 2020). However, fungicide efficiency gradually decreases due to the development of resistance of the pathogens, which is based on variations in specific genes (Chen *et al.* 2013c, Poti *et al.* 2020). Biocontrol and resistance breeding offer more ecological and sustainable solutions.

There are many approaches of biological control of *Colletotrichum* species by other filamentous fungi like *Trichoderma viride* and *Epicoccum dendrobii*, by yeasts such as *Saccharomyces cerevisiae* and *Cryptococcus laurentii*, by bacteria like *Bacillus subtilis* or by essential oils of plants like thyme, sage and peppermint (Ghosh & Chakraborty 2012, Bautista-Rosales *et al.* 2014, Ryu *et al.* 2014, Lopes *et al.* 2015, Morkeliūnė *et al.* 2021, Bian *et al.* 2021). Patel *et al.* (2019) screened bacterial strains for their antifungal activity against *Col. falcatum*, the causal agent of red rot of sugar cane. Most strategies against postharvest diseases focus on *Col. acutatum*, *Col. gloeosporioides* and *Col. truncatum*; promising results with yeast strains were achieved here, however, are not yet commercialised (Shi *et al.* 2021).

Pathogenicity tests are initially important to characterise a fungus as either a pathogen or an endophyte; they play a key role in resistance breeding programs against anthracnose, both to determine the aggressiveness of the *Colletotrichum* strains and to screen the host genotypes for anthracnose resistance (Mongkolporn & Taylor 2018). For example, to develop chili genotypes resistant to the three most important anthracnose pathogens, plant breeders transfer resistance genes from *Capsicum chinense* and *Ca. baccatum* into *Ca. annuum* (Mongkolporn & Taylor 2018). Genotypes of soybeans resistant to *Col. truncatum* have been reported in different countries. However, no studies involving other *Colletotrichum* species have been performed so far (Boufleur *et al.* 2021), and there is currently no breeding program for anthracnose-resistant soybean cultivars (Yang & Hartman 2015). Apart from the problem of multiple species being involved, more than one gene may also be involved in resistance, for example, soybeans against anthracnose caused by *Col. truncatum* (Nataraj *et al.* 2020).

However, several *Colletotrichum* species have been tested as potential biocontrol agents themselves, mostly as bioherbicides against weeds, such as species in the orbiculare complex (Damm *et al.* 2013). *Colletotrichum gloeosporioides* (*s. lat.*) was successfully used to control an obligate parasitic plant *Arceuthobium tsugense* (Askew *et al.* 2011), and the herbicidal activity of metabolites (colletochlorins) of *Col. higginsianum* against leaves of *Sonchus arvensis* and tomato was demonstrated (Masi *et al.* 2017).

Authors: U. Damm and R.S. Jayawardena

15. ***Trametes*** Fr., Fl. Scan.: 339. 1836.

Type species: *Trametes suaveolens* (L.) Fr.

Classification: *Basidiomycota*, *Agaricomycotina*, *Agaricomycetes*, *Polyporales*, *Polyporaceae.*

Background

The genus *Trametes* was established by Elias Magnus Fries treating *Tra. suaveolens* as the type (Fries 1836). Members of the genus are cosmopolitan in distribution and can be easily found in boreal, temperate, and tropical forest ecosystems (Gilbertson & Ryvarden 1987, Ryvarden 1991, Carlson *et al.* 2014, Olou *et al.* 2020). Historically, many genera like *Cerrena*, *Coriolopsis*, *Daedalea*, *Microporus*, *Fomitopsis*, and *Trametopsis* were once placed within the genus *Trametes* by Corner (1989) based on characters like trimitic hyphal systems (Ko & Jung 1999, Tomšovský *et al.* 2006, Tomšovský 2008, Justo & Hibbett 2011). Ryvarden (1991) redefined the *Trametes* group and included most of the genera synonymised by Corner (1989) based on features like the trimitic hyphal system and white-rot type of wood decay.

With the advancement of molecular phylogenetic studies, Ko & Jung (1999) and Tomšovský *et al.* (2006) performed a detailed study and placed most species of *Trametes* in the core polyporoid clade suggesting that the genus is either paraphyletic or polyphyletic. Conflicts over the generic limit of *Trametes*, due to a lack of distinct morphological features, resulted in the genus consisting of a large number of nomenclatural combinations. There are 250 well-recognised species of *Trametes*, according to Index Fungorum. Currently, the genus is circumscribed by the combination of features like a pileate basidiocarp with poroid hymenophore; smooth, thin-walled, IKI-basidiospores, presence of trimitic hyphal system, and symptoms like a white-rot type of decay on hardwood and conifer wood (Gilbertson & Ryvarden 1987, Gomes-Silva *et al.* 2010, Justo & Hibbett 2011).

Traditionally, the genus has long been used in Chinese medicine (Knežević 2015, Soković *et al.* 2018). Several species of the genus are enriched with antioxidant, anti-inflammatory, antimicrobial, and anticancer properties (Yamaç & Bilgili 2006, Kamiyama *et al.* 2013, Knežević *et al.* 2015, Milovanovic *et al.* 2015, Zhao *et al.* 2015g). Maniak *et al.* (2020) discovered a new class of low-molecular-weight hydrazide-hydrazones as laccase inhibitors in *Tra. versicolor*. *Trametes versicolor* is also used to produce higher amounts of divanillin, a bio-based aromatic building block for synthesising semi-aromatic polymers, and this is again polymerised with 2,7-diaminocarbazole and benzene-1,4-diamine to formulate divanillin-based poly-azomethines which show excellent thermal and mechanical properties (Garbay *et al.* 2020).

Ecological and economic significance

Trametes species are a common wood decay fungus due to their lignin degradation ability and can be found on several species of hardwood trees (Roy 1982, Levin & Castro 1998, Hapuarachchi *et al.* 2021). They are commonly known as a predator of natural forest ecosystems (Bari *et al.* 2016). Besides their usefulness as a wood decomposer in natural ecosystems, *Trametes* species are also used in the biodegradation of agricultural waste and bioremediation (Wang *et al.* 2012e, Carlson *et al.* 2014, Wu *et al.* 2016b).

Trametes species are well known to cause white rot decay of wood and details of this decay are given below:

White rot decay of woods

Trametes species have a broad range of host plant species (Eaton & Hale 1993, Schmidt 2006). In the USA and the northern part of Iran, over 90 % of wood decay is due to *Trametes* species causing white rot disease (Gilbertson 1980, Bari *et al.* 2015). These fungi produce filamentous hyphae that are 20–30 times smaller than the invaded wood cell walls (Goodell *et al.* 2008). The filamentous hyphae initially infect the wood ray cells, and then gradually pass from one cell to another cell through the pits. In the growing stages when microclimatic conditions are favourable, the hyphae extend lengthwise through the lumen of the wood cells and secrete enzymatic and non-enzymatic metabolites for the degradation of wood cell wall for the acquisition of nutrients (Goodell *et al.* 2008). The enzymes responsible for decomposing lignin substances include lignin peroxidase, laccase, and manganese peroxidases, which cause oxidisation and mineralisation (Hatakka 1994, Hatakka *et al.* 2002, Karim *et al.* 2017). As a result, a bleached-like appearance develops where fibres and parenchyma cells completely degrade the remaining vessels (Levin & Castro 1998). The wood becomes soft and stringy where the softened wood fibres can be easily separated allowing the wood to be peeled apart (Goodell *et al.* 2008). Besides the simultaneous degradation of lignin, the degradation of cell wall polysaccharides continues, leaving cells perforated with holes and erosion troughs (Eriksson *et al.* 1990). However, in the case of selective removal of lignin present in the middle lamellae and secondary wall there remains in higher quantities (Blanchette 1994).

Apart from wood decay, some *Trametes* species have also been used as biocontrol agents, such as *Tra. versicolor* used to control *Fusarium oxysporum f. sp. lycopersici*, *Fusarium moniliforme*, *Alternaria solani*, *Rhizoctonia solani*, *Cercospora capsici*, *Botrytis cinerea*, and *Verticillium dahliae* (Ruiz-Dueñas & Martınez 1996, Deketelaere *et al.* 2017, Mendieta *et al.* 2019).

Research interests

There are 2 834 publications and 46 427 citations from 2011–2021 in the Web of Science (Fig. 31), with the top 10 most cited articles shown in Table 17. Most publications focused on fungal laccase (production, purification, characterisation, dye synthesis), bioremediation of hazardous chemicals, nutraceutical activities, as well as taxonomy (Fig. 32).

Laccase enzyme from Trametes species

Trametes species are good producers of the enzyme laccase. Studies have focused on the production of laccase from *Tra. gallica* (Dong *et al.* 2005), *Tra. hirsuta* (Rodríguez Couto *et al.* 2004, Rosales *et al.* 2005, Koroleva *et al.* 2002), *Tra. modesta* (Nyanhongo *et al.* 2002), *Tra. pubescens* (Galhaup *et al.* 2002), *Tra. trogii* (Trupkin *et al.* 2003), and *Tra. versicolor* (Fåhraeus & Reinhammar 1967, Mikiashvili *et al.* 2005, Rodríguez Couto *et al.* 2003). Laccase is a promising biocatalyst with a wide range of applications, including chemical synthesis, bioremediation, delignification, biosensing, pulp bleaching, textile finishing, and wine preservation, *etc*. (Dwivedi *et al.* 2011, Fernández-Fernández *et al.* 2013). Laccases can polymerise natural phenols and aid in the development of novel cosmetic dyes, hair colouring materials, toothpaste, deodorants, mouthwashes, and other commodities (Dwivedi *et al.* 2011). These features make laccase a fascinating enzyme to investigate in terms of structure, function, and application (Dwivedi *et al.* 2011). Laccases mediate the oxidation process of various environmental contaminants including non-phenolic and phenolic compounds (Dwivedi *et al.* 2011). As storage and operational stabilities are routinely improved, immobilisation of laccase through adsorption, encapsulation, entrapment, self-immobilisation, and covalent binding offers various advantages for its applications over free enzymes in terms of reusability (Fernández-Fernández *et al.* 2013).

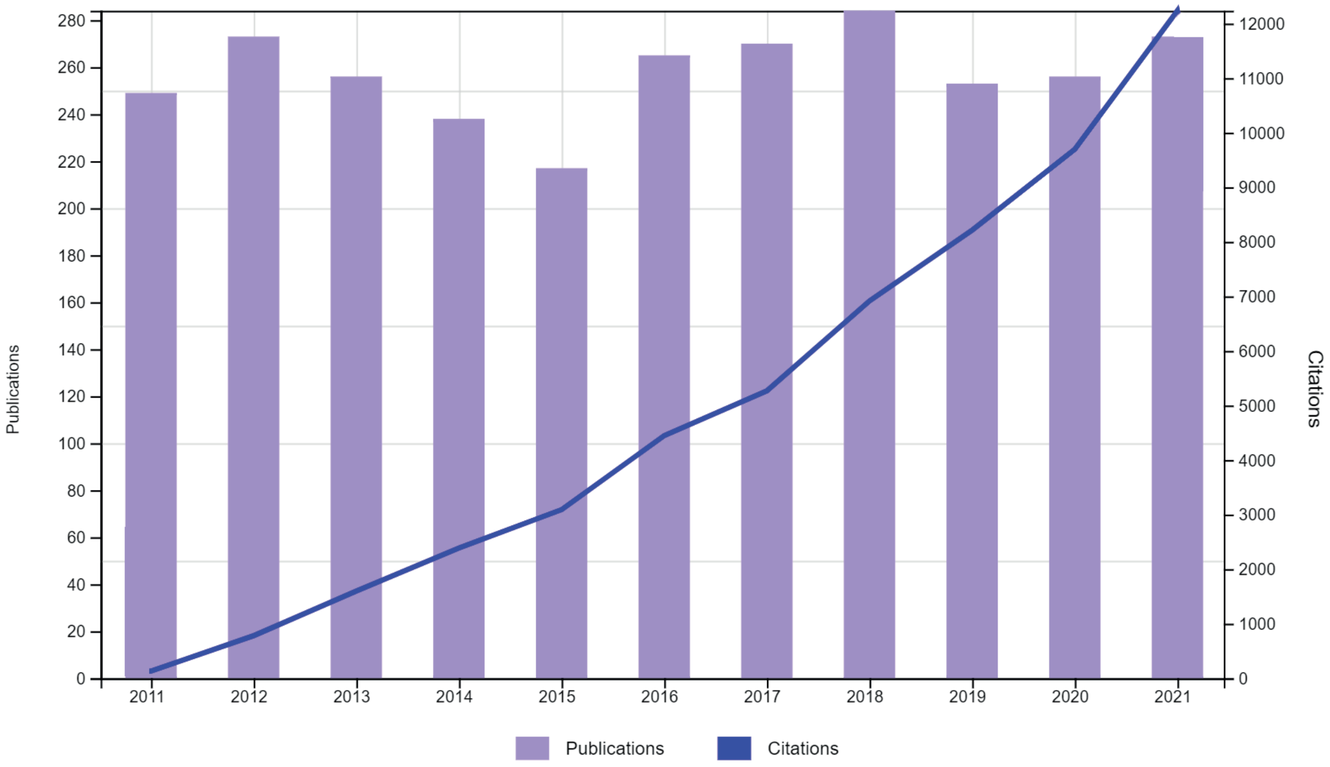

Fig. 31. Trends in research of *Trametes* in the period 2011–2021.

Table 17. Top 10 cited articles related to *Trametes* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Untapped potential: exploiting fungi in bioremediation of hazardous chemicals	491	Harms *et al.* (2011)
2	Enzyme immobilization by adsorption: a review	477	Jesionowski *et al.* (2014)
3	Recent developments and applications of immobilized laccase	401	Fernandez-Fernandez *et al.* (2013)
4	The role of culinary-medicinal mushrooms on human welfare with a pyramid model for human health	341	Chang & Wasser (2012)
5	From the conventional biological wastewater treatment to hybrid processes, the evaluation of organic micropollutant removal: A review	338	Grandclement *et al.* (2017)
6	Enzymes as green catalysts for precision macromolecular synthesis	300	Shoda *et al.* (2016)
7	Structure-function relationship among bacterial, fungal and plant laccases	286	Dwivedi *et al.* (2011)
8	Biotechnological strategies to overcome inhibitors in lignocellulose hydrolysates for ethanol production: review	267	Parawira & Tekere (2011)
9	Potential applications of laccase-mediated coupling and grafting reactions: A review	238	Kudanga *et al.* (2011)
10	Lignin-degrading enzymes	230	Pollegioni *et al.* (2015)

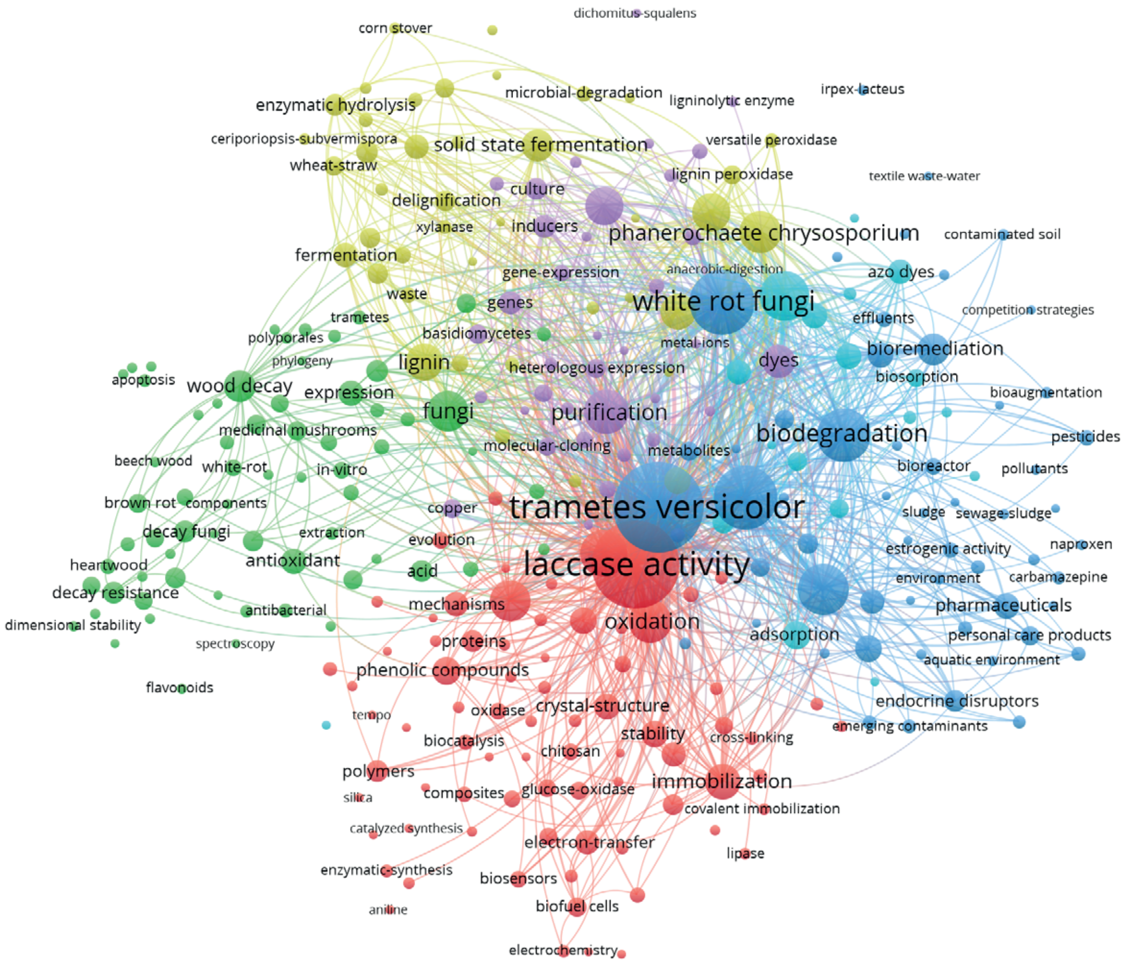

Fig. 32. Network visualisation of keywords of the publications related to *Trametes*. The larger the text and the circle the more often the subject has been cited.

Nutraceutical activities

Trametes versicolor has been widely studied and the acetone extract of the mushroom has been found to contain considerably higher antioxidant activity compared to other extracts like methanol, chloroform, and n-hexane (Kamiyama *et al.* 2013). The major compounds responsible for showing potent antioxidant activities of the mushroom include furfural, furfuryl alcohol, γ-butyrolactone, 2-methoxy-4-vinylphenol, benzaldehyde, and 2,6-dimetoxy-4-vinylphenol (Kamiyama *et al.* 2013, Soković *et al.* 2018). Methanolic extract of *Tra. ochracea* mushrooms contains higher antioxidants compared to the hexane extracts and the mushrooms are enriched with significant amounts of various compounds like phenols, alkaloids, flavonoids, steroids, saponins, tannins, resins, carbohydrates, and proteins (Melappa *et al.* 2015). Experiments performed by Knežević *et al.* (2015) revealed that the antioxidant activities of *Tra. gibbosa* and *Tra. hirsuta* were lower compared to that of *Tra. versicolor*. Cheng & Leung (2008) demonstrated that *Tra. versicolor* proteo-glucans exhibit immunostimulatory properties by promoting the synthesis of interferons, interleukin-6, macrophages, imunoglobulin-G, and T-lymphocytes. The laccase enzyme produced from *Tra. versicolor* showed promising antimicrobial properties against Gram-positive bacteria when encapsulated in a chitosan-nanobiochar matrix suggesting encapsulation as an effective method of keeping the enzyme stable and active for a variety of biological applications (Naghdi *et al.* 2019).

Bioremediation of hazardous chemicals

Trametes spp. are widely used for bioremediation purposes due to their poor specificity of catabolic enzymes, and the formation of long stretches of mycelial mats (Harms *et al.* 2011). These fungi potentially degrade organic molecules in the environment and considerably reduce the harmful effects related to various hazardous substances like metals, radionuclides, and metalloids through chemical alteration or by affecting chemical bioavailability. *Trametes* spp. mineralises various chloro-aromatics, and TNT (Harms *et al.* 2011). *Trametes versicolor* degrades different classes of chemicals (phenols, parabens, and phthalate) in a mixture of endocrine disrupting chemicals (EDCs) in a cost-effective process that enables its application in a water treatment process (Pezzella *et al.* 2017). García-Vara *et al.* (2021) showed that *Tra. versicolor* eliminates bentazone, a widely used herbicide in rice and cereal crops, an average of 48 % from water through the use of laccase and cytochrome P450 enzymatic systems. This fungus is potent for bioremediating diuron [3-(3,4-dichlorophenyl)-1,1-dimethylurea], present in polluted aquatic environments, converting it to two other non-toxic metabolites like 1-(3,4-dichlorophenyl)-urea and 1-(3,4-dichlorophenyl)-3-methylurea under low- and high-nitrogen conditions (Mori *et al.* 2018). Significant breakdown of BPA and decolourisation of commercial colours can also be achieved through the use of *Tra. versicolor* (Manna & Amutha 2017). Species of *Trametes* absorb and accumulate cadmium and are applied in the removal process of heavy metals (Manna & Amutha 2017). In semi-arid and Mediterranean habitats, *Tra. versicolor* decomposes atrazine mixed in low moisture and organic-matter rich calcareous clay soils up to 98 % and is a promising option for atrazine bioremediation (Bastos & Magan 2009). According to Morato (2013), *Tra. versicolor* degrades and reduces overall toxicity of a wide range of xenobiotic and recalcitrant contaminants like antibiotics (ofloxacin), antiepileptics (carbamazepine), analgesics and anti-inflammatory (ketoprofen and diclofenac), lipid regulators (clofibric acid), and an X-ray contrast agent (iopramide) in urban and hospital wastewater through their unspecific enzyme system.

Taxonomy and phylogeny

Phylogenetic reconstruction of the family *Polyporaceae* by the mtSSU rDNA region came into focus with the studies of Hibbett & Donoghue (1995), and Ko & Jung (1999), where the *Trametes*-clade resided within the “core *Polyporaceae* group”. Later, Ko (2000) with the help of sequence data from two marker regions (ITS and mtSSU rDNA) divided the “core *Polyporaceae* group” into two subgroups, where subgroup “B” included the genus *Trametes* together with *Coriolopsis polyzona*, and other members of the genera *Pycnoporus*, and *Lenzites* that was further supported by the study of Rajchenberg (2011) incorporating several morphological and cytological features. Based on the data from two gene sequence regions (*rpb2* and ITS rDNA), Welti *et al.* (2012) demarcated the *Trametes*-clade into three lineages *viz.* a lineage with members of the genus *Trametes* along with its type species, *Tra. suaveolens*, and *Lenzites*, and *Coriolopsis*; another lineage including some species of *Trametes* (*Tra. lactinea*, *Tra. cingulata*, *Tra. menziesii*, and *Tra. ljubarskyi*), together with the genus *Pycnoporus*; and a single lineage with *Artolenzites elegans*. Justo & Hibbett (2011) re-delimited the concept of the genus based on the data from ribosomal markers and protein-coding gene regions where the “trametoid clade” consisted of most of the *Trametes* species together with *Coriolopsis polyzona*, and species of genera *Pycnoporus*, and *Lenzites*. However, according to the studies of Justo & Hibbett (2011), designating the trametoid clade after the name *Trametes* suggested the necessity of incorporating more molecular sequence data together with a few novel nomenclatural combinations.

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16. ***Rhizoctonia*** DC., Fl. franç., Edn 3 (Paris) 5–6: 110. 1815.

Type species: *Rhizoctonia solani* Kühn

Classification: *Basidiomycota*, *Agaricomycotina*, *Agaricomycetes*, *Cantharellales*, *Ceratobasidiaceae.*

Background

Rhizoctonia was first described by De Candolle in 1815 with *R. crocorum* as the original type species. Due to the confusion around what defined members of this genus, a re-definition of the genus concept was later provided by Ogoshi (1987) to include characteristics such as the absence of asexual spores (conidia) and rhizomorphs, hyphal branching from distal septa of vegetative hyphae, constriction at hyphal branching, and sclerotia with no cellular differentiation into rind or medulla. Three main groups are widely recognised as pathogens of crop plants worldwide: *R. solani* (*Thanatephorus*), *R. zeae* (*Waitea*), and *Ceratorhiza* (*Ceratobasidium*). While these groups share important attributes that define the genus *Rhizoctonia*, they can be differentiated based on vegetative characteristics. Members of *Ceratorhiza* have binucleate cell compartments, while *R. solani* and *R. zeae* are multinucleate. The salmon-coloured mature hyphae of *R. zeae* are distinguished from *R. solani* hyphae which are brown in culture.

Rhizoctonia solani is the most studied species of the three genera by virtue of its importance to agricultural production. It was first described on potato plants by Julius Kühn in 1858 and has since been associated with diseases of other economically important crops. The unique characteristics of *R. solani* make laboratory identification straightforward. Isolates are hyaline when young and become brown with age; the mycelia are made up of septate hyphae that branch at 90° angles with constrictions at the point of branching; hyphae consist of dolipore septa that permit cell-to-cell movement of cytoplasmic organelles, mitochondria, and nuclei; and asexual forms do not produce conidia, clamp connections, rhizomorphs, or pigmentations other than brown. All members of this species have the same sexual morph (*Thanatephorus cucumeris*) (Homma *et al*. 1983, Ogoshi 1984, Neate & Warcup 1985, Carling *et al*. 1994), and differentiation based on the sexual morph has yet to be reported.

Earlier attempts to resolve the diversity existent within this species utilised hyphal anastomosis to group isolates into anastomosis groups (AG) (Parmeter *et al*. 1969) and the different AGs of *R. solani* are considered non-interbreeding populations (Anderson *et al*. 1972). Hyphae of isolates belonging to the same AG, when paired on a suitable growth medium, recognise and fuse and may undergo cytoplasmic and nuclei exchange. Fourteen AGs (AGs 1–13 and AG-B1) have been identified to date (Ogoshi 1987, Carling 1996, 1999), and additional characteristics have been used to further delineate subgroups within certain AGs. Aside from genetic diversity, host crop diversity within AGs and AG subgroups makes *R. solani* a remarkable pathogen (Table 18). For the binucleate *Rhizoctonia* spp., *Ceratobasidium*, 18 AGs have been identified (Sneh *et al*. 1991, Sharon *et al*. 2008), and for *Waitea*, two anastomosis groups, WAG-O (*W. circinata* var. *oryzae*, asexual morph *R. oryzae*) and WAG-Z (*W. circinata* var. *zeae,* asexual morph *R. zeae*), are currently defined (Oniki *et al*. 1985).

Ecological and economic significance

Diseases caused by *R. solani* have gathered more attention than those caused by other species of *Rhizoctonia*. Host range includes, but is not limited to, members of *Poaceae*, *Fabaceae*, *Solanaceae*, *Asteraceae*, and *Brassicaceae*, causing symptoms such as root rot, foot rot, seed rot, crown rot, stem rot, sheath blight, web blight, brown patch, *etc*. Below is a summary of some of the most important diseases of crop plants caused by *Rhizoctonia* spp.

Sheath blight of rice, (*Oryza sativa*) caused by *R. solani* AG1-1A, is an economically important disease of rice worldwide. Although first reported in Japan in 1910, the disease has become prominent in high-fertility rice-production systems around the globe (Eizenga *et al*. 2002). It is one of the most devastating diseases of rice in Eastern Asia and one of the leading causes of yield loss in rice-producing states in the USA. Under favourable environmental conditions (high humidity and warm temperatures), yield losses, particularly on susceptible varieties, can be as high as 50 % (Lee & Rush 1983, Savary *et al*. 2000). There are no rice varieties with complete resistance to the pathogen, and resistance is quantitatively inherited (Hashiba 1984, Linscombe *et al*. 1992, Eizenga *et al*. 2002), which has most likely hampered the development of rice varieties for use on a commercial scale. As a result, sheath blight management has relied mostly on an integrated approach involving a combination of cultural practices, such as field sanitation, nutrient management, crop rotation to non-hosts, and fungicides.

Crown and root rot of sugar beet (*Beta vulgaris*) is one of the most important diseases of sugar beet in the USA (Schneider & Whitney 1986) and has gained importance in sugar beet-producing areas in Europe (Buhre *et al*. 2009). In the USA, the disease is caused by two AGs of *R. solani*, AG-2-2 IIIB and AG-2-2 IV, although the former is generally more aggressive on sugar beet (Bolton *et al*. 2010, Windels & Brantner 2007). In Germany and other parts of Europe, AG-2-2 IIIB is the main subgroup causing crown and root rot in sugar beet (Büttner *et al*. 2002). Yield losses as high as 50 % can occur (Herr 1996), and in Europe at least 36 000 ha of fields planted to sugar beet are affected on an annual basis (Garcia *et al*. 2001). In Europe, there are no fungicides registered for the control of the disease. Thus, control is mostly achieved through strategies that combine host resistance with agronomic practices like crop rotation (Herr 1996, Buhre 2009). In the USA chemical control is widely used and is the most effective method (Jacobsen

Table 18. Anastomosis groups of *Rhizoctonia solani* and their host crops.

Anastomosis group (subgroups)	Host crop	References
AG-1 (1A, 1B, 1C, 1D, 1E, 1F)	Rice, corn, soybean, bean, turfgrass, cabbage, lettuce, coffee, sorghum	Mukou *et al.* (1975), Martin & Lucas (1984), Jones & Belmar (1989), Yang *et al.* (1990), Herr (1992), Priyatmojo *et al.* (2001), Grosch *et al.* (2004)
AG-2- (1, t, Nt), AG-2- (2IIIB, 2IV, 2LP, 3, 4)	Soybean, sugar beet, rice, turfgrass, corn, canola, wheat, tulip, tomato	Sumner & Bell (1982), Windels & Nabben (1989), Liu & Sinclair (1991), Muyolo *et al.* (1993a), Watanabe & Matsuda (1966), Engelkes & Windels (1996), Nelson *et al.* (1996), Schneider *et al.* (1997), Dorrance *et al.* (2003), Paulitz *et al.* (2006), Misawa & Kuninaga (2010)
AG-3 (TB, PT, TM)	Potato, tobacco, soybean, tomato	Meyer *et al.* (1990), Nelson *et al.* (1996), Windels *et al.* (1997), Woodhall *et al.* (2007), Misawa & Kuninaga (2010)
AG-4 (HGI, HGII, HGIII)	Soybean, tomato, dry bean, peanut, cotton, potato, melon, broccoli, spinach	Windels & Nabben (1989), Muyolo *et al.* (1993b), Balali *et al.* (1996), Brenneman (1996), Rothrock (1996), Fenille *et al.* (2002), Kuramae *et al.* (2003)
AG-5	Potato, turfgrass, bean, soybean, sugar beet	Martin & Lucas (1984), Balali *et al.* (1995), Nelson *et al.* (1996), Windels *et al.* (1997)
AG-6 (HG-I, GV)	Non-pathogenic (mycorrhizal with orchids)	Carling *et al.* (1999), Pope & Carter (2001)
AG-7	Soybean, potato, cotton, watermelon	Baird *et al.* (1996), Carling *et al.* (1998), Abd-Elsalam *et al.* (2010)
AG-8-ZG (1, 2, 4, 5)	Small grains (wheat, barley)	Neate & Warcup (1985), Roberts & Sivasithamparam (1986)
AG-9 (TP, TX)	Potato, lettuce, carrot	Carling *et al.* (1987)
AG-10	Non-pathogenic	MacNish *et al.* (1995)
AG-11	Wheat, lupin, soybean, cotton, potato, radish	Carling *et al.* (1994), Sweetingham (1989), Kumar *et al.* (1999)
AG-12	Cauliflower, radish, mycorrhizal with orchids	Carling *et al.* (1999), Pope & Carter (2001)
AG-13	Cotton	Carling *et al.* (2002)
AG-BI (Bridging Isolate)	Non-pathogenic	None reported to date

et al. 2001, Khan & Bradley 2010) for controlling the disease, although agronomic practices, such as rotation to non-hosts and host resistance, are also encouraged.

Rhizoctonia root rot and bare patch, caused by *R. solani* AG-8 and *R. oryzae*, is a major disease of direct-seeded cereals in Australia (MacNish & Neate 1996) and the Pacific Northwest region of USA (Weller *et al*. 1986, Paulitz *et al*. 2002) and is considered the most important disease limiting the adoption of no-till technology (Schroeder & Paulitz 2006) in these regions. There is no single method for controlling Rhizoctonia root rot and bare patch, however, various combinations of available management methods can achieve the desired results. Tillage to disrupt pathogen networks (Pumphrey *et al*. 1987), elimination of green bridges (Roget *et al*. 1987, Smiley *et al*. 1992), and the application of nitrogen at seeding (MacNish 1985) are management practices that have proven effective.

Rhizoctonia root and hypocotyl rot is an important seedling disease of soybean (*Glycine max*) in continental America, particularly in the north-central region, where most of the USA soybean is grown (American Soybean Association 2021). Rhizoctonia seedling disease of soybean together with diseases caused by other seedling pathogens (*Pythium*, *Fusarium*, *Phomopsis*) are the second most important group of diseases limiting soybean yields in the USA and Ontario, Canada from 2015 to 2019 (Bradley *et al*. 2021). Several AGs have been associated with this disease, however, isolates of AG-2-2 IIIB, AG-4 and AG-5 (Liu & Sinclair 1991, Muyolo *et al*. 1993a, Nelson *et al*. 1996, Zhao *et al*. 2005, Ajayi-Oyetunde & Bradley 2017) are considered most aggressive on soybean seedlings. Resistant soybean cultivars are not commercially available (Bradley *et al*. 2001), and crop rotation alone may be insufficient to mitigate the risk of infection due to the host range (Nelson *et al*. 1996, Ajayi-Oyetunde & Bradley 2017) and longevity of infection propagules in soil. Thus, seed treatment fungicides are the method of choice for managing the disease (Dorrance *et al*. 2003).

Sharp eyespot of wheat caused by *R. cerealis* (sexual morph: *Ceratobasidium cereale*) is a stem-base disease of wheat (*Triticum aestivum*) in temperate regions of the world. The disease has attracted significant attention only in the past few decades owing to its wide geographical distribution across Europe, North America, Asia, and Africa, widespread use of wheat cultivars susceptible to the pathogen, global climate change, and its ability to infect a wide range of host crops (Cromey *et al.* 2005, Hamada *et al.* 2011). *Rhizoctonia cerealis* also causes disease on other members of the grass family (barley, oats, rye, turf grasses) (Tomaso-Peterson & Trevathan 2007, Lemańczyk & Kwaśna 2013), as well as on other crops, including sugar beet, cotton, potato, and some legumes (Kataria & Hoffmann 1988). While the impacts of the disease on yield can vary (Bateman *et al*. 2000), economic losses of over 150 million US dollars have been reported in wheat production fields in China (Chen *et al.* 2008). Cultural methods such as delayed sowing, mulching, and straw management can reduce sharp eyespot severity in wheat fields (Colbach *et al.* 1997, Diao *et al.* 1998, Miao *et al.* 1998, Bateman & Jenkyn 2001, Cromey *et al.* 2006). Although resistance to sharp eyespot is quantitative (Cai *et al.* 2006b), and germplasm with complete resistance has not been identified, transgenic wheat lines with enhanced resistance to the pathogen have been developed (Chen *et al.* 2008, Li *et al.* 2011f). Despite this, there are no commercially available resistant wheat cultivars, and management has relied mostly on the application of fungicides.

Research interests

There are 3 938 publications and 46 317 citations from 2011–2021 in the Web of Science (Fig. 33), with the top 10 most cited articles shown in Table 19. The major research themes cover fungal identification and disease management strategies such as biological control, host resistance through traditional breeding and biotech approaches, and other control methods (Fig. 34).

Due to the intractable nature of *Rhizoctonia* diseases, extensive research work on the biological control of *Rhizoctonia* diseases has been carried out for the most economically important

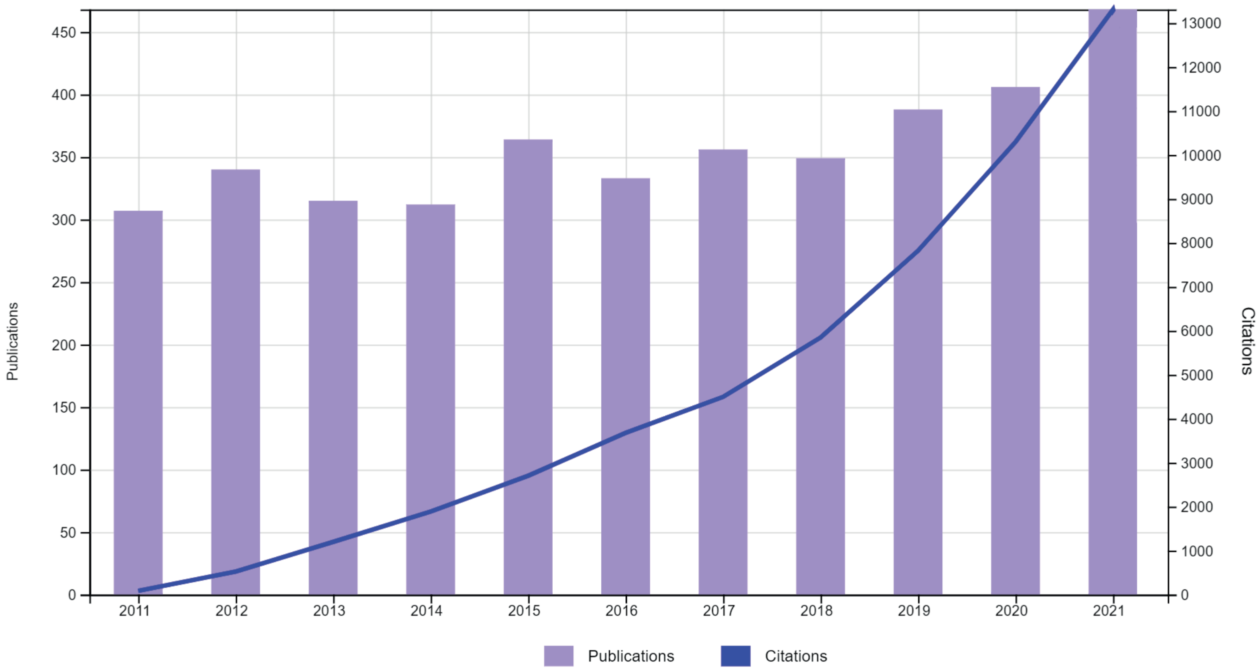

Fig. 33. Trends in research of *Rhizoctonia* in the period 2011–2021.

Table 19. Top 10 cited articles related to *Rhizoctonia* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Optimization for rapid synthesis of silver nanoparticles and its effect on phytopathogenic fungi	202	Krishnaraj *et al.* (2012)
2	Pathogen-induced activation of disease-suppressive functions in the endophytic root microbiome	195	Carrión *et al.* (2019)
3	Effects of *Bacillus amyloliquefaciens* FZB42 on lettuce growth and health under pathogen pressure and its impact on the rhizosphere bacterial community	172	Chowdhury *et al.* (2013)
4	The evolution and pathogenic mechanisms of the rice sheath blight pathogen	166	Zheng *et al.* (2013)
5	Mitochondrial complex II has a key role in mitochondrial-derived reactive oxygen species influence on plant stress gene regulation and defense	157	Gleason *et al.* (2011)
6	Comparative transcriptomics reveals different strategies of *Trichoderma* mycoparasitism	146	Atanasova *et al.* (2013)
7	Constitutive expression of rice *WRKY30* gene increases the endogenous jasmonic acid accumulation, *PR* gene expression and resistance to fungal pathogens in rice	142	Peng *et al.* (2012)
8	Role of bacterial communities in the natural suppression of *Rhizoctonia solani* bare patch disease of wheat (*Triticum aestivum* L.)	126	Yin *et al.* (2013)
9	Compost amendments enhance peat suppressiveness to *Pythium ultimum*, *Rhizoctonia solani* and *Sclerotinia minor*	118	Pane *et al.* (2011)
10	Biocontrol of *Rhizoctonia solani* damping-off and promotion of tomato plant growth by endophytic actinomycetes isolated from native plants of Algerian Sahara	110	Goudjal *et al.* (2014)

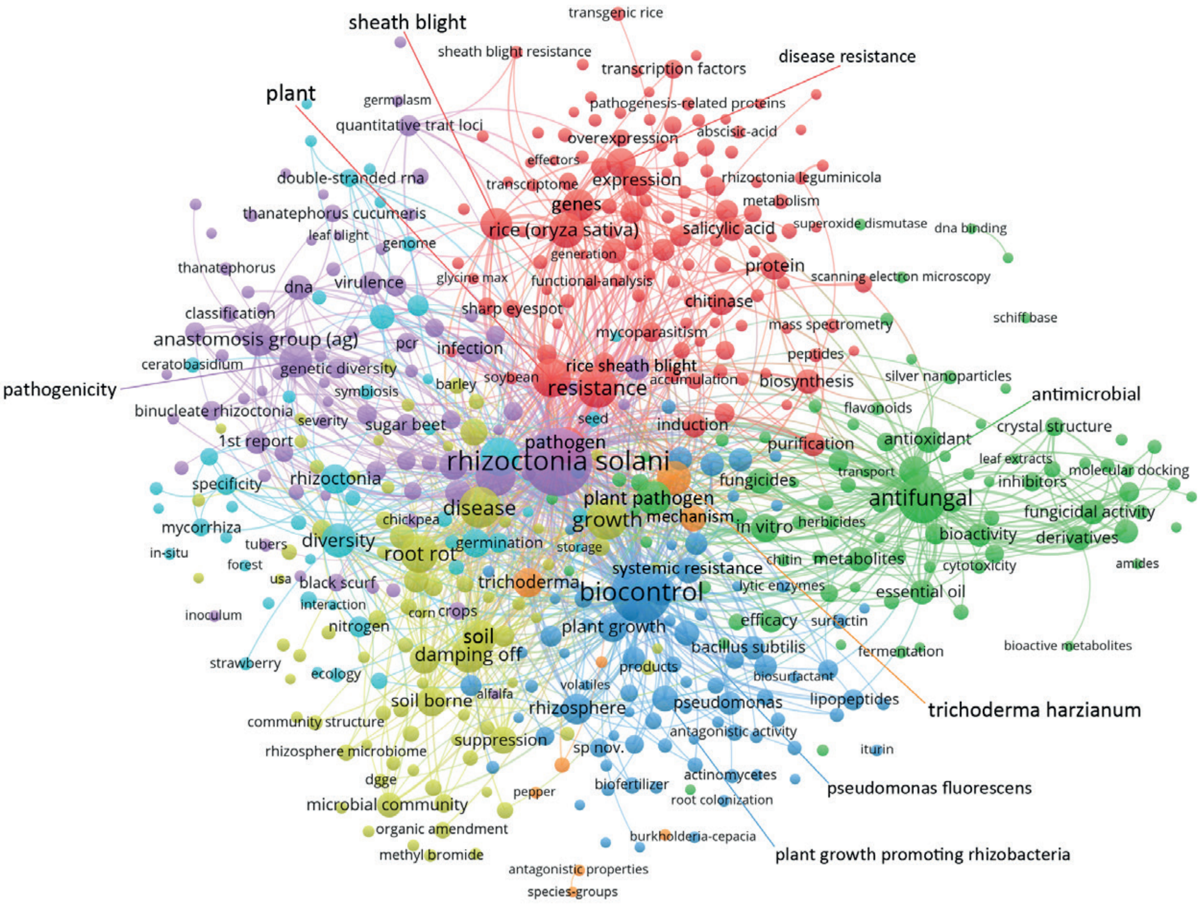

Fig. 34. Network visualisation of keywords of the publications related to *Rhizoctonia*. The larger the text and the circle the more often the subject has been cited.

hosts. Plant-growth promoting rhizobacteria such as *Pseudomonas* and *Bacillus* (Brewer & Larkin 2005, Chen *et al.* 2010, Kumar *et al.* 2012a, Haque & Khan 2021), Actinomycetes such as *Streptomyces* (Kulik 1996), as well as certain fungi including arbuscular mycorrhizae (Larkin 2008), *Trichoderma* (Boogert 1996, Grosch *et al.* 2006), *Gliocladium*, and hypovirulent strains of *Rhizoctonia* (Pascual *et al.* 2000, Sneh *et al.* 2004) have demonstrated varying levels of control of different *Rhizoctonia* species in both controlled environment and field conditions. In rice, control of *R. solani* by *Pseudomonas fluorescens* has been linked to the production of various antimicrobial metabolites, including chitinases, HCN, IAA, *etc*. (Radjacommare *et al.* 2004, Weller 2007), while various *Bacillus* spp. are known to produce pathogenicity-related proteins (He *et al.* 2002). In potatoes, *Trichoderma* species have shown acceptable levels of control of *Rhizoctonia* diseases in commercial applications (Brewer & Larkin 2005, Wilson *et al.* 2008). In wheat, the role of disease-suppressive soils has been investigated, and several bacteria have been associated with the suppression of root rot and bare patches (Barnett *et al.* 2006, Mendes *et al.* 2011, Yin *et al.* 2013). Despite the promise of *Rhizoctonia* disease control, biocontrol agents alone have not provided the level of control needed to mitigate high losses caused by *Rhizoctonia* species in field settings.

Host resistance is not available for the majority of *Rhizoctonia* diseases, and if available, resistance is quantitatively inherited, making traditional breeding methods tedious and lengthy. As a result, approaches to crop improvement for disease resistance other than traditional breeding methodologies have been investigated in a few crops. In rice, RNA interference (Tiwari *et al.* 2017), gene editing technologies such as CRISPR/Cas9 (Gao *et al.* 2018), and transcriptional regulation of gene expression (Singh *et al.* 2015b, Peng *et al.* 2016) have shown promise for the targeted control of sheath blight. Similarly, transgenic wheat lines with enhanced resistance to *R. cerealis* have also been developed but are yet to be deployed for sharp eyespot control.

Other aspects of *Rhizoctonia* biology that warrant further investigation include an in-depth understanding of its interaction with various hosts. Specifically, functional genomics approaches, such as transcriptomics, proteomics, and metabolomics, may be exploited to identify pathogenic determinants of infection and reveal the biochemical pathways underlying quantitative resistance in different host plants, which may ultimately lead to the identification of novel resistance mechanisms in different hosts.

Authors: O. Ajayi-Oyetunde and C.A. Bradley

17. ***Pleurotus*** (Fr.) P. Kumm., Führ. Pilzk. (Zerbst): 24. 1871.

Type species: *Pleurotus ostreatus* (Jacq. ex Fr.) P. Kumm.

Classification: *Basidiomycota*, *Agaricomycotina*, *Agaricomycetes*, *Agaricales*, *Pleurotaceae.*

Background

Pleurotus is a gill mushroom belonging to the family *Pleurotaceae*. *Pleurotus* was described by Paul Kummer in 1871, but over the years has been moved to many genera such as *Favolaschia*, *Hohenbuehelia*, *Lentinus*, *Marasmiellus*, *Omphalotus*, *Panellus*, *Pleurocybella*, and *Resupinatus* (Singer 1986). There are 771 taxon names listed in Index Fungorum (2022), with 25 species recognised by He *et al*. (2019b). Macroscopic and microscopic morpho-characters and molecular data, including colour of the basidiomata, spore print, and type of hyphal system, all play an important role in the taxonomic classification of the genus (Guzmán 2000). Identification of *Pleurotus* is difficult as it is based mostly on morphological characteristics of the basidiomata. *Pleurotus* is an edible mushroom, with *Ple. ostreatus* (oyster mushroom) as the most famous species and cultivated worldwide (Cohen *et al*. 2002, Chang & Miles 2004). There are "species complexes" of commercial strains such as *Pleurotus djamor* (Zervakis *et al*. 2019), *Ple. eryngii* (Zervakis *et al*. 2001), *Ple. ostreatus* (Eger *et al*. 1979), and *Ple. pulmonarius* (Bao *et al*. 2005). The main morphological characteristics of *Pleurotus* are defined by pleurotoid basidiomata, decurrent lamellulae, smooth and elongated to cylindrical basidiospores, dimitic hyphal system with skeletal hyphae and generative hyphae, and presence of clamp connections (Largent 1986, Seelan 2015).

Ecological and economic significance

Mushrooms play important roles in forest ecosystems. Wild strains and commercial strains of *Pleurotus* species can provide diverse ecological, environmental and economic services for local communities around the world. The ecosystem services provided by mushrooms also include provisioning services since many mushroom species are collected as food and for cultural services. Mushroom picking can also be a recreational and physical activity (Olah *et al*. 2020). Gathering *Pleurotus* sporocarps can also provide income for rural economies (Sánchez 2010). *Pleurotus* species can be found in both tropical and temperate areas (Chang & Miles 2004, Laessoe & Petersen 2019), and species are widespread in hardwood forests around the world (Gunde-Cimerman 1999). Most species of *Pleurotus* cause white rot, growing on both decayed and dead hardwoods (Cohen *et al*. 2002, Tsujiyama & Ueno 2013). The mycelia of some *Pleurotus* species can produce adhesive knobs in asexual stages that can attack and consume nematodes (Thorn *et al*. 2000). *Pleurotus* is cultivated worldwide because they can grow with lignocellulosic waste materials that are easy to find. Thus, it is not expensive to cultivate *Pleurotus* for food.

Research interests

There are 4 025 publications and 45 475 citations from 2011–2021 in the Web of Science (Fig. 35), with the top 10 most cited articles shown in Table 20. Most publications focused on biotechnological applications, and cultivation of *Pleurotus* (Fig. 36). *Pleurotus* sporocarps contain several bioactive compounds, have high nutritional value, potential medicinal value, and are important functional foods or nutraceuticals. However, the biochemical mechanisms of healing of disease remain largely unknown (Gregori *et al*. 2007), and future research should focus on ways forward in the therapeutic activities and cultivation of *Pleurotus* species.

Biotechnological applications of Pleurotus species

Pleurotus species are saprobes and can play an important role in managing organic wastes whose disposal has become a problem (Li *et al*. 2020e). *Pleurotus* species have important medical and bioactive properties, producing primary and secondary metabolites (Renuga Devi & Krishnakumari 2015, Mapook *et al*. 2022). Bioactivities include hepatoprotective (Zhang *et al.* 2016a), antioxidant (Jayakumar *et al*. 2011, Zhang *et al*. 2016), antimicrobial (Schillaci *et al.* 2013), antiviral, anticancer, anti-inflammatory, anti-ageing, anti-tumour, antimutagenic, antilipidemic, hepatoprotective, antihyperglycemic, hypotensive, and immunostimulant properties with nutraceutical and pharmaceutical applications (Gunde-Cimerman 1999, Khan & Tania 2012, Patel *et al*. 2012, Wahab *et al*. 2014). *Pleurotus ostreatus* can produce extracellular laccase isoenzymes (Palmieri *et al*. 2000). Pre-treatment with *Ple. ostreatus* for enzymatic hydrolysis of rice straw found increased degrees of enzymatic solubilisation of holocellulose and cellulose fractions as the content of Klason lignin decreased (Taniguchi *et al.* 2000). The β-glucans contained in *Ple. ostreatus* have been clinically identified to possess immunostimulating properties (Patel *et al*. 2012). Kavanagh *et al*. (1951) reported that pleuromutilin was isolated in crystalline form from *Ple. multilus* and *Ple. passeckerianus*, which can be inhibitory for *Staphylococcus aureus*. *Pleurotus djamor* was able to inhibit gram-negative bacteria such as *Vibrio cholera*,

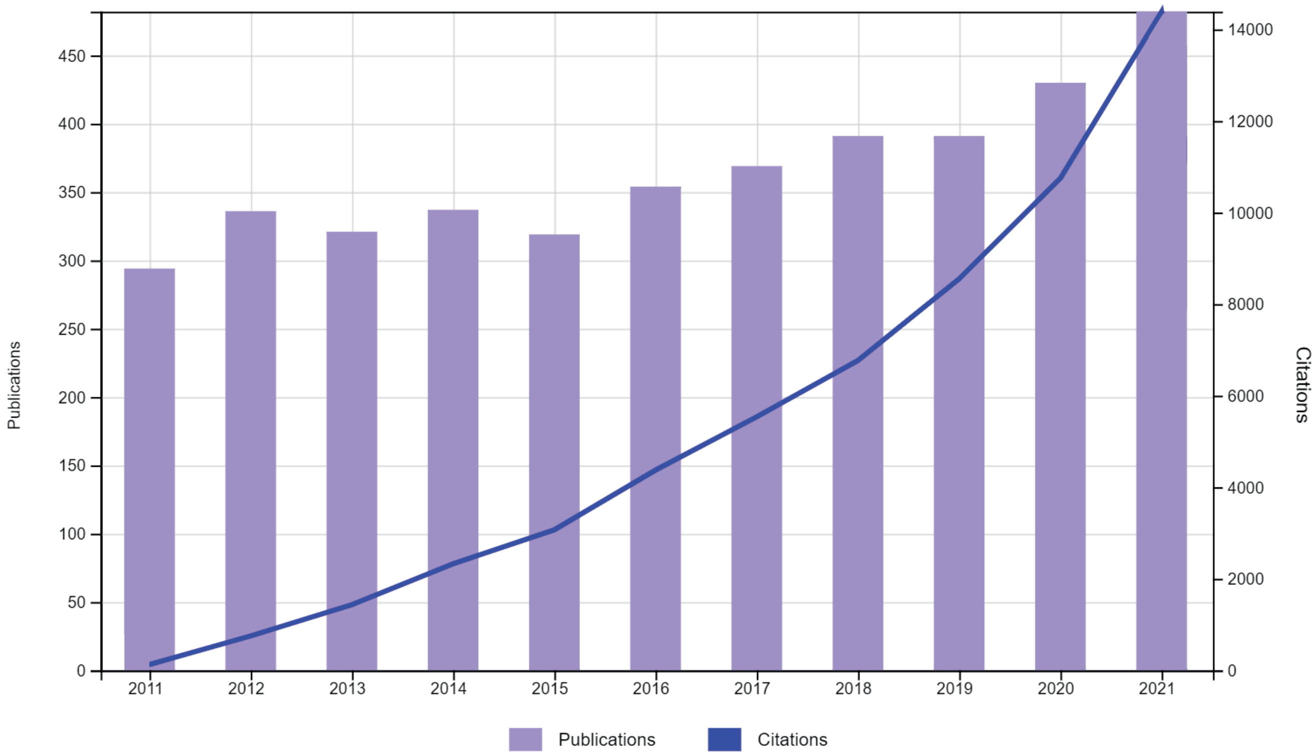

Fig. 35. Trends in research of *Pleurotus* in the period 2011–2021.

Escherichia coli and *Pseudomonas* sp. (Suresh *et al.* 2017). *Pleurotus eryngii* var. *eryngii*, *Ple. eryngii* var. *ferulae*, *Ple. eryngii* var. *elaeoselini*, and *Ple. nebrodensis* inhibited activity of bacterial strains of medical relevance such as *Staphylococcus aureus*, *S. epidermidis*, *Pseudomonas aeruginosa*, and *Escherichia coli* (Schillaci *et al*. 2013). *Pleurotus* species contain a high content of proteins, carbohydrates, fibre, minerals, vitamins, and low-fat content (Cohen *et al*. 2002, Bonatti *et al*. 2004). *Pleurorus* species have been used in traditional medicine for approximately 35 disorders or diseases (Guzmán 2000). *Pleurotus* species are also becoming increasingly attractive as sources for the development of new drugs and functional foods development.

Cultivation of Pleurotus species

Mushrooms have been consumed by humankind for millennia, and have high value. Cultivation of mushrooms is important economically (Girmay *et al*. 2016). *Pleurotus* species are the largest group of cultivated mushrooms in the world, ranking second in the world mushroom market, and the most popular consumed. *Pleurotus* species can be cultivated on a number of low-cost agro-industrial and forestry wastes, and they thrive on hardwood by-products such as sawdust (Girmay *et al*. 2016, Thongklang & Luangharn 2016), paper wastes (Girmay *et al*. 2016), pulp sludge, several agricultural wastes such as cocoa shell waste (Martínez-Carrera 1998), corn (Dias *et al*. 2003, Naraian *et al*. 2009), cotton waste (Chang *et al*. 1981), cotton seed *(Girmay et al*. 2016), diverse plant leaves, grass (Girmay *et al*. 2016), cereal straw (Mehta *et al*. 1990),

Table 20. Top 10 cited articles related to *Pleurotus* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Lignocellulosic agriculture wastes as biomass feedstocks for second-generation bioethanol production: concepts and recent developments	316	Saini *et al.* (2015)
2	Structure–function relationship among bacterial, fungal and plant laccases	286	Dwivedi *et al.* (2011)
3	Fungal pretreatment of lignocellulosic biomass	257	Wan & Li (2012)
4	Antioxidant properties of phenolic compounds occurring in edible mushrooms	250	Palacios *et al.* (2011)
5	Macro and trace mineral constituents and radionuclides in mushrooms: health benefits and risks	238	Falandysz *et al.* (2013)
6	Recent developments in mushrooms as anti-cancer therapeutics: a review	216	Patel & Goyal (2012)
7	Induction and transcriptional regulation of laccases in fungi	200	Piscitelli *et al.* (2011)
8	Fungal laccase, manganese peroxidase and lignin peroxidase: Gene expression and regulation	191	Janusz *et al.* (2013)
9	The amazing potential of fungi: 50 ways we can exploit fungi industrially	186	Hyde *et al.* (2019b)
10	Antioxidant properties and phenolic profile of the most widely appreciated cultivated mushrooms: A comparative study between *in vivo* and *in vitro* samples	182	Reis *et al.* (2012)

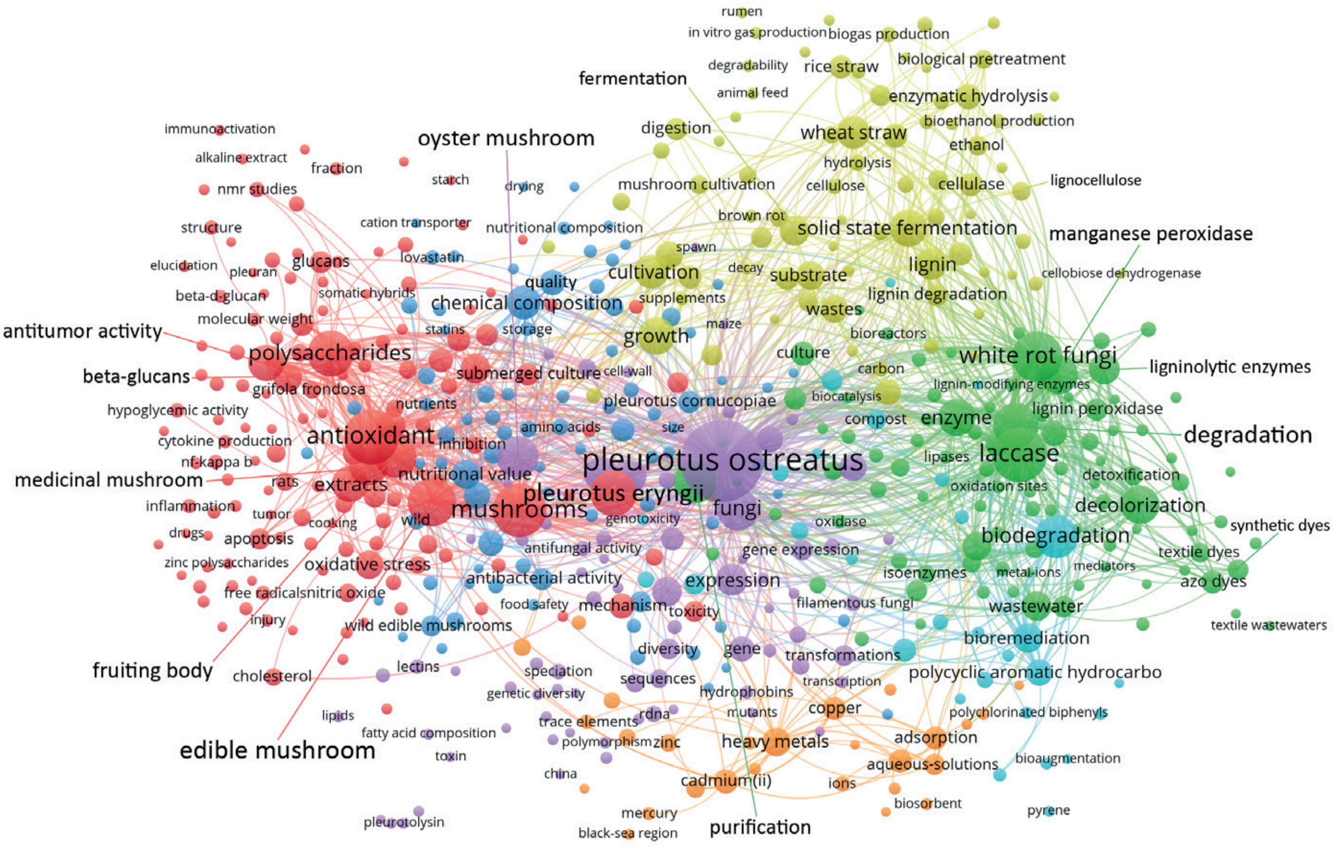

Fig. 36. Network visualisation of keywords of the publications related to *Pleurotus*. The larger the text and the circle the more often the subject has been cited.

sugarcane bagasse (Ragunathan *et al*. 1996), wheat straw (Zhang *et al*. 2002), coffee residues such as coffee grounds (Fan *et al*. 2000), and hulls, stalks, and leaves of banana (Mondal *et al.* 1970). The production and consumption of *Pleurotus* have increased significantly in recent years (Chang 1999), with prices varying between 3.91 and 7.84 US dollars per kg depending on product presentation (Vargas *et al*. 2020). The article "Cultivation of *Ple. ostreatus* and other edible mushrooms" (Sánchez 2010) is ranked among the top 10 cited published articles. Oyster mushrooms are cultivated in a shorter growth time when compared with other edible mushrooms (Sánchez 2010). *Pleurotus ostreatus* is the most cultivated mushroom for food purposes and to obtain income (Cohen *et al*. 2002). Other commercial species reported include *Ple. citrinopileatus* (yellow oyster mushroom or golden oyster mushroom), *Ple. cystidiosus* (abalone mushroom or maple oyster mushroom), *Ple. cornucopiae*, *Ple. djamor* (pink oyster mushroom), *Ple. florida* (white oyster mushroom), *Ple. flabellatus* (red oyster mushroom), *Ple. giganteus* (giant oyster mushroom), *Ple. ostreatus* (tree oyster), *Ple. pulmonarius* (Indian oyster or Italian oyster), *Ple. sapidus* (black oyster mushroom), and *Ple. tuber-regium* (king tuber mushroom) (Samsudin & Abdullah 2019).

Author: M. Phonemany

18. **Ganoderma** P. Karst., Revue Mycol., Toulouse 3(9): 17. 1881.

Type species: *Ganoderma lucidum* (Curtis) P. Karst.

Classification: *Basidiomycota*, *Agaricomycotina*, *Agaricomycetes*, *Polyporales*, *Ganodermataceae.*

Background

Ganoderma was established by Karsten (1881) with *G. lucidum* as the type species. Justo *et al*. (2017) treated *Ganodermataceae* as a synonym of *Polyporaceae*, while Cui *et al*. (2019) stated that *Ganoderma* was not included in *Polyporaceae* because their double-walled basidiospores are quite different from *Polyporaceae*. Sun *et al.* (2022) treated *Ganodermataceae* as an independent family based on its remarkable morphological features. The genus *Ganoderma* has been divided into three subgenera known as *Ganoderma* (which includes two sections *Ganoderma* and *Phaenema*), *Elfvingia*, and *Trachyderma*. *Ganoderma* species delimitation is unique to laccate and non-laccate basidiocarps, truncated double-walled basidiospores, and an apical germinal pore (Moncalvo & Ryvarden 1997, Ryvarden 2004). Kirk *et al*. (2008) mentioned that globally there are 80 species of *Ganoderma*, while Index Fungorum (2022) lists 489 taxa (currently 495) and MycoBank records about 500 taxa (currently 539) (Crous *et al.* 2004). The taxonomy of *Ganoderma* is unclear, and it can be a confusing genus to study due to the highly variable morphological features of the species (Ryvarden 2000, Chen *et al.* 2012b, Papp *et al.* 2017, Hapuarachchi *et al*. 2019, Tchotet-Tchoumi *et al*. 2019). A high level of phenotypic plasticity of the basidiomes at the macroscopic level has led to considerable confusion in the taxonomy of *Ganoderma* (Pilotti *et al.* 2005). Its basidiome features are also influenced by the interaction of both intrinsic and extrinsic factors (Moore *et al.* 2008). *Ganoderma* has high genetic diversity and substantial morphological variation, even within species. *Ganoderma* morphology may alter due to the influence of climate, nutrition, vegetation, and geography (Wu & Dai 2005).

Ganoderma is a cosmopolitan genus and some of the species are pathogenic and grow as facultative parasites that can live as saprobes on decaying logs and stumps or associated with roots of living and dead trees (Moncalvo & Ryvarden 1997, Pilotti *et al*. 2005, Singh *et al*. 2007). Diseases caused by *Ganoderma* species result in lower yields in economically important trees (Wong *et al*. 2012). Most *Ganoderma* species are regarded as plant pathogens of trees, such as *G. australe* which is associated with *Castanopsis* spp. (Luangharn *et al*. 2017), *G. boninense* which is pathogenic to oil palm (Pilotti 2005), *G. leucocontextum* causes diseases in *Cyclobalanopsis glauca* trees (Li *et al*. 2015b), and *G. tropicum*, which grows in a solitary manner on living *Dipterocarpus* species (Luangharn *et al*. 2019).

Ganoderma species have been widely utilised as traditional medicines for millennia in Asia (Chang & Wasser 2012, Li *et al*. 2015b, Zhou *et al*. 2015a, Hapuarachchi *et al*. 2018). *Ganoderma* species are economically important as they have potential nutritional and therapeutic values. Its highly prized medicinal value is widely researched (De Silva *et al*. 2012b, Hapuarachchi *et al*. 2018).

Ecological and economic significance

Ganoderma species are distributed in sub-tropical to tropical and temperate regions but are particularly diverse in tropical regions (Cao & Yuan 2013). They are important wood-decaying fungi. Most species are regarded as pathogens that possess a wide host range (Wong *et al*. 2012) with more than 44 species from 34 genera of host plants (Venkatarayan 1936). *Ganoderma* can cause severe diseases in economically important trees and perennial crops, especially in tropical countries (Pilotti 2005). *Ganoderma* species are white rot fungi and have ecological importance in the breakdown of woody plants. These fungi decay lignin, hemicellulose and cellulose resulting in a severe loss of woody plant strength (Ćilerdžić *et al*. 2017). *Ganoderma* possess lignocellulose decomposing enzymes useful for bioenergy production and bioremediation (Kües *et al*. 2015). There is a high degree of morphological variation, even within species, perhaps due to ecological factors (Pilotti *et al*. 2004).

Ganoderma has been used in traditional medicines for hundreds of years in Asian countries and is increasingly being used in pharmaceutical industries worldwide. However, these fungi are not edible, since their basidiomes are always corky, tough, and bitter in taste (Hapuarachchi *et al*. 2019). Over the past two decades, the *Ganoderma* industry has developed greatly and today offers thousands of products to the markets. *Ganoderma* products are available in many forms such as dried sporocarps, dietary supplements, spore capsules, and cosmetic products (Taofiq *et al*. 2016a, b). Currently, *G. lucidum* is estimated to be worth more than 2.5 billion US dollars in Asian countries such as China, Korea and Japan (Lai *et al*. 2004). *Ganoderma tsugae* is regarded as a healthy food as it enhances the immune system and improves metabolic functions (Lai *et al*. 2004, Singh *et al*. 2013). *Ganoderma lucidum* is a high-priced product which is used as ornamental in Bonsai products to decorate gardens, ornaments and many other art products. However, there are problems with the industry which prevent it from establishing an effective market (Hapuarachchi *et al*. 2018).

Research interests

There are 3 699 publications and 44 643 citations from 2011–2021 in the Web of Science (Fig. 37), with the top 10 most cited articles listed in Table 21. Most of the publications focused on valuable medicinal mushrooms and natural bioactive compounds (polysaccharides, triterpenoids, sterols, and secondary metabolites) for potential use in clinical perspectives applications (anticancer, antioxidant, anti-tumour, immunomodulating) (Fig. 38).

The genus *Ganoderma* is economically important, as its members are regarded as valuable medicinal mushrooms (Dai *et al*. 2009, Chang & Wasser 2012). *Ganoderma* consumption has consistently been shown to have beneficial effects on human health and can be used to remedy a wide range of human diseases (Zong *et al*. 2012, Richter *et al*. 2015, Wang *et al*. 2015e).

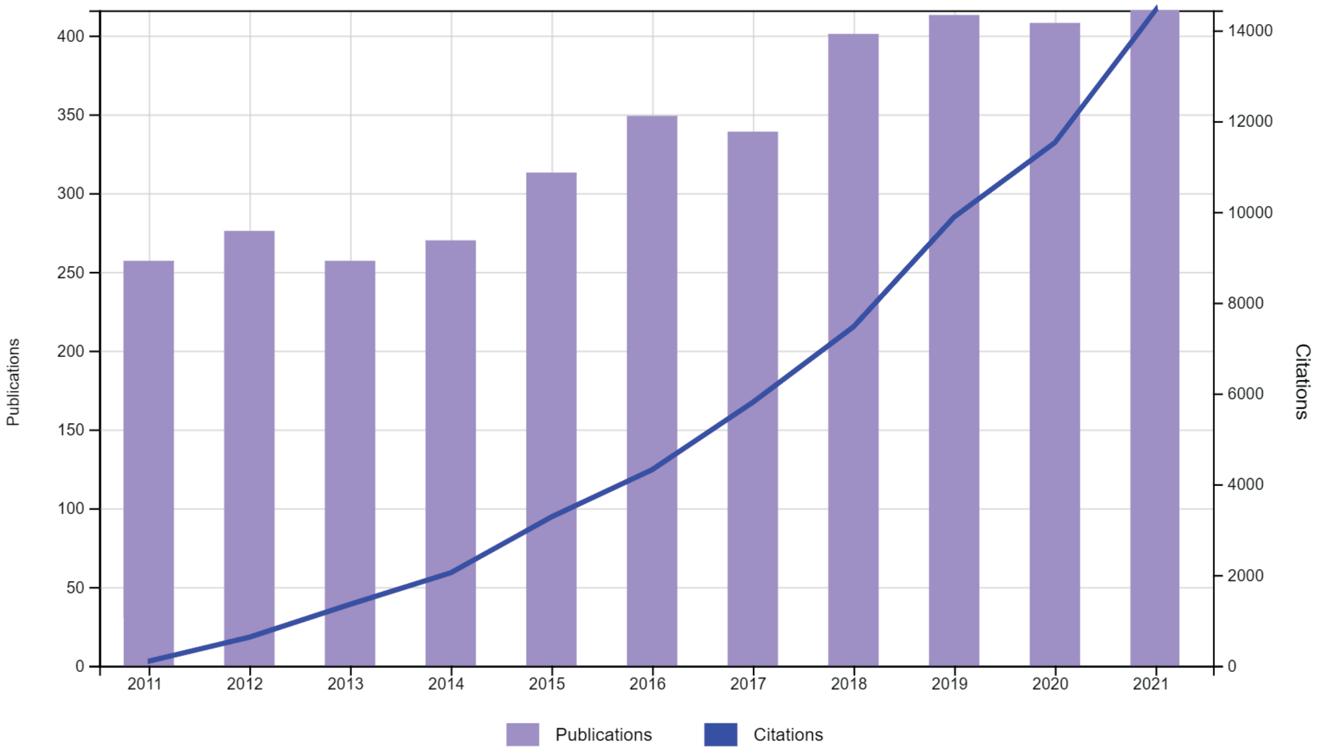

Fig. 37. Trends in research of *Ganoderma* in the period 2011–2021.

Table 21. Top 10 cited articles related to *Ganoderma* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	*Ganoderma lucidum* reduces obesity in mice by modulating the composition of the gut microbiota	702	Chang *et al.* (2015)
2	Immune evasion in cancer: Mechanistic basis and therapeutic strategies	637	Vinay *et al.* (2015)
3	Reviews on mechanisms of *in vitro* antioxidant activity of polysaccharides	399	Wang *et al.* (2015)
4	Anticancer polysaccharides from natural resources: A review of recent research	387	Zong *et al.* (2012)
5	The role of culinary-medicinal mushrooms on human welfare with a pyramid	341	Chang & Wasser (2012)
6	Genome sequence of the model medicinal mushroom *Ganoderma lucidum*	304	Chen *et al.* (2012b)
7	Tissue invasion and metastasis: molecular, biological and clinical perspectives	281	Jiang *et al.* (2015)
8	Antioxidative and immunomodulating activities of polysaccharide extracts of the medicinal mushrooms *Agaricus bisporus*, *Agaricus brasiliensis*, *Ganoderma lucidum* and *Phellinus linteus*	279	Kozarski (2011)
9	Current findings, future trends, and unsolved problems in studies of medicinal mushrooms	267	Wasser (2011)
10	Macro and trace mineral constituents and radionuclides in mushrooms: health benefits and risks	238	Falandysz & Borovička (2013)

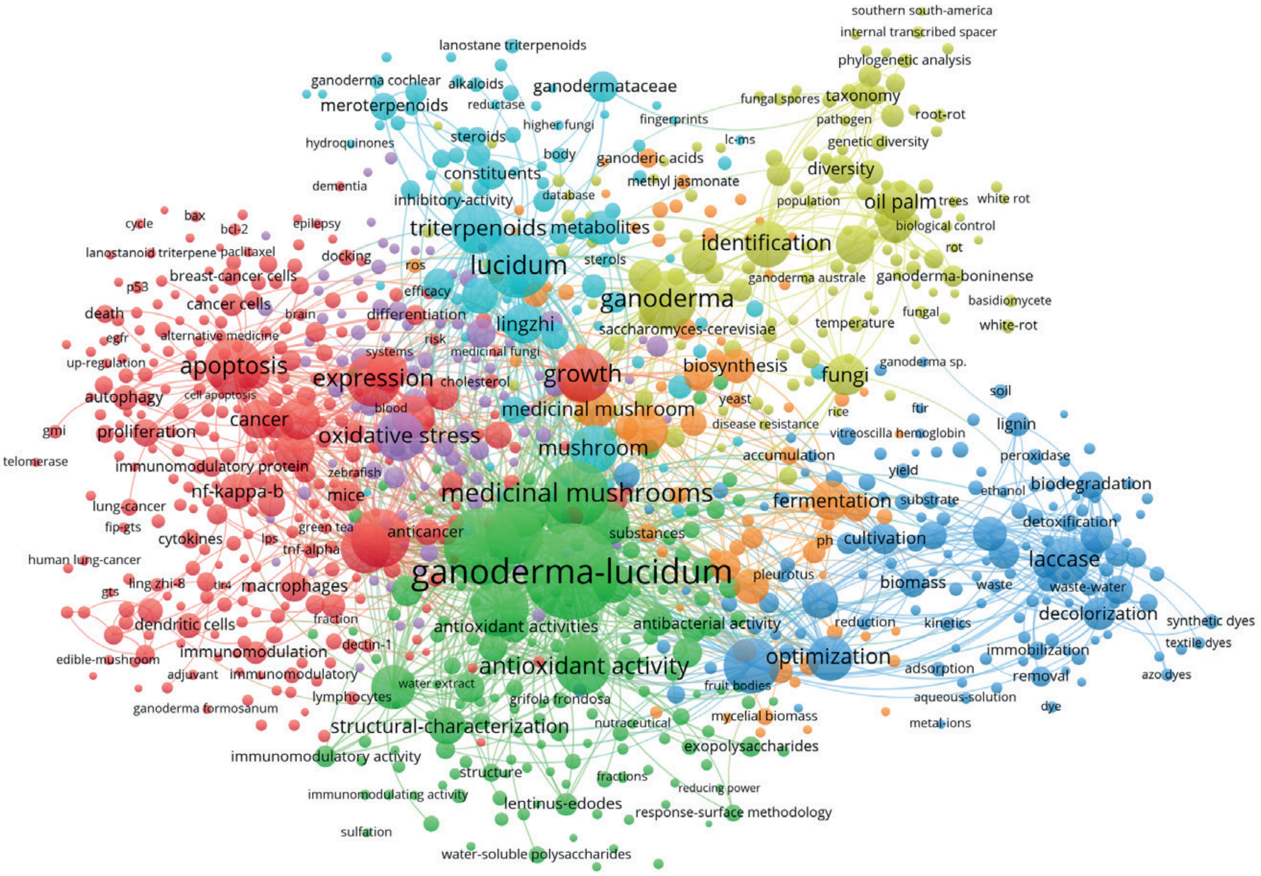

Fig. 38. Network visualisation of keywords of the publications related to *Ganoderma*. The larger the text and the circle the more often the subject has been cited.

More than 400 bioactive compounds have been found in various *Ganoderma* species such as fatty acids, polysaccharides, protein, steroids, triterpenoids, and secondary metabolites (*i.e.*, ganoderic acids, ganodermanondiol, ganodermanontriol, and ganodermadiol) (Shim *et al*. 2004, Qiao *et al*. 2005, Teng *et al*. 2011, Richter *et al*. 2015). Those valuable natural compounds are used to treat and remedy many pathological diseases such as hypertension, hypercholesterolemia, bronchitis, asthma, diabetes, and cancer (Chang & Wasser 2012, De Silva *et al*. 2012a, Richter *et al*. 2015, Abate *et al*. 2020). Additionally, there are reports of several metabolic activities of *G. lucidum* performed in both *in vitro* and *in vivo* studies. The major consideration is given to therapeutic strategies (Chang *et al.* 2015, Vinay *et al.* 2015), the benefits that have been claimed for the use of mushrooms in treating cancer, and the prospects of using medicinal mushrooms (Wasser 2011).

Bioactive metabolites isolated from *Ganoderma* mushrooms have also shown potential success in cancer treatment as biological immunotherapeutic agents that stimulate the immune system against cancer cells (Kozarski 2011). Hence, pharmacologically active constituents of *G. lucidum* contribute to positive immune responses. Improved application methods and further clinical research on *G. lucidum* on human subjects are needed.

Author: T. Luangharn

19. ***Neurospora*** Shear & B.O. Dodge, J. Agric. Res., Washington 34: 1025. 1927.

Type species: *Neurospora sitophila* Shear & B.O. Dodge

Classification: *Ascomycota*, *Pezizomycotina*, *Sordariomycetes*, *Sordariales*, *Sordariaceae*.

Background

The genus *Neurospora* was first found in bakeries in France in 1843 where it formed an asexual morph on bread, and later the discovery of sexual sporocarps by mycologists Cornelius L. Shear and Bernard O. Dodge placed this fungus in a new genus *Neurospora* (Shear & Dodge 1927). Members of this genus were first usually found in burned/unburned vegetation in terrestrial habitats or soil in tropical and subtropical regions but were later identified across the globe (Perkins *et al.* 1976, Perkins & Raju 1986, Perkins & Turner 1988, Turner *et al.* 2001, García *et al.* 2004). The sexual morph of this genus is characterised by dark brown ascospores with ornamented surfaces and the asexual morph is chrysonilia-like with both macroconidia and microconidia (Shear & Dodge 1927, Arx 1981a, b, Jacobson *et al.* 2004). There are three mating strategies in *Neurospora viz.*: homothallism, pseudohomothallism and heterothallism (Shear &

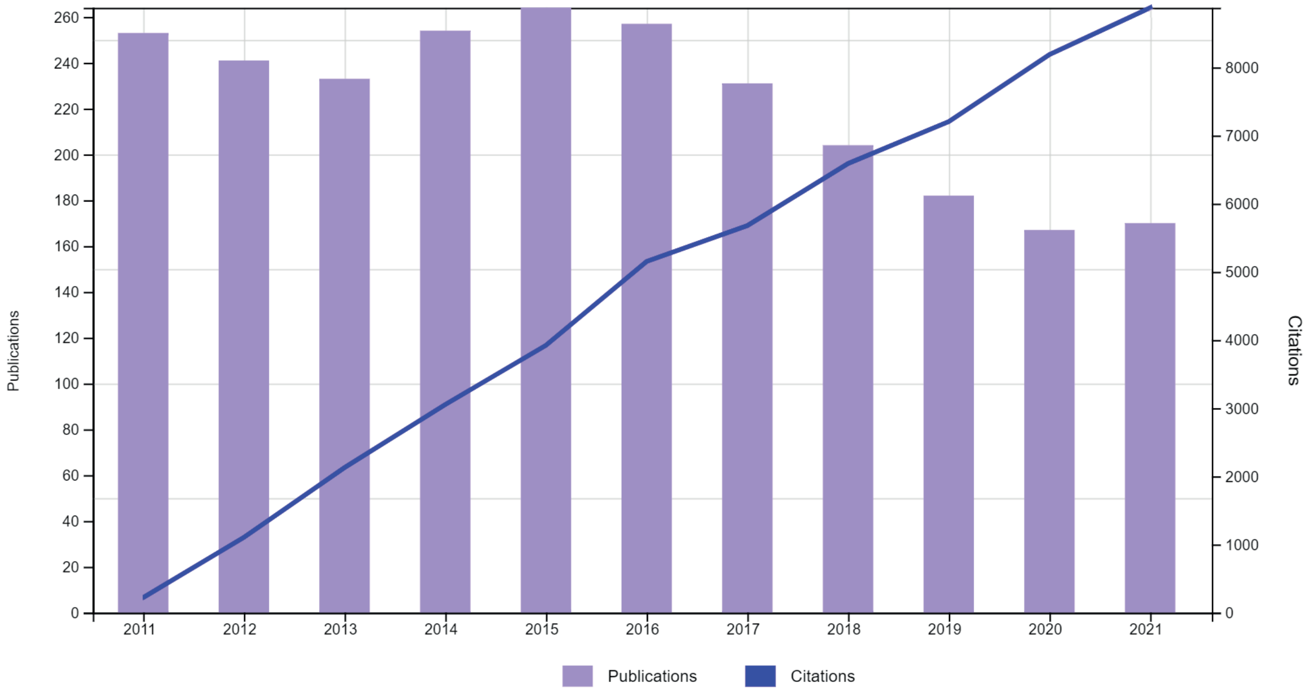

Fig. 39. Trends in research of *Neurospora* in the period 2011–2021.

Table 22. Top 10 cited articles related to *Neurospora* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Cellobiose dehydrogenase and a copper-dependent polysaccharide monooxygenase potentiate cellulose degradation by *Neurospora crassa*	419	Phillips *et al.* (2011)
2	Oxidative cleavage of cellulose by fungal copper-dependent polysaccharide monooxygenases	314	Beeson *et al.* (2012)
3	Fungal cell wall organization and biosynthesis	276	Free (2013)
4	Codon usage influences the local rate of translation elongation to regulate co-translational protein folding	273	Yu *et al.* (2015a)
5	DNA methylation and demethylation in mammals	266	Chen & Riggs (2011)
6	Non-optimal codon usage affects expression, structure and function of clock protein FRQ	250	Zhou *et al.* (2013)
7	Discovery of LPMO activity on hemicelluloses shows the importance of oxidative processes in plant cell wall degradation	249	Agger *et al.* (2014)
8	Quorum sensing in fungi - a review	215	Albuquerque & Casadevall (2012)
9	Extracellular electron transfer systems fuel cellulose oxidative degradation	215	Kracher *et al.* (2016)
10	A C4-oxidizing lytic polysaccharide monooxygenase cleaving both cellulose and cello-oligosaccharides	210	Isaksen *et al.* (2012)

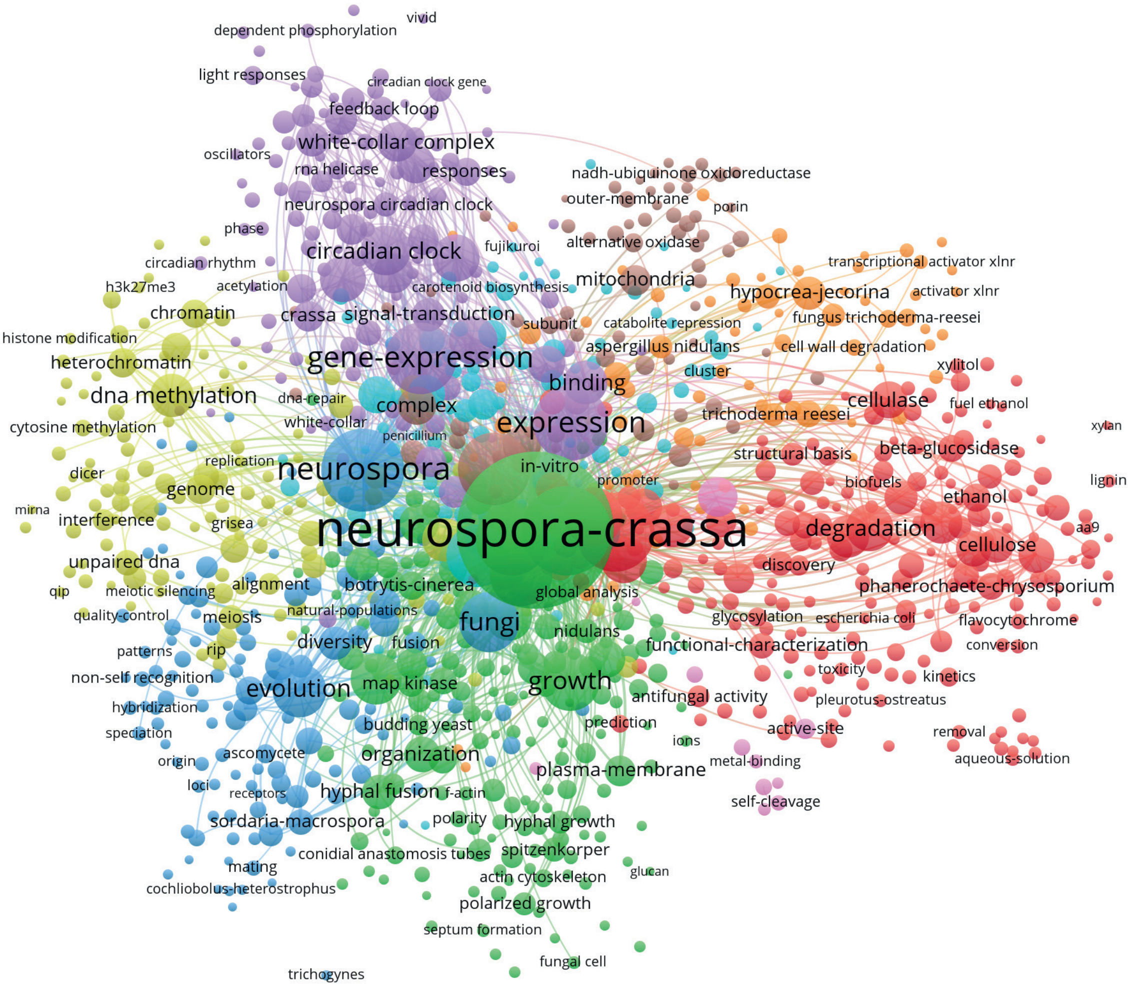

Fig. 40. Network visualisation of keywords of the publications related to *Neurospora*. The larger the text and the circle the more often the subject has been cited.

Dodge 1927, Tai 1935, Mahoney *et al.* 1969, Krug & Khan 1991). The traditional identification of *Neurospora* species is based on distinguishing ascospore wall ornamentation (García *et al.* 2004, Cai *et al.* 2006a). García *et al.* (2004) and Cai *et al.* (2006a) found that only using ascospore wall structure to distinguish *Neurospora* species results in species being polyphyletic in the *Sordariales* phylogenetic analysis. The mating strategy and ornamentation of the epispore are the most important characteristics to define the phylogenetic relationship in *Neurospora* (Whitehouse 1949, Taylor & Natvig 1989, Grognet & Silar 2015, García *et al.* 2004, Cai *et al.* 2006a).

The asexual growth and reproduction, the asexual-sexual transition, and sexual development and reproduction are well-studied developmental phases of the life cycles of *Neurospora* (Lehr *et al.* 2014, Dunlap *et al.* 2007). In addition, *Neurospora crassa* is known as a model eukaryotic multicellular organism which is used in research for the one-gene–one-enzyme, genetics, developmental biology, and molecular biology (Beadle & Tatum 1941, Cogoni & Macino 1999, Loros & Dunlap, 2001, Davis & Perkin 2002, Honda *et al.* 2020). Systematic sampling of natural populations of *Neurospora* was started in 1968 and the results were presented by Perkins *et al.* (1976). A comprehensive review of the genus *Neurospora* was presented with useful information on experimental laboratory studies, field-collection and analysing data together with ecology, geographical distribution, species status, genetic variation, and polymorphism was provided by Perkins and Turner (1988). Studies on biological and phylogenetic species of *Neurospora* (Dettman *et al.* 2001, 2003, 2006) helped to understand the clock variation within different ecotypes of *Neurospora*.

Ecological and economic significance

Among filamentous fungi, *Neurospora* species have been widely used as a model for clock variation studies (Koritala & Lee 2017). Several *Neurospora* species were listed as natural variant studies in Koritala & Lee (2017). *Neurospora* species are well-characterised, especially *Neurospora crassa* (Colot *et al.* 2006, McCluskey *et al.* 2010, Koritala & Lee 2017). *Neurospora* species have multiple advantages and have been widely used as model species to understand the biological aspects of natural variations, *viz.* biochemistry, ecology, evolution, genetics, and circadian biology (Koritala & Lee 2017, Perkins *et al.* 1976, Turner *et al.* 2001).

Research interests

There are 2 456 publications and 44 091 citations from 2011–2021 in the Web of Science (Fig. 39), with the top 10 most cited articles listed in Table 22. Most publications focused on a model for clock variation studies of *Neurospora* (Fig. 40).

Toxins

Neurosporin A and the salicylaldehyde sordarial are toxins produced by *Neurospora* species which have a defense mechanism (Zhao *et al.* 2017c, 2019c).

Taxonomy and phylogeny

Huang *et al.* (2021c) referred to sequence data by Cai *et al.* (2006a), Wang *et al.* (2019d, e) and Vu *et al.* (2019) to build a phylogenetic tree and used combined sequence data from the markers LSU, ITS and *tub*. Based on a multi-gene analysis of *Neurospora*, Huang *et al.* (2021c) divided *Sordaria* into four clades within *Sordariaceae*. They mentioned that the positions of *Neurospora* and *Sordaria* species are usually unstable in single-gene or even multi-gene analyses. Thus, the morphology of *Neurospora* and *Sordaria* can be used to distinguish them.

Author: S. Tibpromma

20. ***Cladosporium*** Link, Mag. Ges. Naturf. Freunde Berlin 7: 37. 1816.

Type species: *Cladosporium herbarum* (Pers.) Link

Classification: *Ascomycota*, *Pezizomycotina*, *Dothideomycetes*, *Cladosporiales*, *Cladosporiaceae.*

Background

Cladosporium is one of the largest genera of hyphomycetes with more than 750 species epithets listed in MycoBank, including about 250 recognised species. Species of *Cladosporium* are among the most common fungi worldwide, being isolated from almost any environmental source and geographic location (Bensch *et al.* 2012). Most species primarily occur in soil, food, paint, textiles and other organic matter (Ma *et al.* 2017, Iturrieta-González *et al.* 2021) or colonise as secondary invaders leaf lesions caused by plant pathogenic fungi (Ellis 1971, 1976, Bensch *et al.* 2012, 2015). Several species are important pathogens of plants (Schubert 2005, Bensch *et al.* 2012, Rosado *et al.* 2019) or occur as hyperparasites on other fungi (Heuchert *et al.* 2005). Some are also able to affect animals and humans (De Hoog *et al.* 2000, Sandoval-Denis *et al.* 2015, 2016, Yew *et al.* 2016, Batra *et al.* 2019, Velázquez-Jiménez *et al.* 2019). *Cladosporium* species are considered among the most widespread fungi in buildings and indoor environments as well as in outdoor and indoor air (Fradkin *et al.* 1987, Flannigan 2001, Horner *et al.* 2004, Bensch *et al.* 2018). With their relatively small conidia, usually formed in branched chains, they are well adapted to be spread easily in large numbers over long distances. Because many *Cladosporium* species are cosmopolitan agents of decay, deterioration, or may cause allergies or even diseases of plants, animals and human beings, and are often of high environmental impact, the genus is of special interest to researchers in a wide variety of disciplines (Bensch *et al.* 2012).

Cladosporium, a monophyletic genus residing in the *Cladosporiaceae* (*Cladosporiales*, *Dothideomycetes*; Abdollahzadeh *et al.* 2020), is well circumscribed by having a unique coronate structure of its conidiogenous loci and conidial hila, consisting of a central convex dome surrounded by a raised periclinal rim (David 1997, Braun *et al.* 2003, Bensch *et al.* 2012). *Cladosporium* was established by Link in 1816, who included four species of which *Cl. herbarum* was proposed as lectotype species by Clements & Shear (1931), a decision followed by De Vries (1952) and Hughes (1958). It developed to be one of the most heterogeneous genera of hyphomycetes as all kinds of unrelated dematiaceous hyphomycetes characterised by having amero- to phragmosporous conidia formed in acropetal chains have been assigned to *Cladosporium s. lat*. Various authors discussed the heterogeneity of *Cladosporium s. lat.* and proposed new, more natural circumscriptions of this genus (*e.g.*, Von Arx 1981, 1983, Morgan-Jones & Jacobsen 1988, McKemy & Morgan-Jones 1990, Morgan-Jones & McKemy 1990, Braun 1995, Partridge & Morgan-Jones 2002, 2003). David (1997) revised *Cladosporium* species previously referred to as *Heterosporium* and demonstrated that the genus *Cladosporium* is well-characterised and easily recognisable by its unique structure of the conidiogenous loci and conidial hila. A few years later, the first attempts were made to revise and monograph *Cladosporium s. lat.* (Crous *et al.* 2001a). Braun *et al.* (2003) published results of the first molecular examination of *Cladosporium s. lat.*, clearly confirming the strong heterogeneity of this genus. In the last two decades, various genera with cladosporium-like morphs could be separated from *Cladosporium s. str.* (De Hoog *et al.* 1995, Seifert *et al.* 2004, Heuchert *et al.* 2005, Crous *et al.* 2006a, 2007, 2017, Braun *et al.* 2008, Bezerra *et al*. 2017), based on re-assessments of morphological features and molecular data. Efforts to clarify the phylogeny and taxonomic structure of *Cladosporium* species and allied fungi have resulted in a modern redefinition of the genus (Crous *et al.* 2007, Schubert *et al.* 2007, Zalar *et al.* 2007, Bensch *et al.* 2010, 2012, 2018). Due to continuous isolations from a wide range of substrates, collected on various continents, the number of *Cladosporium* species has steadily increased (Crous *et al.* 2014a, Bensch *et al.* 2015, Braun *et al.* 2015, Razafinarivo *et al.* 2016, Marin-Felix *et al.* 2017, Sandoval-Denis *et al.* 2016, Ma *et al.* 2017, Crous *et al.* 2018, Tibpromma *et al.* 2018a, Rosario *et al.* 2019, Iturrieta-González *et al.* 2021, Costa *et al.* 2022, Moharram *et al.* 2022, Chethana *et al.* 2023, Lee *et al.* 2023, Yang *et al.* 2023b). Sexual morphs, previously assigned to the genus *Davidiella*, are known for only a few species.

Within *Cladosporium*, three major species complexes are recognised: *Cl. herbarum*, *Cl. sphaerospermum* and *Cl. cladosporioides* species complexes. Morphological features used for the circumscription of these complexes have been summarised in Bensch *et al.* (2012, 2015) and Marin-Felix *et al.* (2017a). Most *Cladosporium* species can be referred to one of the three species complexes based on their morphology. However, within a given species complex, the differentiation of particular species of *Cladosporium* is often difficult based on morphological characters alone since many species have overlapping characteristics. Therefore, polyphasic approaches including multilocal phylogenetic analyses are necessary for species delimitations and proper identifications. Previous studies have already revealed the existence of numerous cryptic species in the three species complexes (Schubert *et al.* 2007, Zalar *et al.* 2007, Bensch *et al.* 2010, 2018, Sandoval-Denis *et al.* 2016), but many more are to be expected.

Ecological and economic significance

Cladosporium cladosporioides

This species represents a species complex of morphologically almost indistinguishable, but phylogenetically distinct species (Bensch *et al.* 2010, 2018). Given their high morphological similarity, the use of a molecular approach for the correct identification of all these species is highly recommended. *Cladosporium cladosporioides s. lat.* is a common air- and soil-borne saprotroph and is frequently encountered as a contaminant. It has been isolated from food sources such as cereal grain, coffee and peas, as fruit contaminants causing spoilage in low-temperature storage and from indoor environment sources such as water-damaged wood, wallpaper and plaster (Samson *et al.* 2019). It is one of the most predominant fungi in outdoor air (Fradkin *et al.* 1987), its spores being important in seasonal allergic diseases. *Cladosporium cladosporioides* rarely causes invasive disease in animals and humans, but is an important agent of plant disease, attacking both the leaves and fruits of many plants (Nam *et al.* 2015). It is found as a common endophytic fungus as well as a secondary invader on necrotic parts of many different host plants, including lesions caused by pathogenic fungi (Bensch *et al.* 2012). Some leaf-spotting races have been reported, but such host-specific pathogenicity is largely untested (Meneses *et al.* 2018, Robles-Yerena *et al.* 2019). Furthermore, this species is relevant as a potential biocontrol agent for plant diseases (Wang *et al.* 2013, Köhl *et al.* 2015, Torres *et al.* 2017). *Cladosporium anthropophilum*, a member of the *Cl. cladosporioides* species complex, represents a clinically relevant fungus, being the second most prevalent species identified in a set of clinical isolates from the USA after *Cl. halotolerans* (Sandoval-Denis *et al.* 2015, 2016).

Cladosporium herbarum

Cladosporium herbarum has been isolated from food sources, such as weathered cereal grain, mouldy fruit and vegetables, living and decaying plant material, cheese, butter and margarine and from indoor environment sources such as water-damaged wood, wallpaper and plaster (Samson *et al.* 2019). It is the most studied species in allergy research (Breitenbach 2008, Poll *et al.* 2009), but in recent studies (Segers *et al.* 2015, Bensch *et al.* 2018) none of the studied strains turned out to be *Cl. herbarum*. The closely allied and morphologically similar species *Cl. allicinum* proved to be one of the most common *Cladosporium* species in indoor environments instead (Segers *et al.* 2015, Bensch *et al.* 2018, Andersen *et al.* 2021).

Cladosporium sphaerospermum

Similar to the other two species, *Cladosporium sphaerospermum* represents a species complex of morphologically similar and closely allied species. *Cladosporium halotolerans* proved to be the most common *Cladosporium* species in indoor environments and is very often isolated from house dust. It is commonly found both indoors and outside and is frequently encountered as a contaminant. It has been isolated from hypersaline water, from indoor environment sources such as water-damaged bathroom and basement walls, gypsum wallboard, inner roofing in attics and from human sputum and skin (Bensch *et al.* 2018, Samson *et al.* 2019). *Cladosporium sphaerospermum* and related taxa develop under low nutrient conditions and easily cope with humidity changes, both very characteristic for indoor situations. Sandoval-Denis *et al.* (2015) reported *Cl. halotolerans* as the most frequent *Cladosporium* species recovered from clinical samples in the USA.

Research interests

There are 2 641 publications and 38 580 citations from 2011–2021 in the Web of Science (Fig. 41). The top 10 most cited articles are listed in Table 23. Most of the publications focused on the identification, diversity and phylogeny of *Cladosporium* species, their occurrence as airborne, endophytic and allergy-inducing microorganisms and their role in biodegradation, biodeterioration and indoor environments, their potential as biocontrol and antifungal agents and their produced metabolites (Fig. 42). *Cladosporium fulvum*, the causal agent of tomato leaf mould, which is frequently used as a model organism to study plant-pathogen interactions, does not belong in the genus *Cladosporium* but is *Fulvia fulva* (Videira *et al.* 2017), which belongs in the *Mycosphaerellaceae*, *Mycosphaerellales*.

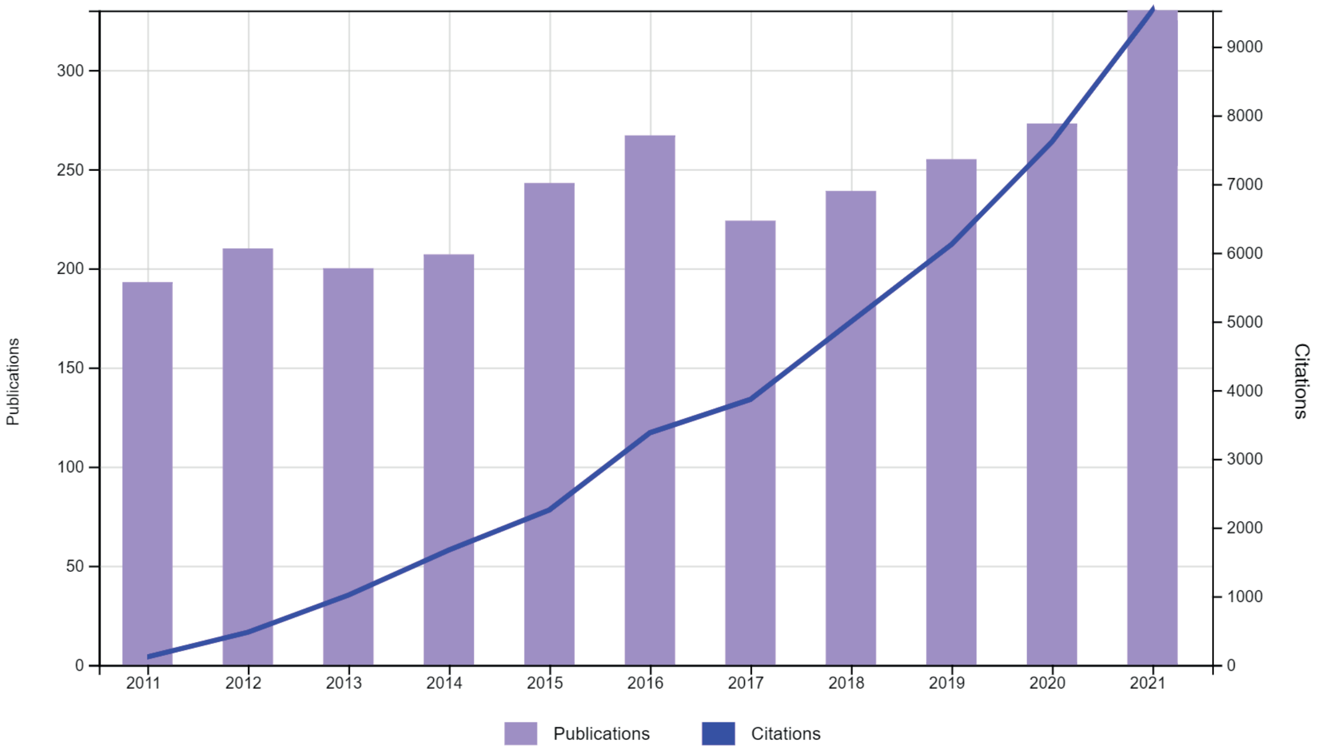

Fig. 41. Trends in research of *Cladosporium* in the period 2011–2021.

Table 23. Top 10 cited articles related to *Cladosporium* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Fungal effectors and plant susceptibility	505	Lo Presti *et al.* (2015)
2	The genus *Cladosporium*	352	Bensch *et al.* (2012)
3	Fungi and allergic lower respiratory tract diseases	305	Knutsen *et al.* (2012)
4	Associations between fungal species and water-damaged building materials	213	Andersen *et al.* (2011)
5	Analysis of two *in planta* expressed LysM effector homologs from the fungus *Mycosphaerella graminicola* reveals novel functional properties and varying contributions to virulence on wheat	196	Marshall *et al.* (2011)
6	Receptor-like kinase SOBIR1/EVR interacts with receptor-like proteins in plant immunity against fungal infection	175	Liebrand *et al.* (2013)
7	Dual disease resistance mediated by the immune receptor Cf-2 in tomato requires a common virulence target of a fungus and a nematode	171	Lozano-Torres *et al.* (2012)
8	Two for all: receptor-associated kinases SOBIR1 and BAK1	163	Liebrand *et al.* (2014)
9	The genomes of the fungal plant pathogens *Cladosporium fulvum* and *Dothistroma septosporum* reveal adaptation to different hosts and lifestyles but also signatures of common ancestry	153	De Wit *et al.* (2012)
10	Fungal effector Ecp6 outcompetes host immune receptor for chitin binding through intrachain LysM dimerization	152	Sanchez-Vallet *et al.* (2013)

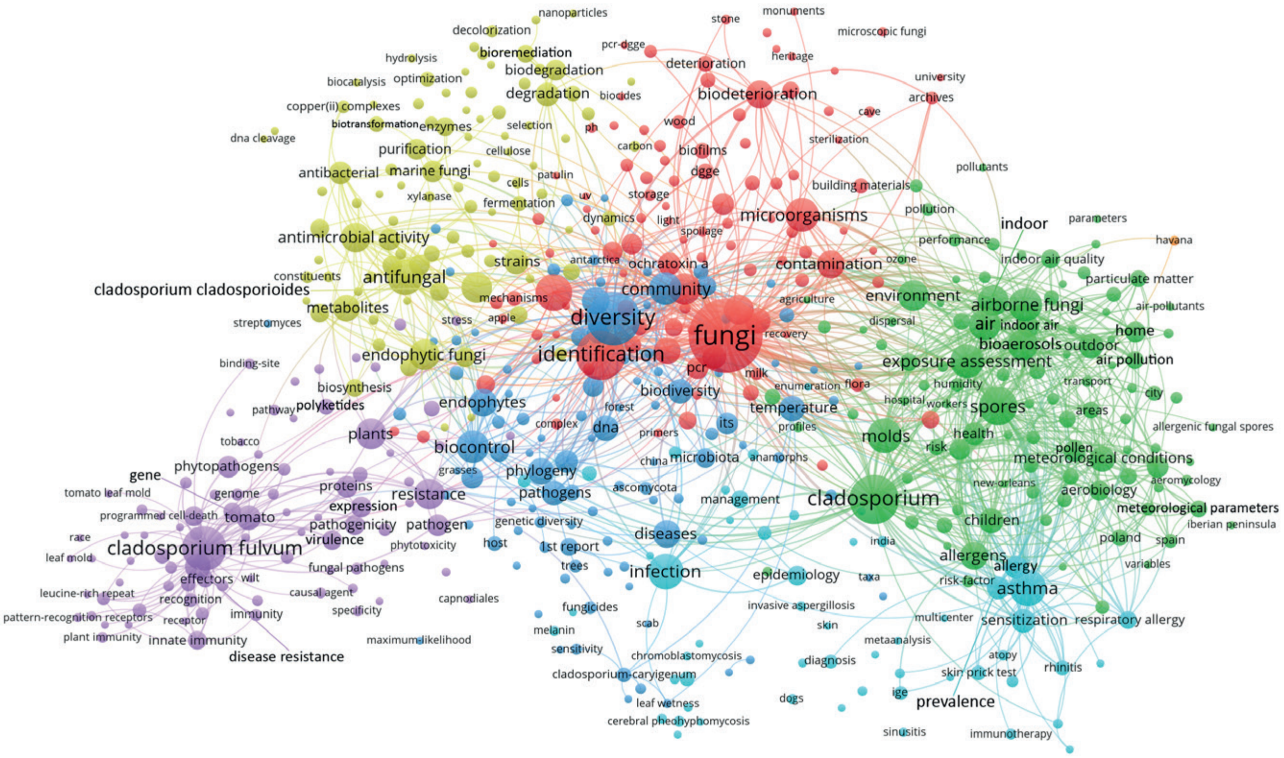

Fig. 42. Network visualisation of keywords of the publications related to *Cladosporium*. The larger the text and the circle the more often the subject has been cited.

Disease management

There are only a few economically important diseases caused by *Cladosporium* species. *Cladosporium* leaf spot of spinach, caused by *Cl. variabile*, occurs to some extent almost every year but is rarely severe. Hot water as well as chlorine seed treatment effectively eliminates *Cladosporium* from spinach seed (Du Toit *et al.* 2005). QoI fungicides have also been shown to control this disease. *Cladosporium cucumerinum*, the causal organism of crown blight and scab or gummosis disease, is widespread among members of the *Cucurbitaceae*. Several fungicides can reduce the severity of this scab if applied on a schedule after the first bloom. Fairy ring leaf spot affecting carnations, caused by *Cl. echinulatum*, can be most effectively treated with sodium bicarbonate and *Trichoderma virens* (Sandoval *et al.* 2009).

Toxins

Several mycotoxins are known to be produced by *Cladosporium* species, *viz.*, cladosporin, isocladosporin, emodin, cladosporid, cladosporol as well as several others, which represent antifungal, anti-bacterial or insecticidal compounds that have plant growth regulators or plant inhibiting activities while others are inhibitors of protein kinase C (Alwatban *et al.* 2016, Wang *et al.* 2013, 2015).

Cladosporinone was found as a new viriditoxin derivative and was studied for its cytotoxicity against the murine lymphoma cell line L5187Y (Liu *et al.* 2016f). Salvatore *et al.* (2021) provided a survey of bioactive natural compounds from *Cladosporium* species, including toxins.

Taxonomy and phylogeny

The most phylogenetically informative markers proved to be *actA* and *tef1*, while ITS sequences are usually identical for species of the same complex (Bensch *et al.* 2010, 2012, 2018, Sandoval-Denis *et al.* 2016). Although ITS is a suitable locus to identify an isolate as belonging to the genus *Cladosporium* and to some extent to a species complex, additional loci are required to reach a conclusive species (or even species complex) identification. The use of a molecular approach is strongly recommended for correct identifications of the species in this complex fungal group. A sufficient number of isolates should be included in the phylogenetic analysis to ensure that the genetic diversity of a species is covered. As starting material, a reliable backbone tree should be used. It is not advisable to blindly go on the names in GenBank as many of the names of older sequences are outdated.

Authors: U. Braun and K. Bensch

21. ***Yarrowia*** Van der Walt & Arx, Antonie van Leeuwenhoek 46: 519. 1981.

Type species: *Yarrowia lipolytica* (Wick. *et al.*) Van der Walt & Arx

Classification: *Ascomycota*, *Saccharomycotina*, *Dipodascomycetes*, *Dipodascales*, *incertae sedis.*

Background

Yarrowia species are widespread and have been isolated from various sources such as food, soil, insects, salt and fresh water as well as humans (Kurtzman *et al.* 2011, Groenewald *et al*. 2014). The first observation of the sexual morph of *Yarrowia lipolytica*, the type species, was made by Wickerham *et al.* (1970a, b) and described as *Endomycopsis lipolytica*. Yarrow (1972) transferred *E. lipolytica* to the genus *Saccharomycopsis*. *Saccharomycopsis lipolytica* appeared distinct from the other members of the genus because of the shape of its ascospores and the presence of coenzyme Q-9. Based on this, the genus *Yarrowia* was proposed by Van der Walt & Von Arx (1980) to accommodate *Y. lipolytica*. This species remained the only member of the genus for more than 30 years until Groenewald & Smith (2013) illustrated the presence of the sexual life cycle of *Candida deformans* and proposed a new combination *Yarrowia deformans*. Most of the sexually reproducing *Yarrowia* species were found to be mainly heterothallic (Knutsen *et al*. 2007, Groenewald & Smith 2013) as asci are formed following the conjugation of complementary mating types. However, a few *Y. lipolytica* isolates were found to be self-sporulating.

In the past years, *Yarrowia* was expanded from comprising only one species to 14 species. Several studies included numerous phylogenetically closely related asexual *Candida* species as new combinations, and novel species were described (Kurtzman *et al*. 2011, Groenewald & Smith 2013, Nagy *et al*. 2014, Crous *et al*. 2017a). The currently described *Yarrowia* species are *Y. deformans*, *Y. lipolytica*, *Y. parophonii* and *Y. porcina* having a sexual morph and the asexual reproducing species *Y. alimentaria*, *Y. bubula*, *Y. brassicae*, *Y. divulgata*, *Y. galli*, *Y. hollandica*, *Y. keelungensis*, *Y. osloensis*, *Y. phangngaensis* and *Y. yakushimensis. Candida hispaniensis*, although not yet proposed as a new combination within *Yarrowia*, clusters with the rest of the *Yarrowia* species in most phylogenetic studies. Most species of *Yarrowia* can assimilate only a few carbon compounds and are almost indistinguishable physiologically from one another (Kurtzman *et al*. 2011, Groenewald & Smith 2013, Nagy *et al*. 2014, Crous *et al*. 2017a).

The currently most used and best method to describe novelties and distinguish among species of this genus is by sequence analysis of the D1/D2 domains of LSU nrRNA gene and the ITS regions (Kurtzman & Robnett 1994, 1995, 1998, Fitzpatrick *et al*. 2006, James *et al*. 2006, Kurtzman *et al*. 2011, Groenewald & Smith 2013, Nagy *et al*. 2014, Crous *et al*. 2017b, Liu *et al*. 2018b). *Yarrowia* is phylogenetically distantly related to most members of the *Saccharomycotina* yeast genera and present at the base of the *Saccharomycetales*. However, multigene and phylogenomic analyses that included a greater number of genera showed genera belonging to the families *Lipomycetaceae*, *Dipodascaceae* and *Phaffomycetaceae* to be basal to *Yarrowia* (Kurtzman *et al*. 2011, Kurtzman & Robnett 2013, Shen *et al*. 2018).

Yarrowia species are commonly found in food products such as meat (beef, pork, poultry) and dairy (cheeses, milk, yoghurt, butter, cream, and margarine), but they have also been isolated from fish, maize, traditional food, soil, insects (beetles), salt and fresh water, human tissue as well as petroleum storage tanks (Kurtzman *et al*. 2011, Groenewald *et al*. 2014). *Yarrowia* has been described as an oleaginous genus indicating that strains can grow on a variety of hydrophobic substrates and those that contain high proportions of lipids (fat and/or protein). It is known that the type species *Y. lipolytica* can accumulate lipids intracellularly to 40 % of its cell dry weight (Beopoulos *et al*. 2011).

Economical and medical significance

It is clear from literature that *Yarrowia* species are widespread and play an essential role in the food industry (beneficial or undesirable), they have importance in medical fields and have industrial utility (Kurtzman *et al*. 2011, Groenewald *et al*. 2014). These characteristics together with the knowledge that *Y. lipolytica* is a "safe-to-use" organism, indicate that this genus has great ecological and economic significance (reviewed in Groenewald *et al*. 2014).

Food and food safety

Yarrowia lipolytica is a species commonly associated with food products (reviewed in Groenewald *et al*. 2014). It is a regular component of food and beverage microbiota, either with desirable and beneficial effects (Wyder *et al*. 1999, Encinas *et al*. 2000, Boekhout & Robert 2003, Ferreira & Viljoen 2003, Patrignani *et al*. 2007) or occasionally it contributes to spoilage (Deak & Beuchat 1987, 1996, Ismail *et al*. 2000, Boekhout & Robert 2003). However, for food safety concerns it is important to know that *Y. lipolytica* is regarded to be a "safe-to-use" organism.

Yarrowia species are often associated with (fermented) dairy products. These include a diversity of cheeses, milk from ewe, water buffalo and cow as well as yoghurt, butter, cream, margarine and traditional products such as kefir, *nunu* and *amas* (reviewed in Groenewald *et al*. 2014). *Yarrowia lipolytica* contributes to the organoleptic characteristics of cheese and is one of the top three most prevalent yeast species in cheese such as mould-ripened, smear-ripened, blue-veined and fresh cheeses. It is frequently used as a cheese starter as it reduces ripening times, extends the shelf life and inhibits the growth of undesirable bacteria and green mould. However, there is sometimes a thin line between the desirable and beneficial effects and its occasional contribution to spoilage as it can produce off-flavours, affects the cheese texture negatively, increases the formation of biogenic amines and causes surface browning that affects appearance.

Yarrowia species also occur on red meat (*e.g.*, Vienna, traditional sausages of southern Italy, Spanish and German fermented sausages, salami, ham, salted bacon, beef, biltong) and occasionally also in poultry and fish products (reviewed in Groenewald *et al*. 2014). *Yarrowia alimentaria* was found to co-exist with *Y. lipolytica* in processed meat products (Nielsen *et al.* 2008). *Yarrowia lipolytica* was also reported from fermented products such as wine, must, cider, tempeh and sourdough, also in products at refrigeration temperatures such as soft drinks, juices, fruit concentrates, mayonnaise, salad dressings and salads, as well as in chilled and frozen, processed food. Whether *Yarrowia* species have a desirable or undesirable effect on the flavor and/or texture of these products is not fully known. However, *Y. galli* was found to be a spoilage organism in non-processed chicken and processed chicken meat due to its lipolytic and proteolytic activities (Kurtzman *et al*. 2011).

Although *Y. lipolytica* is commonly associated with food products it can be hypothesised that some of the earlier identifications of this species in food may refer to closely related *Yarrowia* species, and previously known *Candida* species, that are physiologically not distinguishable from *Y. lipolytica*.

Industrial significance

The great variety of potential commercial applications of *Y. lipolytica* for a more biobased economy is extensively reviewed by Coelho *et al*. (2010), Groenewald *et al*. (2014) and Abeln & Chuck (2021) and it has several physiological properties of industrial significance. It has already been deployed in multiple industrial applications. These applications include (i) as a high-quality protein source for livestock feeding (Bamberg 2000) and production of cell protein (SCP), (ii) as a biotechnological production host for various organic acids and/or hydrophobic substances, and (iii) as a heterologous production host for pharmaceutical and industrial proteins and enzymes, for the mass production of biofuels as well as for bioremediation purposes (reviewed in Groenewald *et al*. 2014, Abeln & Chuck 2021). The affinity of *Y. lipolytica* towards hydrophobic substrates accelerated its industrial relevance to SCP and citric acid and its genetic accessibility makes *Y. lipolytica* an industrially-relevant versatile microbe that can produce a variety of valuable metabolites not limited to SCP and citric acid, but also carotenoids, erythritol, lipids, lipases, mannitol, *etc*. (Ledesma-Amaro & Nicaud 2016). Due to the advanced development of genetic tools and the early genetic accessibility of *Y. lipolytica*, this yeast was already used as a genetically modified organism to produce fatty alcohols (Wang *et al*. 2016g) and unusual fatty acids such as long-chain polyunsaturated fatty acids (Ledesma-Amaro & Nicaud 2016).

The listed current applications are just a selection but there is a great variety of potential commercial usage for this species. *Yarrowia lipolytica* probably has some close relatives with great potential that should be investigated further in order to be used towards more a bio-based economy.

Medical importance

Infections by *Yarrowia* species are very rare with only a few cultures originating from human sources. This is clear from the limited number of cases and publications indicating species of *Yarrowia* cause infections and public culture collections maintaining *Yarrowia* strains isolated from humans. It is also clear that it is mostly immunocompromised patients that have been infected. The low pathogenicity of *Y. lipolytica* was also illustrated by Walsh *et al*. (1989). Some *Yarrowia* species tested by Desnos-Ollivier *et al*. (2012) showed high Minimum Inhibitory Concentrations (MICs) to some antifungals (Table 24). Among the four ascomycetes isolates resistant to all antifungal drugs tested, were *Y. lipolytica* and *C. hispaniensis.* Unlike *Y. lipolytica*, *C. hispaniensis* is not known to be a potential human pathogen but it can also grow at 37 °C (Desnos-Ollivier *et al*. 2012). Although *Y. deformans* was recovered twice from clinical materials, its inability to grow at 37 °C makes it unlikely to be an agent of systemic infection (Kurtzman *et al*. 2011). Jacques & Casaregola (2008) pointed out that the common occurrence of *Y. lipolytica* and probably related species on a variety of food products provide a ready source of inoculum to those people who may be susceptible to infection. Resistance to various antifungals may occur in *Yarrowia* species or close relatives but opportunistic infections by *Y. lipolytica* can be treated well or disappear even without treatment (Hazen 1995, Walsh *et al*. 2004, Belet *et al*. 2006, Groenewald *et al*. 2014); this might be the case for other opportunistic pathogenic *Yarrowia* species.

Research interests

There are 2 558 publications and 37 460 citations from 2011–2021 in the Web of Science (Fig. 43), with the top 10 most cited articles shown in Table 25. Most of the publications focused on biotechnological applications, generic engineering and future processes (Fig. 44).

Table 24. Species tested by Desnos-Ollivier *et al.* (2012) and their corresponding MIC values to different antifungals.

	C. hispaniensis	***Y. deformans***	***Y. galli***	***Y. phangngaensis***	***Y. lipolytica***
Fluconazole	High MIC	High MIC	High MIC	Low MIC	High MIC
Itraconazole	High MIC	Low MIC	Low MIC	Low MIC	High MIC
Posaconazole	High MIC	High MIC	Low MIC	Low MIC	High MIC
Voriconazole	High MIC	High MIC	High MIC	High MIC	High MIC
Caspofungin	High MIC	Low MIC	Low MIC	Low MIC	High MIC
Amphotericin B	High MIC	High MIC	High MIC	High MIC	High MIC
5FC	High MIC	High MIC	High MIC	Low MIC	High MIC
Terbinafine	High MIC	Low MIC	Low MIC	High MIC	High MIC

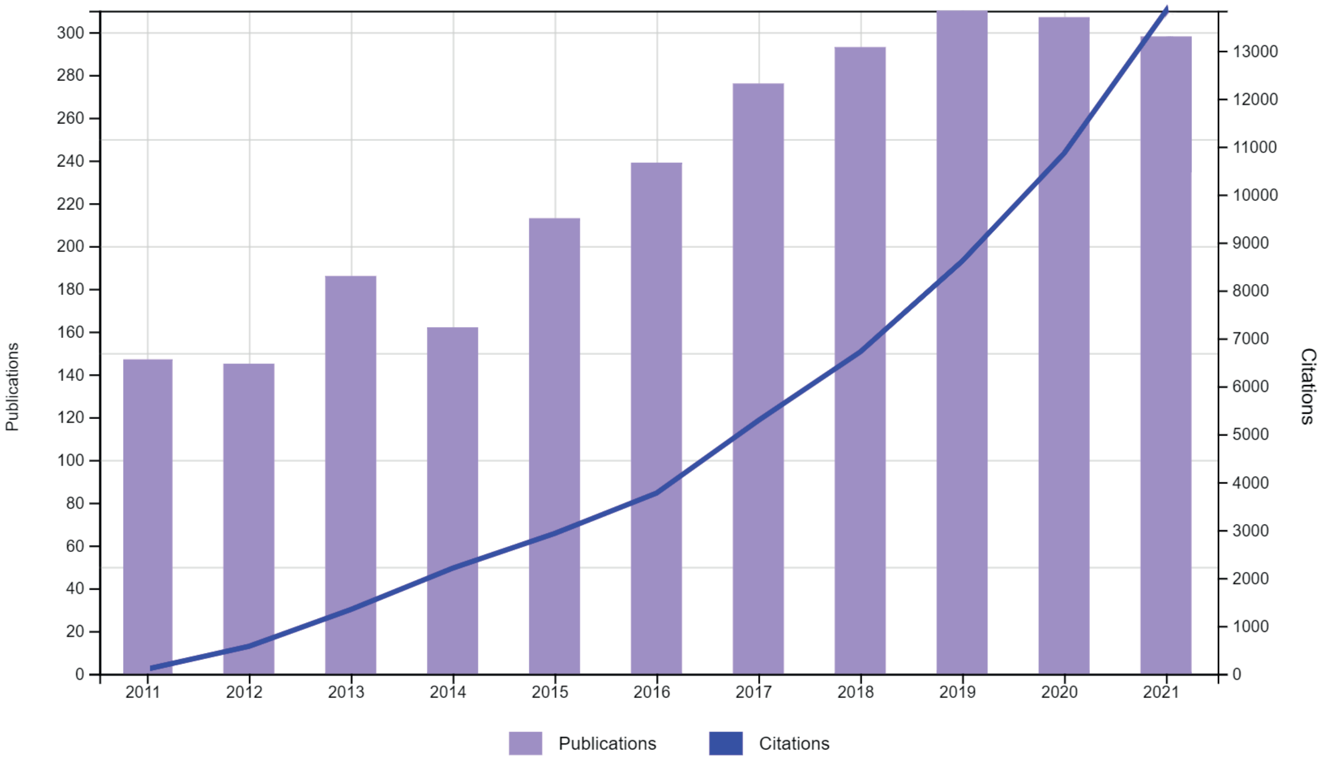

Fig. 43. Trends in research of *Yarrowia* in the period 2011–2021.

Table 25. Top 10 cited articles related to *Yarrowia* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Value-added uses for crude glycerol - a byproduct of biodiesel production	659	Yang *et al*. (2012b)
2	Lipids of oleaginous yeasts. Part I: Biochemistry of single cell oil production	410	Papanikolaou (2011)
3	Engineering the push and pull of lipid biosynthesis in oleaginous yeast *Yarrowia lipolytica* for biofuel production	406	Tai & Stephanopoulos (2013)
4	Harnessing *Yarrowia lipolytica* lipogenesis to create a platform for lipid and biofuel production	361	Blazeck *et al.* (2014)
5	Oily yeasts as oleaginous cell factories	353	Ageitos *et al.* (2011)
6	Production of omega-3 eicosapentaenoic acid by metabolic engineering of *Yarrowia lipolytica*	314	Xue *et al.* (2013)
7	Oil production by oleaginous yeasts using the hydrolysate from pretreatment of wheat straw with dilute sulfuric acid	313	Yu *et al.* (2011a)
8	Macromolecular organization of ATP synthase and complex I in whole mitochondria	310	Davies *et al.* (2011)
9	Lipids of oleaginous yeasts. Part II: Technology and potential applications	273	Papanikolaou & Aggelis (2011)
10	Microbial xylanases: Engineering, production and industrial applications	268	Juturu *et al.* (2012)

(Bio-)industry

As *Y. lipolytica* is regarded to be a “safe-to-use” organism, the study of its use in the food and food-related industries, for *Yarrowia*-derived products or as a production host for biotechnological applications is warranted. Follow-up studies to explore the effectiveness of this species to be used as a probiotic (Liu & Tsao 2009) and its cell-free extract as a prebiotic (Kumura *et al*. 2009) was proposed and reviewed in Groenewald *et al*. (2014). Due to its immense capability to accumulate high concentrations of lipids intracellularly, *Y. lipolytica* featured in the first-ever commercial oleaginous yeast process (Abeln & Chuck 2021). As this species has numerous physiological properties of industrial significance, interest in exploring and developing *Y. lipolytica* for further usage in the (bio-) industry is growing (reviewed in Coelho *et al*. 2010, Groenewald *et al*. 2014, Abeln & Chuck 2021), opening the door for more properties to be discovered and known properties to be explored. Advancing yeast lipid technology as a sustainable source of oil in the place of palm and soybean oil, as a novel route to advanced biofuels (Beopoulos *et al*. 2009, Blazeck *et al*. 2014, Abeln & Chuck 2021), and to produce biofuels sustainably in the form of large biodiesel, will be an important research interest in coming years. It is clear that *Y. lipolytica* and probably some of its close relatives will play an important role in bio-processes, and especially due to its oleaginous ability multiple industrial applications to exploit this species should be considered.

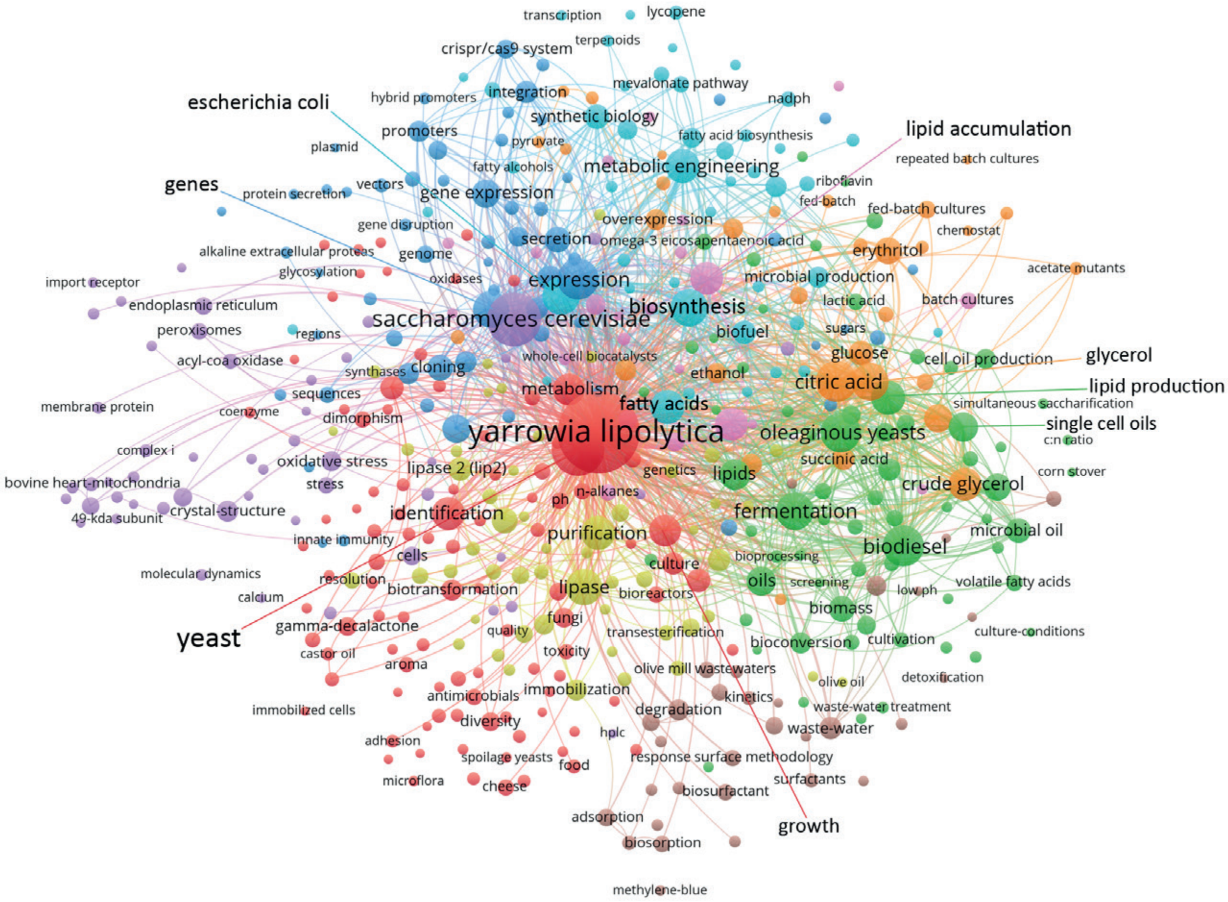

Fig. 44. Network visualisation of keywords of the publications related to *Yarrowia*. The larger the text and the circle the more often the subject has been cited.

Generic engineering and future processes

Yarrowia lipolytica was an early selection for whole genome sequencing. Kerscher *et al*. (2001) reported the sequence for the complete mitochondrial genome, which was then followed by the sequence of the complete nuclear genome (Dujon *et al*. 2004). It is also the most frequently genetically modified yeast (over 50 % of modified yeasts) due to the advanced development of genetic tools that can be applied to this species and due to its genetic accessibility. Approximately 70 % of the genetically engineered oleaginous yeasts cultured are of *Y. lipolytica* (Abeln & Chuck 2021). Recent work has also demonstrated successful adaptive evolution strategies, increasing single cell oil (SCO) production at the expense of citric acid biosynthesis, a process that is still being improved (Juturu & Chuan 2012). Bigey *et al*. (2003) investigated the ability of *Y. deformans* to excrete powerful lipolytic enzymes that are active in a mostly aqueous environment and characterised several genes that code for these enzymes.

Oleaginous yeast processes, with *Y. lipolytica* as one of the main species involved, have been intensively investigated and brought to scale in times of crisis and uncertainty (Abeln & Chuck 2021). With the many problems mankind is facing due to climate change, depletion of fossil resources and ecological damage affecting global food supply chains, *Yarrowia* species could play a vital role in multiple areas due to their extensive lipid production. It is essential that microbial processes are developed, scaled and ready to produce lipids on the industrial scale in the short to medium term and *Yarrowia* species, especially *Y. lipolytica*, can play a crucial role in achieving a sustainable future in these areas.

Author: M. Groenewald

22. *Agaricus* L., Sp. pl. 2: 1171. 1753.

Type species: *Agaricus campestris* L.

Classification: *Basidiomycota*, *Agaricomycotina*, *Agaricomycetes*, *Agaricales*, *Agaricaceae.*

Background

Agaricus is the type genus of *Agaricaceae*. It has a worldwide distribution extending to all continents except Antarctica (Zhao *et al*. 2011, Hyde *et al.* 2017b). Species of *Agaricus* are characterised by sporocarps with an annulate stipe and free lamellae that produce dark brown spore prints. They are saprobic and can be found in natural environments such as forests, grasslands and/or urban areas such as gardens, roadsides and pastures (Parra 2008). There are an estimated 600 species of *Agaricus* (He *et al*. 2022a). Many *Agaricus* species are edible, for example, *Ag. arvensis*, *Ag. augustus* and *Ag. campestris* (Li *et al*. 2021a). *Agaricus* species have long been collected in the wild and are preferred as food worldwide. Some of them are successfully cultivated. The best-known species is *Ag. bisporus*, also called button mushrooms, which has been widely cultivated for at least 300 years (Kerrigan 2016, Bhushan & Kulshreshtha 2018). Many species are of medicinal value as they can produce antimicrobial, antioxidant and anti-allergenic biocompounds (Kerrigan 2005, Stojković *et al*. 2014).

Most monographs of *Agaricus* deal with species from temperate areas, such as those from Europe (Möller 1950, Pilát 1951, Konrad & Maublanc 1952, Kühner & Romagnesi 1953, Wasser 1980,

Table 26. Nutritional value of *Ag. bisporus* (white button mushrooms) per 100 g.

Nutritional components	Amount/per 100 g	Nutritional components	Amount/per 100 g
Protein	2.89 g	Riboflavin	0.444 mg
Calcium, Ca	5 mg	Niacin	3.88 mg
Iron, Fe	0.23 mg	Vitamin B-6	0.077 mg
Magnesium, Mg	10.2 mg	Biotin	9 µg
Phosphorus, P	93 mg	Folate	35 µg
Potassium, K	373 mg	Vitamin D (D2 + D3)	0.02 µg
Sodium, Na	6 mg	Ergosta-7-enol	1.63 mg
Zinc, Zn	0.51 mg	Ergosta-5,7-dienol	5.84 mg
Copper, Cu	0.389 mg	Ergosta-7,22-dienol	1.54 mg
Manganese, Mn	0.054 mg	Ergosterol	56 mg
Selenium, Se	20 µg	Ergothionine	4 mg
Thiamin	0.065 mg	Energy	31 kcal

Cappelli 1984, Parra 2008) and North America (Kerrigan 1986, Singer 1986), although those from tropical areas have been treated by Heinemann (1956, 1978, 1980). With the advent of the molecular era, *Agaricus* has undergone systemic studies with evidence from single and/or multiple sequences (Mitchell & Bresinsky 1999, Challen *et al*. 2003, Geml *et al*. 2004, Kerrigan *et al*. 2005, 2008, Zhao *et al*. 2011, 2016b, Chen *et al*. 2017a, He *et al*. 2017a, Ortiz-Santana *et al*. 2021). The current taxonomic system for *Agaricus* is based on combined phylogenetic analyses, phenotypic characteristics and divergence times. The latest *Agaricus* taxonomic system recognises six subgenera and 26 sections (Zhao *et al*. 2011, 2016, Chen *et al*. 2017a, He *et al*. 2017a, Ortiz-Santana *et al*. 2021). The phylogenetically informative characteristics including the structure of the annulus (superior *vs* inferior; simple *vs* double or two-layered), odour, discolouration of context when cut or rubbed and Schäffer reaction (aniline × nitrogen acid) are the major criteria for the infrageneric classification of *Agaricus*. *Agaricus* is the first genus in ranking fungi with divergence times and using divergence times as an additional criterion to be accepted in fungal systematics studies (Hongsanan *et al*. 2017, Hyde *et al*. 2017a, Liu *et al*. 2017a, Zhao *et al*. 2017b, Tedersoo *et al*. 2018, Ji *et al*. 2022).

Economic significance

Agaricus is a diverse genus with high economic potential. *Agaricus bisporus* and *Ag. subrufescens* are the most widely cultivated species for both edible and medicinal value. Several recently described species are also edible and can be cultivated. For example, *Ag. flocculosipes* and *Ag. sinodeliciosus* are two edible species originally found in Thailand and China (Zhao *et al*. 2012a, Wang *et al*. 2015i). Not all *Agaricus* species are edible and some are poisonous, for example, species of section *Xanthodermatei*. They can cause serious gastrointestinal irritation which requires treatment (Gill & Strauch 1984, Hender *et al*. 2000, Boxshall *et al*. 2021).

Agaricus bisporus

The global edible mushroom market is estimated to be worth 42 000 million US dollars per year and is expected to exhibit a compound annual growth rate (CAGR) of 9.5 % from 2021 to 2028. *Agaricus bisporus* accounts for 61.8 % of the world's total edible mushroom production and was worth 28 500 million US dollars in 2020 (Willis 2018, Grand view research 2022). Due to its high protein, low calories and nutrition-rich features (Table 26, accessed from U.S. Department of Agriculture, FoodData Central, on 21st February 2022), there is an increased demand for this product.

Agaricus subrufescens

Agaricus subrufescens, also called almond mushrooms, was wrongly named *Ag. blazei* for a long time (Kerrigan 2005). It is widely cultivated for its medicinal value. The bioactive compounds isolated from the basidiomes or mycelia proved to be antimicrobial, antioxidant and anti-allergenic (Wisitrassameewong *et al*. 2012, Stojković *et al*. 2014). The reported beneficial properties are listed in Table 27.

Agaricus flocculosipes

Agaricus flocculosipes was originally found in Thailand and Mayotte Island and later found in China (Zhao *et al*. 2012a, Gui *et al*. 2015). This taxon is potentially cultivatable as it is presumably heterothallic and is a member of section *Arvenses*, indicating its edibility (Zhao *et al*. 2012a). Thongklang *et al*. (2014) successfully cultivated this species in Thailand and it has good potential as a new mushroom in the market.

Agaricus sinodeliciosus

Agaricus sinodeliciosus was originally found in northwestern China (Wang *et al*. 2015i). It is widely collected and consumed by the local people in the Xinjiang and Qinghai provinces, even before it was formally named. Studies have focused on its cultivation including the offspring analysis and habitat microbial communities (Zhou *et*

Table 27. Medicinal properties reported for *Agaricus subrufescens*.

Medicinal properties	References
Tumour growth reduction	Pinto *et al.* (2009), Jumes *et al.* (2010)
Immunomodulatory activities	Niu *et al.* (2009), Ramberg *et al.* (2010)
Immunostimulatory effects	Endo *et al.* (2010), Førland *et al.* (2010, 2011)
Antimicrobial activities	Bernardshaw *et al.* (2005, 2006)
Antiviral activities	Bruggemann *et al.* (2006), Faccin *et al.* (2007)
Anti-allergy effects	Ellertsen & Hetland (2009)
Antioxidant activities	Lavitschka *et al.* (2007)

al. 2017a, Ling *et al*. 2019). Some isolates are domesticated and suitable for bagged and industrialised facility cultivation (Xu *et al*. 2021).

Agaricus xanthodermus

Species of section *Xanthodermatei* are poisonous and can cause gastrointestinal irritation. *Agaricus xanthodermus* is from this section and is frequently consumed (Kerrigan 2016). Phenols are thought to be the main toxic agents in the basidiomes. A study from Australia indicated that the concentration of the phenols varies between basidiomatal structures, different developmental stages, and different nutritional substrates (Boxshall *et al.* 2021). Awareness should always be given when collecting *Agaricus* in the wild for food.

Research interests

There are 2 668 publications and 34 079 citations from 2011–2021 in the Web of Science (Fig. 45). The top 10 most cited articles are listed in Table 28. Most publications mostly focused on medicinal properties and systematics (Fig. 46).

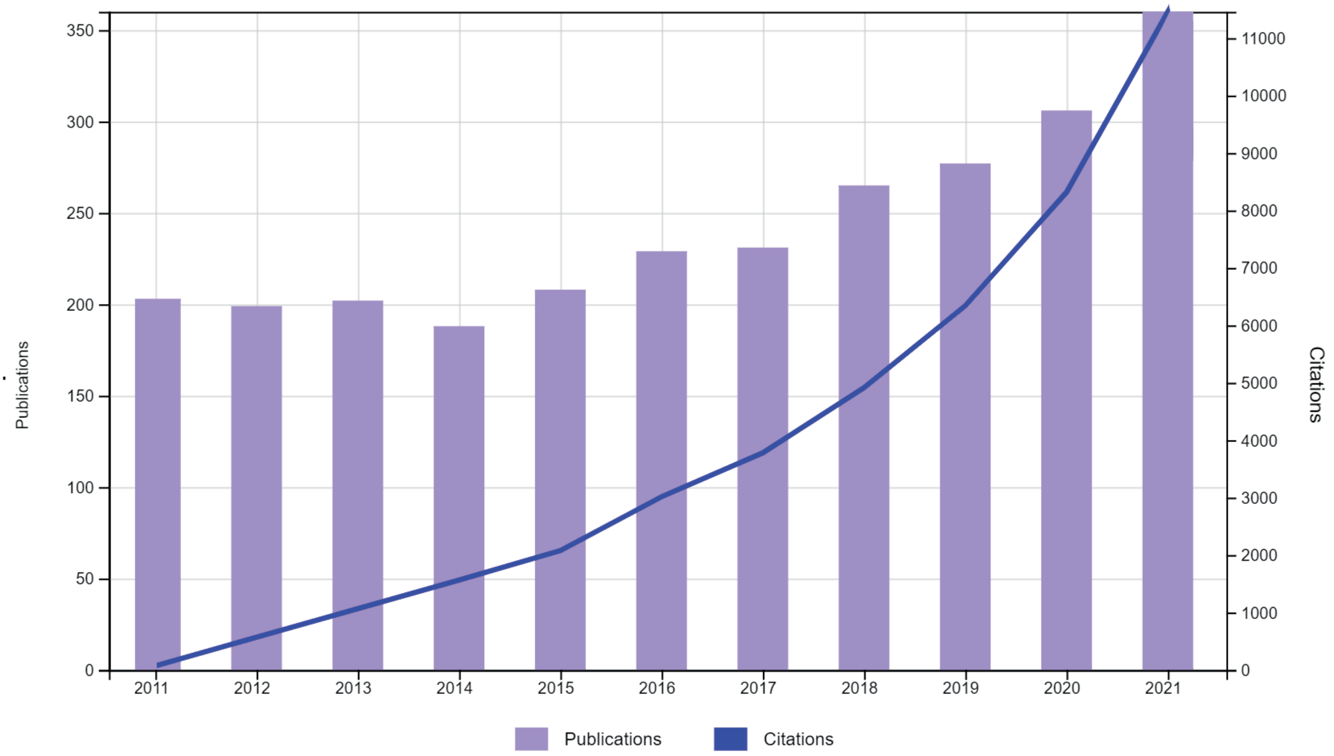

Fig. 45. Trends in research of *Agaricus* in the period 2011–2021.

Table 28. Top 10 cited articles related to *Agaricus* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Crystal structure of *Agaricus bisporus* mushroom tyrosinase: Identity of the tetramer subunits and interaction with tropolone	485	Ismaya *et al.* (2011)
2	*In vitro* and *in vivo* antioxidant activity of ethanolic extract of white button mushroom (*Agaricus bisporus*)	327	Liu *et al.* (2013b)
3	A review of chemical composition and nutritional value of wild-growing and cultivated mushrooms	322	Kalac (2013)
4	A comprehensive review on tyrosinase inhibitors	317	Zolghadri *et al.* (2019)
5	Tissue invasion and metastasis: Molecular, biological and clinical perspectives	281	Jiang *et al.* (2015)
6	Antioxidative and immunomodulating activities of polysaccharide extracts of the medicinal mushrooms *Agaricus bisporus*, *Agaricus brasiliensis*, *Ganoderma lucidum* and *Phellinus linteus*	279	Kozarski *et al.* (2011)
7	Chemical composition and nutritional value of the most widely appreciated cultivated mushrooms: An inter-species comparative study	267	Reis *et al.* (2012a)
8	Current findings, future trends, and unsolved problems in studies of medicinal mushrooms	267	Wasser (2011)
9	Antioxidant properties of phenolic compounds occurring in edible mushrooms	250	Palacios *et al.* (2011)
10	Genome sequence of the button mushroom *Agaricus bisporus* reveals mechanisms governing adaptation to a humic-rich ecological niche	234	Morin *et al.* (2012)

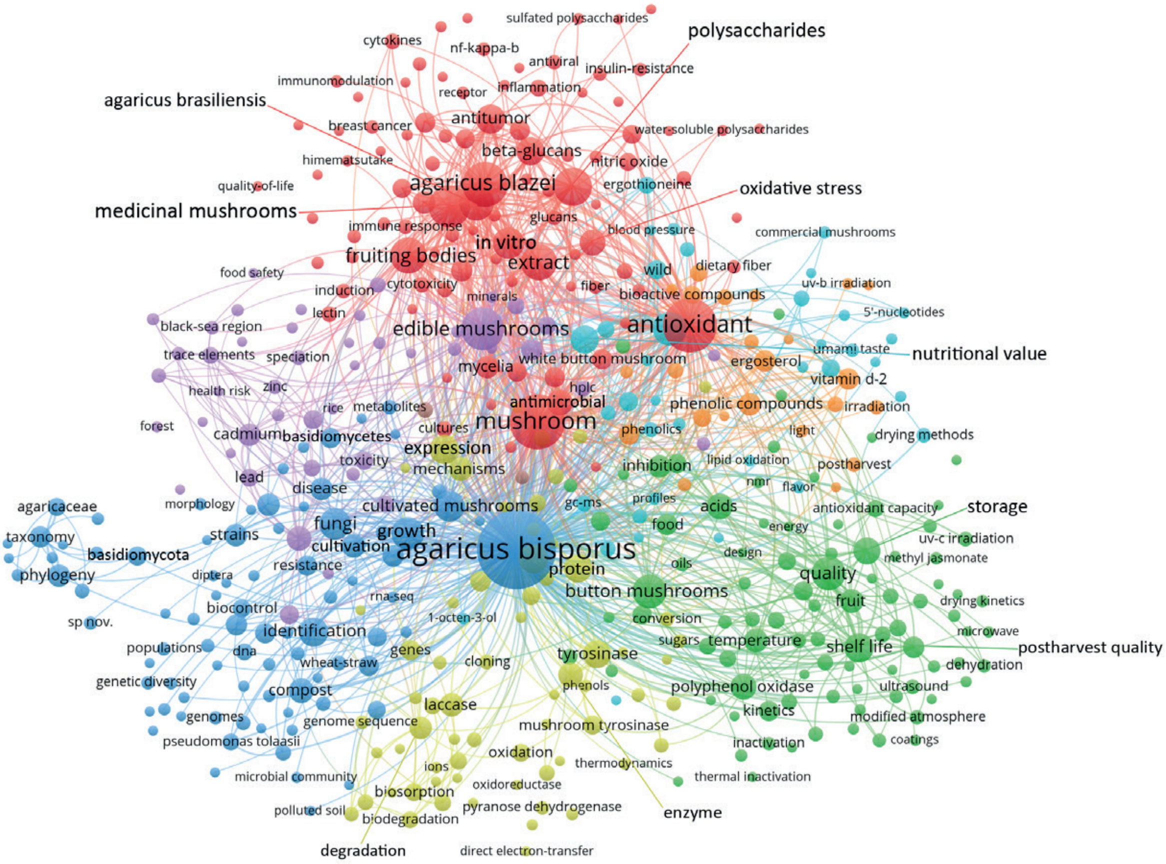

Fig. 46. Network visualisation of keywords of the publications related to *Agaricus*. The larger the text and the circle the more often the subject has been cited.

Medicinal properties

Many bioactive compounds have been isolated from *Agaricus* species and these attract researchers to explore their medicinal values (Wasser 2011). Polysaccharides isolated from *Ag. bisporus* and *Ag. subrufescens* are antioxidative and immunomodulating-active (Kozarski *et al*. 2011). Tyrosinase isolated from *Ag. bisporus* is important in browning reactions in the food industry and medicinal use as an anticancer agent (Ismaya *et al*. 2011, 2017).

Authors: M.Q. He and R.L. Zhao

23. *Kluyveromyces* Van der Walt, Antonie van Leeuwenhoek 22: 271. 1956.

Type species: *Kluyveromyces marxianus* (E.C. Hansen) Van der Walt

Classification: *Ascomycota*, *Saccharomycotina*, *Saccharomycetes*, *Saccharomycetales*, *Saccharomycetaceae.*

Background

Our current understanding of the genus *Kluyveromyces* bears only a passing resemblance with its original conception. Van der Walt (1956) created *Kluyveromyces* to accommodate a fermentative species with the unique property of forming asci containing up to 100 spores, in contrast to most other ascomycetous yeast species, which form up to four (rarely eight) ascospores. The genus was soon emended (Van der Walt 1965) to include several other species, some formerly assigned to *Saccharomyces*, on the basis of deliquescence of the ascus in combination with a vigorous fermentative ability and the formation of smooth ascospores. That definition persisted through the fourth edition of "*The Yeasts, a Taxonomic Study*" (TYTS, Lachance 1998), although the phylogenetic heterogeneity of the genus had already become abundantly clear. The possibility of defining the genus on a unique set of growth characteristics vanished with the discovery of a non-fermentative species (Nagahama *et al*. 1999), and DNA sequence data were making it clear that most *Kluyveromyces* species could not be considered congeneric with the originally proposed type species, *K. polysporus* (Zhan 1994, James *et al.* 1997, Kurtzman & Robnett 1998). To avoid a nomenclatural catastrophe, Kurtzman *et al*. (2001) proposed the conservation of *Kluyveromyces*, but with *K. marxianus* as the new type species. Two-thirds of the species were reassigned to other genera in the family *Saccharomycetaceae* (Kurtzman 2003); this included the original type species, which was renamed *Vanderwaltozyma polyspora*.

Although one nightmare was averted, the changes have had a considerable impact on our ability to retrieve relevant literature, as exemplified by the fact that four of the references listed in Table 29 deal mostly with species that are no longer included in *Kluyveromyces*, as obsolete names continue to be applied. Noteworthy is the transfer of *K. thermotolerans* (syn. *Saccharomyces veronae*) to the genus *Lachancea*, the continued use of names such as *Candida kefyr*, *C. pseudotropicalis*, *K. fragilis*, or even *Saccharomyces fragilis*, all of which are defunct synonyms of *K. marxianus*, or the use of *K. marxianus* to designate other species, including *K. lactis* and *K. dobzhanskii*. Such nomenclatural ambiguities may result in misleading assumptions about the expected properties of strains used in comparative studies (*e.g.*, Alves *et al*. 2019). Details of these nomenclatural changes have been reviewed by Lachance (2007,

Table 29. Top 10 cited articles related to *Kluyveromyces* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Production of liquid biofuels from renewable resources	1 257	Nigam & Singh (2011)
2	Selected non-saccharomyces wine yeasts in controlled multistarter fermentations with *Saccharomyces cerevisiae*	366	Comitini *et al.* (2011)
3	Extraction of genomic DNA from yeasts for PCR-based applications	247	Lõoke *et al.* (2011)
4	Past and future of non-saccharomyces yeasts: from spoilage microorganisms to biotechnological tools for improving wine aroma complexity	243	Padilla *et al.* (2016b)
5	*Lachancea thermotolerans* and *Saccharomyces cerevisiae* in simultaneous and sequential co-fermentation: a strategy to enhance acidity and improve the overall quality of wine	233	Gobbi *et al.* (2013)
6	Structure of yeast Argonaute with guide RNA	212	Nakanishi *et al.* (2012)
7	Biotechnological potential of inulin for bioprocesses	192	Chi *et al.* (2011)
8	Production of recombinant proteins by yeast cells	182	Çelik & Çalık (2012)
9	Efficient multiplexed integration of synergistic alleles and metabolic pathways in yeasts via CRISPR-Cas	175	Horwitz *et al.* (2015)
10	Inulin-type fructans: a review on different aspects of biochemical and pharmaceutical technology	159	Apolinario *et al.* (2014)

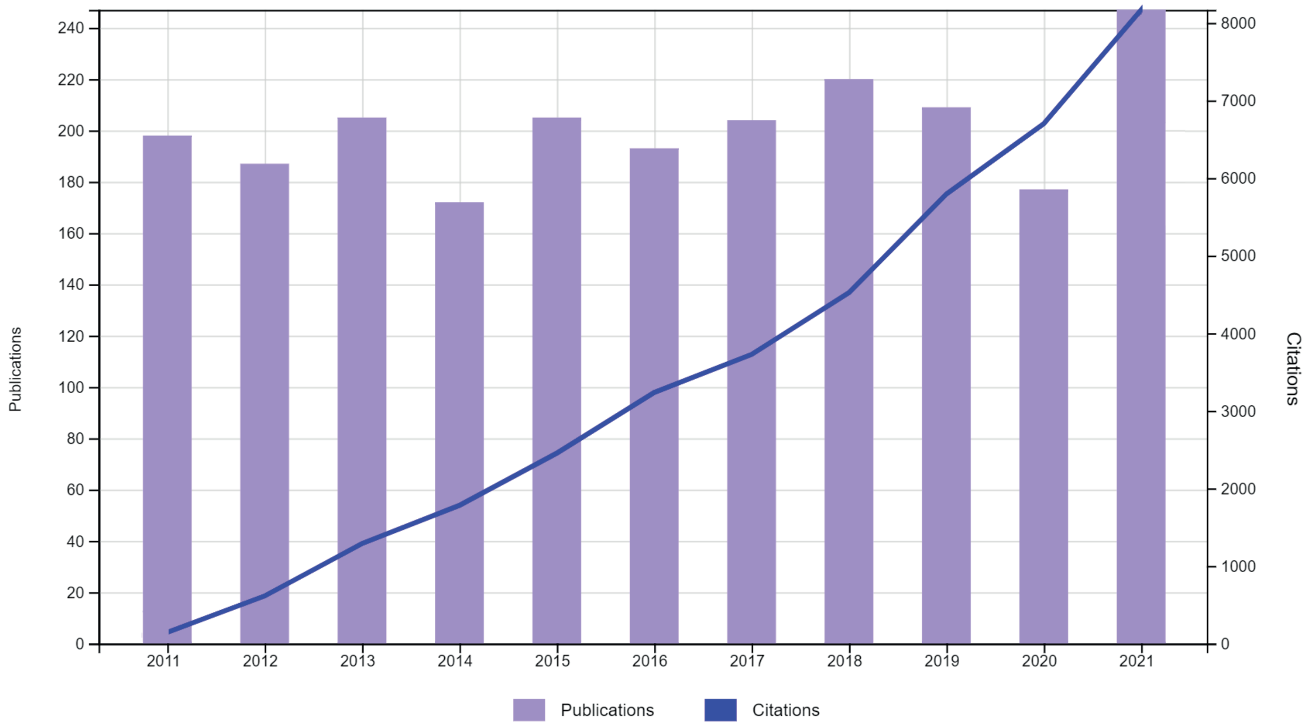

Fig. 47. Trends in research of *Kluyveromyces* in the period 2011–2021.

2011). The genus as it now stands consists of eight species (Freitas *et al*. 2020). All form evanescent asci which release up to four spheroidal, ovoid, or reniform ascospores that tend to agglutinate. The mitotic state is normally haploid and undergoes isogamous or mother-bud diploidisation prior to ascus formation. Most species form the iron-containing pigment pulcherrimin and assimilate lactose oxidatively, both of which are infrequent properties among ascomycetous yeasts. Three species, namely *K. aestuarii*, *K. nonfermentans*, and *K. siamensis*, form a distinct clade and are confined to marine sources. The most recently described, *K. starmeri*, is known only from Brazilian cacti. The remaining species are isolated with regularity in wild *Drosophila* species and their plant habitats. *Kluyveromyces lactis* and *K. marxianus* are also frequently isolated from cheese and other dairy products, due to their unique ability to ferment lactose. The taxonomy of *K. lactis* has received some attention in the past due to the polymorphic nature of the species. Lactose-negative biotypes are assigned to the variety *drosophilarum*; some of the biotypes were originally described as separate species and do show a small amount of divergence at the level of ITS sequences (Lachance 2011b).

Ecological and economic significance

As indicated in Fig. 48, two species, *K. lactis* and *K. marxianus*, attract much of the attention. The former serves as a rival model organism to *Saccharomyces cerevisiae* (Fukuhara 2006, Morrissey 2010). Of prime interest is their shared ability to assimilate and

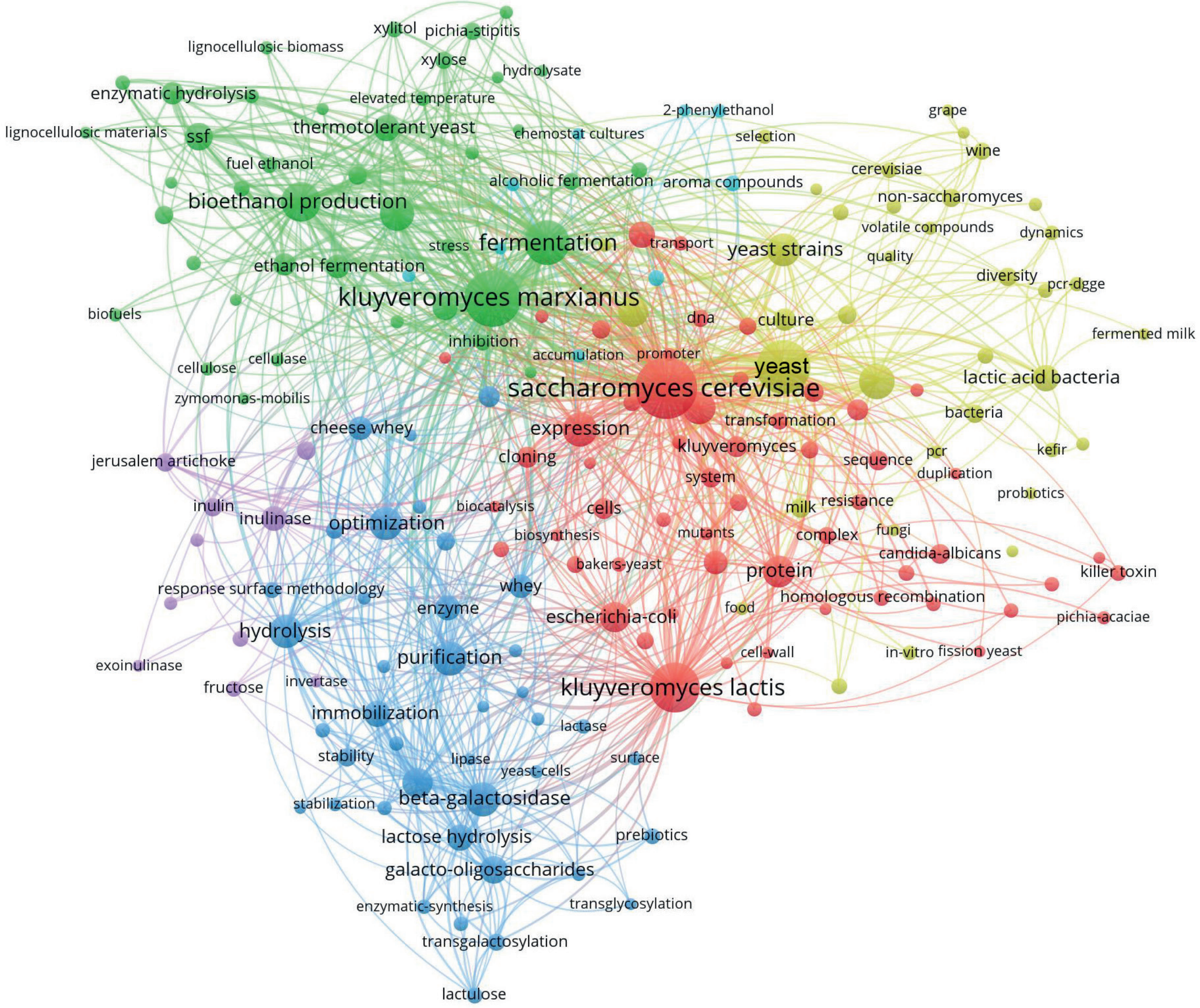

Fig. 48. Network visualisation of keywords of the publications related to *Kluyveromyces*. The larger the text and the circle the more often the subject has been cited.

ferment lactose combined with a GRAS (generally regarded as safe) status. As already noted, the former *Kluyveromyces* (now *Lachancea*) *thermotolerans* has also become a focal point.

Lactose utilisation and fermentation are confined to only about 1 % of ascomycetous yeasts (Lyutova *et al*. 2021). Although β-galactosidase is present in several *Kluyveromyces* species, only *K. lactis* var. *lactis* and *K. marxianus* possess the respiration-independent permeases required for uptake of lactose under low oxygen conditions, which allows them to metabolise the sugar by ethanol-yielding fermentation. The ability to ferment lactose has been used extensively to provide value added to whey, the major by-product of cheese making. Worldwide generation of whey approaches 200 million tonnes annually, equivalent to 10 million tonnes of lactose (Guimarães *et al*. 2010). A large proportion of recycled whey is dried into a protein powder for use primarily as animal feed, leaving behind a dilute lactose solution that has the potential to be converted to about 3.5 % of the bioethanol produced worldwide. Some industrial plants successfully execute the fermentation of whey permeate using *K. marxianus*. The process can be adapted to benefit small cheesemakers, allowing them to alleviate the environmental impact of whey disposal and even profit financially by generating potable alcohol products. Whey gin and vodka involving *K. marxianus* are available in several countries (Hughes *et al.* 2018). *Kluyveromyces* species are also the main source of commercial β-galactosidase (Zolnere & Ciprovica 2017).

Of much interest is the evolution of lactose genes among *Kluyveromyces* species. Naumov *et al*. (2006) demonstrated that the *LAC4LC12* gene cluster is absent in the known biotypes of *K. lactis* var. *drosophilarum*, indicating that the variety *lactis* acquired the genes by introgression. Based on gene phylogenies, they identified *K. marxianus* as the most likely source. Varela *et al*. (2019) provided strong support for this by using chromosome-size sequences to demonstrate the transfer of a 15-kb region from *K. marxianus* to *K. lactis*. The region contained *LAC4* and *LAC12* as well as a flocculin gene that subsequently pseudogenised in *K. lactis*. They dated the acquisition of lactose genes by *K. lactis* to a time that coincides with the beginnings of dairy agriculture.

***Kluyveromyces lactis* as a model organism** was chosen in the 1960s for its interesting sugar metabolism and the availability of heterothallic mating types, which would favour the design of genetic analyses (Fukuhara 2006). Interest in the species was further stimulated by the discovery of plasmids and killer systems that can be used in the expression and secretion of heterologous proteins. The species soon followed *S. cerevisiae* in having its genome sequenced. As a result of these attributes, *K. lactis* has figured prominently among yeasts used to produce recombinant proteins (Çelik & Çalık 2012). Its early use to produce bovine chymosin, the major component of rennet used in cheesemaking, established the species as a battle horse. Inserted genes can be put under the control of the inducible and repressible *LAC4* promoter, well understood after seven decades of β-galactosidase production. The yeast is even part of an easy-to-use commercial kit for heterologous gene expression. Among the approximately 100 successfully expressed proteins figure interleukin-1β, a granulocyte colony-stimulating factor, a hepatitis B surface antigen, human serum albumin, and several enzymes such as D-amino acid oxidase, glucoamylase, lipase, xylanase, and esterase. Spohner *et al*. (2016) provided a detailed overview of the proteins along with the various genetic techniques that made this possible. Horwitz *et al*. (2015) demonstrated the feasibility of using the CRISPR-Cas system to insert a complete novel metabolic pathway in yeast. The production of muconic acid was first acquired by the single-step integration of six large DNA fragments at three different locations in *S. cerevisiae*. The successful transformation of *K. lactis*, reported as the first use of the CRISPR-Cas system in the species served to show that its application is not limited to *S. cerevisiae*.

Kluyveromyces marxianus is a rare thermotolerant yeast

Less than a third of described yeast species share the ability to grow at 37 °C or above, and only a handful have maximum growth temperatures exceeding 40 °C. *Kluyveromyces marxianus* stands out by its ability to grow at temperatures up to 52 °C and it can produce ethanol at 50 °C (Banat *et al*. 1992). Matsumoto *et al*. (2018) attributed this unique property to a higher resistance to heat shock and a greater ability to deal with the elevated levels of reactive oxygen species triggered by high temperatures. A higher cellular concentration of trehalose compared to *S. cerevisiae* is also thought to play a role. In a broad review of the production of biofuels, Nigam & Singh (2011) singled out *K. marxianus* by virtue of its thermotolerance. Biofuel research is the target of intense research activity in view of humanity's desperate need to wean itself off fossil fuels.

***Kluyveromyces marxianus* assimilates inulin** due to a powerful *exo*-β-fructosidase capable also of invertase activity, as demonstrated in the former variety *bulgaricus* (Kushi *et al*. 2000). The potential significance of this property should be seen in the light of the biotechnology of β-fructans used by a wide variety of plants for energy storage (Chi *et al*. 2011). A simplistic taxonomy of β-fructans divides them into inulin, with β(2-1) bonds, and levan, with β(2-6) bonds (Apolinario *et al*. 2014). Inulin may constitute over 50 % of tuber biomass and is more readily converted to fermentable sugars than cellulose, starch, or xylan. Intact inulin may be used as a food ingredient for its properties as a low-calorie sweetener, a source of dietary fibre, or a prebiotic. Of major interest in biotechnology are methods for the extraction, purification, and transformation of inulin. *Kluyveromyces marxianus* may come in next as a source of enzyme for the production of fructose to be used directly or as an intermediate in the biosynthesis of other metabolites, including bioethanol. The yeast itself is also used in the direct transformation of inulin into biomass or ethanol.

Lachancea thermotolerans is gaining popularity in winemaking

Kluyveromyces species are among those that may appear as secondary components of spontaneous fermentations and are known to influence wine aroma (Padilla *et al*. 2016b). Of these *K. lactis* has been reported as a minor producer of volatile activity, but much of the interest is focused on a former member of the genus, *L. thermotolerans*. Comitini *et al*. (2011) found *L. thermotolerans* in mixed culture with *S. cerevisiae* to be unique in the ability to generate lactic acid, a low amount of volatile acidity, and a high yield of glycerol and 2-phenylethanol. Larger scale studies (Gobbi *et al*. 2013) indicated that such mixed cultures result in a more complex profile, with notably spicier and more acidic notes. This is due in part to enzyme activity. Of five such enzymes, two were detected in *L. thermotorans*, namely β-glucosidase and carbon-sulfur lyase (Padilla *et al*. 2016b). The former enzyme catalyses the release of a vast array of terpenols and other floral flavour compounds, whereas the latter enzyme cleaves fruity thiols from non-volatile molecules. The species is notable for its ability to release 4-mercapto-4-methylpentan-2-one and 3-mercaptohexan-1-ol in grape must, imparting wines with special floral notes. The release of lactic acid has also been put to use by Benito *et al*. (2015) as a substitute for the spontaneous and temperamental malolactic fermentation process. *Schizosaccharomyces pombe* consumes the malic acid and *L. thermotolerans* generates lactic acid. One should also mention the use of the species in the fermentation of sour beer (Domizio *et al.* 2016), a product of growing interest in the world of artisanal brewing.

Research interests

There are 2 217 publications and 33 194 citations from 2011–2021 in the Web of Science (Fig. 47), with the top 10 most cited articles shown in Table 29. The results presented in Table 29 exemplify the perils of performance metrics combined with the caprices of taxonomic nomenclature. As a result, some of the papers listed deal only peripherally with *Kluyveromyces* species. Of these, the report by Nakanishi *et al*. (2012) is concerned with the Argonaute protein of *Vanderwaltozyma polyspora* (formerly *K. polysporus*, original type species of the genus). The protein is a component of the RNA interference phenomenon. The species had been chosen in a previous study (Drinnenberg *et al.* 2009) due to its intermediate phylogenetic position with respect to *S. cerevisiae*, which does not engage in RNA interference. It is noteworthy that of the eleven species considered in that study, six were designated by names that were obsolete at the time of publication.

The report by Lõoke *et al*. (2011) explores a method for the extraction of DNA to be used for PCR amplification from yeasts. The study used the model species *K. lactis*, *Ogataea* (*Hansenula*) *polymorpha*, *Schizosaccharomyces pombe*, *Candida albicans*, *Komagataella* (*Pichia*) *pastoris*, and *S. cerevisiae*. Cells are heated in the presence of lithium acetate and sodium dodecyl sulfate, and DNA is precipitated with ethanol, redissolved in buffer, and debris is removed by centrifugation, resulting in a solution that is suitable for PCR amplification. Conspicuously absent is a simpler control where intact yeast cells are added directly to the reaction mixture (Lachance *et al*. 1999).

Author: M.A. Lachance

24. ***Mucor*** Fresen., Beitr. Mykol. 1: 7. 1850.

Type species: *Mucor mucedo* Fresen.

Classification: *Mucoromycota*, *Mucoromycotina*, *Mucoromycetes*, *Mucorales*, *Mucoraceae.*

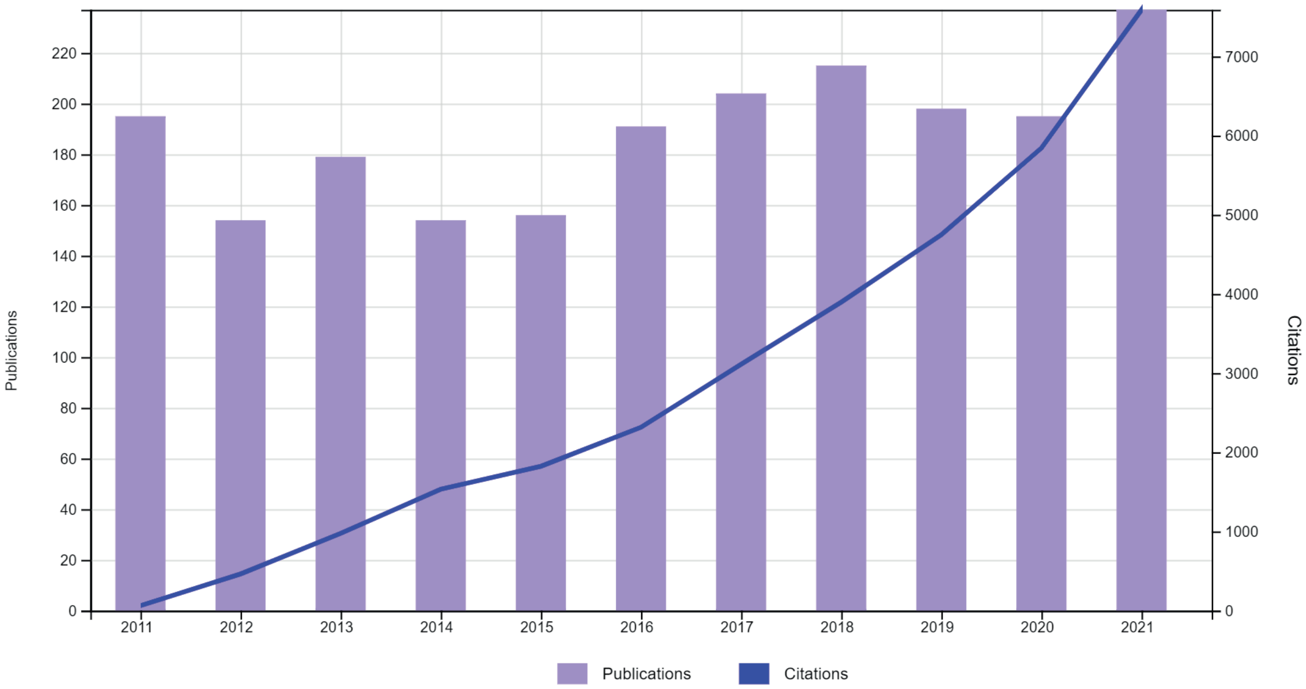

Fig. 49. Trends in research of *Mucor* in the period 2011–2021.

Table 30. Top 10 cited articles related to *Mucor* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	One stop shop: backbones trees for important phytopathogenic genera: I (2014)	235	Hyde *et al.* (2014)
2	Global epidemiology of mucormycosis	217	Prakash & Chakrabarti (2019)
3	Associations between fungal species and water-damaged building materials	213	Andersen *et al.* (2011)
4	DNA barcoding in *Mucorales*: an inventory of biodiversity	176	Walther *et al.* (2013)
5	Complex microbiota of a Chinese "Fen" liquor fermentation starter (Fen-Daqu), revealed by culture-dependent and culture-independent methods	146	Zheng *et al.* (2012)
6	Quantitative polymerase chain reaction detection of circulating DNA in serum for early diagnosis of mucormycosis in immunocompromised patients	141	Millon *et al.* (2013)
7	Obesity changes the human gut mycobiome	140	Rodriguez *et al.* (2015)
8	Chondroitin sulfate, hyaluronic acid and chitin/chitosan production using marine waste sources: characteristics, applications and eco-friendly processes: a review	137	Antonio Vazquez *et al.* (2013)
9	Survival outcomes in acute invasive fungal sinusitis: a systematic review and quantitative synthesis of published evidence	134	Turner *et al.* (2013)
10	Bioethanol production from sweet sorghum bagasse by *Mucor hiemalis*	115	Goshadrou *et al.* (2011)

Background

Mucor is the largest genus within the order *Mucorales* (phylum *Mucoromycota*). The genus is one of the most studied groups of *Mucorales* and early diverging lineages of fungi (Jayawardena *et al.* 2020). More than 300 species have been described (Lima *et al.* 2020), but recent studies (*e.g.*, Wijayawardene *et al.* 2018b) accept around 60 *Mucor* species while others suggest 50–76 valid taxa (Walther *et al.* 2020). The genus has 734 epithets in Index Fungorum (2022) which includes infra-specific taxa, invalid names, and synonyms. *Mucor* species are mostly saprobes, ubiquitous, and collected from a wide range of substrates such as soil and herbivore dung (Lima *et al.* 2020). The genus consists of coprophilous and non-coprophilous species which are involved in the decomposition of organic matter, and carbon and nitrogen cycles. They are also known to be opportunistic pathogens, causing cutaneous and subcutaneous mucormycosis (Lima *et al.* 2020).

Mucor species are valued for being fast-growing and have many biotechnological benefits. Most mucoralean species are mesophilic while some are psychrophiles. They are used in bioremediation, the production of biofuels, pharmaceuticals, and industrial enzymes. Some species have also been used for fermenting food, especially in Asian and African foods such as tempeh (Chai *et al.* 2019). This genus is one of the main causes of mucormycosis with 12 species known to be involved in human infections. The infections range from cutaneous, and rhino cerebral, or have gastrointestinal manifestations. In plants, *Mucor* species can cause rot and soft rot. *Mucor fragilis*, *Mu. piriformis*, *Mu. racemosus,* and *Mu. irregularis* are known to cause postharvest diseases mentioned above. Infection is usually possible if the crop or fruit has wounds or cracks on the surface (Jayawardena *et al.* 2020).

Mucor species are characterised by the formation of non-apophysate sporangia with pigmented and ornamented zygosporangia walls, simple or branched sporangiophores, and

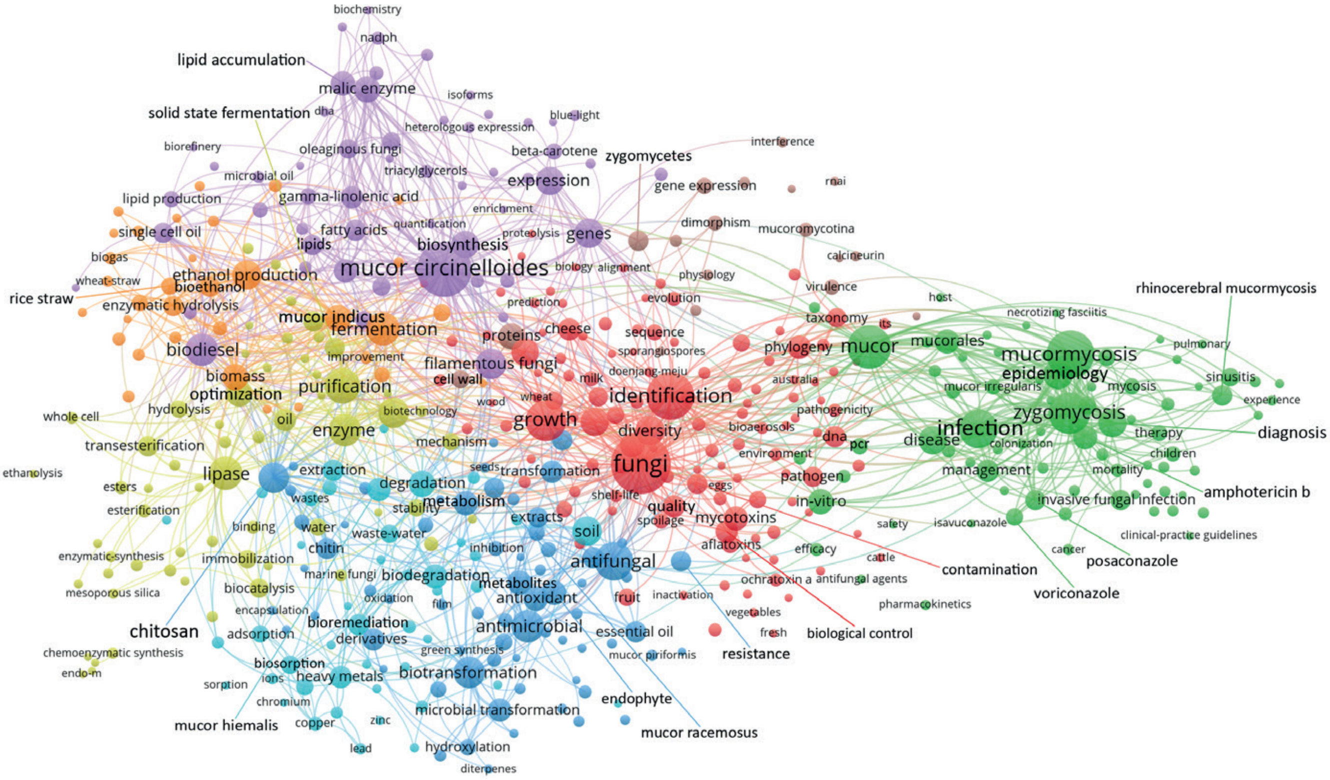

Fig. 50. Network visualisation of keywords of the publications related to *Mucor*. The larger the text and the circle the more often the subject has been cited.

zygospores with opposed or tong-like suspensors (Nguyen *et al.* 2019). Though the absence of rhizoids was considered a primary characteristic of *Mucor*, recent studies did notice the production of rhizoids in some species under specific environmental conditions. The sporangium produced is typically globose and contains a columella. The spores are normally ellipsoidal, round, or slightly elongated. Once the sporangiospores have been released, a collarette can be seen in most cases.

Previously, the taxonomic classification of *Mucor* largely depended on morphological characters, infertility tests mostly incorporating biological species and morphological species recognition. However, with the incorporation of DNA-based molecular phylogeny, it is noted that identification based solely on morphology can be problematic as the two may not be congruent (Hyde *et al.* 2023a). Primarily, ITS and LSU genetic markers are used for the delimitation of species within the genus. The use of protein-coding genes is not possible in all complexes as molecular data are not available. For the *Mucor circinelloides* group, recent studies and analyses have used protein-coding genes (Wagner *et al.* 2019).

Ecological and economic significance

Mucor rot is caused by species such as *Mu. fragilis*, *Mu. irregularis*, and *Mu. racemosus* but primarily by *Mu. piriformis* (Jayawardena *et al.* 2020). The disease affects crops such as strawberries and citrus fruits. One such fruit is mandarin which had a production value exceeding 500 million US dollars in 2014 (Saito *et al.* 2016). In Nigeria, *Mucor* species are responsible for 25 % of decayed fruits, and in Pakistan 1.65 % (Saito *et al.* 2016). Mucor rot produces similar initial symptoms to several other moulds (green mould and blue mould) (Jayawardena *et al.* 2020). In comparison to blue and grey mould, Mucor rot is less frequent and considered a minor problem (Sardella *et al.* 2016). Mucor rot causes significant losses in strawberry production and sales. *Mucor* species usually lead to soft rot disease in strawberries (Agyare *et al.* 2020). Over years, the occurrence of postharvest spoilage by this fungus has increased in countries such as the UK. It has been reported that spoilage by *Mucor* and *Rhizopus* is more common if harvested late (Dennis & Davis 1977, Agyare *et al.* 2020). Unlike other genera infecting strawberries, *Mucor* and *Rhizopus* cannot infect flowers. The white and ripe fruit are more susceptible to infection. Abiotic factors such as relative humidity, temperature, water availability, and factors such as the number of spores deposited on the fruit, impact the growth of the fungi (Kubicek & Druzhinina 2007, Agyare *et al.* 2020).

Research interests

There are 2 078 publications and 30 923 citations from 2011 to 2021 in the Web of Science (Fig. 49), with the top 10 most cited articles listed in Table 30. Most publications are related to the taxonomy of *Mucor*, postharvest diseases, and human pathogenicity (mucormycosis) (Fig. 50).

Taxonomy and phylogeny

Delimitation of *Mucor* species primarily involves morphophysiological characters and molecular phylogeny based on ITS-LSU sequence data. Protein-coding genes are usually lacking in the phylogenetic inference of most species in this genus due to the unavailability of sequence data. For the *Mucor circinelloides* complex, Wagner *et al.* (2020) used a five-locus phylogeny (*cfs*, ITS, *mcm*7, *rpb*1, *tsr*1) to provide a phylogenetic tree and introduced several new species. Among the genes used, *tsr*1 had the highest resolution power but other markers are considered appropriate for species delimitation (Wagner *et al.* 2020).

Mucormycosis

Mucor irregularis is a common causative agent of mucormycosis globally (Prakash & Chakrabarti 2019). It is the main cause of cutaneous mucormycosis in Australia, China, India, Japan, and the USA. To date, more than 20 cases of cutaneous mucormycosis caused by *Mu. irregularis* have been reported in China. However, the causative agent of mucormycosis may vary depending on the geographical area (Liang *et al*. 2018a, Skiada *et al.* 2020). Studies reviewing the global incidence of the disease state that mucormycosis caused by *Rhizopus*, *Mucor,* and *Lichtheimia* species account for 75 % of all cases (Skiada *et al.* 2020). Unlike other mucormycosis cases, this species mostly involves immunocompetent individuals. Main factors such as injuries and surgeries increase susceptibility to infections. The disease is characterised by progressive swelling, necrosis of the tissues, ulceration, and in severe cases leads to disfiguration (Liang *et al.* 2018a, Wang *et al.* 2019).

Author: V.G. Hurdeal

25. ***Verticillium*** Nees, Syst. Pilze (Würzburg): 56. 1816.

Type species: *Verticillium dahliae* Kleb.

Classification: *Ascomycota*, *Pezizomycotina*, *Sordariomycetes*, *Trichosphaeriales*, *Trichosphaeriaceae.*

Background

Verticillium is a large and heterogeneous hyphomycetous genus that was introduced by Nees von Esenbeck (1816) to accommodate the monotypic species *V. tenerum*. The type species is now accommodated in *Acrostalagmus* (Zare *et al.* 2004). In order to preserve the important plant pathogenic name *Verticillium*, *V. dahliae* was proposed as a neotype for this genus (Gams *et al.* 2005). There are 274 records in Index Fungorum (2022) and 292 records in MycoBank (Crous *et al.* 2004). However, this genus has changed dramatically, especially after molecular evidence became widely used for fungal taxonomy (Zare *et al.* 2000, 2001, 2004, 2007, Gams & Zare 2001, Sung *et al.* 2001, Zare & Gams 2001a, b, Fahleson *et al.* 2004, Gams 2017). Gams (1971) introduced the sect. *Prostrata* and provided a key to some *Verticillium* species. Gams & Van Zaayen (1982) accepted four sections, *viz.* sect. *Verticillium*, sect. *Nigrescentia*, sect. *Prostrata*, sect. *Albo-erecta*, and a residual group. A key to these sections and detailed descriptions for some fungicolous *Verticillium* species were provided by Gams & Van Zaayen (1982). However, the sections singled out by Gams (1971) and Gams & Van Zaayen (1982) are still heterogeneous. Gams & Zare (2001) introduced the genera *Haptocillium* and *Lecanicillium*, while *V. balanoides* and *V. lecanii* were transferred to *Haptocillium* and *Lecanicillium*, respectively. In addition, *V. chlamydosporium* was synonymised under *Pochonia chlamydosporia* by Gams & Zare (2001). Zare & Gams (2001a) transferred several *Verticillium* species to *Lecanicillium*, and several were placed under the new genus *Simplicillium*. *Verticillium nigrescens* and *V. theobromae* were transferred to *Gibellulopsis* and *Musicillium*, respectively (Zare *et al.* 2007). Inderbitzin *et al.* (2011) provided conclusive phylogenetic analyses for this genus based on ITS, partial sequences of the protein coding genes *act*, *tef*1, *gapdh* and tryptophan synthase (*ts*). Ten species were accepted, *viz. V. albo-atrum*, *V. alfalfa*, *V. dahlia*, *V. isaacii*, *V. klebahnii*, *V. longisporum*, *V. nonalfalfae*, *V. nubilum*, *V. tricorpus*, *V. zaregamsianum*. These 10 species represent *Verticillium s. str*. An annotated checklist of epithets published in *Verticillium* and *Acrostalagmus*, some similar genera, and sexual morphs associated with verticillium-like asexual morphs was provided by Gams (2017).

Verticillium is characterised by having verticillate, septate, hyaline to brown conidiophores, monophialidic, hyaline conidiogenous cells, aseptate, or rarely 1-septate, hyaline, ellipsoidal or cylindrical with rounded ends, slimy conidia. Some species can produce chlamydospores, brown monilioid hyphae or microsclerotia (Zare *et al.* 2004, Seifert *et al.* 2011, Giraldo & Crous, 2019, Hyde *et al.* 2020d). It is similar to *Chlorocillium*, *Gibellulopsis*, *Haptocillium*, *Lecanicillium*, *Leptobacillium*, *Musicillium*, *Ovicillium*, *Pochonia*, *Rotiferophthora*, *Simplicillium*, *Sphaerostilbella* (Gams & Zare 2001, Zare & Gams 2001a, b, 2016, Zare *et al.* 2001, 2007, Seifert *et al.* 2011, Giraldo & Crous 2019, Wei *et al.* 2019). A key to verticillium- and gliocladium-like genera bearing one or several whorls of awl-shaped or flask-shaped phialides was provided by Seifert *et al.* (2011).

Ecological and economic significance

Verticillium species are important plant pathogens and causal agents of wilt in many host plants. *Verticillium albo-atrum* and *V. dahliae* are the two species that cause the most economic damage, including wilt on a wide range of plant hosts, including high-value crops such as cotton, lettuce, mango, olive, potato and strawberry (Pegg & Brady 2002, Jimenez-Diaz *et al.* 2017, Jayawardena *et al.* 2019), resulting in high yield losses.

There are seven plant-pathogenic species historically associated with the genus *Verticillium*, *viz*. *V. albo-atrum*, *V. dahliae*, *V. fungicola* (now known as *Lecanicillium fungicola*), *V. nigrescens* (now known as *Gibellulopsis nigrescens*, *V. nubilum*, *V. theobromae* (now known as *Musicillium theobromae*) and *V. tricorpus* (Pegg & Brady 2002, Barbara & Clewes 2003, Klosterman *et al.* 2009).

Verticillium species infect many important crops, *e.g*., banana, bean, beet, cherry, coffee, cotton, cucumber, eggplant, gold kiwifruit, lettuce, mango, muskmelon, olive tree, peach, pepper, potato, pumpkin, tomato, watermelon (Rudolph 1931, Himelick, 1969, Bhat & Subbarao 1999, Pegg & Brady, 2002, Klosterman *et al.* 2009, Jayawardena *et al.* 2019). Because of their soil habitat, their ability to produce resting structures and their capacity to infect a wide range of hosts, *Verticillium* wilt is a challenge for agricultural production (Barbara & Clewes, 2003, Klosterman *et al.* 2009).

Research interests

There are 2 545 publications and 30 674 citations from 2011–2021 in the Web of Science (Fig. 51), with the top 10 most cited articles listed in Table 31. Most of the publications focused on disease management, and research on pathogenic *Verticillium* species and *Verticillium* wilt (*V. albo-atrum* and *V. dahliae*), as well as taxonomic and phylogenetic studies (Fig. 52).

Verticillium wilt

Verticillium wilt is a common plant disease caused by *Verticillium* spp., especially *V. albo-atrum* and *V. dahliae*, and it is the most extensively researched area related to *Verticillium* species. Because *Verticillium* species infect such a large number of crops and ornamental plants, Verticillium wilt has caused economic losses of billions of dollars (Lazarovits & Subbarao 2009). Many studies have reported and introduced this widespread disease (Van Zaayen & Gams 1982, Bhat & Subbarao 1999, Barbara & Clewes 2003, Klosterman *et al.* 2009, Hyde *et al.* 2014, Jayawardena *et al.* 2019).

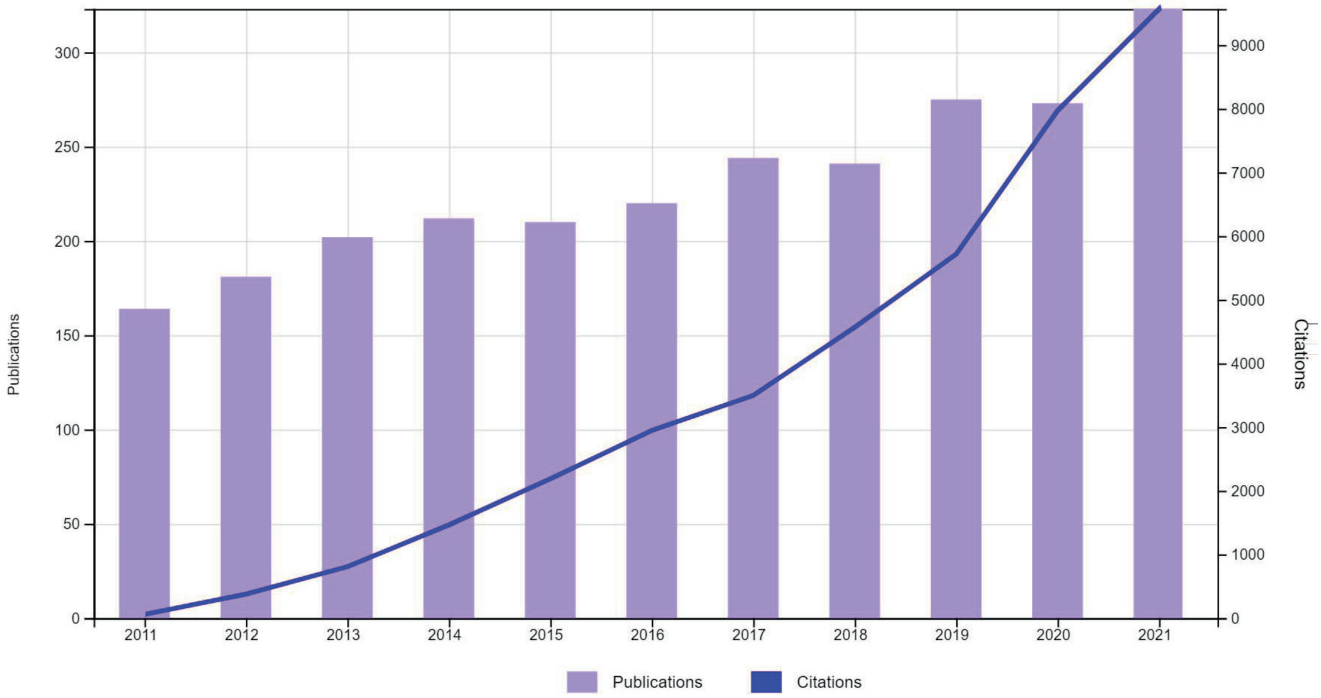

Fig. 51. Trends in research of *Verticillium* in the period 2011–2021.

Table 31. Top 10 cited articles related to *Verticillium* published in the period 2011–2021.

Rank	Article	No. of citations	References
1	Genome sequence of the cultivated cotton *Gossypium arboreum*	580	Li *et al.* (2014b)
2	Machine learning for high-throughput stress phenotyping in plants	360	Singh *et al.* (2016a)
3	Tomato immune receptor Ve1 recognizes effector of multiple fungal pathogens uncovered by genome and RNA sequencing	329	De Jonge *et al.* (2012)
4	Towards a natural classification and backbone tree for *Sordariomycetes*	326	Maharachchikumbura *et al.* (2015)
5	Comparative genomics yields insights into niche adaptation of plant vascular wilt pathogens	314	Klosterman *et al.* (2011)
6	Bidirectional cross-kingdom RNAi and fungal uptake of external RNAs confer plant protection	277	Wang *et al.* (2016d)
7	Lignin metabolism has a central role in the resistance of cotton to the wilt fungus *Verticillium dahliae* as revealed by RNA-Seq-dependent transcriptional analysis and histochemistry	272	Xu *et al.* (2011b)
8	MYB72-dependent coumarin exudation shapes root microbiome assembly to promote plant health	269	Stringlis *et al.* (2018)
9	One stop shop: backbones trees for important phytopathogenic genera: I (2014)	235	Hyde *et al.* (2014)
10	Families of *Sordariomycetes*	159	Maharachchikumbura *et al.* (2016)

Disease management

Reducing the populations of microsclerotia in soil, which are resting structures produced by *Verticillium* spp., is an effective approach to reduce losses due to Verticillium wilt (Lazarovits & Subbarao 2009). Soil fumigation with methyl bromide plus chloropicrin was used in some areas and in some conditions it is useful (Klosterman *et al.* 2009). However, soil fumigation can bring environmental pollution problems. Because of the wide host range of *Verticillium* species, crop rotation is not a good option for the management of Verticillium wilt (Klosterman *et al.* 2009). In some conditions, high nitrogen organic amendments and products containing volatile fatty acids (VFAs) can significantly reduce disease severity (Lazarovits & Subbarao 2009). Studies on the management of Verticillium wilt are ongoing, and an effective method that can be adapted to different environmental conditions and host plants is particularly needed.

Taxonomy and phylogeny

Because phylogenetic analyses are widely used in *Verticillium*, great changes have taken place in this genus (Zare *et al.* 2000, 2001, 2004, 2007, Gams & Zare 2001, Sung *et al.* 2001, Zare & Gams 2001a, b, Fahleson *et al.* 2004, Gams 2017). There are many *Verticillium* species recorded in Index Fungorum (2022) and MycoBank, however, most of them have been synonymised or transferred to other genera (Gams & Van Zaayen 1982, Zare & Gams 2001a, b, Zare *et al.* 2001, 2004, 2007, Seifert *et al.* 2011). The most conclusive study for this genus was carried out by Inderbitzin *et al.* (2011) and ten species were accepted in *Verticillium s. str*. However, it is necessary to recollect and epitypify the described taxa and amplify all the necessary genes for this genus.

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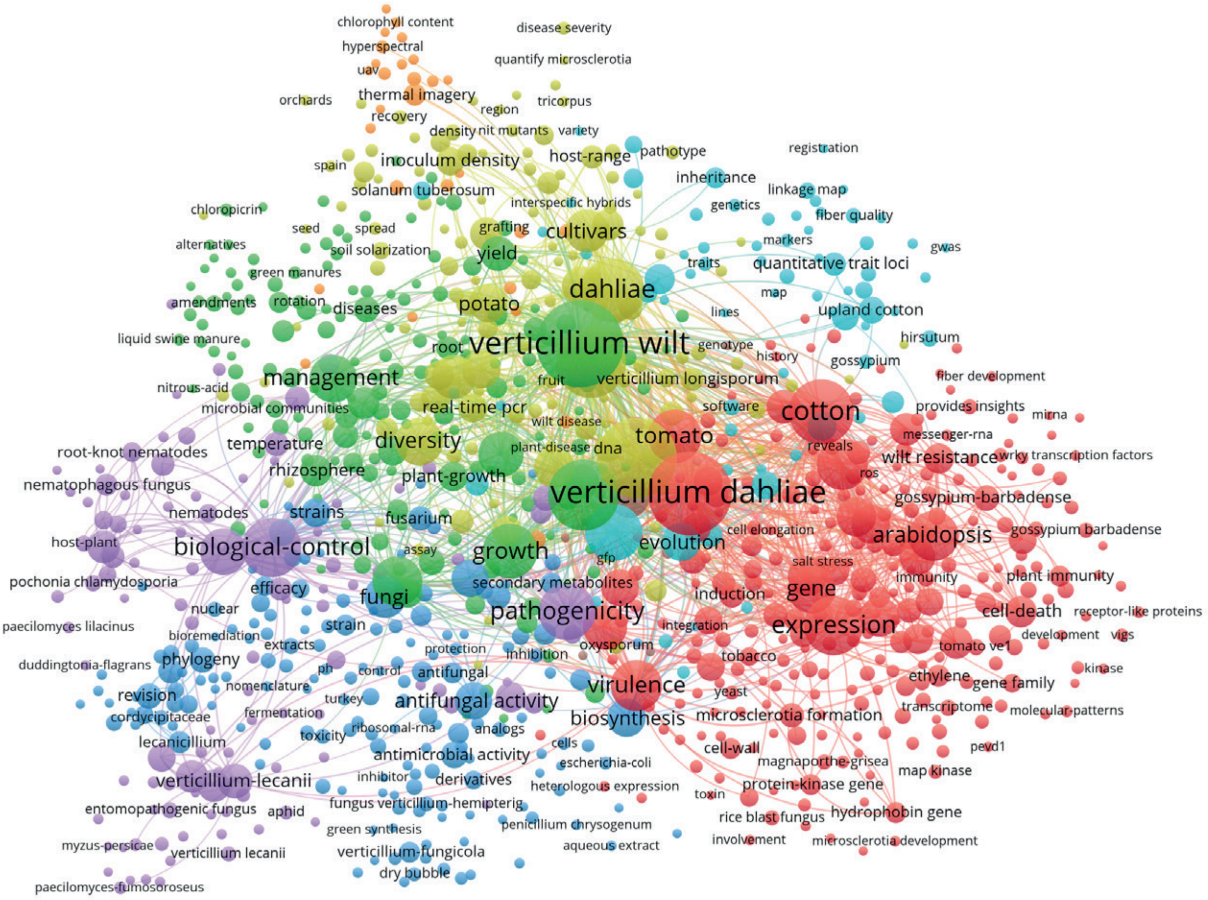

Fig. 52. Network visualisation of keywords of the publications related to *Verticillium*. The larger the text and the circle the more often the subject has been cited.

26. ***Sclerotinia*** Fuckel, Jb. Nassau. Ver. Naturk. 23–24: 330. 1870.

Type species: *Sclerotinia libertiana* Fuckel (syn. *Scl. sclerotiorum*)

Classification: *Ascomycota*, *Pezizomycotina*, *Leotiomycetes*, *Helotiales*, *Sclerotiniaceae.*

Background

Sclerotinia is a genus of plant pathogenic hyphomycetes with more than 200 epithets listed in Index Fungorum (2022). *Sclerotinia* was introduced by Fuckel (1870), based on the type species *Scl. libertiana* found on *Sclerotium compactum* in Germany. Despite the importance of *Sclerotinia* as a devastating plant pathogen, there are few studies on taxonomic classification available besides early monographic works on the *Sclerotiniaceae* (Whetzel 1945, Dumont & Korf 1971, Carbone & Kohn 1993, Holst-Jensen *et al.* 1997) and on the genus *Sclerotinia* (Kohn 1979a, b, Kohn *et al.* 1988). The complexity of *Sclerotinia* taxonomic classifications is illustrated by the recent reclassification of *Clarireedia* homoeocarpa (*Scl. homoeocarpa*), associated with dollar spot of turf grass (Salgado-Salazar *et al*. 2018). Although there are 122 currently accepted *Sclerotinia* names, it has been universally accepted that *Sclerotinia s. str.* contains three valid species only: *Scl. minor*, *Scl. sclerotiorum*, and *Scl. trifoliorum* (Kohn 1979a, b, Kohn *et al.* 1988, Bolton *et al.* 2006) and the vast majority of *Sclerotinia* diseases are caused by these three species. *Sclerotinia asari* and *Scl. nivalis* were later found as members of *Sclerotinia* based on DNA analyses (Wu & Wang 1983, Saito 1997, Clarkson *et al*. 2017). However, recent research is exploring *Scl. subarctica*, a morphologically indistinguishable species related to *Scl. sclerotiorum*. *Sclerotinia subarctica* requires unique climatic conditions for germination and disease initiation than that of *Scl. sclerotiorum* (Clarkson *et al*. 2017). Additionally, *Scl. subartica* has been distinguished from three accepted *Sclerotinia* spp. through adapted qPCR primers (Leyronas *et al.* 2018). The genetic variability of *Sclerotinia* populations is 'typically' considered clonal (Lehner *et al.* 2015, Steyn 2015), although, reports vary depending on the specific host plant, the origin of the isolate, climatic zones, and continuous availability of host crops (Lehner *et al.* 2017). This is illustrated by contrasting studies that have reported high variability and populations which are genetically and phenotypically distinct from one another (Attanayake *et al.* 2013, Aldrich-Wolfe *et al.* 2015). Due to the lack of contemporary studies on the taxonomy and classification of species in *Sclerotinia*, our understanding of species diversity and genetic relationships in this group remains obscure.

Plant pathogens in the genus *Sclerotinia* are among the few considered to be necrotrophs, deriving nutrients from killed host cells (Amselem *et al.* 2011). The active modulation of the host redox status and the subversion of the host (programmed) cell death pathways by *Sclerotinia* spp. appear to be crucial for disease development (Kim *et al.* 2008a, Amselem *et al.* 2011). A wide array of substances that facilitate a necrotrophic lifestyle are secreted, including cell-wall-degrading enzymes and oxalic acid (OA) (Kim *et al.* 2008a, b). Oxalic acid is known to play a key role in pathogenesis and fungal development, as its absence renders non-pathogenic isolates incapable of infecting host plants and unable to produce sclerotia (Kim et al. 2008a). Furthermore, the absence of OA plays a role in the processes leading to the development of melanised hyphal masses associated with pathogen survival *i.e.*, sclerotia. The formation of sclerotial stromata is commonly associated with Sclerotinia and members of *Sclerotiniaceae* (Willetts 1997, Bolton *et al.* 2006).

The most common pathogenic species, S*cl. minor*, *Scl. sclerotiorum*, and *Scl. trifoliorum* are distributed worldwide and occur on more than 440 different hosts, including numerous cultivated grains, oil- and protein seed, horticultural and vegetable crops (Bardin & Huang 2001, Heffer & Johnson 2007, Peltier *et al*. 2012, Farr & Rossman 2022, Khan *et al*. 2022). Wild plant hosts, such as broad-leaved weeds and wildflowers, are also known hosts of *Sclerotinia* spp. (Boland & Hall 1994, Heffer & Johnson 2007). Common disease names are derived from the symptoms and signs observed on the respective host crop (Purdy 1979); for example, cottony rot (carrot), blight (groundnut), drop (lettuce), head rot (sunflower), stem rot (canola and soybean) and white mould (multiple crops) (Purdy 1979, McDonald & Boland 2004, Heffer & Johnson 2007, Peltier *et al.* 2012, Khan *et al.* 2022). Due to the extensive host range, there are no unique symptoms that belong to all the plants affected by *Sclerotinia* diseases. However, initial symptoms, depending on the host, include a bleached appearance of infected tissues or a watery soft rot, a general characteristic associated with necrotrophic fungi (Amselem *et al.* 2011, Kabbage *et al.* 2015). Subsequently, white cottony mycelial mats form, a characteristic sign of infection, and in severe scenarios, the complete necrosis and shredding of plant organs may be evident (Purdy 1979, Bolton *et al.* 2006). As the disease progresses, the cottony hyphae of the pathogen aggregate into clumps of mycelium that eventually mature into hard black melanised sclerotia (Willets & Bullock 1992). Sclerotia can be found on the outer surface of the diseased tissue, inside of soft host tissues or cavities such as floral receptacles, fruits, and the pith of stems.

Pathogenic species within *Sclerotinia* spend a significant portion of their life cycle in and on soil in the form of sclerotia. The survival efficiency of sclerotia is attributed to the melanised rind, playing an important role in protection from adverse conditions and microbial degradation, as well as in some cases a function in virulence (Bell & Wheeler 1986, Henson *et al.* 1999, Butler *et al.* 2009). Sclerotia can survive for prolonged periods, ranging from one to 10 years before viability starts to decline (Ben-Yephet *et al.* 1993, Barding & Huang 2001, Amselem *et al.* 2011). The size, shape, and weight of sclerotia are dependent on multiple factors, however, the host crop is one of the primary driving variables (Bolton *et al.* 2006, Taylor *et al.* 2018). The disease cycle is initiated through carpogenic or myceliogenic germination depending on conducive environmental conditions. Carpogenic germination produces apothecia, containing inoperculate asci with ellipsoid ascospores, which are forcibly ejected into the air. The production of both large and small ascospores within one ascus and differences between ascospore length/width was used for the early morphological identification of *Scl. trifoliorum* from *Scl. sclerotiourum* and *Scl. minor* (Kohn 1979, Ekins *et al.* 2005). Airborne ascospores are chiefly responsible for infecting above-ground tissues, resulting in stem blights, stalk rot, head rot, pod rot, white mould, and blossom blights (Barding & Huang 2001, Bolton *et al.* 2006). In contrast, myceliogenic germination produces mycelia directly from sclerotia, able to infect crown and root tissues, causing crown and root rots (Barding & Huang 2001). Stipes (associated with carpogenic germination) have been observed on sclerotia which germinated myceliogenically, suggesting that sclerotia are capable of simultaneous dual-germination pathway events (Hao *et al.* 2003). *Sclerotinia* includes species that do not produce macroconidial asexual morphs, however, microconidia can be produced on hyphae or the apothecial hymenium. These microconidia might function as spermatia in some *Sclerotinia* species; however, they do not germinate and their role in the biology of these fungi is mostly unknown (Kohn 1979, Willetts 1997). Infected seed and sclerotia-infested seed bags are associated with the long-distance dissemination of *Sclerotinia* spp. (Hoes & Huang 1976, Mueller *et al.* 1999). Dispersal of the pathogen among regions and on-farm can be due to farm equipment, animal or human activities, runoff irrigation water and plant residues (Schwartz & Steadman 1978, Adam & Ayers 1979, Barding & Huang 2001). Localised in-field dissemination is associated with windblown ascospores and colonised plant material encountering healthy plant material (Ben-Yephet & Bitton 1985).

Ecological and economic significance

Sclerotinia species cause many significant diseases on economically important plants; three of the most well-known are detailed below.

Sclerotinia stem rot of soybean (*Glycine max*) caused by *Scl. sclerotiorum* is considered the second most important cause of yield loss in soybean-producing areas (Savary *et al.* 2019). When environmental conditions are conducive, Sclerotinia stem rot can reduce seed number and weight, seed quality and price discounts for foreign material (sclerotia) delivered at the grain elevator. Infected seeds are an important source of inoculum and can have reduced germination, and in some cases, oil and protein concentrations can be reduced (Peltier *et al.* 2012). The long-term survival of sclerotia in the soil is one of the biggest challenges for disease management (Peltier *et al.* 2012, Willbur *et al.* 2019). Selecting soybean cultivars with resistance to Sclerotinia stem rot is an important part of a disease management plan, although only partial resistance is available (Kim & Diers 2000, Chen & Wang 2005, McCaghey *et al.* 2019). Stem rot is also associated with other leguminous crops, such as dry beans (*Phaseolus vulgaris*) and peanuts (*Arachis hypogaea*) (Purdy 1970, McCreary *et al.* 2016).

Sclerotinia stem rot of *Brassica* oilseeds caused by *Scl. sclerotiorum* is a damaging disease of oilseed brassicas (*B. juncea*, *B. napus* and others). *Brassica* crops are important commodities in Europe, North America, and Indo-Pacific region (India, Australia, and China), with oilseed rape, *B. napus,* accounting for 13 % of total world edible oil production (Taylor *et al.* 2017). The oil-rich seeds of oilseed rape are also processed as biodiesel and high-quality animal feed (Derbyshire & Denton-Giles 2016). Management of *Sclerotinia* diseases is still difficult as sown rapeseed cultivars do not have high levels of resistance, and fungicide-resistant strains are increasingly reported. *Sclerotinia sclerotiorum* does not exhibit a gene-for-gene response during interactions with the host unlike other *B. napus* pathogens such as *Leptosphaeria maculans* (syn. *Plenodomus lingam*) or *Plasmodiophora brassicae*, and therefore despite advances made in the understanding of the *B. napus*–*Scl. sclerotiorum* interaction, few control strategies using genetic tools have proven successful (Wytinck *et al.* 2022).

Sclerotinia stalk/stem and head rot of sunflower (*Helianthus annuus*) caused by *Sclerotinia sclerotiorum* is one of the most destructive diseases of sunflowers. *Sclerotinia sclerotiorum* causes the most damage to sunflowers in cool and humid production regions resulting in more than 50 % seed yield loss. This disease has been reported in all important sunflower-producing regions of the world (Talukder *et al.* 2014). Unlike other hosts, sunflowers are vulnerable to infection by *Scl. sclerotiorum* both via floral and root infection, subsequently, causing head and stalk/stem rot. Myceliogenic germination of sclerotia leads to infection of nearby sunflower roots result in basal stalk rot and wilt. Head rot occurs when sclerotia germinate carpogenically releasing airborne ascospores and infecting senescing florets. Cultivated sunflowers generally lack complete resistance to *Scl. sclerotiorum*, although differences in susceptibility exist yielding variation of host responses under various environmental conditions. However, in over 51 species of *Helianthus*, a diverse pool of potential sources of *Sclerotinia* resistance exists. Evaluation of wild germplasm has indicated that several wild perennial species possess high levels of resistance to Sclerotinia head rot and stalk rot (Seiler *et al.* 2017).

Research interests

There are 2 705 publications and 27 698 citations from 2011–2021 in the Web of Science (Fig. 53), with the top 10 most cited articles listed in Table 32. Most publications focused on *Sclerotinia sclerotiorum* plant-pathogen interaction (host defense process, host resistance, pathogen virulence), disease management (disease suppression by cultural practices), fungal viruses (Sclerotinia ssDNA virus) and research on the host and pathogen genomes to understand host defences and defences and pathogen virulence. Shared research interests between *Botrytis*, *Monilinia* and *Sclerotinia* are often cited as they have shared taxonomic features belonging to the *Sclerotiniaceace* and may co-occur in field (Fourie *et al*. 2002).

Plant pathogen interaction

As necrotrophs, *Sclerotinia* spp*.* produce a wide array of degradative lytic enzymes (*e.g.*, endo- and exo-pectinase, cellulase, hemicellulase, protease) as well as oxalic acid, believed to facilitate colonisation and host cell wall degradation. Oxalic acid contributes to numerous physiological processes (*e.g.*, reduction in pH, acidity-induced activation of enzymes, the elevation of Ca2+, guard cell regulation, vascular plugging with oxalate crystals) that augment fungal colonisation of host plants (Williams *et al.* 2011). Studies with OA-deficient mutants strongly suggest that OA is an essential pathogenicity determinant and a key factor governing the broad pathogenic success of *Sclerotinia*. Oxalic acid also aids *Sclerotinia* pathogenicity indirectly by acting as a signalling molecule, via manipulation of the host reactive oxygen system (ROS) (Williams *et al.* 2011, Heller & Witt-Geiges 2013). Understanding of host-*Sclerotinia* interactions can contribute to the efforts of breeding for resistance.

Disease management

Diseases caused by *Sclerotinia* spp. require an integrated pest management program that includes a combination of cultural practices, cultivar selection with host resistance and crop rotation, chemical control, and biological control (Bardin & Huang 2001, Peltier *et al*. 2012). For economically important crops, targeted disease forecasting programs based on epidemiological data for fields have been developed, however, these programs are targeted for specific growing regions (Derbyshire & Denton-Giles 2016). Breeding programs are also exploring sources of partial resistance in wild relatives of cultivated plants, which can help reduce losses associated with *Sclerotinia* diseases (Taylor *et al.* 2017).

Biological control

Research groups in China, the USA, and New Zealand found that *Scl. sclerotiorum* hosts various mycoviruses, including double-stranded RNA (dsRNA) viruses, positive-sense single-stranded RNA (+)ssRNA viruses, DNA viruses and negative-sense single-stranded RNA (−)ssRNA viruses (Xie & Jiang 2014). *Sclerotinia sclerotiorum* hypovirulence-associated DNA virus 1 (SsHADV-1) was the first DNA mycovirus to be found to confer hypovirulence to the fungi infected (Yu *et al.* 2010). The investigation of different *Scl. sclerotiorum*-mycovirus interaction systems might supply new insights regarding virus-host interactions as well as control

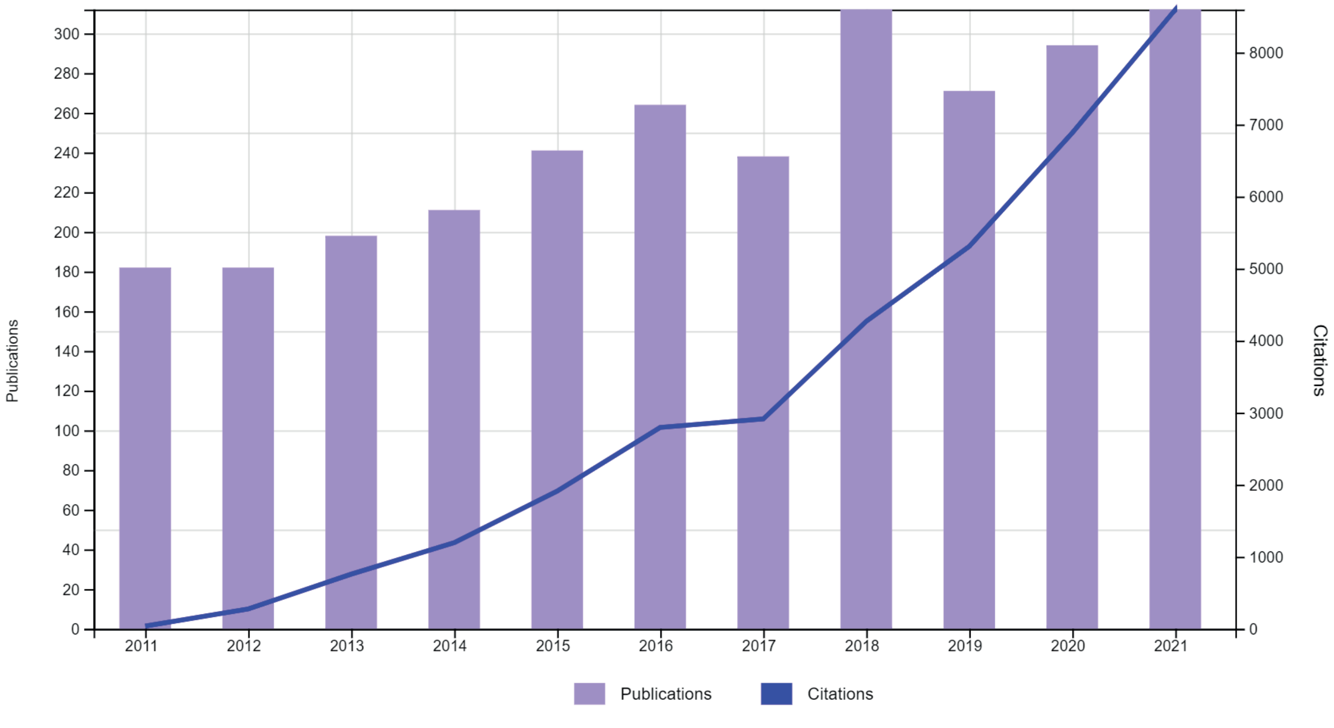

Fig. 53. Trends in research of *Sclerotinia* in the period 2011–2021.

Table 32. Top 10 cited articles related to *Sclerotinia* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Evolution of jasmonate and salicylate signal crosstalk	678	Thaler *et al.* (2012)
2	Genomic analysis of the necrotrophic fungal pathogens *Sclerotinia sclerotiorum* and *Botrytis cinerea*	603	Amselem *et al.* (2011)
3	Have biopesticides come of age?	348	Glare *et al.* 2011
4	50-plus years of fungal viruses	323	Ghabrial *et al.* (2015)
5	Plant immunity to necrotrophs	311	Mengiste (2012)
6	Tipping the balance: *Sclerotinia sclerotiorum* secreted oxalic acid suppresses host defenses by manipulating the host redox environment	277	Williams *et al.* (2011)
7	Crops that feed the World 2. Soybean-worldwide production, use, and constraints caused by pathogens and pests	238	Hartman *et al.* (2011)
8	A review of current knowledge of resistance aspect for the next-generation succinate dehydrogenase inhibitor fungicides	235	Sierotzki & Scalliet (2013)
9	New insights into mycoviruses and exploration for the biological control of crop fungal diseases	213	Xie & Jiang (2014)
10	*Bacillus* strains isolated from rhizosphere showed plant growth promoting and antagonistic activity against phytopathogens	208	Kumar *et al.* (2012)

strategies for *Sclerotinia* diseases (Xie & Jiang 2014). Additionally, (−)ssRNA viruses are also known to be dangerous human viruses, however, the discovery of these viruses in fungi can provide a safe model system to study function and to screen antiviral compounds against them (Xie & Jiang 2014).

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27. ***Rhodotorula*** F.C. Harrison, Proc. & Trans. Roy. Soc. Canada, ser. 3 21(5): 349. 1927.

Type species: *Rhodotorula glutinis* (Fresen.) F.C. Harrison

Classification: *Basidiomycota*, *Pucciniomycotina*, *Microbotryomycetes*, *Sporidiobolales*, *Sporidiobolaceae.*

Background

The genus *Rhodotorula* was introduced by Harrison (1928), with *Rho. glutinis* (bas. *Cryptococcus glutinis*) as the type species. The genus has about 190 records registered in Index Fungorum (2022); however, several species have been transferred to other genera and a new generic concept was introduced by Wang *et al.* (2015b). In the most recent outline of fungi, *Rhodotorula* is placed in the family *Sporidiobolaceae* with about 15 accepted species (Wijayawardene *et al.* 2022). The recently introduced species, *Rho. sampaioana* (from subsurface waters, Argentina) and *Rho. frigidialcoholis* (from permafrost, Antarctica), were described by Tiwari *et al.* (2021) and Touchette *et al.* (2022), respectively.

Morphologically, *Rhodotorula* species are mainly characterised by having subglobose, ovoid, ellipsoid or elongate cells, occasionally producing pseudohyphae or true hyphae. Species produce red or yellow pigments and asexual reproduction is by multilateral or polar budding (Sampaio *et al.* 2011). Fermentative ability is absent but the capacity to assimilate several carbon sources has been reported. However, *Rhodotorula* species are positive for diazonium blue B (DBB) reaction and production of urease (Sampaio *et al.* 2011). The genus description was emended to include the sexual morph *Rhodosporidium*, based on multi-gene phylogenetic analyses (Wang *et al.* 2015c), which revealed that some species of *Rhodotorula* were also described as having sexual reproduction by producing transversely septate basidia and ovoid basidiospores germinating by budding.

In the Global Biodiversity Information Facility (GBIF) (https://www.gbif.org/species/2518125/metrics), there are 5 433 occurrences registered in the database, with the most registrations (1 404) from Australia, and the years 2011 to 2016 having the highest numbers of registration (*e.g.*, 379–508). *Rhodotorula* species have been mostly reported as environmental yeasts (*i.e.*, saprobes and psychrophiles), being frequently isolated from plant material, soil, and water (Sampaio *et al.* 2011, Li *et al.* 2020b, Tiwari *et al.* 2021, Touchette *et al.* 2022). For instance, most of the species accepted by Wang *et al.* (2015b) were first isolated from plant materials and water obtained in the USA, Chile, Japan, and New Zealand, among other countries. However, some studies have reported some *Rhodotorula* species as opportunist pathogens, mainly among immunocompromised individuals (Sampaio *et al.* 2011, Ioannou *et al.* 2019), causing nosocomial and opportunist infections (Sampaio *et al.* 2011, Ioannou *et al.* 2019), with bloodstream, central nervous system, and ocular infections as the most commonly observed manifestations (Ioannou *et al.* 2019).

Importance in public health (pathogenesis)

Rhodotorula species have not been included as important etiological agents of mycosis (Sampaio *et al.* 2011). However, there are several case reports of *Rhodotorula* species causing disease, mainly in immunocompromised patients (Miceli *et al.* 2011, Wirth & Goldani 2012, Ioannou *et al.* 2019). Ioannou *et al.* (2019) reviewed cases of infections caused by *Rhodotorula* species in all five continents, with Asian, European and North American countries having the highest number of cases. Ioannou *et al.* (2019) showed that *Rhodotorula* infections usually manifest as fungemia, central nervous system (CNS) and ocular infections, as well as peritoneal dialysis-associated peritonitis. *Rhodotorula mucilaginosa*, *Rho. glutinis*, *Rho. minuta*, and *Rho. marina* were the most reported species in these infections. However, *Rho. minuta* and *Rho. marina* are not accepted as species of *Rhodotorula* (Wang *et al.* 2015c), being treated in *Cystobasidium* (Yurkov *et al.* 2015) and *Symmetrospora* (Wang *et al.* 2015c), respectively.

Different factors were observed in the *Rhodotorula* lifestyle acting as an opportunistic etiologic agent of infections. For example, Ioannou *et al.* (2019) outlined that fungemia is more frequent in male patients (with a mean age of 33.5 years) that had previous malignancy (mainly hematologic malignancies), or presented an immune depression condition (by AIDS or due to chemotherapy and organ transplant), or autoimmune diseases. Most of these infections were associated with the use of central venous catheter (CVC) and parenteral nutrition (Ioannou *et al.* 2019). These authors also observed a tendency in which AIDS patients have more common CNS infections, and the patients with ocular infections were preceded by trauma or surgery (Ioannou *et al.* 2019). The mortality rate of patients affected by *Rhodotorula* infection is around 10–15 % (Toun & Costa 2008, Miceli *et al.* 2011, Ioannou *et al.* 2019), but in some cases, such as for the CNS infections, overall mortality can reach 41 % (Ioannou *et al.* 2019); however, these rates should be treated independently and the characteristics of each patient need to be evaluated (Ioannou *et al.* 2019).

Research interests

There are 1 810 publications and 26 581 citations from 2011–2021 in the Web of Science (Fig. 54), with the top 10 most cited articles listed in Table 33. Most of the publications focused on applied microbiology (*e.g.*, biotechnology, food science, energy fuel), and some papers report the medical importance of *Rhodotorula* species.

Taxonomy and phylogeny

Since the introduction of *Rhodotorula* (Harrison 1928), and over subsequent years, species in this genus were mainly characterised based on morphology and physiology/biochemistry, including red-pigmented yeasts with no formation of ascospores (Sampaio *et al.* 2011). Later, Lodder (1934) included all yeasts producing carotenoid pigments in *Rhodotorula*. Following this treatment, little change was included in the generic concept of *Rhodotorula* (Lodder & Kreger-van Rij 1952, Lodder 1970). Another important fact was the increase in the number of *Rhodotorula* species, growing from seven (Lodder & Kreger-van Rij 1952) to 47 accepted species (Sampaio *et al.* 2011). One of the most important steps in *Rhodotorula* classification and taxonomy was the establishment of the genus as a basidiomycetous yeast and the sexual related species classified in *Rhodosporidium* (Lodder 1970). Sampaio *et al.* (2011) highlighted that *Rhodotorula* is polyphyletic with species classified into two subphyla (*Pucciniomycotina* and *Ustilaginomycotina*) and four classes (*Microbotryomycetes*, *Cystobasidiomycetes*, *Ustilaginomycetes* and *Exobasidiomyetes*). These authors recommended including species related to the type species, *Rho. glutinis*, from the order *Sporidiobolales* for a modern classification for this genus.

Wang *et al.* (2015b) conducted a large study of the classification of yeasts and related taxa and based on multi-locus phylogeny and morphological, physiological and biochemical information known over years, introduced a new generic concept to *Rhodotorula* and several species were transferred to other genera. The generic description of *Rhodotorula* was emended to include the sexual morph features of species previously treated in *Rhodosporidium* and 15 species were accepted in the genus. *Rhodotorula* was initially considered a polyphyletic genus, as highlighted by Sampaio *et al.* (2011), but its polyphyly was resolved by Wang *et al.* (2015b) based on DNA markers and the genus was placed in *Sporidiobolaceae* (*Sporidiobolales*); the same treatment was followed by Wijayawardene *et al.* (2022).

Environment and biotechnology

Rhodotorula species are frequently isolated from the environment (*e.g.*, living as saprobes and mainly obtained from plants, soils, and water) (Sampaio *et al.* 2011, Li *et al*. 2020) and also reported from spoiled foods and beverages (Barata *et al.* 2012, Wirth & Goldani 2012, Garnier *et al.* 2017). Species in this genus are among the most important fungi to be used in biotechnological processes (Kot *et al.* 2016) being known as "biotechnological machine" used in industries for the production of pigments, lipids, and enzymes capable of degrading rejected low-cost materials (Ageitos *et*

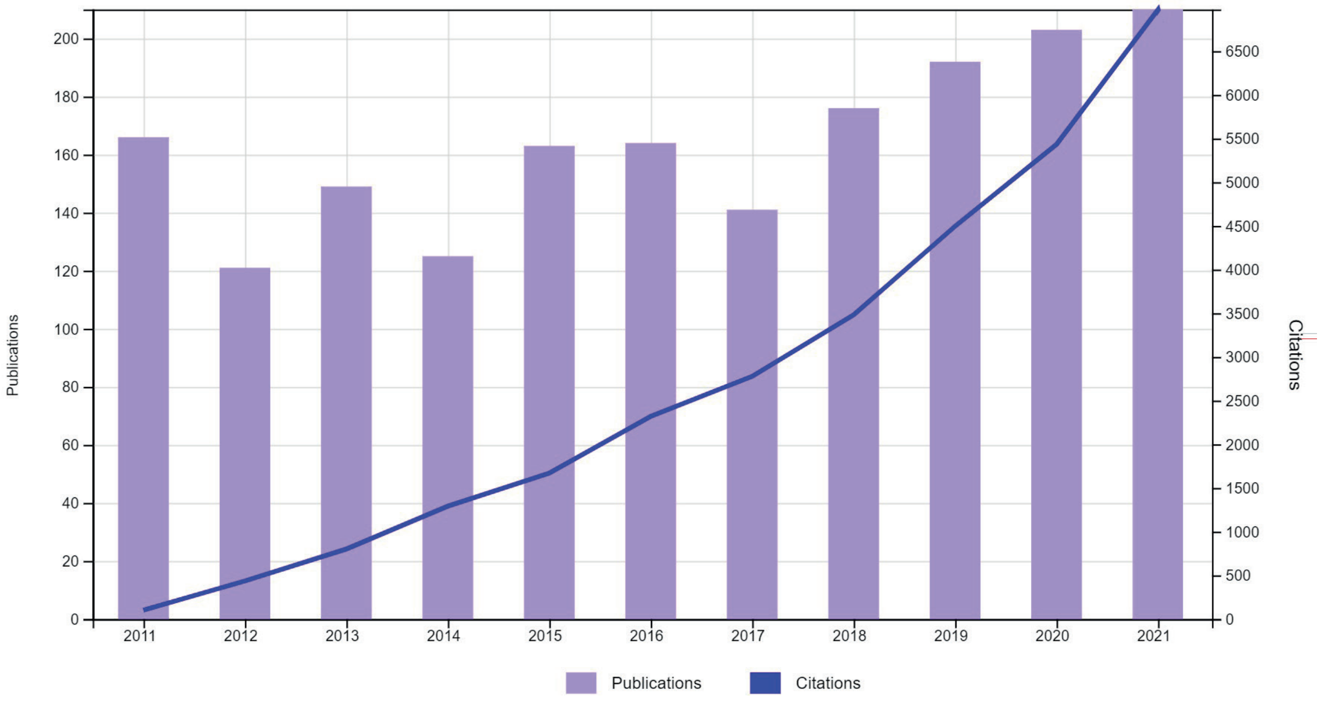

Fig. 54. Trends in research of *Rhodotorula* in the period 2011–2021.

Table 33. Top 10 cited articles related to *Rhodotorula* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Emerging opportunistic yeast infections	530	Miceli *et al.* (2011)
2	Neonatal gut microbiota associates with childhood multisensitized atopy and T cell differentiation	477	Fujimura *et al.* (2016)
3	The microbial ecology of wine grape berries	360	Barata *et al.* (2012)
4	Oily yeasts as oleaginous cell factories	353	Ageitos *et al.* (2011)
5	Oil production by oleaginous yeasts using the hydrolysate from pretreatment of wheat straw with dilute sulfuric acid	313	Yu *et al.* (2011a)
6	ESCMID and ECMM joint clinical guidelines for the diagnosis and management of rare invasive yeast infections	305	Arendrup *et al.* (2014)
7	Characterization of the fungal microbiota (mycobiome) in healthy and dandruff-afflicted human scalps	250	Park *et al.* (2012b)
8	Potential use of oleaginous red yeast *Rhodotorula glutinis* for the bioconversion of crude glycerol from biodiesel plant to lipids and carotenoids	220	Saenge *et al.* (2011)
9	Terminal olefin (1-alkene) biosynthesis by a novel P450 fatty acid decarboxylase from *Jeotgalicoccus* species	219	Rude *et al.* (2011)
10	Biotechnological conversions of biodiesel derived waste glycerol by yeast and fungal species	203	Chatzifragkou *et al.* (2011)

al. 2011, Chatzifragkou *et al.* 2011, Saenge *et al.* 2011, Yu *et al.* 2011a, Kot *et al.* 2016). Over the years, some researchers have focused on the potential of *Rhodotorula* species/isolates to be used in the production of oils (Ageitos *et al.* 2011, Chatzifragkou *et al.* 2011, Saenge *et al.* 2011, Yu *et al.* 2011a, Mussagy *et al.* 2021), carotenoids and enzymes (Kot *et al.* 2016, Mussagy *et al.* 2021).

Carotenoids produced by *Rhodotorula* species are important in the food industry as pigments and diet supplements (Saenge *et al.* 2011, Kot *et al.* 2016). Because of the health benefits of carotenoids, they have also been used in cosmetic and pharmaceutical industries (Kot *et al.* 2016, Mussagy *et al.* 2021), with promising global markets (see the reports of "The Global Market for Carotenoids" in 2018 and "Yeasts, Yeast Extracts, Autolysates and Related Products: The Global Market" in 2017).

Diagnosis in human health

Similar to other yeasts already known as etiologic agents of mycosis, *e.g.*, *Candida* and *Cryptococcus* species, *Rhodotorula* is a genus that needs attention during the treatment of hospitalised patients (Toun & Costa 2008, Miceli *et al.* 2011, Ioannou *et al.* 2019). Over the years, *Rhodotorula* isolates have been frequently reported as etiologic agents of human infections, mainly in immunocompromised patients (Toun & Costa 2008, Miceli *et al.* 2011, Arendrup *et al.* 2013, Ioannou *et al.* 2019). Diagnostic methods broadly used for other mycoses, *e.g.*, candidiasis and cryptococcosis, could also be used for the isolation and identification of *Rhodotorula* species. The molecular markers usually studied for analyses of DNA sequences are ITS and D1/D2 domain of the LSU rDNA regions (Arendrup *et al.* 2013). In addition, protein analysis by MALDI-TOF has been applied for yeast identification (Fraser *et al.* 2016). In 2013, a panel of experts proposed a clinical guideline for the diagnosis and management of rare invasive yeast infections, including important highlights for *Rhodotorula* species (Arendrup *et al.* 2013).

Virulence factors

Virulence factors of *Rhodotorula* species is an understudied topic. Some studies suggest that virulence is related to the capacity of *Rhodotorula* isolates to form biofilm on medical devices (*e.g.*, catheter fragments) (Arendrup *et al.* 2013, Thomson *et al.* 2017, Maciel *et al.* 2019, Jarros *et al.* 2020, 2021). These studies showed that these isolates also have the potential to form biofilm and should be studied similarly to other medically important yeasts. For example, species of *Candida* are widely studied because of their medical importance, and their virulence factors are also well understood (Rocha *et al.* 2021). Other surveys showed that similar to *Cryptococcus* cells, *Rhodotorula* capsules may act as a resistance mechanism against phagocytosis (Yockey *et al.* 2019). The emergence of *Rhodotorula* species as opportunistic pathogens needs more attention.

Management of the disease

Rhodotorula species have been associated with healthcare workers and found in hospital environments (Khodavaisy *et al.* 2011, Sham *et al.* 2021). Due to their capacity to adhere to surfaces, medical equipment (*e.g.*, flexible endoscopes) could also be a source of contamination (Arendrup *et al.* 2013, Ioannou *et al.* 2019). Good biosafety practices in the hospital environment could also minimise external contamination of patients. For the treatment of hospitalised patients due to *Rhodotorula* infection, amphotericin B is the most common antifungal drug used, followed by fluconazole, 5-fluocytosine, itraconazole, voriconazole, and ketoconazole (Ioannou *et al.* 2019); however, there are reports of resistance of *Rhodotorula* species to azoles and echinocandins (Arendrup *et al.* 2013, Yockey *et al.* 2019). Combined use of drugs is necessary in some cases (Ioannou *et al.* 2019). Ioannou *et al.* (2019) reported a high clinical cure rate for patients with *Rhodotorula* infection.

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28. ***Beauveria*** Vuill., Bull. Soc. Bot. France 59: 40. 1912.

Type: *Beauveria bassiana* (Bals.-Criv.) Vuill.

Classification: *Ascomycota*, *Pezizomycotina*, *Sordariomycetes*, *Hypocreales*, *Cordycipitaceae.*

Background

The discovery of *Beauveria bassiana* dates back to the causal agent of white muscardine disease on silkworms that was found by an Italian entomologist, Agostino Bassi di Lodi (Bassi 1835, 1836). *Beauveria bassiana* was initially described as *Botrytis bassiana* by Giuseppe Gabriel Balsamo-Crivelli, in honour of Bassi's discovery (Rehner 2005). Later, Vuillemin (1912) formally erected the genus *Beauveria* and designated *Beauveria bassiana* as the type species, in honour of Beauveria who had studied the fungus in 1911. *Beauveria brongniartii* was the second species described in this genus by the end of the 19th century (MacLeod 1954). Since then, many *Beauveria* species have been introduced from soil and arthropod hosts (Zimmermann 2007).

Beauveria originally was known as an anamorphic genus which was placed in *Moniliacea* (*Moniliales*, *Hyphomycetes*, *Deuteromycotina*) (Imoulan *et al*. 2017). Nowadays, multi-loci phylogenies have necessitated the transfer of *Beauveria* to *Cordycipitaceae* (*Hypocreales*) (Sung *et al.* 2007, Maharachchikumbura *et al.* 2016a, b) and the sexual-asexual connection between *Beauveria* and *Cordyceps* has been established based on molecular analyses (Liu *et al.* 2002, 2001, Rehner *et al.* 2005, Shrestha *et al.* 2014). The sexual morph of *Beauveria* is characterised by brightly-pigmented, stipitate, fleshy stromata and semi-immersed, ovoid perithecia which are produced on the upper part of stromata and cylindrical asci with thickened apex and hyaline, filiform, multiseptate ascospores which disarticulate into cylindrical, one-celled secondary spores when mature (Khonsanit *et al.* 2020). The key diagnostic character of asexual *Beauveria* species is the basally inflated conidiogenous cells with a zig-zag rachis from which the conidia are produced (De Hoog 1972). Cultural and morphological characteristics present a low resolution on interspecific delimitation within *Beauveria*, due to the extensive overlap in conidial shape and dimensions (Imoulan *et al.* 2017). For a long time, many strains were consigned to *Beauveria bassiana* and *Be. brongniartii*, based on the shape of conidia, which included many cryptic species, leading to taxonomic confusion in *Beauveria* (Zimmermann 2007, Imoulan *et al.* 2017). Recently, some cryptic species of *Beauveria* were restudied employing both maximum likelihood and neighbor-net phylogenetic analyses based on combined markers (*tef*–*rpb*1–*rpb*2–ITS–*Bloc*) (Khonsanit *et al.* 2020). To date, 40 morphological species are accepted in *Beauveria*, including 25 species with sequence data (Hyde *et al.* 2020d).

Ecological and economic significance

Beauveria includes some of the most well-known species used in biological control against insect pests (Lacey *et al.* 2015, García-Estrada *et al.* 2016). *Beauveria* species can persist in soil as dormant propagules; in plants as endophytes or associated with the rhizosphere (Ownley *et al.* 2008, Vega *et al.* 2009, Greenfield *et al*. 2016, Vega 2018); they are also plant disease antagonists (Dara 2019). Thanks to the great diversity in ecological niches and wide arthropod host range, this genus has huge potential in pest management with significant ecological and economic impacts.

Beauveria bassiana is the most widely used species and can infect insects belonging to over 521 genera (Imoulan *et al.* 2017). From its discovery 200 years ago as the cause of devastating disease in economically important silkworm, *Be. bassiana* became a popular entomopathogenic fungus used as an agent against various agricultural pests (Lacey *et al.* 2015, García-Estrada *et al*. 2016, Baron *et al*. 2019, 2020) with many mycopesticide products developed from *Beauveria* and available in niche markets (Zimmermann 2007). *Beauveria*, especially *Be. bassiana* and *Be. brongniartii*, were shown also to be effective against invasive insects causing damage to trees in natural habitats such as Eucalyptus weevil, Asian long-horned beetle, emerald ash borer and oak lace bug (Dara 2019). *Beauveria* species have been used also against insect vectors of protozoan and bacterial diseases to humans and animals such as *Triatoma infestans* (kissing bug) carrying Chaga's disease that has infected over 20 million people in South America (Forlani *et al.* 2015); ticks carrying *Borrelia burgdorferi*, a bacterium causing Lyme disease (Kirkland *et al.* 2004). *Beauveria bassiana* has been used also against mosquito vectors of important human diseases such as malaria (Kikankie *et al.* 2010, Ragavendran *et al.* 2017) and Zika virus (Deng *et al.* 2019).

Research interests

There are 3 620 publications and 26 077 citations from 2011–2021 in the Web of Science (Fig. 55), with the top 10 most cited articles shown in Table 34. The publications cover the evolution and mechanisms of virulence, production of secondary metabolites and virulence-associated molecules, the interest for biocontrol and appropriate formulation for practical use, and also diversity and taxonomy.

Phylogeny and taxonomy

Beauveria includes many cryptic species with ambiguous morphological characters. The size and shape of conidia can be used to some extent to discriminate species but multigene phylogenies have been the basis for circumscribing new species during the last decade (Rehner & Buckley 2005, Rehner *et al.* 2011, Imoulan *et al.* 2017, Khonsanit *et al.* 2020). The species status of certain taxa might be doubtful as they were proposed based on a few samples with incomplete species sampling (Chen *et al.* 2018d). Future studies should include comprehensive data for the genus, and propose detailed morphometric analyses on conidia size and shape to propose new species.

Virulence and host specificity

Beauveria is well known for *Be. bassiana*, largely studied for its virulence and pathogenicity against arthropods (Xiao *et al.* 2012). The variation of virulence and host specificity are generally elusive with contrasting results. For example, some studies found a strong to intermediate association between hosts and genetic groups (Maurer *et al.* 1997, Chen *et al.* 2015f) while other studies (Wang *et al.* 2005, Meyling *et al.* 2009, Mei *et al.* 2020) found that genetic structure cannot be explained by host association but rather by geographic origins. The level of virulence can be highly variable between strains toward specific insect groups (Boston *et al.* 2020) without apparent association to population genetic structure. Variation in virulence seems to be due to the mutation and positive selection of some categories of genes, particularly toxin-producing genes (Zhang *et al.* 2020). Highly virulent strains seem to arise by gaining specific genes such as polyketide synthases (PKSs) and bacterial toxins (Xiao *et al.* 2012, Valero-Jiménez *et al.* 2016).

Toxins and secondary metabolite

Beauveria produces a diverse array of biologically active secondary metabolites that include non-peptide pigments and polyketides, non-ribosomally synthesised peptide antibiotics and other secreted metabolites implicated in insect pathogenesis and

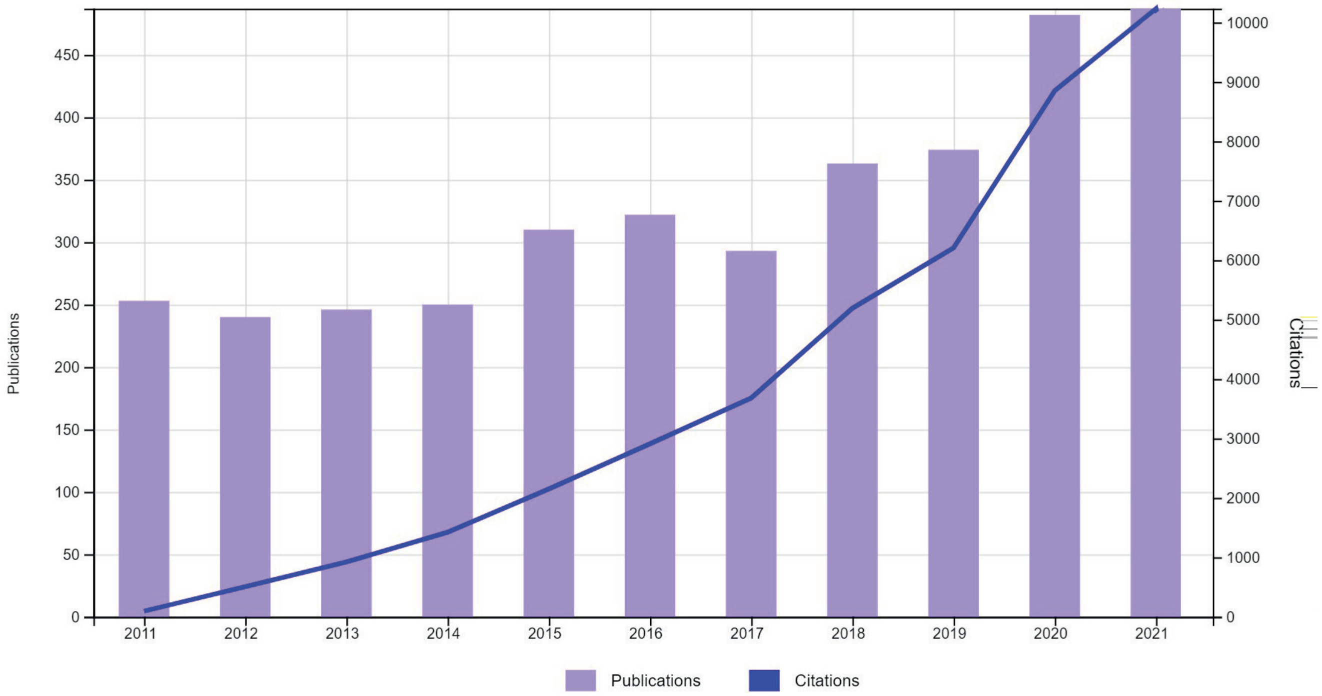

Fig. 55. Trends in research of *Beauveria* in the period 2011–2021.

Table 34. Top 10 cited articles related to *Beauveria* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Insect pathogens as biological control agents: back to the future	623	Lacey *et al.* (2015)
2	Genomic perspectives on the evolution of fungal entomopathogenicity in *Beauveria bassiana*	370	Xiao *et al.* (2012)
3	Phylogeny and systematics of the anamorphic, entomopathogenic genus *Beauveria*	232	Rehner *et al.* (2011)
4	Insect pathogenic fungi: genomics, molecular interactions, and genetic improvements	168	Wang & Wang (2017)
5	Two hydrophobins are involved in fungal spore coat rodlet layer assembly and each play distinct roles in surface interactions, development and pathogenesis in the entomopathogenic fungus, *Beauveria bassiana*	161	Zhang *et al.* (2011)
6	Fungal secondary metabolites as modulators of interactions with insects and other arthropods	155	Rohlfs & Churchill (2011)
7	Additive contributions of two manganese-cored superoxide dismutases (MnSODs) to antioxidation, UV tolerance and virulence of *Beauveria bassiana*	137	Xie *et al.* (2012)
8	More than a colour change: insect melanism, disease resistance and fecundity	118	Dubovskiy *et al.* (2013)
9	Evolutionary interaction networks of insect pathogenic fungi	109	Boomsma *et al.* (2014)
10	A phylogenetically based nomenclature for *Cordycipitaceae* (*Hypocreales*)	89	Kepler *et al.* (2017)

virulence that have potential use in industrial, pharmaceutical and agricultural aspects (Rehner *et al.* 2012). These metabolites exhibit insecticidal, antiviral, antibacterial, antifungal, anticancer, anti-tumour, antiatherosclerotic, cytotoxic, herbicidal activities, *etc*. (Strasser *et al.* 2000 a, b, Gurulingappa *et al.* 2011, Sahab 2012, Lozano-Tovar *et al.* 2017, Cheong *et al.* 2020, Du *et al.* 2020). Some important mycotoxins derived from *Beauveria* species have been elucidated with chemical structure, synthesis mechanism, physicochemical properties and bioactive activity (Logrieco *et al.* 2002, Zobel *et al.* 2016, Amobonye *et al.* 2020). Beauvericin and pyridovericin have significant cytotoxicity to a variety of cancer cell lines, showing high potential in cancer therapeutics (Strasser *et al.* 2000b, Wu *et al.* 2018b, Amobonye *et al.* 2020). Oosporein, bassianin and tenellin have ability to inhibit insect immunity, allowing the fungus to overcome and kill its hosts (Basyouni *et al.* 1968, Jeffs & Khachatourians 1997, Zibaee *et al.* 2011, Fan *et al.* 2013, Feng *et al.* 2015a, Mc Namara *et al.* 2019). The compound S-(-)-10,11-dihydroxyfarnesic acid methyl ester (**I**) can inhibit melanin synthesis and does not irritate the skin or eyes of humans, for which it can be developed as cosmetic biomaterials (Son & Lee 2013). Additionally, batryticated silkworms infected by *Be. bassiana* have traditionally been used as folk medicine to treat stroke, urticaria, diabetes, *etc*. (Patocka 2016). Much research has been conducted to investigate the pharmacological activities, main compositions and clinical uses of batryticated silkworms (Hu *et al.* 2017).

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29. *Puccinia* Pers., Syn. Meth. Fung. 1: 225. 1801.

Type species: *Puccinia graminis* Pers.

Classification: *Basidiomycota*, *Pucciniomycotina*, *Pucciniomycetes*, *Pucciniales*, *Pucciniaceae.*

Background

Puccinia graminis on cultivated Triticum was designated as the type species of Puccinia by Cunningham (1931) and subsequently lectotypified by Jørstad (1958). Over the last century, *Puccinia* has typified taxonomic ranks up to the *Pucciniomycotina*.

Puccinia (*Pucciniaceae*) has almost 6 000 named species, which accounts for almost half of the known species of rust fungi (He *et al.* 2022a). *Puccinia* species are obligate plant pathogens on hosts in many plant families, especially *Asteraceae*, *Cyperaceae*, *Fabaceae*, *Lamiaceae*, *Liliaceae s. lat.*, *Malvaceae* and *Poaceae* (Fig. 56). Some species of *Puccinia* cause rust diseases on agriculturally important hosts in the *Poaceae* and *Asteraceae* (Aime & McTaggart 2021) while others have been utilised as beneficial biological control agents for invasive weeds, *e.g.*, *Puccinia chondrillina*, *Pu. myrsiphylii* and *Pu. xanthii*.

Most species of *Puccinia* form conspicuous, powdery, yellow to red pustules (uredinia) on leaves and stems. The rusty colour of uredinia reveals the etymology of both the name that applies to

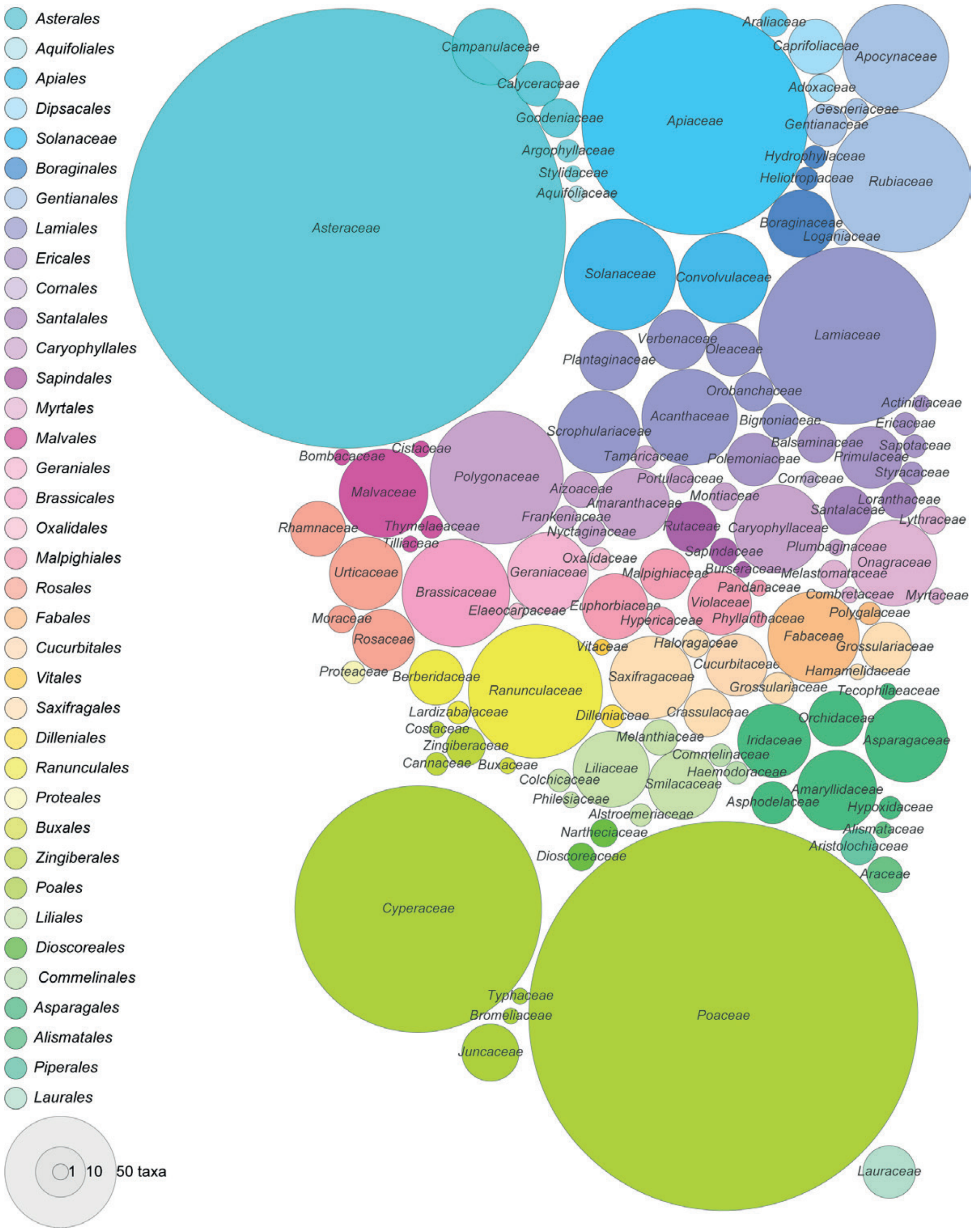

Fig. 56. Bubble plot of 3 214 species of *Puccinia* based on the telial host family. Bubbles are coloured by host at order rank, and size is proportional to the biodiversity of described rust fungi.

disease symptoms as well as the collective name for the *Pucciniales* (the order of rust fungi). Life cycles of *Puccinia* are variable, with species that produce between 1–5 different spore types, and species that complete their life cycle on one (autoecious) or two (heteroecious) host plants. The five spore stages of *Puccinia* are (i) spermogonia that exude hundreds of haploid spermatia, which fertilise other compatible spermogonia; (ii) aecia, which are formed adjacent to spermogonia after dikaryotisation (or fertilisation) and produce dikaryotic aeciospores that disperse new genotypes; (iii) uredinia, which are also dikaryotic and produce urediniospores, the primary means of inoculum that spread one genotype; (iv) telia, which produce teliospores that are 2-celled, with each cell dikaryotic and able to germinate and undergo karyogamy and meiosis; and (v) basidia, which are four-celled and produce haploid basidiospores.

Puccinia and related genera are the crown radiation of rust fungi, sharing a most recent common ancestor between 15–65 million years ago (McTaggart *et al.* 2016b, Aime *et al.* 2018, Aime & McTaggart 2021). There are four main clades in the *Pucciniaceae*, each having species primarily on (i) *Asteraceae*, *Cyperaceae* and *Fabaceae*; (ii) *Amaranthaceae* and *Poaceae*; (iii) ferns, *Apocynaceae*, *Araceae* and *Loranthaceae*; and (iv) *Poaceae* (Van der Merwe *et al.* 2008, Dixon *et al.* 2010, Marin-Felix *et al.* 2017a). *Puccinia* is paraphyletic with respect to many other genera in the *Pucciniaceae*, such as *Baeodromus*, *Ceratocoma*, *Cumminsiella*, *Desmella*, *Didymopsora*, *Dipyxis*, *Hapalophragmium*, *Macruropyxis*, *Uromyces* and *Stereostratum* (Aime & McTaggart 2021). Many rust fungi, particularly species of *Aecidium* and *Uredo*, which have been described only from aecial and uredinial stages, respectively, will need recombination in *Puccinia* or other monophyletic genera, pending their taxonomic resolution.

Species of *Puccinia* on cultivated grasses have become model organisms to study the genomes of rust fungi (Aime *et al.* 2017). The genomes of *Pu. graminis* (Duplessis *et al.* 2011), *Pu. coronata* (Miller *et al.* 2018), *Pu. striiformis* (Schwessinger *et al.* 2018) and *Pu. sorghi* (Rochi *et al.* 2018) have been assembled to near-chromosome resolution. Fully phased nuclei of *Pu. graminis f. sp. tritici* have been used to support somatic hybridization of rust fungi (Li *et al.* 2019b, Wu *et al.* 2019c), and a phased genome of *Pu. triticina* has been used to support tetrapolar mating in *Puccinia* (Wu *et al.* 2020a).

Ecological and economic significance

There are 5 845 species names in *Puccinia* listed on MycoBank, of which 140 have been described in the last 10 years (accessed 12 April 2022). The reduction in the discovery of new rust species may reflect that only rare and cryptic species remain to be discovered. Six examples have been chosen to illustrate the ecological and/or economic significance of *Puccinia*.

Leaf rust of peanut/groundnut (*Arachis hypogaea*) caused by *Puccinia arachidis* can significantly reduce pod and fodder yield, as well as oil quality. The rust co-evolved with its host in South America and the last 200 years has spread around the world to wherever *A. hypogaea* are cultivated. Spermogonia and aecia have not been reported for *Pu. arachidis*, which is considered brachycylic and autoecious. *Puccinia arachidis* spreads in the field by repeated cycles of urediniospores that are dispersed by wind and rain.

Crown rust of oats (*Avena sativa*) caused by *Puccinia coronata* and **leaf rust of wheat** (*Triticum aestivum*) caused by *Puccinia graminis* are two species that demonstrate the diagnostic difficulties and taxonomic confusion that surround the cereal rusts. *Puccinia coronata* has been reported from about 290 species of grass (Nazareno *et al.* 2018, Liu & Hambleton 2013). *Puccinia graminis* has been reported on hosts in 77 grass genera (Cummins 1971). The emergence of the Ug99 race of *Pu. graminis* on wheat has been a threat to wheat production worldwide for more than a decade, with the potential to cause crop losses on widely used varieties that are not resistant (Singh *et al.* 2015a).

Puccinia coronata and *Pu. graminis* share some similar characteristics in that each (i) causes economic diseases on some cultivated grasses; (ii) is macrocylic and heteroecious; and (iii) has been divided into numerous *formae speciales* based on host identity. Taxonomic resolution of species of *Puccinia* on grasses remains mostly unresolved, by molecular methods alone or in combination with morphology, host range, host taxonomy, and geographic origin. One exception is the excellent work of Liu & Hambleton (2013), who used a polyphasic approach to resolving taxonomic issues in *Puccinia coronata s. lat.* The inevitable molecular phylogenetic solutions have been complicated by agriculture and the global movement of populations. Complex species or species complex well applies.

Orange rust of sugarcane (*Saccharum* spp. and cultivated hybrids) caused by *Puccinia kuehnii* is endemic in the southeast Asian and Oceania regions. *Puccinia kuehnii* is hemicyclic, producing only teliospores and urediniospores on *Saccharum* and some closely related grass genera (*Erianthus*, *Sclerostachya*, *Narenga*) (Ryan & Egan 1989). In 2000, *Pu. kuehnii* was responsible for the largest single-season loss (200 million AUS dollars) caused by a disease in the history of the Australian sugarcane industry (Magarey *et al.* 2001).

Rust on *Asteraceae* (*Asteroideae*) caused by *Puccinia lagenophorae* is an example of an endemic Australian rust that has spread worldwide infecting about 150 species (Scholler *et al.* 2011, McTaggart *et al.* 2014). *Puccinia lagenophorae* has spread to Europe (Mayor 1962), North America (Scholler *et al.* 2001) and South America (Delhey *et al.* 1988). *Puccinia lagenophorae* is an autoecious species that forms aecia and telia.

Rust of Noogoora burr (*Xanthium pungens*) caused by *Puccinia xanthii* was considered a biological control agent for this introduced weed in Australia prior to its detection in 1975 (Alcorn 1976). *Puccinia xanthii* is native to North America where it is widespread and commonly infects Noogoora burr, *Ambrosia trifida* (giant ragweed), and other plants in the tribe *Heliantheae* of the *Asteraceae* (Morin *et al.* 1993). *Puccinia xanthii* is microcyclic and autoecious.

Research interests

Puccinia species were collectively listed in the top 10 plant pathogens based on socio/economic importance in a survey of plant pathologists conducted by *Molecular Plant Pathology* (Dean *et al.* 2012). There are 3 123 publications and 25 970 citations from 2011–2021 in the Web of Science (Fig. 57), with the top 10 most cited articles shown in Table 35.

Research into *Puccinia* is dominated by studies on the wheat infecting *Puccinia* spp. This research covers the threats that cereal rusts pose to global food production (Huerta-Espino *et al.* 2011, Singh *et al.* 2011, Wellings *et al.* 2011, Savoury *et al.* 2019) as well

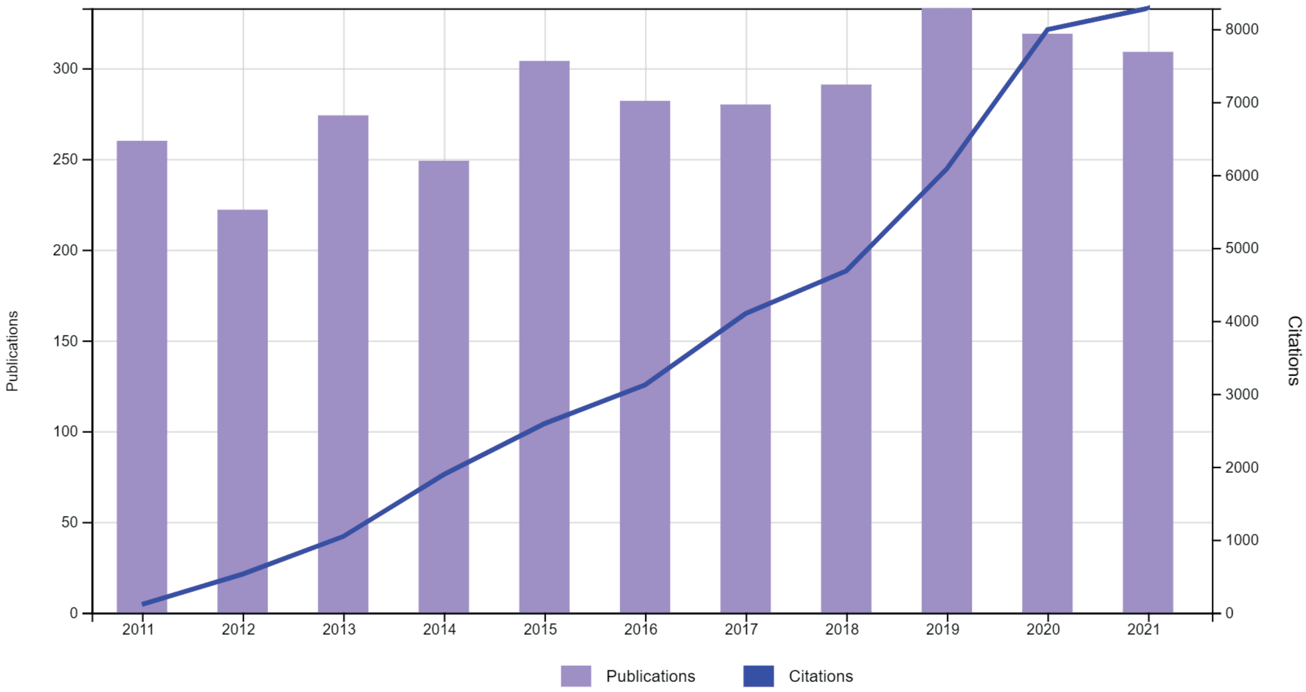

Fig. 57. Trends in research of *Puccinia* in the period 2011–2021.

Table 35. Top 10 cited articles related to *Puccinia* published in the period 2011–2021.

Rank	Article	No. of citations	References
1	The top 10 fungal pathogens in molecular plant pathology	1 769	Dean *et al.* (2012)
2	The global burden of pathogens and pests on major food crops	524	Savary *et al.* (2019)
3	Obligate biotrophy features unraveled by the genomic analysis of rust fungi	415	Duplessis *et al.* (2011)
4	The emergence of Ug99 races of the stem rust fungus is a threat to world wheat production	390	Singh *et al.* (2011)
5	Evaluation of the antibacterial potential of liquid and vapor phase phenolic essential oil compounds against oral microorganisms	346	Wang *et al.* (2016e)
6	Global status of stripe rust: a review of historical and current threats	314	Wellings *et al.* (2011)
7	The two-speed genomes of filamentous pathogens: waltz with plants	240	Dong *et al.* (2015)
8	One stop shop: backbones trees for important phytopathogenic genera: I (2014)	235	Hyde *et al.* (2014)
9	The gene Sr33, an ortholog of barley Mla genes, encodes resistance to wheat stem rust race Ug99	226	Periyannan *et al.* (2013)
10	Global status of wheat leaf rust caused by Puccinia triticina	217	Huerta-Espino *et al.* (2011)

as insights into how these threats may be mitigated (Periyannan *et al.* 2013, Watson *et al.* 2018, Dinh *et al.* 2020).

Authors: R.G. Shivas and A.R. McTaggart

30. *Cordyceps* Fr., Observ. Mycol. (Havniae) 2: 316 (cancellans). 1818.

Type species: *Cordyceps militaris* Fr.

Classification: *Ascomycota*, *Pezizomycotina*, *Sordariomycetes*, *Hypocreales*, *Cordycipitaceae.*

Background

Cordyceps is a hypocrealean entomogenous genus, parasitising several orders of arthropods from larva to adult stages (Sung *et al*. 2007, Shrestha *et al*. 2016, Araújo & Hughes 2016) and comprises 280 recognised species (Index Fungorum 2022). It is named after the Latin "*cord*" meaning club and "*ceps*" meaning head, as it describes the club-shaped stroma emerging from the insect larva as depicted in *Cor. militaris*. In the past, taxonomic classifications were mainly based on morphological characters on the host and were extensively studied by Kobayasi (1941, 1982) and Mains (1958). Less than two decades ago *Cordyceps s. lat.* belonged to the family *Clavicipitaceae s. lat.* characterised by the presence of cylindrical asci, thickened ascus apices, and filiform ascospores that often disarticulate into secondary ascospores (Mains 1958, Kobayasi 1941, 1982, Rossman *et al*. 1999, Sung *et al*. 2007).

This genus is the most diverse group of *Clavicipitaceae s. lat.* due to the large number of species and wide host range. Understanding the evolutionary relationships and host-switching over the past decades have come through molecular studies and these have provided stable phylogenies. The analyses of multi-gene sequences to reconstruct the phylogeny of *Cordyceps*, including the morphologies of its sexual and asexual morph, led Sung *et al.* (2007) to split *Cordyceps s. lat.* into three families, *Clavicipitaceae*, *Cordycipitaceae*, and *Ophiocordycipitaceae*.

Cordyceps militaris, the type species, is nested in the *Cordycipitaceae*; it is a cosmopolitan species reported from North and South America, Europe and Asia (Mains 1958, Shrestha *et al*. 2005a). Most species in *Cordyceps* have been reported from several countries in Asia such as China, Japan, Korea, Nepal, Taiwan and Thailand, while others have been reported from Europe, South America (Columbia), and North America (Kobayasi & Shimizu 1978, 1982).

Cordyceps species are parasitic on spiders (*Araneae*) and insects belonging to orders *Coleoptera*, *Diptera*, *Hemiptera*, *Hymenoptera*, *Lepidoptera* and *Orthoptera*, in which infections occur at various stages of the arthropod life cycle from larvae to adults (Torres *et al*. 2005, Liang *et al*. 2008, Cabanillas *et al*. 2013, Yan & Bau 2015, Tasanathai *et al*. 2016, Chiriví *et al*. 2017, Mongkolsamrit *et al*. 2018, 2020b, Crous *et al*. 2019b, Zha *et al*. 2019). *Cordyceps* species are characterised by fleshy, pallid to bright yellow, orange or red stromata with crowded or loosely embedded perithecia. Three kinds of ascospore morphologies are known: (1) bola-shaped, whole ascospores characterised by a thin filamentous middle part and fusiform ends, like a skipping rope, (2) filiform, multiseptate, whole ascospores, and (3) filamentous, multiseptate ascospores disarticulating into part-ascospores (Tasanathai *et al*. 2016, Mongkolsamrit *et al*. 2018, 2020b, Crous *et al*. 2019b, Zha *et al*. 2019). The asexual morph associated with *Cordyceps* includes species in *Isaria*, *Lecanicillium*, and *Evlachovaea.*

Ecological and economic significance

Bioactive compounds and medicinal value

The past decades have witnessed an increasing interest in seeking bioactive compounds from *Cordyceps* species. *Cordyceps militaris* is a renowned traditional Chinese medicine and edible fungus, receiving considerable attention due to its plentiful bioactive compounds (Chiu *et al.* 2016). Experimental evidence has shown that *Cor. cicadae* (*Isaria cicadae*), *Cor. takaomontana*, *Cor. pruinosa* and *Cor. kyushuensis* possess similar biological activity and chemical composition as found in *Cor. militaris* and *Ophiocordyceps sinensis* (Lee *et al.* 2009, Ling *et al.* 2009, Kim *et al.* 2010, Deng *et al.* 2020, Nxumalo *et al.* 2020). The aforementioned *Cordyceps* species have been successfully cultivated *in vitro* and advanced progress has been made in their pharmacological research (Xiao *et al.* 2004, Gui & Zhu 2008, Hama *et al.* 2019, Li *et al.* 2019d, Zhao *et al.* 2019b).

Many pharmacological experiments have been conducted based on aqueous, ethanolic and methanolic extracts from sporocarps, cultured mycelia and fermentation broth (Zhou *et al.* 2009). These crude extracts exert broad biological activities, such as anti-ageing, anti-bacterial, antifungal, antihypertensive, anti-inflammatory, anti-lupus, antimalarial, anti-metastatic, antioxidant, antiproliferative, antithrombotic, anti-tumour, antiviral, hepatic-protective, hypoglycaemic, hypolipidaemic, immunomodulatory, insecticidal, neuroprotective, renal-protective, *etc*. (Ng & Wang 2005, Zhang *et al*. 2006, Lee *et al*. 2015, Kim *et al*. 2017, Jin *et al*. 2018, Hu *et al*. 2019, Ke & Lee 2019, Liu *et al*. 2019c). To understand the pharmacological mechanism of these raw extracts, an array of effective components has been purified and their structure and biological activities elucidated (Zhou *et al.* 2009, Zhao *et al.* 2014a). These components include adenosine, amino acids, carotenoids, cordycepic acid, cordycepin, cyclic dipeptides, ergosterol, fatty acids and their derivatives, lectins, nucleosides, nucleotides, phenolic compounds, polyamines, polysaccharides, proteins, proteoglycans, saccharides, steroids, sterols, sugar derivatives, terpenoids, vitamins and metal elements, volatile components, *etc*. (Cheng *et al.* 2011, Zheng *et al.* 2012, Dong *et al*. 2013, Cohen *et al*. 2014, Zhao *et al.* 2014a, Nallathamby *et al*. 2015, Yin *et al*. 2018b, Zhu *et al*. 2016, Wang *et al*. 2017a, Lu *et al*. 2019, Singpoonga *et al*. 2020, Zhang *et al*. 2020a).

Biological control

Cordyceps farinosa (syn. *Isaria farinosa*) and *Cor. fumosorosea* (syn. *I. fumosorosea*) are entomopathogenic fungi that have shown great potential in the control of a wide range of insect pests (Zimmermann 2008). *Cordyceps fumosorosea* under laboratory conditions was able to control the solanum whitefly *Aleurothrixus trachoides*, a polyphagous pest known to attack more than 70 crops worldwide. It is also effective against ambrosia beetles, *Anisandrus dispar* and *Xylosandrus germanus* (*Coleoptera*: *Curculionidae*: *Scolytinae*), which are significant pests of hazelnuts. There are important reports that nymphs and adults of *Bemisia tabaci* are also highly sensitive to *Cor. fumosorosea* (Avery *et al*. 2010, Mascarin *et al*. 2014, Murillo-Alonso *et al*. 2015, Tian *et al*. 2015). Due to its safety to non-target organisms and humans, despite its broad insecticidal activity and host range, *Cor. fumosorosea* has been commercialised for the management of various insect pests, causing a significant reduction in insect pest population (Ali *et al.* 2010a, b, 2017, Huang *et al*. 2010).

Research interests

There are 2 073 publications and 23 831 citations from 2011–2021 in the Web of Science (Fig. 58), with the top 10 most cited articles shown in Table 36. The publications are mostly about the bioactive compounds produced by *Cor. militaris* for pharmacological and therapeutic implications, as well as the potential use in biological control, diversity, and taxonomy.

Pharmacological and therapeutic implications

Cordycepin (3’-deoxyadenosine) is a crucial bioactive compound commonly found in *Cordyceps* species (Zheng *et al.* 2011a, Cohen *et al.* 2014). Clinical trials have shown that cordycepin exhibits therapeutic potential against many types of cancers (Khan & Tania 2020). With these properties, cordycepin is considered an important supplement or substitute medicine drug for cancer treatment (Jin *et al.* 2018). The market price of cordycepin has reached more than 500 000 US dollars per kilogram (Yang *et al.* 2020). To satisfy market needs, the metabolic pathways and synthesis mechanism of some important compounds, such as carotenoid and cordycepin, including their antioxidant and anti-ageing activities have been elucidated (Liu *et al.* 2020b, Wang *et al.* 2020e, Zhu *et al.* 2020c), which could facilitate the mass production of target compounds. Additionally, the optimisation of culture conditions and the extraction process has enabled the harvest of more sporocarps and the production of more target bioactive compounds (Chou *et al.* 2020). *Cordyceps* species typically have fleshy sporocarps, for which different drying approaches have been exploited to prolong their shelf life and retain their commercial value (Wu *et al.* 2019e).

Toxins and other secondary metabolites

Although there has been a lot of research on the application of various bioactive metabolites isolated from *Cordyceps* spp.

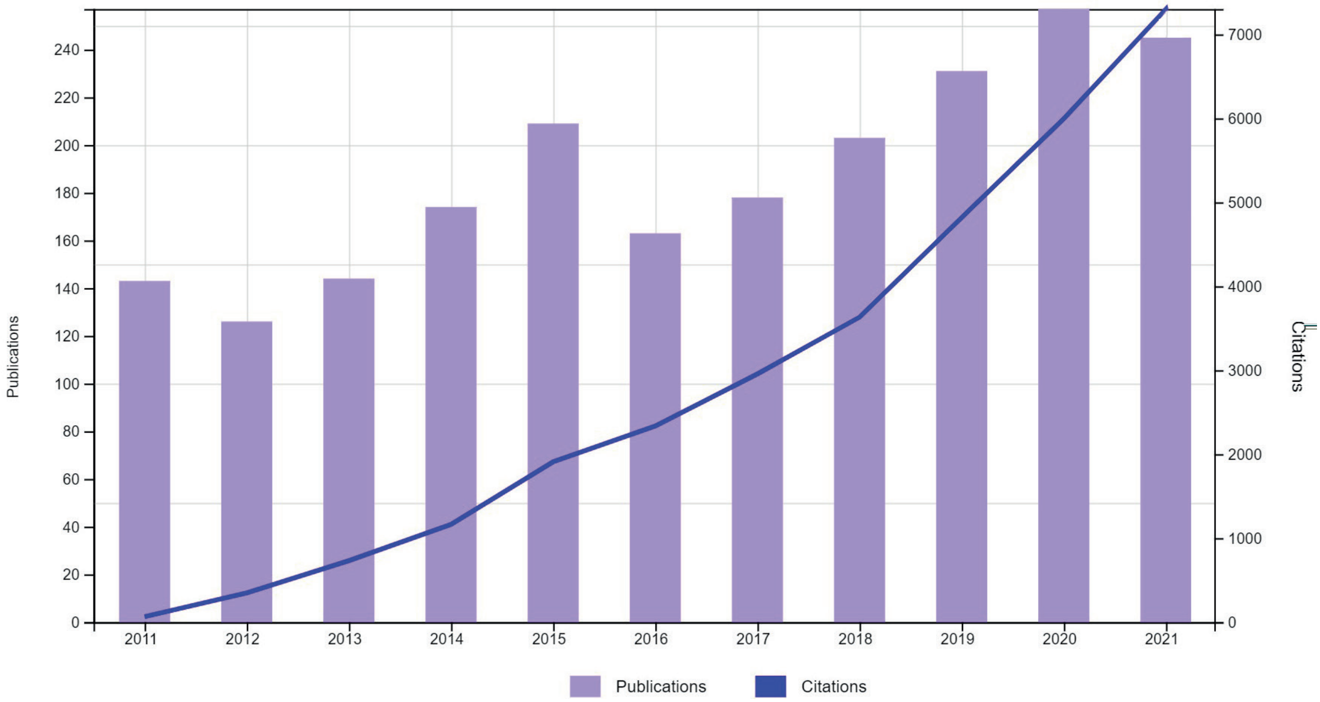

Fig. 58. Trends in research of *Cordyceps* in the period 2011–2021.

Table 36. Top 10 cited articles related to *Cordyceps* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Tissue invasion and metastasis: molecular, biological and clinical perspectives	281	Jiang *et al*. (2015)
2	Genome sequence of the insect pathogenic fungus *Cordyceps militaris*, a valued traditional chinese medicine	275	Zheng *et al*. (2011a)
3	Recent developments in mushrooms as anti-cancer therapeutics: a review	216	Patel & Goyal (2012)
4	A review on the effects of current chemotherapy drugs and natural agents in treating non-small cell lung cancer	191	Huang *et al*. (2017)
5	Cordycepin: a bioactive metabolite with therapeutic potential	167	Tuli *et al*. (2013)
6	A phylogenetically-based nomenclature for *Cordycipitaceae* (*Hypocreales*)	139	Kepler *et al*. (2017)
7	Toll-like receptor 4-related immunostimulatory polysaccharides: primary structure, activity relationships, and possible interaction models	111	Zhang *et al*. (2016f)
8	Advances in fundamental and applied studies in China of fungal biocontrol agents for use against arthropod pests	106	Wang & Feng (2014)
9	Enhancement of the antioxidant capacity of chickpeas by solid state fermentation with *Cordyceps militaris* SN-18	101	Xiao *et al*. (2014b)
10	Induction of apoptosis by cordycepin via reactive oxygen species generation in human leukemia cells	83	Jeong *et al*. (2011)

to develop biocontrol agents or to use in traditional Chinese medicine, safety and health issues in the consumption and use of these fungi have long been a concern. Thus, research on their secondary metabolites (SMs) is considered beneficial to improving the safety of these fungal products. In the case of *Cor. cicadae* (syn. *Isaria cicadae*), its SMs mainly include nucleosides, amino acids, beauvericins, myriocin, and oosporein while trichothecene derivatives, isariotins, cyclopenta benzopyrans and PKs are found in *Cor. tenuipes* (syn. *Isaria tenuipes*, *Paecilomyces tenuipes*). Among them, beauvericins, myriocin, oosporein and many trichothecene derivatives are toxic compounds. Most of these SMs for pharmaceutical or beneficial uses are dependent on the dose and can show cytotoxicities, neurological toxicities and or toxicological effects in humans and animals (Zhang *et al*. 2019c, Chen *et al*. 2020a).

Taxonomy and phylogeny

Cordyceps is a genus with diverse sexual and asexual morph morphologies. The sexual morphs of *Cordyceps* vary in the structure of the stromata, possessing brightly coloured, fleshy stromata as in the type species, *Cor. militaris* or having pallid stromata as in the case of many spider pathogens. There is no evident morphological difference between species found in *Cordyceps*, *Blackwellomyces*, *Flavocillium* and *Samsoniella* in *Cordycipitaceae* (Mongkolsamrit *et al*. 2018, 2020b, Wang *et al*. 2020f). The sexual morphs are known as isaria-, evlachovaea-, or lecanicillium-like. Species used in traditional Chinese medicine, *e.g.*, *Cordyceps cicadae*, known as “chanhua” or cicada flower, or producing a compound that could be used in medicine, *e.g.*, *Isaria sinclairii* (syn. *Cordyceps sinclairii*) producing myriocin have turbulent taxonomic histories and proper identification of these species are imperative for further applications.

Authors: D.P. Wei, J. Luangsa-ard and S. Mongkolsamrit

31. *Trichophyton* Malmsten, Arch. Anat. Physiol. Wiss. Med. 14. 1848.

Type species: *Trichophyton tonsurans* Malmsten

Classification: *Ascomycota*, *Pezizomycotina*, *Eurotiomycetes*, *Onygenales*, *Arthrodermataceae.*

Background

Trichophyton is a member of the best-known group of pathogenic fungi in medical mycology, the dermatophytes. *Trichophyton* species inhabit animals, humans and soil, including several anthropophilic, zoophilic, and geophilic species. Some species are distributed worldwide, while others are geographically restricted, such as *Trichophyton concentricum*, an endemic species located in the Pacific Islands, Southeast Asia, and Central America (Angra & Norton 2015). *Trichophyton* species are one of the most important etiological agents of superficial mycoses infecting hair, skin, and nails in humans. These mycoses are traditionally known as tineas or “ringworm”. *Trichophyton* species belong to *Onygenales*, family *Arthrodermataceae* with teleomorphs in the genus *Arthroderma*. The most prevalent etiologic agents are *Tri. rubrum* and *Tri. mentagrophytes* (Wu *et al*. 2013b). In humans, dermatophytes can infect the stratum corneum, nails and hair but rarely progress deeper than the basal layer (Toussaint *et al.* 2019). Occasionally, they can penetrate deeply and cause invasive infections involving hair follicles, subcutaneous tissue, and even lymph nodes (Cheikhrouhou *et al.* 2009, Lanternier *et al.* 2013, Rouzaud *et al.* 2015). The same pattern is observed in animals, invading hairs, with lesions appearing in the head, neck and less commonly in the back, flank and limbs (as *Tri. verrucosum* in cattle), and inflammatory and necrotising lesions (*Tri. simii* in poultry) (Gugnani & Rhandawa 1973, Guo *et al.* 2020).

Identification of *Trichophyton* species is based mainly on their macro- and micromorphological characteristics, in addition to physiological tests, which are helpful in some cases, as evidenced by the use of the urease test to differentiate *Tri. rubrum* from *Tri. mentagrophytes*.

A brief history

The first records of infections attributed to *Trichophyton* date back to Roman times. They were reported by Celsus, who described a suppurative infection of the scalp (as “porrigo” currently known as “kerion of Celsus” or “kerion celsi”) in De Medicina (Celsus 30 A.D.). Later, Cassius Felix called tinea the alopecic lesions observed on the head of humans. Then, in 1806, Alibert coined the term “*teigne faveuse*” or “*favus*” to describe the yellowish exudate observed in some tinea capitis (tinea favus for *Tri. schoenleinii*). Notwithstanding the above citations, it was Robert Remak who first described fungi as the causative agents of tinea, observing hyphae in tinea favosa, but these results were not published. Later, Remak self-inoculated the fungus on his hands and later recovered it in mycological culture, naming the agent *Achorion schoenleinii* (*Tri. schoenleinii*) in honour of his mentor Johann Lucas Schoenlein (Remak 1842). Gruby reported the current *Tri. tonsurans* as an agent related to endothrix (Gruby 1844). Malmsten proposed the new genus *Trichophyton*, with *Tri. tonsurans* as the type species (Malmsten 1848). A few years later, Robin reported *Tri. mentagrophytes* (Robin 1853). In 1910, Raymond Sabouraud published the first book, including a compilation of the species of the genus *Trichophyton*: “*Les teignes*” (Sabouraud 1910). Sabouraud also introduced the most famous isolation medium for fungal cultures, sabouraud dextrose agar (SDA). Nannizzi (1927) reported sexual status while Emmons (1934) published what we can consider the first taxonomic classification based on fungal structures.

Morphology in the genus *Trichophyton*

Trichophyton species present hyaline and septate hyphae in agar cultures. Some show spiral hyphae (*Tri. mentagrophytes*), antler-like hyphae or favic chandeliers (*Tri. schoenleinii*). Two types of aleuriospores (conidia) are produced, macroconidia and microconidia. Macroconidia are commonly club-shaped, around 100 µm long, with blunt ends and several transverse septa. They are not frequently seen and their occurrence seems to depend on the culture medium used and the strain viability. Microconidia are hyaline, small, spherical to tear-shaped, solitary or grouped in clusters. They are usually abundant in mycological cultures. In skin and nail scrapings, *Trichophyton* species are commonly observed producing arthroconidia and hyphae.

Laboratory identification of the four most prevalent *Trichophyton* species

Trichophyton mentagrophytes

The taxonomy associated with *Tri. mentagrophytes* has been confusing. Until recently, *Tri. mentagrophytes* was a species complex, among which *Tri. interdigitale* was included as a variety (*Tri. mentagrophytes* var. *interdigitale*). Molecular studies have shown that both species correspond to separate taxa. According to some authors, *Tri. mentagrophytes* would be a zoophilic species, responsible for more inflammatory mycoses when infecting humans (Cabañes *et al*, 1996), while *Tri. interdigitale* appears to be an antrophophilic species (De Hoog *et al*. 2017).

Trichophyton mentagrophytes is a cosmopolitan species and is one of the most commonly isolated dermatophytes from animals, but also from humans. Macroscopically, colonies of *Tri. mentagrophytes* are flat with a cream-to-buff or tan, powdery surface. Sometimes, colonies can produce intensely pigmented colonies. Microscopically they produce abundant microconidia, some macroconidia and spiral hyphae. Microconidia are commonly round-subglobose, borne along the sides and ends of repeatedly branched hyphae to form clusters. Macroconidia, when present, are cylindrical, 20–50 × 7–10 µm, thin and smooth-walled and mainly three to four septa. Usually, these species react positively in the urease and hair perforation tests.

Trichophyton interdigitale

Trichophyton interdigitale is considered an antrophophilic species. It is commonly isolated from tinea pedis and tinea unguium. Colonies are usually velvety, white to cream; reverse yellowish, pink or brown in the centre. Microconidia are subspherical to pyriform, 2 µm diam, sessile, grouped in grape-like clusters or alongside the hyphae. Spiral hyphae and macroconidia are occasionally present in cultures (Campbell & Johnson 2013). The species is urease and hair perforation tests positive.

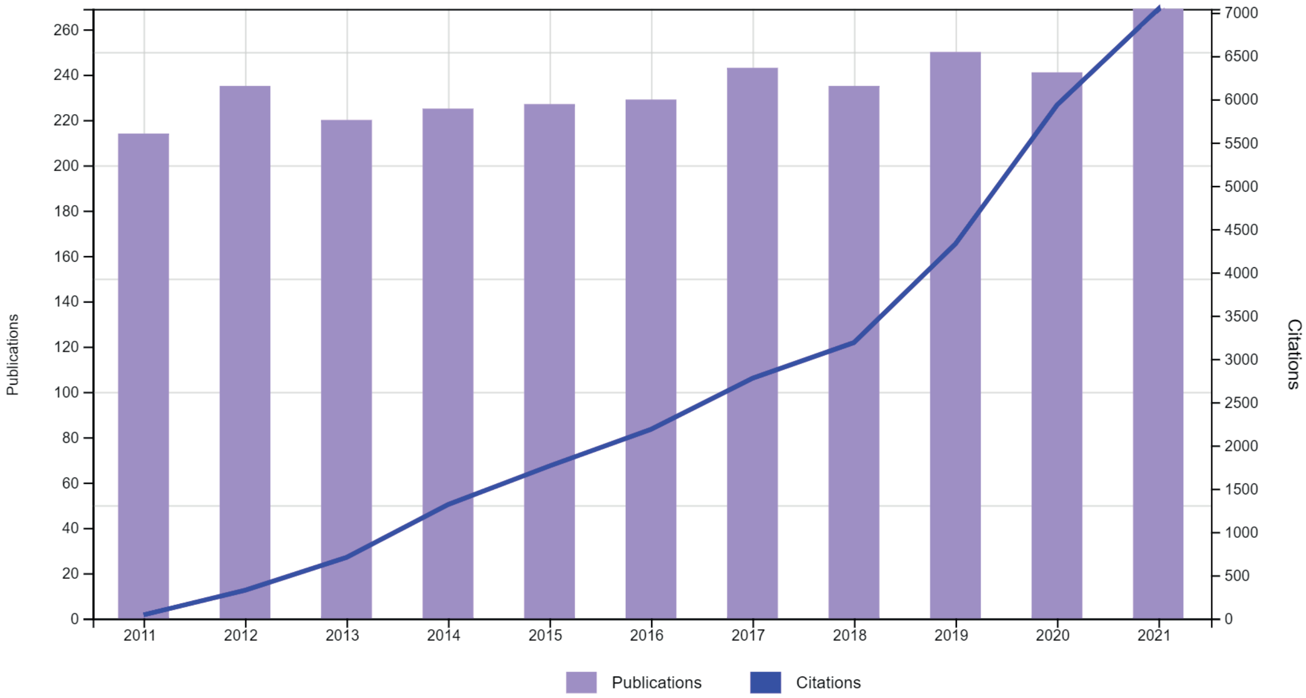

Fig. 59. Trends in research of *Trichophyton* in the period 2011–2021.

Table 37. Top 10 cited articles related to *Trichophyton* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Concepts and principles of photodynamic therapy as an alternative antifungal discovery platform	375	Dai *et al*. (2012)
2	Toward a novel multilocus phylogenetic taxonomy for the dermatophytes	264	De Hoog *et al*. (2017)
3	Deep dermatophytosis and inherited CARD9 deficiency	215	Lanternier *et al*. (2013)
4	International Society of Human and Animal Mycology (ISHAM)-ITS reference DNA barcoding database-the quality controlled standard tool for routine identification of human and animal pathogenic fungi	175	Irinyi *et al*. (2015)
5	Mycology - an update. Part 1: Dermatomycoses: Causative agents, epidemiology and pathogenesis	162	Nenoff *et al*. (2014)
6	Comparative genome analysis of *Trichophyton rubrum* and related dermatophytes reveals candidate genes involved in infection	150	Martinez *et al*. (2012)
7	High terbinafine resistance in *Trichophyton interdigitale* isolates in Delhi, India harbouring mutations in the squalene epoxidase gene	145	Singh *et al*. (2018)
8	Terbinafine resistance of *Trichophyton* clinical isolates caused by specific point mutations in the squalene epoxidase gene	141	Yamada *et al*. (2017)
9	Comparative and functional genomics provide insights into the pathogenicity of dermatophytic fungi	137	Burmester *et al*. (2011)
10	Can Phlorotannins purified extracts constitute a novel pharmacological alternative for microbial infections with associated inflammatory conditions?	124	Lopes *et al*. (2012)

Trichophyton rubrum

Trichophyton rubrum colonies are slow-growing, white, cottony to velvety, with a red to purple pigment on the reverse. They developed numerous microconidia, which are oval, pyriform to club-shaped, 2–3 × 3–5 µm, formed along the sides of hyphae. Macroconidia are rare, but when present are cylindrical or cigar-shaped, multiseptate with smooth-thin walls, 40–55 × 6.0–7.5 µm. Urease negative, cannot perforate hair when grown in hair culture *in vitro* and can grow in the presence of cycloheximide.

Trichophyton tonsurans

Trichophyton tonsurans produces granular to velvety colonies, sometimes with surface cracks, white, cream to yellowish or brown, and reverse yellow or brown. Microconidia are clavate, subspherical, produced abundantly along the hyphae, sessile, and sometimes appear as inflated balloon shaped. Macroconidia are cylindrical to cigar-shaped, often somewhat thick-walled, 2–6(–10)-celled, 10–65 × 4–12 µm, and usually distorted with age. Chlamydospores are formed in abundance. The urease test is positive and the hair perforation test is negative.

Classification

As with other dermatophytes, *Trichophyton* species can be grouped into three groups according to their habitat: geophilic (soil), zoophilic (animals), and anthropophilic (human). Geophilic species are saprotrophic and obtain nutrients from keratin present in the soil. An example is *Tri. terrestre*.

Zoophilic species tend to have species-specific parasitism but can also infect humans. Some examples of zoophilic agents are *Tri. simii* in monkeys, *Tri. equinum* in horses, and *Tri. mentagrophytes* in rodents.

Anthropophilic species are usually confined to humans but can also affect other animals. Examples of such species are *Tri. rubrum*, *Tri. schoenleini*, *Tri. concentricum* and *Tri. tonsurans*. The first proposal for classifying *Trichophyton* species and related fungi (Emmons 1934) placed dermatophytes into three genera based on asexual structures, *Microsporum*, *Trichophyton* and *Epidermophyton*. However, from 1960 onwards, several studies revealed that dermatophytes could reproduce sexually through ascospores (Griffin 1960, Nannizzi 1961); thus, they were classified as ascomycetes within the family *Gymnoascaceae*. Currah (1985) established a taxonomic classification scheme for keratinolytic fungi based on the morphology of the ascospores, the type and organisation of the peridium and the type of substrate on which these fungi develop (keratin or cellulose). The sexual morphs of dermatophytes (*Arthroderma* and *Nannizzia*) were classified within the family *Arthrodermataceae* belonging to the order *Onygenales*.

Recently, De Hoog and co-workers proposed a new classification scheme based on sequence data of five genes. In their molecular analyses, *Trichophyton* is accompanied by eight other genera: *Arthroderma*, *Ctenomyces*, *Epidermophyton*, *Guarromyces*, *Lophophyton*, *Microsporum*, *Nannizzia*, and *Paraphyton*. *Trichophyton* species are closely related, with low genetic variation (De Hoog *et al*. 2017).

Research interests

There are 2 588 publications and 21 756 citations from 2011–2021 in the Web of Science (Fig. 59), with the top 10 most cited articles shown in Table 37. *Trichophyton* species implicated in infections in animals and humans are probably the most prevalent etiologic agents worldwide. Although infections by dermatophytes are not life-threatening diseases, they are contagious and prone to recurrence. It is estimated that about 20–25 % of the world's population is affected by superficial mycosis (Havlickova *et al.* 2008). A 30-year systemic review carried out in China focused on onychomycosis showed that *Tri. rubrum* (49.93 %) was the most prevalent etiological agent in onychomycosis, followed by *Candida albicans* (10.99 %) and *Aspergillus* (3.11 %) (Song *et al.* 2022). Another study in Canada showed that in 2 046 patients with proven onychomycosis, 51.7 % of the cases were caused by *Tri. rubrum*, followed by *Tri. mentagrophytes* with 19.6 % (Gupta *et al.* 2016). Furthermore, dermatophytoses have a high economic impact, both for the patient and for the health centres. Costs related to physician visits, treatments, creams and lotions for managing skin conditions (OTC/self-care products), and sick leaves were estimated at 802 million US dollars in 2017, representing 11 % of total fungal infection costs (Benedict *et al*. 2019). Dermatophyte infections in animals are highly prevalent in some countries, becoming a public health and economic problem, and affecting livestock production. In India, a prevalence of 45–53 % in goats and dogs has been reported, with *Tri. mentagrophytes* being the most isolated agent (38 %) (Begum & Kumar 2021). Similarly, a study in Nigeria that considered dermatophytoses in cattle reported the isolation of *Tri. verrucosum* at 54.2 %, followed by *Tri. mentagrohpytes* with 45.8 % (Dalis *et al*. 2018).

Author: E. Álvarez-Duarte

32. ***Metarhizium*** Sorokīn, Veg. Parasitenk. Mensch Tieren 2: 268. 1879.

Type species: *Metarhizium anisopliae* (Metschn.) Sorokīn

Classification: *Ascomycota*, *Pezizomycotina*, *Sordariomycetes*, *Hypocreales*, *Clavicipitaceae.*

Background

Invertebrate-pathogenic fungi in the genus *Metarhizium* commonly occur on a wide range of arthropod hosts worldwide. Historically known to only comprise asexual morph species, members of *Metarhizium* are known to have diverse asexual reproductive morphologies and life cycle stages (Bischoff *et al*. 2009, Kepler *et al.* 2012, Luangsa-ard *et al.* 2017, Mongkolsamrit *et al.* 2020a, Thanakitpipattana *et al.* 2020). It was known to cause the "green muscardine disease", and was first described by Metchnikoff (1879) on a wheat cockchafer *Anisoplia austriaca* (scarab beetle, *Coleoptera*) in Russia (Zimmermann *et al.* 1995). The specific epithet of the type species, *Metarhizium anisopliae* was derived from the generic name of this beetle.

Tulloch (1976) monographed *Metarhizium*, accepting only two species, *Met. anisopliae* and *Met. flavoviride.* However, she also recognised two varieties based on the size of conidia, *Met. anisopliae* var. *minus* and *Met. anisopliae* var. *anisopliae*. Rombach *et al*. (1986) thereafter recognised a short-spored variety of *Met. flavoviride.* Further species were added occurring on various hosts from China, *viz*. *Met. cylindrosporum*, *Met. guizhouense*, and *Met. pingshaense.* With the advent of molecular phylogenetics to infer relationships among fungi, Driver *et al.* (2000) used ITS rDNA and RAPD patterns to study relationships within species of *Metarhizium* and recognised five additional varieties, *viz*. *Met. anisopliae* var. *acridum*, *Met. anisopliae* var. *lepidiotae*, *Met. flavoviride* var. *pemphigi*, *Met. flavoviride* var. *acridum* and *Met. flavoviride* var. *novozealandicum*. More informative genetic loci (*tef1*, *tub*, *rpb*1, *rpb*2) were used to better define species and understand relationships in *Metarhizium* and the varieties recognised by Driver *et al*. (2000) were elevated to species ranks accordingly. In 2006, Bischoff *et al*. recognised *Met. frigidum* as a separate species from *Met. anisopliae* that has closer affinities to *Met. flavoviride.* Subsequently, Bischoff *et al.* (2009) studied the collections of *Met. anisopliae* and recognised nine species in this species complex. In an extensive molecular phylogenetic study revising *Cordyceps* and the *Clavicipitaceae*, Sung *et al.* (2007) showed *Metarhizium* as a monophyletic clade that included species formerly classified in *Nomuraea*, *Paecilomyces*, *Pochonia* and *Tolypocladium.* A new genus *Metacordyceps* was established to accommodate cordyceps-like sexual morphs. Kepler *et al*. (2012) thereafter transferred additional species of *Cordyceps* to the genus. Following the concept of single nomenclature (One Fungus = One Name), Kepler *et al.* (2014) proposed to suppress *Metacordyceps* in favour of a broad concept of *Metarhizium* recognising taxa with uncertain placement in the basal clades. Several species were added over the last decade (Li *et al*. 2010, Montalva *et al*. 2016, Luangsa-ard *et al*. 2017, Lopes *et al*. 2018, Gutierrez *et al*. 2019, Luz *et al*. 2019, Thanakitpipattana *et al*. 2020, Yamamoto *et al*. 2020). Mongkolsamrit *et al*. (2020a) revisited the genus and recognised 19 species from Thailand. In the reconstructed phylogeny based on six genomic loci, six genera were established for basal monophyletic clades, moving diverse species that were in previous revisions to various genera.

Ecological and economic significance

Metarhizium species are extremely versatile and include species that are generalists. *i.e.*, infecting a broad range of insect hosts (*e.g.*, *Met. anisopliae*, *Met. robertsii*), while other species show host specificity (*e.g.*, *Met. acridum*, *Met. album*). The asexual morph generalist species have been used for the biological control of a wide range of insect pests that damage economically important crops and are known to play multiple roles in nature, with the ability to switch to different kinds of lifestyles (St Leger & Wang 2020).

Multiple roles in nature

Metarhizium species have long been recognised for their biological control potential against arthropods due to their ability to invade the cuticles of insects and proliferate in the hemolymph. As early as 1879, fungi from this genus were being evaluated for control of wheat chafer beetles, *Anisoplia austriaca*, and sugar beet curculio, *Cleonus punctiventris*, in Ukraine and since then have been developed as biopesticides. *Metarhizium* species are also known to play multiple roles in nature, surviving as saprobes or rhizosphere-competent fungi, as well as plant endophytes (Vega 2008, 2018, Vega *et al*. 2009, Greenfield *et al*. 2016) resulting in increased plant growth and providing increased tolerance against pests and diseases (Liao *et al*. 2017, Liu *et al*. 2017d). The benefits *Metarhizium* provides to host plants are varied: resistance to salt stress (Khan *et al*. 2012), antagonism towards plant pathogens (Sasan & Bidochka 2013, Keyser *et al*. 2016), and acquisition of insect-derived nitrogen (Behie *et al*. 2012, 2017, Behie & Bidochka 2014, Barelli *et al*. 2019).

Transgenic fungi

Malaria is a serious infectious disease affecting humans and other animals caused by the bite of the mosquito *Anopheles* carrying the parasite *Plasmodium falciparum.* A genetically modified (GM) *Metarhizium* strain expressing a spider toxin represents a new army for malaria parasites within mosquitoes (Wang & St Leger 2007, Fang *et al*. 2011). Studies on transgenic *Metarhizium* spp. have shown the potential to reduce malaria transmission in the world.

Research interests

There are 3 002 publications and 21 615 citations from 2011–2021 in the Web of Science (Fig. 60), with the top 10 most cited articles shown in Table 38. The publications cover research on biological control using *Met. anisopliae* and related taxa, studies on virulence, toxins, plant-growth promoting qualities as endophytes and also diversity and taxonomy.

Field Management

The use of *Metarhizium* against insect pests in agricultural ecosystems is one of the most successful and long-lasting biological control programs using an entomopathogenic fungus in the world. Their use has been extensively studied including in the laboratory and the field (Magalhães *et al*. 2000, Maniania *et al*. 2003, Peng *et al*. 2008, Hussain *et al*. 2011, Carolino *et al*. 2014, Iwanicki *et al*. 2019), and they have attributes to promote plant growth.

Toxins and other secondary metabolites

Destruxins (Dtxs) are cyclic depsipeptides produced by *Metarhizium* spp. that are recognised as important virulence determinants and assumed to be an important virulence factor accelerating the death of insects (Dumas *et al*. 1994, Brousseau *et al*. 1996, Kershaw *et al*. 1999, Wang *et al*. 2004a, Golo *et al*. 2014). They are, by far, the most exhaustively researched toxins produced by entomopathogenic fungi. The ability to produce the toxin varies from species to species, and toxigenic species are capable of killing multiple orders of insects, whereas the nontoxigenic *Metarhizium* spp. have narrow host ranges (Wang *et al*. 2012a).

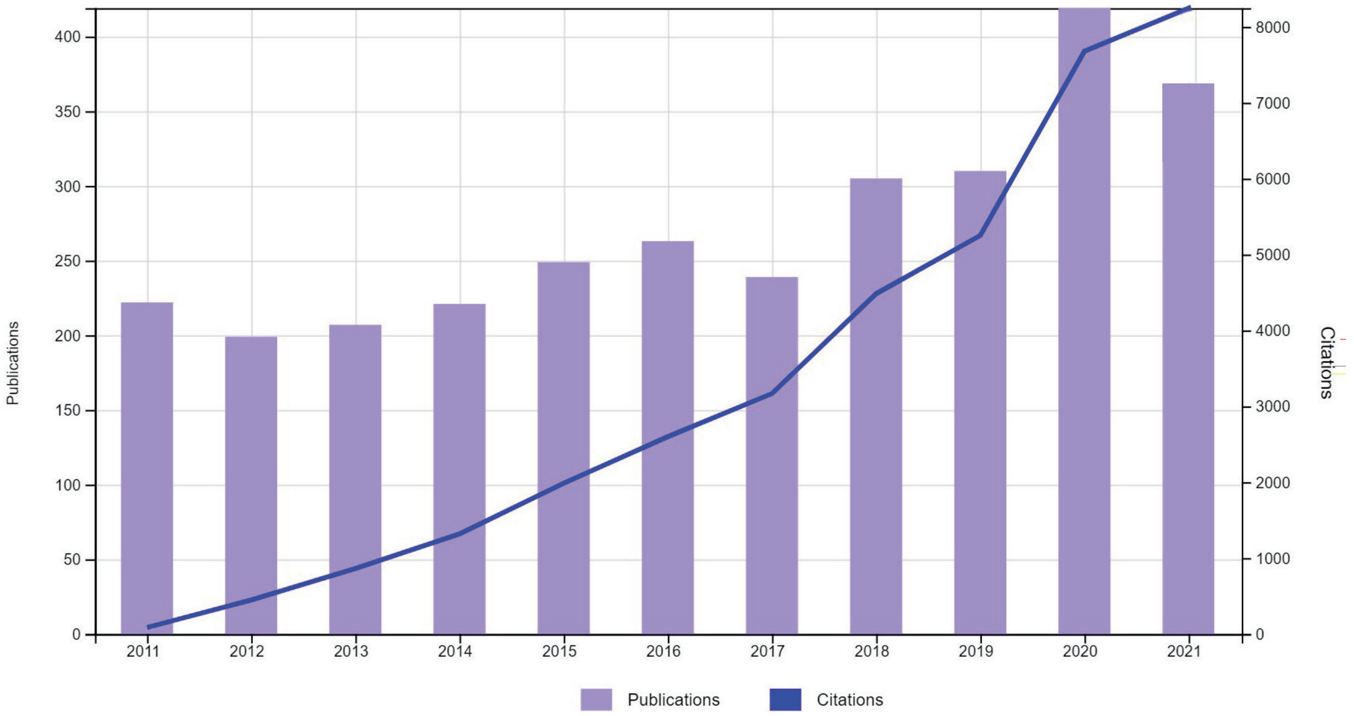

Fig. 60. Trends in research of *Metarhizium* in the period 2011–2021.

Table 38. Top 10 cited articles related to *Metarhizium* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Insect pathogens as biological control agents: back to the future	623	Lacey *et al*. (2015)
2	Genome sequencing and comparative transcriptomics of the model entomopathogenic fungi *Metarhizium anisopliae* and *M. acridum*	439	Gao *et al*. (2011)
3	Endophytic insect-parasitic fungi translocate nitrogen directly from insects to plants	220	Behie *et al*. (2012)
4	Development of transgenic fungi that kill human malaria parasites in mosquitoes	179	Fang *et al*. (2011)
5	Trajectory and genomic determinants of fungal-pathogen speciation and host adaptation	176	Hu *et al*. (2014b)
6	Insect pathogenic fungi: genomics, molecular interactions, and genetic improvements	168	Wang & Wang (2017)
7	The insect-pathogenic fungus *Metarhizium robertsii* (*Clavicipitaceae*) is also an endophyte that stimulates plant root development	163	Sasan & Bidochka (2012)
8	Fungal secondary metabolites as modulators of interactions with insects and other arthropods	155	Rohlfs & Churchill (2011)
9	Clarification of generic and species boundaries for *Metarhizium* and related fungi through multigene phylogenetics	148	Kepler *et al*. (2014)
10	Unveiling the biosynthetic puzzle of destruxins in *Metarhizium* species	146	Wang *et al*. (2012)

Genomics

Annotated genomes of *Metarhizium* species, including *Met. acridum*, *Met. anisopliae* and *Met. rileyi* are valuable resources providing additional insights for the presence and identification of virulence genes, interactions with hosts and the development of species- and strain-specific assays to screen unique combinations of pathogenicity factors important for the development of biopesticides (Gao *et al*. 2012, Pattemore *et al*. 2014, Binneck *et al*. 2019, Tong *et al*. 2020). The genome of host-specific *Met. acridum* gave insights into the core metabolism of high virulence of this locust-specialistic fungus as compared to the generalist *Met. anisopliae* to provide an improved basis for designing mycoinsecticide strains. These genome sequences provide the basis for a comprehensive understanding of the interactions between fungus, plant and insect and thus contribute to our understanding of fungal evolution and ecology.

Habitats

Metarhizium species are commonly thought of as soil saprobes and are most frequently found in habitats with human disturbance like agricultural fields as compared to forest ecosystems (Meyling & Eilenberg 2007). Findings of Hu & St Leger (2002) suggest that these fungi form associations with plant roots in the rhizosphere and survive better in that environment than in surrounding potting soil over extended periods (Bruck 2005). Studies on the survival of *Metarhizium* in soils have focused on a diverse range of field crops, including sugar beet (Pingel *et al*. 1999), cabbage (Hu & St Leger 2002), maize (Pilz *et al*. 2011, Guerrero-Guerra *et al*. 2013), sugar cane (Milner *et al*. 2003, Vieira Tiago *et al*. 2012), strawberry (Klingen *et al*. 2015), peanut (Liu *et al*. 2016d), coffee (Moreira *et al*. 2019a), sweet potato (Putnoky-Csicsó *et al*. 2020) and tobacco (Yang *et al*. 2019a).

Taxonomy and phylogeny

About 60 species are recognised in *Metarhizium* (Index Fungorum 2022). The use of morphological characters to identify *Metarhizium* species can be imprecise due to the overlap of dimensions of characters among species. Taxonomic classification has to rely heavily on multi-gene approaches to study cryptic speciation among closely related species. In species complexes recognised in *Metarhizium* there are 21 species in the *Met. anisopliae* species complex, and 13 species in the *Met. flavoviride* species complex. *Metarhizium anisopliae* culture CBS 130.71 isolated from *Avena sativa* root, a cereal crop, is considered the closest strain to Metchnikoff's *Metarhizium anisopliae* in terms of geography (Mongkolsamrit *et al*. 2020a). *Metarhizium* is characterised by the production of conidia that are predominantly in various shades of green, but may also be white or in shades of brown or yellow. There are three kinds of phialide and conidiophore morphologies found in this genus. The first is the characteristic *Metarhizium* conidiophore wherein a palisade layer of conidiophores with cylindrical phialides that form a hymenium-like layer on an arthropod host is produced. Secondly, nomuraea-like phialides and conidiophore arrangement can be seen in species found on cicada nymphs, cicada adults and small planthoppers. Thirdly, the presence of paecilomyces-like phialides in certain species, especially those that are found on animals (*e.g.*, *Met. granulomatis* and *Met. viride*).

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33. ***Pythium*** Pringsh., Jahrb. Wiss. Bot. 1: 304. 1858.

Type species: *Pythium monospermum* Pringsh.

Classification: *Peronosporomycetes*, *Oomycetes*, *Pythiales*, *Pythiaceae.*

Background

The genus *Pythium* includes approximately 220 recognised species recorded from a broad diversity of hosts and substrates. The type species, *Py. monospermum*, was described from mealworms that had fallen into water (Pringsheim 1858) and subsequent early records of *Pythium* species were similarly from dead insects and algae in water (Schenk 1858, De Bary 1860, Lohde 1874). Hesse (1874) was the first to document *Pythium* as a plant pathogen in his study of *Globisporangium debaryanum* (syn. *Py. debaryanum*) as a seedling pathogen of various agricultural crops. Since then, *Pythium* species have been recorded as pathogens of algae, crustaceans, fish, fungi (including other oomycetes), insects, mammals and nematodes (Van der Plaats-Niterink 1981, De Cock *et al.* 1987, Hatai 1988, Miura *et al.* 2010, Hyde *et al.* 2014). Host associations and interactions of many *Pythium* species are not well-known and many species have been recorded only as saprobes in soil or water. Nevertheless, the fact that the genus is primarily known as plant pathogens testifies to its importance, especially in crop production, and food safety and security.

Pythium has a global distribution, with records originating from all continents and most major islands across the globe (Van der Plaats-Niterink 1981, Farr & Rossman 2022). With such a wide distribution, *Pythium* species have adapted to a diverse set of climates. Species like *Globisporangium ultimum* (syn. *Py. ultimum*) and *Py. aphanidermatum* are widespread in temperate climates including arid, Mediterranean, and tropical regions (Van der Plaats-Niterink 1981, Farr & Rossman 2022). *Globisporangium ultimum* has even been reported in the sub-arctic zone (Johnson 1971). Other species appear to be more limited in their climatological tolerance or distribution, *e.g.*, *G. polare* (syn. *Py. polare*) has only been recovered from the polar regions (Tojo *et al.* 2012), or *Py. insidiosum*, the causal agent of pythiosis in mammals, is generally limited to tropical and sub-tropical regions (Gaastra *et al.* 2010). *Pythium* species are mostly found in soil or water, and on parts of their hosts that occur in, or have been exposed to, these substrates. Accordingly, symptoms of plant diseases caused by *Pythium* species are usually typical of soilborne pathogens that directly affect below-ground plant parts, *e.g.*, wilt, root rot and damping off (Martin & Loper 1999). Diseases of above-ground plant parts also occur, but these are relatively uncommon, *e.g.*, fruit rots of cucurbits, solanaceous crops and durian (Tompkins *et al.* 1939, Anwar *et al.* 2017, Solpot & Cumagun 2021, Türkölmez *et al.* 2021), snow rot or mould of grasses and mosses (Lipps & Bruehl 1980, Takamatsu & Ichitani 1986, Tojo & Newsham 2012, Bouket *et al.* 2015), and web blight of spinach (Liu *et al.* 2018a). Although *Pythium* species are commonly encountered in freshwater aquatic environments, a few species are also known from saline environments. These include *Py. grandisporangium*, a presumably saprobic species associated with decaying leaf litter in mangroves (Fell & Master 1975), and *Py. porphyrae*, the causal agent of red rot on *Porphyra* and *Pyropia* spp. (Kawamura *et al.* 2005, Diehl *et al.* 2017).

Reproduction in *Pythium* occurs asexually via zoospores, zoosporangia and hyphal swellings, or sexually via oogonia, antheridia and oospores. The shape of zoosporangia varies from filamentous or inflated filamentous, lobulate or toruloid, to (sub-) globose or ovoid (Van der Plaats-Niterink 1981, Dick 1990, De Cock *et al.* 2015). Hyphal swellings may be indistinguishable from globose to sub-globose zoosporangia; however, hyphal swellings germinate directly to form hyphae, while zoosporangia produce motile zoospores (Van der Plaats-Niterink 1981). Amino acids and other components of root and seed extracts attract zoospores chemotactically towards suitable host material and induce encystment of zoospores once they arrive at the roots or seeds (Deacon & Donaldson 1993). Van West *et al.* (2002) showed that electrical fields generated by roots also play an important role in guiding zoospores to specific regions on the roots through electrotaxis. Once zoospores reach their target, they attach to the host, encyst by forming cell walls, and produce germ tubes that infect the host (Jones *et al.* 1991, Martin & Loper 1999).

During sexual reproduction, *Pythium* species produce oogonia that are fertilised by antheridia to form thick-walled sexual oospores (Van der Plaats-Niterink 1981). Most *Pythium* species are homothallic, *i.e.*, compatible antheridia and oogonia are produced by single isolates. Some species have a heterothallic mating system where two compatible isolates are required for the production of sexual structures, although single isolates occasionally exhibit homothallic production of oogonia (Dick 1990). Examples of heterothallic species include *Py. catenulatum*, *Globisporangium heterothallicum*, *G. intermedium*, *G. polare* and *G. sylvaticum*. The thick-walled oospores can withstand desiccation and are consequently important survival structures that allow for the persistence of *Pythium* species in soil for long periods under adverse conditions (Van der Plaats-Niterink 1981, Martin & Loper 1999). Oospores can germinate either by producing zoosporangia with subsequent release of zoospores for dispersal and infection or by forming hyphae for infection or colonisation (Stanghellini & Burr 1973).

The paraphyly of *Pythium* was already recognised in early molecular phylogenetic studies with limited numbers of species (Briard *et al.* 1995, Cooke *et al.* 2000). Lévesque & De Cock (2004) conducted the first comprehensive phylogenetic investigation that included 96 species. They divided *Pythium* into 11 clades that grouped according to sporangial shape, with clades A–D including species with more or less filamentous or contiguous sporangia, clades E–J including species with globose sporangia, and clade K (also globose sporangia) forming a distinct clade. Later, Bala *et al.* (2010) introduced the new genus *Phytopythium* for species from clade K, while Uzuhashi *et al.* (2010) introduced the genera *Elongisporangium* (clade H) and *Globisporangium* (clades E–G, I, and J) and emended *Pythium* to include only the species from clades A–D. The introduction of *Phytopythium* has been well accepted in the scientific community, however, the revisions of Uzuhashi *et al.* (2010) have been met with some resistance and have not been widely implemented (Hyde *et al.* 2014). This reluctance partly stems from poor phylogenetic support for the relationships and distinction between *Globisporangium* and *Elongisporangium* in phylogenies based on conventional markers, *i.e.*, ITS, 18S, 28S, *cox1*, *cox2* and *tub* (Uzuhashi *et al.* 2010, Hyde *et al.* 2014). This lack of support was addressed in a recent phylogenomic study by Nguyen *et al.* (2022), who found strong support for the revisions of Uzuhashi *et al.* (2010), and made new combinations in *Globisporangium* and *Elongisporangium* to consolidate generic concepts in *Pythium*, and urged the scientific community to adopt these revisions. One of the remaining challenges in this regard is the paraphyly of *Pythium s. str.* (*i.e.*, clades A–D) with regards to *Lagena*, and the relationships of these taxa with *Pythiogeton* (Hyde *et al.* 2014, Spies *et al.* 2016, Nguyen *et al.* 2022). In this overview, the name *Pythium* is applied in the broad sense (*i.e.*, clades A–K) unless specified otherwise, but the names introduced by Bala *et al.* (2010), De Cock *et al.* (2015), Uzuhashi *et al.* (2010), and Nguyen *et al.* (2022) are used when referring to specific species from clades K (*Phytopythium*), H (*Elongisporangium*), and E–G and I–J (*Globisporangium*).

Ecological and economic significance

A search on the Web of Science identified six species with more than 100 publications during 2011–2021: *Globisporangium ultimum* (505 publications), *Py. aphanidermatum* (436 publications), *Py. insidiosum* (292 publications), *G. irregulare* (176 publications), *Py. oligandrum* (116 publications), and *Py. myriotylum* (109 publications). These six species illustrate the three main ecological roles in which *Pythium* species have a significant economic impact, *i.e.*, as plant pathogens (*Py. aphanidermatum*, *Py. myriotylum*, *G. irregulare* and *G. ultimum*), mycoparasites or biological control agents (*Py. oligandrum*), and mammalian pathogens (*Py. insidiosum*). Four of these species were also mentioned in a publication on the top 10 oomycetes in molecular plant pathology, with *G. ultimum* featuring at the eighth position, *Py. aphanidermatum* ranking 27th, *Py. oligandrum* 28th, and *Py. insidiosum* receiving votes, but not being ranked (Kamoun *et al.* 2015).

The fact that four of the six species mentioned above, and the two most published *Pythium* species are plant pathogens, shows the importance of this genus primarily as plant pathogens. Most plant pathogenic *Pythium* species are well adapted to infect and rapidly colonise young succulent tissues such as germinating seeds, seedlings, and feeder roots (Hendrix & Campbell 1973). For this reason, *Pythium* species are among the most important causal agents of seed and seedling diseases, such as damping-off, on a wide range of crops, including cereals, oilseeds, forage crops, vegetables, ornamentals, and trees (fruit and forestry) (Van der Plaats-Niterink 1981). As plant cells mature, cell walls undergo secondary thickening, which reduces their susceptibility to *Pythium* (Hendrix & Campbell 1973). Consequently, *Pythium* infections on older plants and more herbaceous or woody crops are usually associated with feeder roots, resulting in root rot that translates to stunting of foliar growth or wilt (Hendrix & Campbell 1973, Martin & Loper 1999). In some cases, *Pythium* species have been associated with severe decline and death of mature plants, *e.g.*, *Py. aphanidermatum* causing vine decline, a disease affecting mature cucumber and musk melon plants (Al-Sadi *et al.* 2011, Al-Mawaali *et al.* 2013). In fruit trees like apples and peaches, *Pythium* species play a significant role in replanting diseases. These diseases are characterised by uneven growth, reduced root systems and, in severe cases, death of young trees planted on soil previously planted to the same crop (Hendrix & Campbell 1973, Mazzola 1998, Bent *et al.* 2009, Tewoldemedhin *et al.* 2011b).

The impact of plant diseases caused by *Pythium* species is difficult to assess since soilborne diseases usually involve a complex of organisms that may include *Pythium* along with true fungi such as *Fusarium* and *Rhizoctonia*, nematodes, and other organisms (You *et al.* 2020). Losses due to seedling diseases of soybean, caused by a complex of pathogens including *Diaporthe*, *Fusarium*, *Pythium* and *Rhizoctonia* species, have been estimated at 8 755 million US dollars across 28 states in the USA from 1996–2016 (av. 420 million US dollars per year) (Bandara *et al.* 2020). Cook *et al.* (1980) observed 40 % yield increases in wheat when eliminating the effect of *Pythium* using the oomycete-selective fungicide, metalaxyl. Other studies applying fungicides to selectively suppress oomycetes have also highlighted *Pythium* as one of the main contributors to soilborne disease complexes of barley, apple trees and other crops (Harvey & Lawrence 2008, Tewoldemedhin *et al.* 2011b). In the USA and Ontario (Canada), annual losses due to seedling blight and root rot of maize caused by *Pythium* have been estimated at 25 million US dollars (Bickel & Koehler 2021). *Globisporangium irregulare* can reduce the germination of subterranean clover by up to 60 % with a 50 % reduction in plant productivity (You *et al.* 2020). Losses due to soft rot of ginger caused by various *Pythium* species vary between seasons and countries but can be as high as 100 % (Le *et al.* 2014).

Several *Pythium* species are mycoparasites including *Py. acanthicum*, *Py. oligandrum*, *Py. periplocum*, *G. nunn* and *G. acanthophoron* (Lodha & Webster 1990, Jones & Deacon 1995, Ribeiro & Butler 1995). However, most published articles on *Pythium* for biological control of plant diseases are focused on *Py. oligandrum*. This species exhibits various modes of action for reducing disease, including antibiosis, direct parasitism, competitive exclusion from infection sites, and the induction of host resistance (Benhamou *et al.* 1999, 2001, Gerbore *et al.* 2014). Mycoparasitism of a wide range of plant pathogens has been illustrated, including species of *Fusarium*, *Phytophthora*, *Pythium* and *Rhizoctonia*, as well as parasites of animals such as roundworms (Benhamou *et al.* 1999, Luca *et al.* 2022). Furthermore, host resistance, induced by *Py. oligandrum* in plants, is non-specific and effective against various pathogens including bacteria, fungi and phytoplasmas (Gerbore *et al.* 2014). Martin & Hancock (1987) reported similar efficacy of *Py. oligandrum* seed treatment and the fungicide fenaminosulf against pre-emergence damping-off of beetroot caused by *Py. ultimum*. Under controlled conditions, Yacoub *et al.* (2016) demonstrated a 40–50 % reduction in wood necrosis caused by the trunk pathogen *Phaeomoniella chlamydospora* in grapevines whose root systems had been colonised by *Py. oligandrum*. The ability of *Py. oligandrum* to significantly reduce grapevine trunk disease incidence and severity has also been demonstrated in field trials (del Pilar Martínez-Diz *et al.* 2021a). In pepper (*Capsicum annuum*) plants inoculated with *Verticillium dahliae*, *Py. oligandrum* significantly reduced pathogen populations in the rhizosphere and non-rhizosphere soil and increased fresh fruit weight by 78 % (Al-Rawahi & Hancock 1998).

Pythium insidiosum is considered the only causal agent of pythiosis in mammals, a rare disease manifesting as granulomatous lesions or tumour-like growths mostly occurring in or on the skin or intestines, although infections of other organs or tissues such as lungs or bone have also been recorded (Gaastra *et al.* 2010). Pythiosis is most frequently encountered on horses, dogs, and humans, but has also been reported on cats, cattle, sheep and other mammals. The disease mainly occurs in tropical and sub-tropical climates, with some records from other temperate climates, in Oceania, Southeast Asia, Africa, and South, Central and North America (Gaastra *et al.* 2010). Although pythiosis is rare and not contagious, infections tend to progress rapidly and can be fatal if not treated at an early stage. The most effective treatment seems to be excision or amputation to remove affected tissue (Chitasombat *et al.* 2020).

Research interests

There are 2 158 publications with 20 902 citations from 2011–2021 in the Web of Science (Fig. 61), with the top 10 most cited articles shown in Table 39. Important research topics in these publications include the characterisation of *Pythium* species in various hosts and environments, as well as disease management and pathogen detection.

Characterisation of Pythium spp. associated with various hosts and environments

Surveys and first reports provide data on the global diversity, distribution and host ranges of *Pythium* species, and form the basis for the development or implementation of disease management strategies. In this capacity, such studies will remain important in *Pythium* research. Two of the most highly cited surveys of *Pythium* species over the past 12 years include that of Rojas *et al.* (2017a), who identified 54 *Pythium* species while investigating the diversity of oomycete species on soybeans in North America, and Tewoldemedhin *et al.* (2011a), who identified nine *Pythium* species as part of a fungal complex contributing to apple replant disease in South Africa. Both of these studies also performed pathogenicity trials to give an indication of the relative importance of the species recovered. These and most other published surveys of *Pythium* species made use of direct plating or baiting techniques to

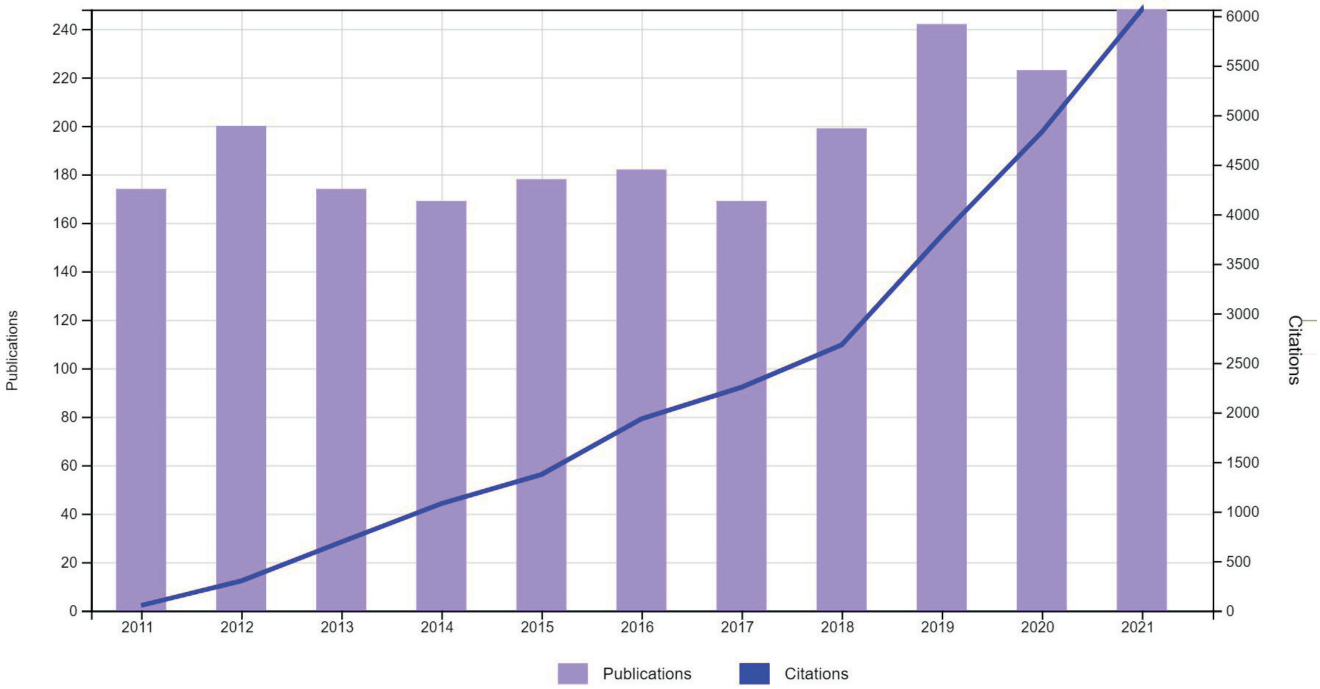

Fig. 61. Trends in research of *Pythium* in the period 2011–2021.

recover *Pythium* isolates. Some more recent surveys have started implementing next-generation sequencing (NGS) technologies that can capture the diversity of *Pythium* species more fully (Redekar *et al.* 2019, Rojas *et al.* 2019, Navarro-Acevedo *et al.* 2021).

Disease management

Management of diseases caused by *Pythium* species relies heavily on the use of fungicides. The phenylamide fungicide metalaxyl (or its active isomer mefenoxam) has long been very effective as soil drench or seed treatment against *Pythium* diseases of many crops, such as apple trees, cucumber, maize, soybean, sugar beet and wheat (Cook & Zhang 1985, Utkhede & Smith 1991, Larkin *et al.* 1995, Brantner & Windels 1998, Al-Sa'di *et al.* 2008). There are, however, various reports of fungicide resistance against metalaxyl in some *Pythium* populations (Cook & Zhang 1985, Brantner & Windels 1998, Moorman & Kim 2004, Chen & Van Vleet 2016). Matić *et al.* (2019) compared the sensitivity of *Pythium* species to azoxystrobin (strobilurin) and mefenoxam, and found considerable variation in the sensitivity of species to mefenoxam while almost all species were sensitive to azoxystrobin. Radmer *et al.* (2017), however, found reduced sensitivity of *Pythium* species to strobilurin fungicides in comparison to mefenoxam. Other fungicides that have shown some promise against *Pythium* species, either as alternatives or supplements to the abovementioned fungicides, include ethaboxam, fluopicolide, fosetyl-Al, phosphorous acid and zoxamide (Martinez *et al.* 2005, Lu *et al.* 2012, Weiland *et al.* 2014, Radmer *et al.* 2017, White *et al.* 2019, Scott *et al.* 2020). *Pythium* species may vary in their sensitivities to different fungicides, *e.g.*, in an investigation of *Pythium* species from maize and soybean, *G. recalcitrans* had reduced sensitivity to ethaboxam, but was the most sensitive to pyraclostrobin, while *Py. oopapillum* was highly sensitive to trifloxystrobin, but least sensitive to mefenoxam (Radmer *et al.* 2017). Oxathiapiprolin is a relatively new fungicide that has shown promise for controlling foliar diseases caused by *Phytophthora* species and the downy mildew genera (Miao *et al.* 2016). Investigations of the sensitivity of *Pythium* species toward this fungicide suggest that *Phytopythium* and some *Globisporangium* species (*e.g.*, *G. splendens* and *G. ultimum*) are moderately sensitive, but many *Pythium s. str.* and *Globisporangium* species are not (Miao *et al.* 2016, 2020, Vargas *et al.* 2022). Further structural optimisation of oxathiapiprolin might yield a novel fungicide with better efficacy against *Pythium* (Miao *et al.* 2020).

Soil amendments with compost, seed meal, and other organic materials have received considerable attention in research on the management of soilborne diseases caused by *Pythium* and other pathogens. The mode of action for disease suppression is linked to the impact of these amendments on microbial populations in the soil, rhizosphere or spermosphere (Scheuerell *et al.* 2005, Bonanomi *et al.* 2010, Weerakoon *et al.* 2012, Hadar & Papadopoulou 2012). Mazzola & Freilich (2017) argued for the harnessing of this effect to selectively enrich disease suppressive components of indigenous microbial populations for more sustainable soilborne disease management. The efficacy of soil amendments can be very dependent on the specific material, pathogen (species or even isolate), and host (Mazzola *et al.* 2009). Several studies over the past 12 years have investigated the disease suppressive ability of composts and are working towards identifying indicators of this ability (Pane *et al.* 2011, Vestberg *et al.* 2014, Mayerhofer *et al.* 2021). Mayerhofer *et al.* (2021) compared the suppressiveness of 17 composts towards wilt of cress caused by *G. ultimum*, and identified 75 bacterial sequence variants that were associated with highly suppressive composts. Such sequence variants could be useful as indicators of disease suppressiveness to support targeted compost production for improved disease management.

Molecular detection

Rapid and sensitive molecular detection assays for pathogens are valuable tools for diagnostic purposes, as well as for monitoring pathogens in ecological studies and evaluations of management strategies. PCR-based detection and quantification assays have been developed for many plant pathogenic *Pythium* species, the mycoparasite *Py. oligandrum*, and the mammalian pathogen *Py. insidiosum* (Le Floch *et al.* 2007, Spies *et al.* 2011, Ishiguro *et al.*

Table 39. Top 10 cited articles related to *Pythium* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	The top 10 oomycete pathogens in molecular plant pathology	383	Kamoun *et al.* (2015)
2	DNA barcoding of oomycetes with cytochrome c oxidase subunit I and internal transcribed spacer	375	Robideau *et al.* (2011)
3	Antifungal effects of silver nanoparticles (AgNPs) against various plant pathogenic fungi	252	Kim *et al.* (2012)
4	One stop shop: backbones trees for important phytopathogenic genera: I (2014)	235	Hyde *et al.* (2014)
5	Apple replant disease: Role of microbial ecology in cause and control	214	Mazzola & Manici (2012)
6	Ecology of root colonizing *Massilia* (*Oxalobacteraceae*)	148	Ofek *et al.* (2012)
7	Lipopeptides as main ingredients for inhibition of fungal phytopathogens by *Bacillus subtilis/amyloliquefaciens*	145	Cawoy *et al.* (2015)
8	Disruption of OPR7 and OPR8 reveals the versatile functions of jasmonic acid in maize development and defense	138	Yan *et al.* (2012)
9	Brassinosteroids antagonize gibberellin- and salicylate-mediated root immunity in rice	133	De Vleesschauwer *et al.* (2012)
10	A multi-phasic approach reveals that apple replant disease is caused by multiple biological agents, with some agents acting synergistically	110	Tewoldemedhin *et al.* (2011)

2013, Schroeder *et al.* 2013, Keeratijarut *et al.* 2015). Schroeder *et al.* (2013) provided an overview of molecular detection and quantification techniques for *Pythium* species with a summary of published PCR and real-time PCR assays up to 2012. Over recent years, loop-mediated isothermal amplification (LAMP) has been gaining popularity for the development of *Pythium* detection assays, due to its rapidity and ease of use (Takahashi *et al.* 2014, Feng *et al.* 2015b, Li *et al.* 2017b). Since 2013, LAMP assays have been developed for the detection of several important *Pythium* species, including *Py. aphanidermatum*, *Py. inflatum*, *Py. insidiosum*, *Py. myriotylum*, *G. irregulare*, *G. ultimum*, *Phytopythium helicoides*, and *Phytopythium. vexans* (Fukuta *et al.* 2013, 2014, Ishiguro *et al.* 2013, Takahashi *et al.* 2014, Keeratijarut *et al.* 2015, Feng *et al.* 2015b, 2018, 2019, Cao *et al.* 2016, Miyake *et al.* 2017, Shen *et al.* 2017a, Htun *et al.* 2020, Wang *et al.* 2021). Some of these studies improved the sensitivity of the assays by incorporating a baiting or plating step prior to LAMP detection from infected water, soil or plant material (Feng *et al.* 2015b, Miyake *et al.* 2017). Recombinase polymerase amplification (RPA) is another isothermal amplification technique that is more and more being used for the development of detection assays of plant pathogens, including *Phytophthora*, a genus that is closely related to *Pythium* (Rojas *et al.* 2017b, Dai *et al.* 2019, McCoy *et al.* 2020). The advantages of RPA over LAMP include amplification at lower temperatures and simpler primer design requirements (Dai *et al.* 2019). Although RPA-based assays for *Pythium* species have not yet been published, this technology is likely to feature for *Pythium* detection in coming years.

Author: C.F.J. Spies

34. *Funneliformis* C. Walker & A. Schüßler, The *Glomeromycota*, A species list with new families and new genera (Gloucester): 13. 2010. *emend*. Oehl *et al.*

Type species: *Funneliformis mosseae* (T.H. Nicolson & Gerd.) C. Walker & A. Schüßler

Classification: *Glomeromycota*, *Glomeromycotina*, *Glomeromycetes*, *Glomerales*, *Glomeraceae.*

Background

Arbuscular mycorrhizal fungi (AMF), belonging to the phylum *Glomeromycota*, live in symbiosis with the majority of vascular land plant species. There is undeniable evidence that AMF, among others, increase plants' water and nutrient supply, as well as their growth, yield, and tolerance to abiotic and biotic stresses (Smith & Read 2008). *Funneliformis* (*Glomeraceae*, *Glomerales*) is one of 49 genera of *Glomeromycota* (Błaszkowski *et al.* 2023, Da Silva *et al.* 2023). The genus was erected by Schüßler & Walker (2010) based on molecular evidence from SSU rRNA and the funnel-shaped spore base observed in 11 species originally described in the genera *Endogone* and *Glomus*. The type species, *Fun. mosseae*, was first described as *E. mosseae* (Nicolson & Gerdemann 1968), and then as *Glomus mosseae* Gerdemann & Trappe (1974). Species of *Funneliformis* usually produce spores blastically at tips of funnel-shaped or cylindrical sporogenous hyphae, occasionally spores are produced intercalary. The spores arise in soil singly or loose clusters, sometimes in compact glomerocarps. Oehl *et al.* (2011), based on molecular phylogeny of rDNA, and morphology of the spore base and the spore subtending hypha, transferred three of the 11 *Funneliformis* species mentioned above to a new genus, *Septoglomus* (*S. africanum*, *S. constrictum*, and *S. xanthium*) and six species of *Glomus* to *Funneliformis*. Recently, *Fun. vesiculiferus* was transferred to *Rhizoglomus* (Błaszkowski *et al*. 2018) and *Fun. pilosus* was described (Guillén *et al*. 2020), both actions were performed following morphological and molecular phylogenetic evidence. Oehl *et al*. (2011) left *G. badium* described by Oehl *et al*. (2005) in *Glomus*, despite Schüßler & Walker (2010) transferring this species to *Funneliformis*. Phylogenetically, *G. badium* is characterised by only one short (617 bp long) sequence covering partially the 18S nrRNA gene and the ITS1 region (Oehl *et al*. 2011). Although *Funneliformis* currently comprises only 13 species (*F. mosseae*, *F. coronatus*, *F. geosporus*, *F. caledonius*, *F. pilosus*, *F. fragilistratus*, *F. verruculosus*, *F. caesaris*, *F. dimorphicus*, *F. halonatus*, *F. kerguelensis*, *F. monosporus*, *F. multiforus*), molecular inventories of AMF communities associated with plant roots and soil samples indicated numerous Operational Taxonomic Units (OTU) belonging to this genus (Geoffroy *et al*. 2017) as potential novel species waiting to be described.

Ecological and economic significance

Species of *Funneliformis* occur frequently and abundantly in different ecosystems (Sun *et al*. 2013, Geoffroy *et al*. 2017, Winagraski *et al*. 2019), even in aquatic environments (Queiroz *et al.* 2020). *Funneliformis mosseae* and *Fun. geosporus* are among the most widely distributed AMF in the world (Öpik *et al*. 2006, Furrazola *et al*. 2021, Stürmer & Kemmelmeier 2021). Because of their common occurrence and wide distribution, *Funneliformis* species certainly play an important role in influencing the productivity and condition of plants growing in cultivated and natural sites (Rodrigues & Rodrigues 2015). Countless experiments have revealed that among the *Funneliformis* species, *F. mosseae* significantly increased plant growth, nutrient absorption (Mirzaei *et al*. 2015, Sahodaran *et al*. 2019), chlorophyll production (Tuo *et al*. 2015, Bahraminia *et al*. 2020), resistance to pathogens (Qian *et al*. 2015, Lu *et al*. 2020), as well as tolerance to salinity (Mirzaei *et al*. 2015, El-Gazzar *et al*. 2020), drought (Bahraminia *et al*. 2020), heavy metals (Degola *et al*. 2015, Berthelot *et al*. 2018) and hydrocarbons (Malicka *et al.* 2021).

Funneliformis mosseae can coexist with communities of actinobacteria, producing high amounts of idole-3-acetil acid (IAA) (Lasudee *et al*. 2018), and yeasts, able to solubilize low-soluble phosphate sources and accumulate polyphosphates (Alonso *et al*. 2008), mitigating the adverse effects of low nutrient and drought stress. *Funneliformis mosseae* also appeared to be important in bioactive compound production in medicinal and aromatic plants (Karimi *et al*. 2016, Weisany *et al*. 2016). Due to the various beneficial effects on plants and environment, as well as the abundant sporulation and the high colonisation potential, *Fun. mosseae* has been widely used in the production of biofertilizers and phytoremediation (Hassan *et al*. 2013, Huang *et al*. 2019).

Research interests

There are 1 452 publications and 20 832 citations from 2011–2021 in the Web of Science (Fig. 62), with the top 10 most cited articles shown in Table 40. The most cited article was published by Latef & Chaoxing (2011) and it represents one of the most important topics in AM research – the role of AM fungi on plant growth, nutrient uptake, and tolerance to abiotic stresses like salinity, drought, and heavy metals. The importance of these fungi to enhance the growth and quality of horticultural crops such as tomatoes is considerable, as among the top 10 articles, five addressed this topic (Table 40). The mycorrhizal network is also a hot research topic (Walder *et al*. 2012). The connection between plants via the mycelial network allowing "talk" among plants mediated by the transfer of signals is in the spotlight and has already reached science fiction movies – Star Trek Discovery from CBS Television Studios INC – "USS Discovery Enters the Mycelial Network" to travel between dimensions and through space and time. The contributions to plant protection (Schausberger *et al.* 2012) and bioremediation (Yu *et al*. 2011b, Barnawal *et al*. 2014) were also discussed in a large number of publications.

The most extensively studied species within the genus is *Funneliformis mosseae.* This species is deeply rooted in the history of AM research, and was named in honour of Dr Barbara Mosse, considered the mother of modern mycorrhizology. Using this species, Dr Mosse demonstrated for the first time, the connection between fructification (sporocarps) of this fungus and AM symbiosis in strawberry roots and later the role of AM fungi in plant nutrition (Mosse 1953, 1956, 1973). *Funneliformis mosseae* has been important to comprehend the molecular basis of AMF symbiosis. Furthermore, it was used as a model species for proteomic and transcriptomic studies of *Glomeromycota* (Zhang & Franken 2014, Sui *et al*. 2018, Lu *et al*. 2020, Zhang *et al*. 2020f). The complete sequence of *Fun. mosseae* mitochondrial (mt) genome showed intriguing characteristics: length (134 925 bp) greater than several mt fungal genomes, different types of introns and insertions in rnl, and alternative genetic codes in both initiation (GUG) and termination (UGA) codons (Nadimi *et al*. 2016).

Authors: B.T. Goto, F.A. de Souza, F. Magurno, J. Błaszkowski and M.B. de Queiroz

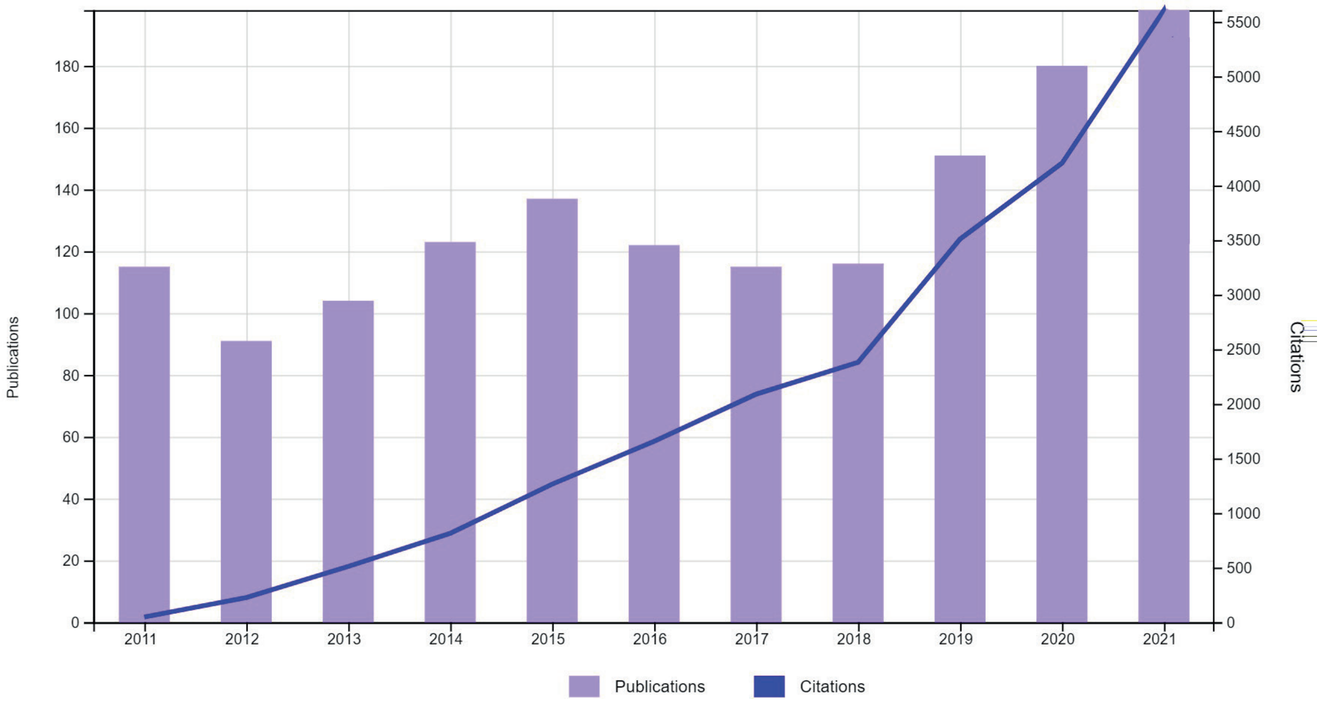

Fig. 62. Trends in research of *Funneliformis* in the period 2011–2021.

Table 40. Top 10 cited articles related to *Funneliformis* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Effect of arbuscular mycorrhizal fungi on growth, mineral nutrition, antioxidant enzymes activity and fruit yield of tomato grown under salinity stress	238	Latef & Chaoxing (2011)
2	Mycorrhizal networks: common goods of plants shared under unequal terms of trade	210	Walder *et al.* (2012)
3	Arbuscular mycorrhizal fungi act as biostimulants in horticultural crops	204	Rouphael *et al.* (2015)
4	Enhanced tomato disease resistance primed by arbuscular mycorrhizal fungus	134	Song *et al.* (2015)
5	Insights on the impact of arbuscular mycorrhizal symbiosis on tomato tolerance to water stress	121	Chitarra *et al.* (2016)
6	ACC deaminase-containing *Arthrobacter protophormiae* induces NaCl stress tolerance through reduced ACC oxidase activity and ethylene production resulting in improved nodulation and mycorrhization in *Pisum sativum*	107	Barnawal *et al.* (2014)
7	Community structure of arbuscular mycorrhizal fungi associated with *Robinia pseudoacacia* in uncontaminated and heavy metal contaminated soils	105	Yang *et al.* (2015)
8	Enhanced dissipation of PAHs from soil using mycorrhizal ryegrass and PAH-degrading bacteria	100	Yu *et al.* (2011b)
9	Mycorrhiza changes plant volatiles to attract spider mite enemies	88	Schausberger *et al.* (2012)
10	Increasing the productivity and product quality of vegetable crops using arbuscular mycorrhizal fungi: a review	85	Baum *et al.* (2015)

35. ***Ustilago*** (Pers.) Roussel, Fl. Calvados, Edn. 2: 47. 1806.

Type species: *Ustilago hordei* (Pers.) Lagerh.

Classification: *Basidiomycota*, *Ustilaginomycotina*, *Ustilaginomycetes*, *Ustilaginales*, *Ustilaginaceae.*

Background

Ustilago is an important basidiomycetous genus of plant pathogens that mainly parasitises members of the grass family (*Poaceae*). The genus is classified in the family *Ustilaginaceae* in class *Ustilaginomycetes* and comprises approximately 200 species (Vánky 2012) with some of them causing major damage to important crops. The morphology of sori and spores, and the host range have been used as major features to distinguish among the various genera and species in *Ustilaginaceae*, and more recently molecular phylogenies have been used to circumscribe genera (Begerow *et al*. 2014, Hyde *et al.* 2014, Wang *et al.* 2015b). *Ustilago s. str.* is mainly restricted to hosts of the tribe *Pooideae* (*Poaceae*) and is further characterised by the absence of soral structures, such as a columella, spore balls, and sterile cells (McTaggart *et al.* 2012, 2016a). One of the major observations resulting from the molecular phylogenies is that the type species of the genus, *U. hordei*, a pathogen on barley, belongs to a different clade (Clade 6) together with *U. tritici*, a pathogen of wheat, whereas the corn smut, *U. maydis*, arguably the most well-known *Ustilago* species belongs to Clade 2 (Wang *et al*. 2015b, McTaggart *et al*. 2016a). Various comparative genomics and phylogenomic investigations supported the phylogenetic separation of *U. hordei* and *U. maydis* (*e.g.*, Bakkeren *et al*. 2008, Laurie *et al*. 2008, Kellner *et al.* 2011). For instance, Laurie *et al*. (2008, 2012) compared the genomes of barley and corn smuts and found that RNA silencing components were lost in the *U. maydis* genome, and species-specific presence of transposable elements occurred. More extensive comparative genomics studies need to include a broader taxonomic sampling to support these initial findings. The polyphyletic nature of *Ustilago* species also made taxonomic and nomenclatural reassessments needed. Several attempts were made to split or reorganise the genus; however, convincing data or clear species delimitations are lacking (Vánky 1987, Stoll *et al.* 2005). Thines (2016) proposed to conserve *Ustilago* with *U. maydis*, and this was further discussed by McTaggart *et al*. (2016a) who concluded that it is preferred to recognise *Ustilago* with its conserved type species *U. hordei* and to reintroduce the generic name *Mycosarcoma*, a genus originally proposed by Brefeld (1912), for the clade containing *U. maydis* (McTaggart *et al.* 2016a, Thines 2016). Eventually, the mycological community must decide on either proposal. In addition, asexually reproducing yeast-like taxa were described in the genus *Pseudozyma* (Bandoni 1985, Boekhout 2011), but later molecular phylogenetic studies found *Pseudozyma* to be polyphyletic, hence, several species have been reclassified in various hitherto sexually defined genera of *Ustilaginales* (Wang *et al.* 2015b). Additionally, genome analyses revealed mating and meiosis genes being present in most *Pseudozyma* species, indicating a sexual but maybe saprobic lifestyle (Steins *et al.* 2023). Importantly, *Pseudozyma prolifica* the type species of *Pseudozyma*, was found to be conspecific with *U. maydis* (Boekhout 1995, 2011, Begerow *et al.* 2000, 2014, Wang *et al.* 2015b).

Ecological and economic importance

Ecologically, smut fungi seem to be well adapted as biotrophic, host-specific parasites, without causing serious damage in natural populations. Even in cereals such as corn, oats or barley they only cause disease in parts of the clonal or inbred host population (*e.g.*, Müller 2006, Thomas & Menzies 1997). *Ustilago maydis* causes hypertrophic tumour-like galls on corn cobs (*Zea mays*), and the introduction of hybrid corn races has strongly reduced the severity and economic loss from the disease (Pataky & Snetselaar 2006). In Mexico, the fungus-plant galls are known as huitlacoche and are considered a delicacy (Valverde *et al*. 1995, Juárez-Tracy *et al.* 2007, Montiel *et al.* 2011). In 2007, 400 to 500 tons of huitlacoche were sold in Mexico (Villanueva 1997) and new markets elsewhere in South America and the USA are emerging.

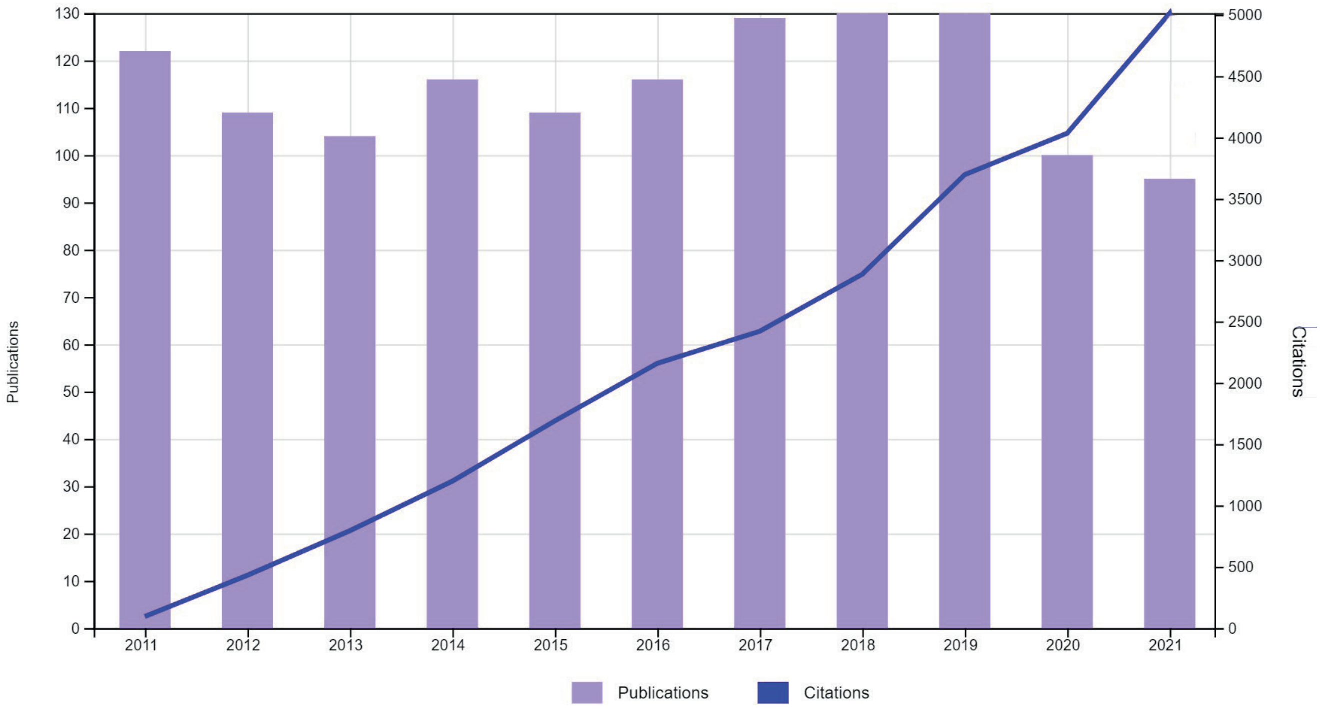

Fig. 63. Trends in research of *Ustilago* in the period 2011–2021.

Table 41. Top 10 cited articles related to *Ustilago* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	The top 10 fungal pathogens in molecular plant pathology	1 769	Dean *et al.* (2012)
2	One stop shop: backbones trees for important phytopathogenic genera: I (2014)	235	Hyde *et al.* (2014)
3	Biosurfactants: a sustainable replacement for chemical surfactants?	232	Marchant & Banat (2012)
4	Mitogen-activated protein kinase signaling in plant-interacting fungi: distinct messages from conserved messengers	169	Hamel *et al.* (2012)
5	Filamentous pathogen effector functions: of pathogens, hosts and microbiomes	151	Rovenich *et al.* (2014)
6	Evolution and genome architecture in fungal plant pathogens	121	Möller & Stukenbrock (2017)
7	Genome comparison of barley and maize smut fungi reveals targeted loss of RNA silencing components and species-specific presence of transposable elements	113	Laurie *et al.* (2012)
8	Multigene phylogeny and taxonomic revision of yeasts and related fungi in the *Ustilaginomycotina*	111	Wang *et al.* (2015b)
9	Fungal development of the plant pathogen *Ustilago maydis*	101	Vollmeister *et al.* (2012)
10	Two linked genes encoding a secreted effector and a membrane protein are essential for *Ustilago maydis*-induced tumour formation	100	Doehlemann *et al.* (2011)

Research interests

There are 1 260 publications and 20 809 citations from 2011–2021 in the Web of Science (Fig. 63), with the top 10 most cited articles shown in Table 41. The high number of citations of *Ustilago*-based research is mainly because *U. maydis* has evolved as a model species to better understand fundamental and applied research issues in plant pathology related to biotrophic basidiomycetous fungi. Aspects studied are regulation of sexual and asexual reproduction, morphogenesis, interactions with the host, including signalling, the role of secreted effector molecules in virulence and the suppression of host immunity, and imaging of intracellular transport and interaction of organelles (Dean *et al.* 2012, Tanaki *et al.* 2012, Vollmeister *et al*. 2012, Rovenich *et al.* 2014, Schuster *et al.* 2016a, b). Several of the highly cited publications are reviews that address several of these aspects. *Ustilago maydis* was in the top 10 fungal plant pathogens according to votes given by an expert community (Dean *et al.* 2012). *Ustilago maydis* emerged as a model species because 1) it grows in culture using defined media; 2) it grows as a haploid budding yeast; 3) the infection cycle can be completed in the laboratory; 4) genetics tools are available for the targeted construction of mutants allowing homologous recombination and the construction of haploid, solopathogenic strains; 5) advanced microscopy tools allow imaging of cell components in a dynamic mode; and, 6) the genome is known (Kämper *et al.* 2006, Dean *et al.* 2012, Schuster *et al.* 2016a, b).

Ustilago and related species are also of biotechnological interest as they can produce itaconic acid (Haskins *et al.* 1955, Tabuchi *et al.* 1981, Klement *et al.* 2012, Becker *et al.* 2020) and biosurfactants, such as mannosylerythritol lipids (Kitamoto *et al.* 2001, Hewald *et al.* 2006, Marchant & Bawat 2012). A species formerly known as *Candida*/*Pseudozyma antarctica*, but that is now classified as *Moesziomyces antarcticus*, accumulates up to 40 % fatty acids dry weight (Gill *et al.* 1977). Lipases (*e.g.*, lipase B) produced by this species find broad application in lipid engineering and biotechnology (Chandra *et al.* 2020). *Ustilago maydis* was also found to be an efficient degrader of lignocellulosic plant biomass with a 57 % improvement in the release of general sugars and 22 % of glucose (Couturier *et al.* 2012). *Ustilago maydis* is also known as a producer of β-carotenes (Estrada *et al.* 2009). *Pseudozyma flocculosa* produces a glycolipid named flocculosin that might have the potential for biocontrol (Mimee *et al.* 2005, 2009). Further information on biotechnological applications of *Ustilaginomycotina* yeasts can be found in Boekhout (2011) and Kitamoto (2019).

Authors: T. Boekhout and D. Begerow

36. ***Rhizoglomus*** Sieverd. *et al*., Mycotaxon 129: 377. 2014.

Type species: *Rhizoglomus intraradices* (N.C. Schenck & G.S. Sm.) Sieverd. *et al*. [≡ *Glomus intraradices* N.C. Schenck & G.S. Sm. = *Rhizophagus intraradices* (T.H. Nicolson & N.C. Schenck) C. Walker & A. Schüßler]

Classification: *Glomeromycota*, *Glomeromycotina*, *Glomeromycetes*, *Glomerales*, *Glomeraceae.*

Background

During the last two decades, the evolutionary history of *Glomeromycota* forming glomoid spores was extensively improved, with paraphyletic and polyphyletic issues identified and solved (Morton & Redecker 2001, Schwarzott *et al*. 2001, Schüssler & Walker 2010, Oehl *et al*. 2011). All species with glomoid spore development were previously classified in *Glomus* (Gerdemann & Trappe 1974, Morton & Benny 1990). Since the acknowledgement of the lack of synapomorphic features in the glomoid spore development, the identification at the genus level of unknown glomoid species has been generally obtained through molecular and phylogenetic analysis (Błaszkowski *et al*. 2021a, b, 2023). Until 2010, almost 100 species were classified in the genus *Glomus*, including species that are currently found in the genus *Rhizoglomus* (Schüssler & Walker 2010, Oehl *et al*. 2011, Sieverding *et al*. 2015). As a result, *Glomus* has a higher citation count than *Rhizoglomus.* However, those citations cover species that no longer belong to the genus *Glomus* (Wijayawardene *et al*. 2020, Index Fungorum 2022). Currently, *Glomus* comprises over 55 species (names), but only six hold phylogenetic positions based on a robust molecular data set (Błaszkowski *et al*. 2021a, b, 2023, Yu *et al*. 2022a), while most lack molecular confirmation and were placed as *incertae sedis* by Schüßler & Walker (2010). Schüssler & Walker (2010) resurrected the genus *Rhizophagus* for species in the *Glomeraceae* forming abundant spores in the roots of vascular plants. *Rhizophagus populinus*, described by Dangeard (1896) as a root-inhabiting fungus forming AM intraradical structures, was erected as the type species despite no material being available for the species. *Glomus intraradices* and species belonging to the phylogenetic group *Glomus* Group Ab were accommodated in the resurrected genus. Interestingly, the name *Rhizophagus* was already in use since 1793 for a genus in the order *Coleoptera* (*Insecta*).

Later the genus *Rhizoglomus* was proposed by Sieverding *et al*. (2015) with *Rh. intraradices* as type species. Currently, *Rhizoglomus* comprises 22 species, 18 of which have been recognised by barcode sequences (*i.e.*, 18S-ITS-28S, *rpb1*) and morphological characters of the glomerospores (Sieverding *et al*. 2015, Turrini *et al*. 2018, Corazon-Guivin *et al*. 2022). Spores of *Rhizoglomus* species present glomoid development, arising blastically at the end of sporogenous hyphae, but some species also produce intercalary spores (De Souza & Berbara 1999). Frequently, they produce abundant assemblages of spores in soil and roots, in loose or compact clusters comprising hundreds, or even thousands of spores (Błaszkowski *et al*. 2019). The spore wall consists of two to, more rarely, five layers, and the subtending hypha, which usually is cylindrical and generally has an open pore at the spore base (Błaszkowski *et al.* 2014, 2019, Kokkoris *et al.* 2023). *Rhizoglomus* root colonisation is characterised by the formation of vesicles, arbuscules and also intraradical spores in the root cortex (Błaszkowski 2012) of plants in terrestrial, including litterfall (Lima *et al.* 2023) and aquatic environments (Gomes *et al.* 2022).

Ecological and economic significance

Bioenhancers and biofertiliser for plant performance

Rhizoglomus species are considered a generalist species of AM fungi in all kinds of environments (Öpik *et al*. 2010, Davison *et al*. 2011). They can improve nutrient and water use efficiency of symbiotically associated plants, promoting the growth and yield of a wide range of economically important crops, having an enormous interest as bio-enhancers of plant performance and biofertiliser for agricultural production, ecosystem restoration and biotechnology.

Although, AM fungi are obligate biotrophs – *Rhizoglomus* species can be grown aseptically in monoxenic systems associated with Ri T-DNA transformed roots of several dicotyledonous species. This system is the base for large-scale AM fungi contaminated-free inoculum production in bioreactors and is also a model for basic and applied studies of AM symbiosis. *Rhizoglomus clarum* and *Rh. irregulare*, two species produced in monoxenic culture, have shown field inoculation response for soybean, cotton, maize, potato and cassava crops (Ceballos *et al*. 2013, Cely *et al*. 2016, Hijri 2016, Barazetti *et al*. 2019, Kokkoris *et al*. 2019) among many other crops and timber species. Together with *Rh. intraradices*, these species are recognised for conferring a stronger tolerance to saline (Bharti & Garg 2019, He *et al*. 2019a) and drought stresses (Zuccarini & Savé 2016), improving phosphorus and nitrogen use efficiency (Abou El Seoud 2019, Lopes *et al.* 2019) and also acting as biocontrol agents of phytopathogens such as *Fusarium* spp. (Ismail *et al*. 2013b, Olowe *et al*. 2020). Due to these benefits, several inoculants using *Rhizoglomus* spp. are sold in different countries.

Research interests

There are 1 393 publications and 17 651 citations from 2011–2021 in the Web of Science (Fig. 64), with the top 10 most cited articles shown in Table 42. Most publications focused on AMF symbiosis, plant performance and the environmental role of the AM fungi among other issues.

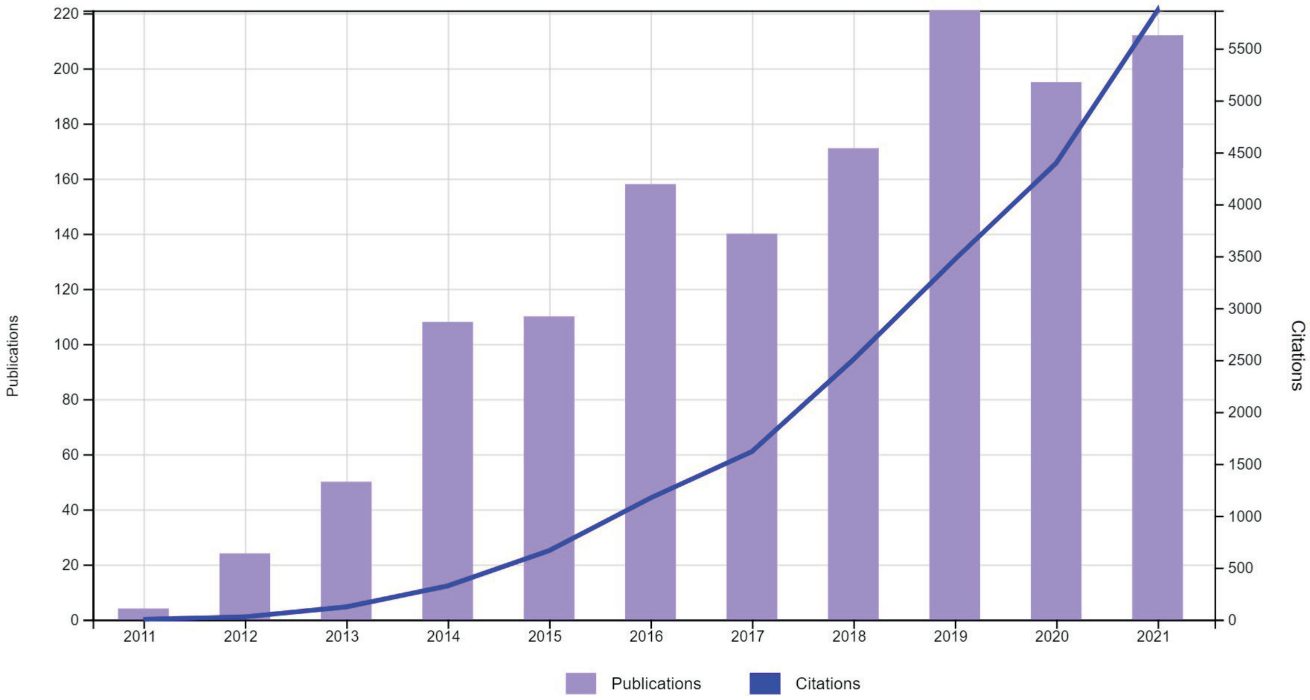

Fig. 64. Trends in research of *Rhizoglomus* in the period 2011–2021.

Table 42. Top 10 cited articles related to *Rhizoglomus* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Mycorrhizal ecology and evolution: the past, the present, and the future	843	Van der Heijden *et al*. (2015)
2	Fungal lipochitooligosaccharide symbiotic signals in arbuscular mycorrhiza	605	Maillet *et al*. (2011)
3	Phylogenetic reference data for systematics and phylotaxonomy of arbuscular mycorrhizal fungi from phylum to species level	440	Krueger *et al*. (2012)
4	Genome of an arbuscular mycorrhizal fungus provides insight into the oldest plant symbiosis	418	Tisserant *et al*. (2013)
5	A secreted fungal effector of *Glomus intraradices* promotes symbiotic biotrophy	305	Kloppholz *et al*. (2011)
6	Regulation by arbuscular mycorrhizae of the integrated physiological response to salinity in plants: new challenges in physiological and molecular studies	300	Ruiz-Lozano *et al*. (2012)
7	Short-chain chitin oligomers from arbuscular mycorrhizal fungi trigger nuclear Ca^{2+} spiking in *Medicago truncatula* roots and their production is enhanced by strigolactone	285	Genre *et al*. (2013)
8	Arbuscular mycorrhizal fungi as natural biofertilizers: let's benefit from past successes	282	Berruti *et al*. (2016)
9	Carbon availability triggers fungal nitrogen uptake and transport in arbuscular mycorrhizal symbiosis	249	Fellbaum *et al*. (2012)
10	The transcriptome of the arbuscular mycorrhizal fungus Glomus intraradices (DAOM 197198) reveals functional tradeoffs in an obligate symbiont	216	Tisserant *et al*. (2012)

Model organisms to study plant root symbiosis

The arbuscular mycorrhiza is an ancient symbiosis that is thought to have played a fundamental role in the transition of plants to terrestrial environment and has become widespread among vascular plants (Wang *et al*. 2010, Corradi & Bonfante 2012, Radhakrishnan *et al*. 2020). Bi-directional nutrient exchange is the key to the function of AM symbiosis – the fungus trades inorganic nutrients and water with the associated plant through specialised structures called arbuscules that develop temporally inside root cortical cells (Gutjahr & Parniske 2017), where symbiotically induced protein transporters are expressed (Balzergue *et al*. 2011, Casieri *et al*. 2012, Gutjahr *et al*. 2012, Tamura *et al*. 2012, Tian *et al*. 2013, Basu *et al.* 2018, Kameoka *et al*. 2019, Plassard *et al*. 2019, Wipf *et al*. 2019). A deep comprehension of the regulation of the arbusculated cell would certainly open the possibility of engineering plants and root organ cultures for more efficient mycorrhization and inoculum production.

The core set of genes that control the genetic program and signalling pathway of the AM symbiosis is also essential for actinorhizal and legume-rhizobial symbioses (Hocher *et al*. 2011, Tromas *et al*. 2012, Bravo *et al*. 2016, Kamel *et al*. 2017). Contrary to AMF, these two younger symbioses have a restricted occurrence among plant families. Understanding and engineering the symbiosis genetic program might favor nitrogen-fixing rhizobial associations with any plant of interest, ending the nitrogen dependency of chemical fertilizer and overcoming yield limitations of several crops with greater environmental benefits. The AM fungus *Rhizoglomus irregulare* together with legume plants *Medicago truncatula*, *Lotus japonicum* and bacteria from *Rhizobium* group are the main model organisms to study the AM symbiosis and nodulation in legumes, while rice is the model plant for *Poaceae* (Horváth *et al*. 2011, Casieri *et al*. 2012, Gutjahr *et al*. 2012, Harrison 2012, Ivanov *et al*. 2012, Tromas *et al*. 2012, Bravo *et al*. 2016, Dreher *et al*. 2017, Floss *et al*. 2017, Volpe *et al*. 2020).

Rhizoglomus irregulare as a model fungus for Glomeromycota genomic studies

Rhizoglomus irregulare is a model species for genomic studies in *Glomeromycota*. It was the first AM fungus to have its complete genome sequenced (Tisserant *et al*. 2013). This work and following studies on other *Rhizoglomus* genotypes shed light on important questions related to the metabolism and obligate biotrophic nature, genome organisation, mating-type genes, sexual status (sexual, parasexual or clonal), and intragenomic polymorphism (Halary *et al*. 2011, Corradi & Bonfante 2012, Ehinger *et al*. 2012, Riley & Corradi 2013, Spatafora *et al*. 2016, Corradi & Brachmann 2017, Koch *et al*. 2017, Chen *et al*. 2018, Kobayashi *et al*. 2018, Mathieu *et al*. 2018, Morin *et al*. 2019, Yildirir *et al*. 2020). Currently, there are 19 genome assemblies available in GenBank for *Rh. irregulare* and *Rh. clarum* (Kobayashi *et al*. 2018).

Environmental role of Rhizoglomus spp. symbiosis

Arbuscular mycorrhizal fungi are undoubtedly one of the most important rhizosphere microorganisms engaged in beneficial symbiosis with the root system of 72 % of vascular plants (Brundrett & Tedersoo 2018) which invest up to 20 % of the fixed carbon to sustain their fungal partner (Siddiqui & Pichtel 2008). Among the AMF species detected in environmental studies across various climatic zones and vegetation types globally, *Rhizoglomus* spp., in particular *Rh. irregulare*, rule the roost (Oehl *et al.* 2017, Malicka *et al.* 2022). Davison *et al.* (2015b) analysed 1 014 DNA samples from plant roots collected worldwide. The data from this publication revealed that within the various virtual taxa (VTs) detected, those representing *Rhizoglomus* (*e.g.*, *Rh. intraradices*, *Rh. irregulare*, *Rh. fasciculatum*, *Rh. vesiculiferum*) were ranked among the most abundantly found. Kivlin *et al.* (2017) used 18S gene DNA sequences from GenBank to model the global distribution of *Rh. irregulare* and found that the distribution was influenced by climatic and resource variables. Considering the different continents, the distribution was driven by climate in North America and Eurasia, soil carbon in South America and climate and soil phosphorus in Africa.

Authors: B.T. Goto, F.A. de Souza, F. Magurno, J. Błaszkowski and M.B. de Queiroz

37. ***Acremonium*** Fr., Syst. Mycol. 3(2): 425. 1832.

Type species: *Acremonium alternatum* Link

Classification: *Ascomycota*, *Pezizomycotina*, *Sordariomycetes*, *Hypocreales*, *Bionectriaceae.*

Background

Acremonium is a ubiquitous fungal genus belonging to *Bionectriaceae* (*Hypocreales*), with more than 200 species epithets recorded in Index Fungorum (2022). This genus contains many of the simplest structured species of all filamentous asexual fungi. Most species of *Acremonium* are saprobes that are geographically widespread and reported to live in various substrates, including soil, sediment, dead plant material, rocks, marine organisms, foods and indoor air (Gams 1971, 1975, Domsch *et al.* 2007, Giraldo *et al.* 2012). It also accommodates endophytes or epiphytes of plants, animals, or other fungi (Gams 1971, 1975, Alfaro-García *et al.* 1996, Summerbell 2003, Lin *et al.* 2004, Domsch *et al.* 2007, Perdomo *et al.* 2011, Guarro 2012), saprotrophs on rotten materials (Weisenborn *et al.* 2010, Zhang *et al.* 2017b), or weak to virulent, facultative or obligate pathogens on plants or human beings (Niknam *et al.* 2017, Nasir *et al.* 2018, Rashed 2018, Zbiba *et al.* 2018, De Hoog *et al.* 2015) and parasites on fungi, lichens, insects or arthropods (Weisenborn *et al.* 2010, Patil *et al.* 2011, Brackel *et al.* 2012, Sherief & Bhaskar 2018, Summerbell *et al.* 2018, Hou *et al.* 2023).

Acremonium was introduced by Link (1809) for a novel species that produces solitary spores at the ends of its fertile cells. This genus was named according to its morphological characteristics of “acro-”, which means “situated at the top”, and “mono-”, which means “single” (Link 1809, Summerbell & Scott 2015). After examination of Link’s herbarium material, Gams (1968) illustrated the type species, *Ac. alternatum*, producing conidia in chains from thin, tapering phialides, rather than single conidia. Subsequently, a morpho-taxonomic groundwork for *Acremonium* conceived by Gams (1971) further demonstrated that many species formerly referred to as *Cephalosporium*, which was characterised by the production of simple unbranched conidiophores and conidiogenous cells bearing at the tip a group or “head” of unicellular conidia, should be re-located in *Acremonium* (Gams 1971). *Acremonium* was reinterpreted as hyaline fungi that produce septate hyphae giving rise to narrow, tapered, mostly lateral phialides with unicellular conidia arranged in mucoid heads or unconnected chains, and differentiated conidiophores with or without verticillate branches which may be observed in some species (Gams 1971, 1975, Domsch *et al.* 2007, Perdomo *et al.* 2011, Summerbell *et al.* 2011, Hou *et al.* 2023). Based on morphological characteristics, *Acremonium* was subdivided into three sections: *Simplex*, *Nectrioidea* and *Gliomastix* (Gams 1971). After an extensive study of the *Cephalosporium*-related and acremonium-like genera, the number of *Acremonium* species increased rapidly with the addition of new species and new combinations that were morphologically similar to *Acremonium* but previously disposed under other genera, such as *Gliomastix*, *Paecilomyces*, *Oospora*, and *Monosporium* (Gams 1971). Three additional sections, *Chaetomioidea*, *Albolanosa*, *Lichenoidea*, were added, for the acremonium-like asexual genera *Chaetomium* and *Epichloe* (Gams 1975, Morgan-Jones & Gams 1982), and the section *Lichenoidea* was added for lichenicolous species (Lowen 1995). However, *Acremonium* has been perceived to be a heterogeneous taxon. Taxonomic placement at the species level is difficult based only on morphology, which is indicated by its association with diverse morphologically distinct sexual genera that are classified in different orders of *Ascomycota* (Wijayawardene *et al.* 2017b). Most of the sexually typified *Acremonium* members were identified as *Nectria* species (Gams 1971, Samuels 1973, 1976a, b, Lowen 1995), but the many genera of *Hypocreales* known from their sexual morphs, such as *Epichloe*, *Emericellopsis*, *Hypocrea*, *Hypomyces*, *Mycoarachis*, *Nectriopsis*, *Nigrosabulum*, *Pronectria*, *Thielavia*, even *Gabarnaudia* in *Microascales*, *Lecythophora* in *Coniochaetales*, and *Pseudogliomastix* in *Sordariales* also have *Acremonium* asexual morphs (Malloch & Cain 1970, Gams 1971, Morgan-Jones & Gams 1982, Samuels 1976, 1988, Lowen 1995, Tubaki 1973). Rapid progress in molecular phylogenetic methods contributed to a substantial revision of acremonium-like genera and offers an effective approach to identifying species into different species or complexes (Glenn 1996, Summerbell *et al.* 2011, 2018, Giraldo *et al.* 2015, 2017, Giraldo & Crous 2019, Hou *et al.* 2023). Glenn (1996) provided a preliminary study of the phylogenetic relationships of *Acremonium* and other genera based on SSU sequences for the first time, indicating that the genus *Acremonium* is highly polyphyletic and previously recognised representatives have affiliations to at least three groups in distinct orders of Ascomycetes, including *Hypocreales*, *Microascales* and *Sordariales*. Summerbell *et al.* (2011) provided a DNA-based phylogenetic overview for more than 100 *Acremonium* species and related or similar taxa available in pure culture and further demonstrated that acremonium-like species are phylogenetic divergent. Epitypification of the type species, *Ac. alternatum*, linked *Acremonium s. str.* to the *Bionectriaceae* (Summerbell *et al.* 2011). Summerbell *et al.* (2018) revealed that many previously reported isolates from clinical and contaminated food were misidentified due to the high plasticity of morphological characters, and that very few historic identifications of *Acremonium* spp. from substrates of practical interest could be trusted.

Ecological and economic significance

Considering the importance of this genus to the agro-forestry, industrial and pharmaceutical industries, a concerted effort must be undertaken to fully elucidate the species of economic importance.

Plant disease

Numerous economically significant plants are infected by *Acremonium* species. *Acremonium strictum* is pathogenic to many monocotyledonous and dicotyledonous crops, and because of its ubiquitous prevalence in soil, it has negatively impacted many agricultural plants including *Gossypium*, *Triticum* and *Zea* (El-Shafey *et al.* 1979, Rashed 2018). Infection by *Ac. strictum* is commonly systemic (Bandyopadhyay 1987), causing plant wilt and abnormal leaf desiccation on one side of the midrib, discoloured vasculature of the stalk near the soil line (Specht 1989), and vasculature of the plant forms orange, red and brown bundles, usually resulting in death (Rashed 2018). In Argentina (Forbes & Crespo 1982), the USA (Natural *et al.* 1982) and India (Bandyopadhyay 1987), *Ac. strictum* (syn. *Sarocladium strictum*) was reported as one of the most common agents of sorghum wilt disease, incorrectly attributed to *Cephalosporium acremonium*. Symptoms initially appear on the lower leaves of corn plants before spreading upward. This disease frequently causes chlorosis, leaf necrosis, stem necrosis without plant lodging, barren plant and wilting symptoms (Natural *et al.* 1982, Bandyopadhyay 1987, Tagne *et al.* 2002), resulting in small, shrunken grains with reduced weight, poor germination, weak seedlings, and a 50 % reduction in grain yield in affected plants (Natural *et al.* 1982, Bandyopadhyay 1987). *Acremonium sclerotigenum* causes “Acremonium brown spot” on bagged apple fruit in China (Li *et al.* 2014a), and has resulted in up to 30 % annual yield losses in Shandong Province from 2010 to 2012, resulting in significant economic losses (Li *et al.* 2014). Additionally, *Acremonium* spp. are notorious as endophytes in stock farming. Cattle, sheep and rabbits feeding on tall fescue grasses infected by acremonium-like endophytes may have reduced growth and milk production, and show intolerance to heat (Morgan-Jones & Gams 1982, Hill *et al.* 1990, Putnam *et al.* 1991, Hoveland 1993).

Food spoilage

Acremonium is frequently isolated from a variety of foods, and it is well established as being among the food-spoiling microorganisms (Summerbell & Scott 2015). Numerous *Acremonium* species were isolated from food-related sources, such as *Ac. atrogriseum* from noodles, *Ac. charticola* from rotten apples, *Ac. egyptiacum* from stored wheat, *Ac. sclerotigenum* from fish meal and lenticel in apple peel (Gams 1971, Summerbell & Scott 2015). Some acremonioid fungi were also reported from corked wine, rice, spoiled bottles of mineral water, postharvest peaches, Brazil nut or stored apples (Gams 1971, Abdel-Hafez 1987, Fujikawa 1997, Fernández-Trujillo 1997, Alvarez-Rodríguez 2002). However, considering many *Acremonium* species are also plant endophytes, those species reported from food sources are perhaps the components of plant stems contacted with food.

Clinical pathogen

Over 300 clinical cases have been linked to *Acremonium*-related species within various reports (Pérez-Cantero 2020). Human clinical cases involving *Acremonium* species, particularly *Ac. kiliense* (currently *Sarocladium kiliense*), *Ac. egyptiacum* and *Ac. strictum*, are frequently reported, mainly associated with mycetomas, and other serious lung or catheter-related bloodstream infections (Negroni *et al.* 2006, Geyer *et al.* 2006, Virgilio *et al.* 2015, Etienne *et al.* 2016, Niknam *et al.* 2017). Onychomycoses, or following traumatic inoculation, infections resulting in fungemia, ocular infections (keratitis), cutaneous and subcutaneous infections and mycetoma have also been commonly detected (Gupta *et al.* 2000a, Perdomo 2011, Summerbell *et al.* 2018, Pérez-Cantero & Guarro 2020). Locally invasive infections such as arthritis, osteomyelitis, peritonitis, sinusitis, and less frequently central nervous system infections have also been frequently reported in recent years (Guarro *et al.* 1997, 2009, De Hoog *et al.* 2000, Gupta *et al.* 2000a, Das *et al.* 2010, Pérez-Cantero & Guarro 2020). The most common clinical manifestation caused by infections of *acremonium*-related species is fungaemia (Pérez-Cantero 2020). Chile and Colombia reported an outbreak of *Ac. kiliense* (*Sarocladium kiliense*) bloodstream infection in more than 50 oncology patients who received contaminated anti-nausea medication during 2013–2014 (Etienne *et al.* 2016).

Cephalosporin producer

Cephalosporins were originally discovered from the fungus *Cephalosporium acremonium* isolated from seawater near sewage. This fungus was later reclassified as *Acremonium chrysogenum* (Lemke & Brannon 1972) and more recently as *Ac. strictum*. Cephalosporins together with penicillins belong to the family of beta-lactam antibiotics, which are among the most widely used anti-infectious drugs (Tollnick *et al.* 2004). In industry, cephalosporin C (CPC) as one of the metabolites of *Ac. chrysogenum*, is the major resource for the production of 7-amino cephalosporanic acid (7-ACA), an important intermediary in the synthesis of many first-line anti-infectious cephalosporins-antibiotics (Hu & Zhu 2016). Currently, genetic engineering on *Acremonium* spp. has developed into a potent technique for manipulating antibiotic-producing strains and obtaining mutant strains with high yields (Hu & Zhu 2016).

Research interests

There are 1 060 publications and 17 481 citations from 2011–2021 in the Web of Science (Fig. 65), with the top 10 most cited articles

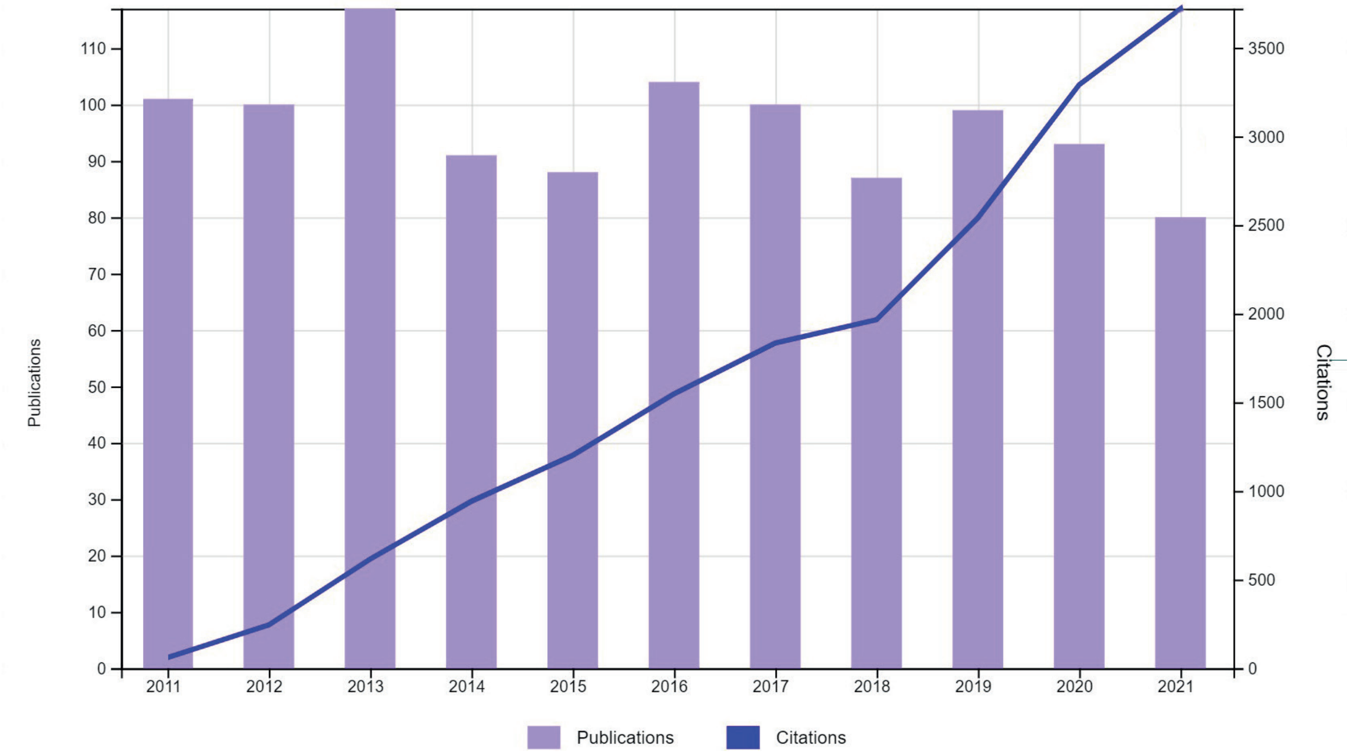

Fig. 65. Trends in research of *Acremonium* in the period 2011–2021.

listed in Table 43. Most of the publications focused on secondary metabolites of *Acremonium* species (*in vitro*, cercosporin toxin biosynthesis, host-species interaction), as well as taxonomy.

Metabolites

Acremonium species are rich sources of novel bioactive secondary metabolites and over 350 metabolites with a wide range of biological activities have been obtained from *Acremonium* fungi. The majority of these metabolites are isolated from saprobic species; however, an increasing number of interesting metabolites have been reported from endophytic or marine-derived species (Tian *et al.* 2017). For example, *Ac. chrysogenum* (syn. *Cephalosporium acremonium*) derived from the sea, produces the beta-lactam antibiotic cephalosporins that have been marketed (Hamilton-Miller 2000). *Acremonium lolii* produces tremorgenic alkaloids that cause ryegrass staggers (a neurological disorder) in livestock grazing on this endophyte-infected perennial ryegrass (*Lolium perenne*) (Fletcher & Harvey 1981, Rowan 1993, Ball *et al.* 1995). These metabolites display a wide range of biological activities including antimicrobial, cytotoxic, anti-tumour, immunosuppressive, antioxidant, anti-inflammatory, antimalarial, phytotoxic, tremorgenic, antiviral, neuritogenic, insecticidal, enzymes-inhibiting and other bioactivities that can be used for the development of pharmaceuticals, agrochemicals and food additives (Tian *et al.* 2017). Additionally, genetic engineering, omics studies, and molecular breeding have been widely applied to

Table 43. Top 10 cited articles related to *Acremonium* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Regulation of fungal secondary metabolism	569	Brakhage (2013)
2	Characterization of the fungal microbiota (mycobiome) in healthy and dandruff-afflicted human scalps	250	Park *et al.* (2012b)
3	Microbial degradation and deterioration of polyethylene - A review	231	Restrepo-Florez *et al.* (2014)
4	Associations between fungal species and water-damaged building materials	213	Andersen *et al.* (2011)
5	*Acremonium* phylogenetic overview and revision of *Gliomastix*, *Sarocladium*, and *Trichothecium*	173	Summerbell *et al.* (2011)
6	An overview of the taxonomy, phylogeny, and typification of nectriaceous fungi in *Cosmospora*, *Acremonium*, *Fusarium*, *Stilbella*, and *Volutella*	165	Grafenhan *et al.* (2011)
7	Plants and endophytes: equal partners in secondary metabolite production?	139	Ludwig-Muller *et al.* (2015)
8	The diversity of ant microbial secondary metabolites produced by fungal endophytes: an interdisciplinary perspective	132	Mousa *et al.* (2013)
9	Fungal community composition in soils subjected to long-term chemical fertilization is most influenced by the type of organic matter	124	Sun *et al.* (2016)
10	Genera in *Bionectriaceae*, *Hypocreaceae*, and *Nectriaceae* (*Hypocreales*) proposed for acceptance or rejection	93	Rossman *et al.* (2013)

industrial strains of *Acremonium* to better serve the pharmaceutical industry (Hu & Zhu 2016). Therefore, further exploration of novel secondary metabolites from *Acremonium* with distinctive structural characteristics and various biological activities will be important and should lead to the development of further pharmaceuticals, agrochemicals and food additives.

Taxonomy and phylogeny

The first systematic phylogenetic analysis of *Acremonium* and its related taxa was carried out by Summerbell *et al.* (2011) based on SSU and LSU sequences. A phylogenetic overview was provided for these morphologically simple fungi and most *Acremonium* species examined clustered within *Hypocreales*, which are divided into two major clades and clustered with diverse known genera. The other species fell into four groups across different classes of *Ascomycota* (*Coniochaetales*, *Microascales*, *Sordariales* and *Cephalothecaceae*), showing them to be highly polyphyletic (Summerbell *et al.* 2011). Therefore, the phylogeny and taxonomic limits of these taxa await to be resolved with additional effective genes and more strains. Giraldo & Crous (2018) revised the phylogenetical relationship of *Acremonium* species and other genera in *Plectosphaerellaceae* based on ITS, LSU, *rpb2*, and *tef1* sequences, revealing that *rpb2* and *tef1* sequences are possible candidates for generic species delimitation in *Acremonium*. All previous studies underlined the fact that the taxonomy and phylogeny of a great number of genera and families with acremonium-like morphs remain undefined (Hou *et al.* 2023).

Author: L. Hou

38. ***Chaetomium*** Fr., Syst. Mycol. 3(1): 253. 1829.

Type species: *Chaetomium globosum* Kunze

Classification: *Ascomycota*, *Pezizomycotina*, *Sordariomycetes*, *Sordariales*, *Chaetomiaceae.*

Background

Chaetomium was assumed to be one of the largest genera of saprobic ascomycetes with more than 400 species epithets listed in Index Fungorum (2022). After being reduced to synonymy and transferred to other genera based on phylogenetic analysis, only 42 species are now accepted in the monophyletic genus (von Arx *et al.* 1986, Wang *et al.* 2016h, i, Zhang *et al.* 2017a, Raza *et al.* 2019).

Chaetomium species are cosmopolitan and can be readily isolated from a great variety of substrates in different environments, such as terrestrial soils, dung, seed, various other plant materials, air, paper, textiles, water-damaged building materials, bird feathers, cheese (Ames 1963, von Arx *et al.* 1986, Kopytina 2005, Andersen *et al.* 2011, Yamada *et al.* 2012, Pangallo *et al.* 2014, Barret *et al.* 2015, Wang *et al.* 2016h, i, Nelson 2018), plant debris submerged in stream water (Luo *et al.* 2019), arthropods such as *Armadillidium vulgare* (Chen *et al.* 2015a, b), lichens as endolichenic fungi (Chen *et al.* 2013b), guts of marine fish (Yamada *et al.* 2011, Yan *et al.* 2014), or even in the troposphere over the Pacific Ocean (Smith *et al.* 2012). They are also common endophytes of different species of plants (Momesso *et al.* 2008, Gutierrez *et al.* 2012, Li *et al.* 2014d, Yadav *et al.* 2014, Fatima *et al.* 2016).

Chaetomium was introduced by Kunze based on *Ch. globosum* (Kunze & Schmidt 1817) with ostiolate sporocarps, membranous wall with dark hairs, and dark spores, but the origin of the spores was initially uncertain. Fries (1849) first discerned the asci which were evanescent and usually deliquesced before ascospores were mature. The first monograph of *Chaetomium* was published by Zopf (1881) who noted the presence of germ pores in ascospores and described the species under two subgenera; subgenus *Chaetomium* with ostiolate ascomata and subgenus *Chaetomidium* with non-ostiolate ascomata. Saccardo (1882) elevated subgenus *Chaetomidium* to genus and this was followed by subsequent researchers (Bainier 1910, Von Arx 1975, Von Arx *et al.* 1988). After Zopf (1881), more than 300 species were described and the morphology of ascomatal hairs was used as the important character for species identification (Chivers 1915, Skolko & Groves 1953, Udagawa 1960, Ames 1963, Seth 1970). The taxonomic value of ascomatal hair characteristics was argued (Hawksworth & Wells 1973, Dreyfuss 1976, Von Arx *et al.* 1984). Von Arx *et al.* (1986) re-described *Chaetomium* as having ostiolate ascomata with a membranous perithecial wall covered by relatively well-developed hairs, producing fasciculate and evanescent asci and single-celled, smooth and pigmented ascospores with germ pores. They emphasised on the morphology of asci, ascospores, germ pores, and the structure of the ascomata wall, but paid less attention to the morphology of ascomatal hairs, only accepting 91 of 310 described species (Von Arx *et al.* 1986). However, molecular evidence suggested the polyphyly of *Chaetomium sensu* Von Arx *et al.* (Greif *et al.* 2009, Asgari & Zare 2011, Zhang *et al.* 2017a, Wang *et al.* 2016h). Phylogeny inference based on six loci (ITS, LSU, *tub*, *rpb1*, *rpb2*, *tef1*) resulted in the establishment of *Chaetomium s. str.* (Wang *et al.* 2016h, i). Three species of *Chaetomidium*, including the type *Chd. fimeti*, were found to be closely related to the type species of *Chaetomium*; the genus *Chaetomidium* was then rejected and its three non-ostiolate species were transferred into *Chaetomium* (Wang *et al.* 2016h, i). The definition of *Chaetomium* is now modified as “ascomata globose, ellipsoid to ovate or obovate, ostiolate or non-ostiolate in a few species, with walls usually composed of *textura intricata* or *epidermoidea* in surface view, or of *textura angularis* in a few species; ascomatal hairs hypha-like, flexuous, undulate, coiled or dichotomously branched, with verrucose surface, or smooth in a few species; asci clavate or fusiform with 8 biseriate or irregularly arranged ascospores, evanescent; ascospores limoniform to globose, or irregular in a few species, bilaterally flattened, usually more than 7 µm in length; asexual morphs, if present, acremonium-like.” Based on the study of ex-type cultures, many chaetomium-like species are now classified in several other existent or newly-proposed genera, such as *Amesia*, *Arcopilus*, *Arxotrichum*, *Botryotrichum*, *Brachychaeta*, *Chrysanthotrichum*, *Chrysocorona*, *Collariella*, *Dichotomopilus*, *Floropilus*, *Humicola*, *Ovatospora*, *Parachaetomium*, *Subramaniula*, and *Trichocladium* (Crous *et al.* 2018, Wang *et al.* 2016h, 2019e, Mehrabi *et al.* 2020).

Ecological and economic significance

Degradation and enzymes

The genus is well-known as decomposers of organic materials, particularly cellulose-rich ones, working together with other fungi and bacteria, they play a role in carbon turnover (Harreither *et al.* 2011, Eichorst & Kuske 2012, Glass *et al.* 2013, Banerjee *et al.* 2016). *Chaetomium globosum* also showed potential in degrading plastics such as poly(ε-caprolactone) (PCL), polyvinyl chloride (PVC), polyethylene adipate (PEA), poly(β-propiolactone) (PPA) and polybutylene adipate (PBA) (Ghosh *et al.* 2013, Vivi *et al.*

2019). Because of their capacity to degrade organic materials, *Chaetomium* species have the potential in biodegradation of waste plant material and other industrial applications (Umikalsom *et al.* 1998, El-Gindy *et al.* 2003, Ahammed *et al.* 2008, Prokhorov & Linnik 2011, Longoni *et al.* 2012, Singh *et al.* 2013, Kim *et al.* 2016, Hu *et al.* 2018b, Yadav *et al.* 2019). On the other hand, biodegradation by *Chaetomium* species can damage cellulose-rich materials like books, military goods, archaeological relics and building materials (Ames 1963, Andersen *et al.* 2011, Wang *et al.* 2016h, Abdel-Rahim *et al.* 2018, Abdel-Azeem *et al.* 2019).

Metabolites and bioactivity

Chaetomium is a rich source of novel secondary metabolites with various biological activities (Zhang *et al.* 2012b). Over 300 secondary metabolites have been discovered from *Chaetomium* species, with most from *Ch. globosum* obtained from various environments (Momesso *et al.* 2008, Yamada *et al.* 2011, Gutierrez *et al.* 2012, Zhang *et al.* 2012b, Yan *et al.* 2014, Fatima *et al.* 2016, Liang *et al.* 2018b). The metabolites can be chaetoglobosins, epipolythiodioxopiperazines, azaphilones, xanthones, anthraquinones, chromones, depsidones, terpenoids, steroids, *etc*. (Zhang *et al.* 2012b, Fatima *et al.* 2016, Liang *et al.* 2018b). Most of these metabolites exhibit bioactivity and are of considerable importance as new lead compounds for medicine as well as for plant protection: cytotoxic or anticancer Sekita *et al.* 1973, Ge *et al.* 2008, Kharwar *et al.* 2011, Yamada *et al.* 2011, Gutierrez *et al.* 2012, Awad *et al.* 2013, Li *et al.* 2013c, Li *et al.* 2014d, Hani & Eman 2015, Wang *et al.* 2015a, Xu *et al.* 2015, Wang *et al.* 2017b, Wang *et al.* 2018g, Yang *et al.* 2018a), antioxidant (Huang *et al.* 2007, Ye *et al.* 2013, Yadav *et al.* 2014); anti-bacterial (Ge *et al.* 2011, Gond *et al.* 2012, Casella *et al.* 2013, Talontsi *et al.* 2013), some show anti-bacterial activity against drug-resistant bacterial pathogens such as methicillin-resistant *Staphylococcus aureus* (Wu *et al.* 2013a, Gao *et al.* 2019, Garcia *et al.* 2021b), which may contribute to the development of new anti-bacterial agents against drug-resistant microbial pathogens; antimalarial (Kharwar *et al*. 2011, Zhang *et al.* 2012b); antifungal with potential in plant disease biocontrol (Andrews 1992, Dipietro *et al.* 1992, Vilich *et al.* 1998, Istifadah & McGee 2006, Tarafdar & Gharu 2006, Qin *et al.* 2009, González & Tello 2011, Li HQ, Li *et al.* 2011b, Vujanovic *et al.* 2012, Wang *et al.* 2012g, Zhang *et al.* 2013a, b, Zhang *et al.* 2014b, Kawasaki *et al.* 2016, Larran *et al.* 2016); nematicidal with potential in biocontrol of nematode (Hu *et al.* 2013b); and enzyme inhibitors (Selim *et al.* 2014).

Common indoor contaminants

Chaetomium is a common indoor fungus. Six species have been detected in the indoor environments, among them, *Ch. globosum* is the most abundant, followed by *Ch. cochliodes*, *Ch. elatum*, *Ch. coarctatum*, *Ch. cervicicola* and *Ch. testifimeti* (Wang *et al.* 2016h). They can be in the air or on various kinds of building materials like concrete, wood, plaster, gypsum, wallpaper, glass fibre and plywood (Andersen *et al.* 2011, Wang *et al.* 2016c). These moulds not only damage building material but produce mycotoxins (chaetoglobosins), which may cause skin irritation and non-specific hypersensitivity reactions or even contribute to the symptoms of rhinitis, asthma and other health problems (Griffin *et al.* 1982, Vesper *et al.* 2007, Apetrei *et al.* 2009, Polizzi *et al.* 2009, Mason *et al.* 2010, Miller & McMullin 2014, Abdel-Rahim *et al.* 2018).

Human infection

Chaetomium globosum is one of the causal agents of human onychomycosis (Naidu *et al.* 1991, Stiller *et al.* 1992, Aspiroz *et al.* 2007, Latha *et al.* 2010, Tullio *et al.* 2010, Hubka *et al.* 2011, Hwang *et al.* 2012, Lagacé & Cellier 2012, Kim *et al.* 2013b) and skin infection of other animals (Sugiyama *et al.* 2008). However, whether this species and its close relatives can cause systemic and deep infections remains controversial (Hoppin *et al.* 1983, Anandi *et al.* 1989, Abbott *et al.* 1995, Yeghen *et al.* 1996, Lesire *et al.* 1999, Barron *et al.* 2003, Paterson *et al.* 2005, De Hoog *et al.* 2013). A single isolate from a clinical case of fatal brain abscess was originally identified as *Ch. globosum* (Anandi *et al.* 1989). Abbott *et al.* (1995) later re-classified this isolate as *Ch. atrobrunneum* (syn. *Amesia atrobrunnea*) based on its morphology and its ability to grow at 42 °C, and they suggested that infections by *Ch. globosum* were confined to cooler areas of the human body due to its restricted growth at 37 °C. The growth response of a fungal species at 37 °C is used as an indicator of its potential for internal infection in humans (Abbott *et al.* 1995, Barron *et al.* 2003). Correct identification of clinical fungal isolates is very important. More research is required to clarify the adaptation of *Chaetomium* species to human bodies.

Plant disease

Recently, a few cases of plant diseases were reported to be caused by *Chaetomium globosum*. At the University of Tennessee, leaf spots of hemp (*Cannabis sativa*) were found in the greenhouse, which began as chlorotic lesions near the margins and then progressed to necrotic lesions with chlorotic halos (Chaffin *et al.* 2020). In another case (Zhu *et al.* 2020a), leaf blight of cabbage (*Brassica oleracea* var. *capitata*) was found in greenhouses of the Chinese Academy of Agricultural Sciences (Beijing). The disease showed the symptoms of leaf wilt and can make the plants gradually die. It is uncertain whether the infection by *Ch. globosum* only occurs in controlled environments like greenhouses or not.

Research interests

There are 1 154 publications and 16 519 citations from 2011–2021 in the Web of Science (Fig. 66), with the top 10 most cited articles listed in Table 44. The majority of the publications focused on their ecology and ecological function (indoor contamination, human infection), novel metabolites they produce and their bioactivity as well as taxonomy.

Exploring more novel metabolites with different bioactivities

In addition to isolating new metabolites produced by *Chaetomium* species from different or special environments, metabolites were also induced in laboratories by co-culturing with some other organisms (Wang *et al.* 2018d), in the presence of some special additive (Ancheeva *et al.* 2018), or by gene engineering or genetic manipulation (Nakazawa *et al.* 2013, Yan *et al.* 2014) to activate the silent or less-active biosynthetic pathways in the fungus.

Genetics and biology

Chaetomium globosum, the type species of the genus, is often used as a representative species to investigate the general genetics and biology of *Ascomycota* (Clutterbuck 2011, Jedd 2011, Muszewska

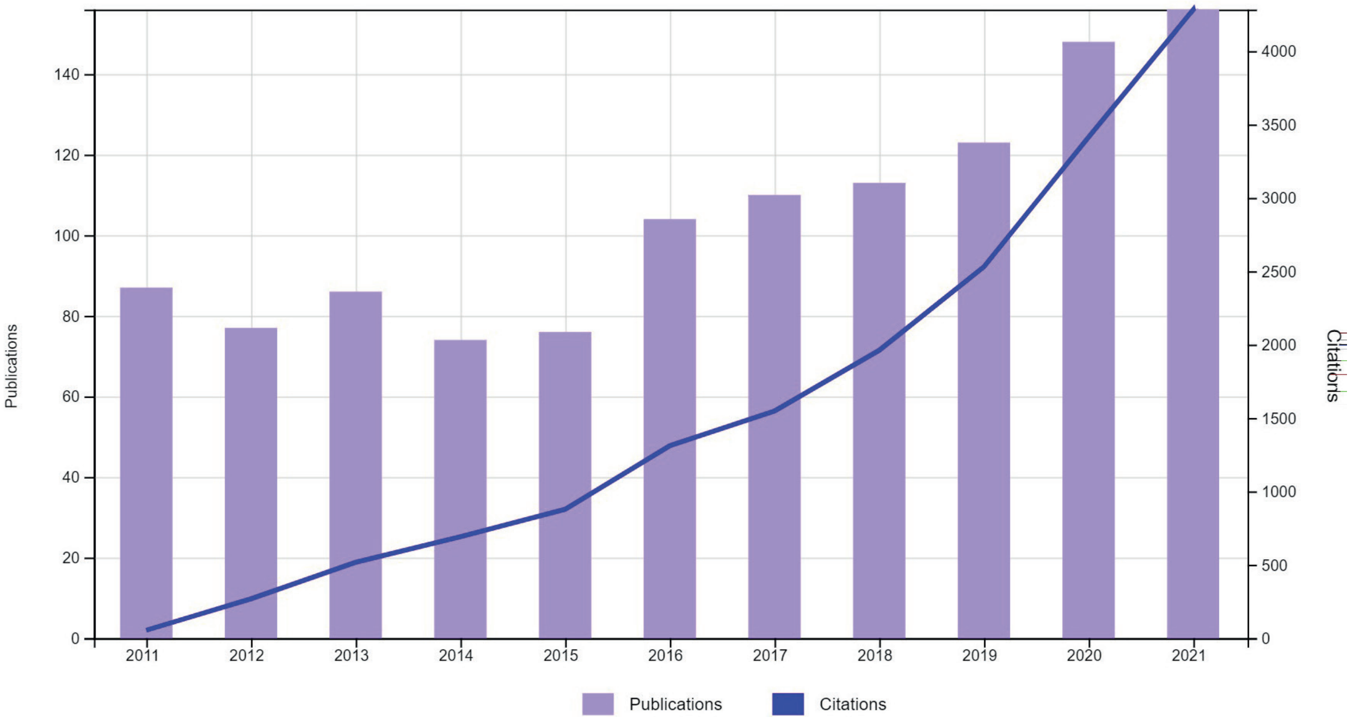

Fig. 66. Trends in research of *Chaetomium* in the period 2011–2021.

Table 44. Top 10 cited articles related to *Chaetomium* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Network analysis reveals functional redundancy and keystone taxa amongst bacterial and fungal communities during organic matter decomposition in an arable soil	318	Banerjee *et al.* (2016)
2	Anticancer compounds derived from fungal endophytes: their importance and future challenges	313	Kharwar *et al.* (2011)
3	Associations between fungal species and water-damaged building materials	213	Andersen *et al.* (2011)
4	Plant cell wall deconstruction by ascomycete fungi	203	Glass *et al.* (2013)
5	Antiviral activity of mycosynthesized silver nanoparticles against herpes simplex virus and human parainfluenza virus type 3	192	Gaikwad *et al.* (2013)
6	Endophytic fungi from medicinal plants: a treasure hunt for bioactive metabolites	154	Kaul *et al.* (2012)
7	The endophytic mycota associated with *Vitis vinifera* in central Spain	123	González & Tello (2011)
8	Common foliar fungi of *Populus trichocarpa* modify *Melampsora* rust disease severity	97	Busby *et al.* (2016)
9	Chemical and bioactive diversities of the genus *Chaetomium* secondary metabolites	92	Zhang *et al.* (2012)
10	Illumina MiSeq investigations on the changes of microbial community in the *Fusarium oxysporum f. sp. cubense* infected soil during and after reductive soil disinfestation	89	Huang *et al.* (2015b)

et al. 2011). This species has been whole-genome sequenced (Cuomo *et al.* 2015), which will help to better understand this fungus as well as the whole *Ascomycota*.

Taxonomy and phylogeny

Chaetomium has been phylogenetically revised, and *tub* is proposed as a secondary molecular marker for species delimitation (Wang *et al.* 2016h, i). There are several *Chaetomium* isolates in the literature which remain to be identified at the species level (Talontsi *et al.* 2013, Wang *et al.* 2015a, 2017b, Ancheeva *et al.* 2018). A review of "*Chaetomium* endophytes: a repository of pharmacologically active metabolites" covered 71 published articles, of which, however, 31 kept their isolates as poorly-identified "*Chaetomium* sp." (Fatima *et al.* 2016). Proper identification of species will help to understand the potential of *Chaetomium* species in producing metabolites in association with its phylogeny and evolution. For example, Rank *et al.* (2011) noticed that in *Chaetomium s. lat.*, *Ch. cellulolyticum*, *Ch. longicolleum*, *Ch. malaysiense* and *Ch. virescens* were able to produce O-methylsterigmatocystin, the immediate precursor for aflatoxin. But these species currently belong to *Humicola* and *Collariella*. It is necessary to screen other species in these two genera for their potential to produce this mycotoxin. In addition, there are still some chaetomium-like species that remain to ascertain their place in the family.

Author: X.W. Wang

39. *Paecilomyces* Bainier, Bull. Soc. Mycol. France. 23(1): 26. 1907.

Type species: *Paecilomyces variotii* Banier

Classification: *Ascomycota*, *Pezizomycotina*, *Eurotiomycetes*, *Eurotiales*, *Thermoascaceae.*

Background

In 1907, Bainier introduced the genus *Paecilomyces* with *Paec. variotii* as the type species. In the century after this introduction, several other species were described or combined in the genus and the generic concept changed over time. For example, the monograph of Brown & Smith (1957) accepted 23 species and 10 years later, Onions & Barron (1967) broadened the concept and included species having orthotropic awl-shaped phialides. In time, the genus *Paecilomyces* became a heterogeneous assemblage of species with diverse ecology. Samson (1974) noted this diversity and restricted *Paecilomyces* to species producing verticillate conidiophores, bearing divergent whorls of branches and having phialides that consist of a cylindrical or swollen basal portion, tapering abruptly into a long distinct neck. Based on conidial colours and growth temperatures, he introduced section *Paecilomyces* (incl. the generic type *Paec. variotii*) for mesophilic, thermotolerant and thermophilic species that produce yellow brown to brownish-coloured conidia. Section *Isarioidea* contained mesophiles and species with purple, pink, green or yellow conidial colours. Certain section *Paecilomyces* species can produce a sexual morph and these were classified as *Byssochlamys*, *Talaromyces* and *Thermoascus*.

Using 18S rDNA sequences, Luangsa-Ard *et al.* (2004) showed that *Paecilomyces sensu* Samson (1974) is polyphyletic across two subclasses, *Sordariomycetidae* and *Eurotiomycetidae. Paecilomyces variotii*, and its thermophilic relatives, belong in the *Eurotiales*. Not all of Samson's (1974) section *Paecilomyces* species are nowadays classified as *Paecilomyces*. For example, *Talaromyces* (*Paecilomyces*) *byssochlamydoides* is classified in the phenotypically related genus *Rasamsonia* and *Talaromyces* (*Paecilomyces*) *leycettanus* is combined in the recently introduced genus *Evansstolkia* (as *E. leycettana*) (Houbraken *et al.* 2012, 2020). Other species not belonging to *Paecilomyces* are, for example, *Purpureocillium lilacinum* (syn. *Paec. lilacinus*), *Keithomyces carneus* (syn. *Paec. carneus*), *Marquandomyces marquandii* (syn. *Paec. marquandii*) but the old species names are still used in recent literature. In the dual nomenclature era, the ascomycete genus *Byssochlamys* was linked to *Paecilomyces s. str.* and Samson *et al.* (2009) accepted five *Byssochlamys* and four *Paecilomyces* species. The asexual species *Paec. fulvus*, *Paec. niveus*, *Paec. variotii* and *Paec. zollerniae* were linked to the sexual species *B. fulva*, *B. nivea*, *B. spectabilis* and *B. zollerniae*, respectively. With the introduction of a single name nomenclature system, *Paecilomyces* got priority over *Byssochlamys*. Currently, *Paecilomyces* includes 12 accepted species: *Paec. brunneolus*, *Paec. clematidis*, *Paec. formosus*, *Paec. lagunculariae*, *Paec. dactylethromorphus*, *Paec. divaricatus*, *Paec. fulvus*, *Paec. niveus*, *Paec. penicilliformis*, *Paec. tabacinus*, *Paec. variotii* and *Paec. zollerniae* (Houbraken *et al.* 2020, Crous *et al.* 2020b, Spetik *et al.* 2022).

Paecilomyces variotii

The best-known and most studied species of the genus is *Paec. variotii*. Due to taxonomic changes and the move to a single name nomenclature system, *Paec. variotii* can be found in the literature under multiple synonym names. The fungus was first described by Bainier, who dedicated the name to the French doctor and paediatrician Dr Variot (Bainier 1907). Two years later, the genus *Byssochlamys* was described to accommodate a sexually reproducing species *B. nivea* (Westling 1909). In 1994, a new sexually reproducing species, *Talaromyces spectabilis* with a *Paecilomyces* asexual morph was described (Udagawa & Suzuki 1994). Later, morphological observations showed that this fungus had a *Byssochlamys* morph instead of *Talaromyces* sexual morph (Houbraken *et al.* 2006). Molecular data and the discovery of its heterothallic sexual life cycle revealed that *B. spectabilis* is conspecific with *Paec. variotii* and therefore the same species as *T. spectabilis* (Houbraken *et al.* 2008, Samson *et al.* 2009). After the abolition of the dual nomenclature, *Paecilomyces* has priority, hence the name *Paec. variotii* should be used (Hawksworth *et al.* 2011, Rossman *et al.* 2016).

Peacilomyces variotii is a common cosmopolitan filamentous fungus found in soil, indoor environments, plants, animals, food and beverages, and can also be an opportunistic human pathogen (Houbraken *et al.* 2008, 2010, Pitt & Hocking 2009, Samson *et al.* 2019). It is a thermotolerant species, able to grow at temperatures up to 50 °C (Samson *et al.* 2019). In addition, it can grow at low oxygen concentrations and in the presence of preservatives. Therefore, this fungus is a spoilage organism of many food products. It is considered a heat-resistant mould because of its heat-resistant ascospores (Houbraken *et al.* 2008). Consequently, *Paec. variotii* can spoil heat-treated products or resources, such as pectin, canned fruits, fruit juices and non-carbonated sodas. However, it is also able to spoil a wide range of other products like margarine and bakery products, which are more likely to be contaminated through airborne conidia than by ascospores. The fungus can produce viriditoxin of which the biosynthetic gene cluster was recently described (Urquhart *et al.* 2019), and which was shown to be toxic to mice (Lillehoj & Ciegler 1972). Viriditoxin has anti-bacterial activity by inhibiting the cell division protein FtsZ (Wang *et al.* 2003), while it also has cytotoxic activity against cancer cells (Kundu *et al.* 2014, Park *et al.* 2015). Whether viriditoxin is also produced in foodstuffs is unknown and the significance for food safety needs to be studied.

Three different spore types can be formed by *Paec. variotii*. Asexually, it produces abundant conidia and chlamydospores are usually present in colonies. Conidia are smooth and ellipsoid with usually flat apical edges. When two compatible mating strains encounter each other, they can mate and reproduce sexually through ascospore formation (Fig. 67). Although the heat resistance of *Paec. variotii* ascospores has not been studied in detail, there are indications that they can survive heat treatments of 85 °C for more than an hour (Houbraken *et al.* 2006). This makes them potentially more resistant than ascospores of the related heat-resistant *Paec. niveus* and *Paec. fulvus* (Beuchat & Rice 1979). Chlamydospores and ascospores of *Paec. variotii* are considered more localised within the mycelium and less prone to distribution than its conidia. Ten strains of *Paec. variotii* showed notable heterogeneity in conidial spore size distribution and heat resistance (Van den Brule *et al.* 2020a, b).

The full genome sequences of *Paec. variotii* strains CBS 101075 and CBS 144490 are available at the Joint Genome Institute (JGI, jgi.doe.gov). Authors found evidence for an active repeat induced point mutation (RIP) system for the first time in an *Eurotiales* species (Urquhart *et al.* 2018). It is thought that RIP is a fungal specific protection mechanism against the deleterious effects of transposons (Hane *et al.* 2015). Recently, a large transposable element of approximately 85 kbp was identified in some, but not all, *Paec. variotii* strains (Urquhart *et al.* 2022). Genes located in this cluster are involved in stress resistance against the metals cadmium, lead, zinc, copper and arsenic. The genome of another strain was also sequenced under the name *Paec. variotii* No. 5 (Oka *et al.* 2014) but was reclassified as *Paec. formosus* (Urquhart *et al.* 2018).

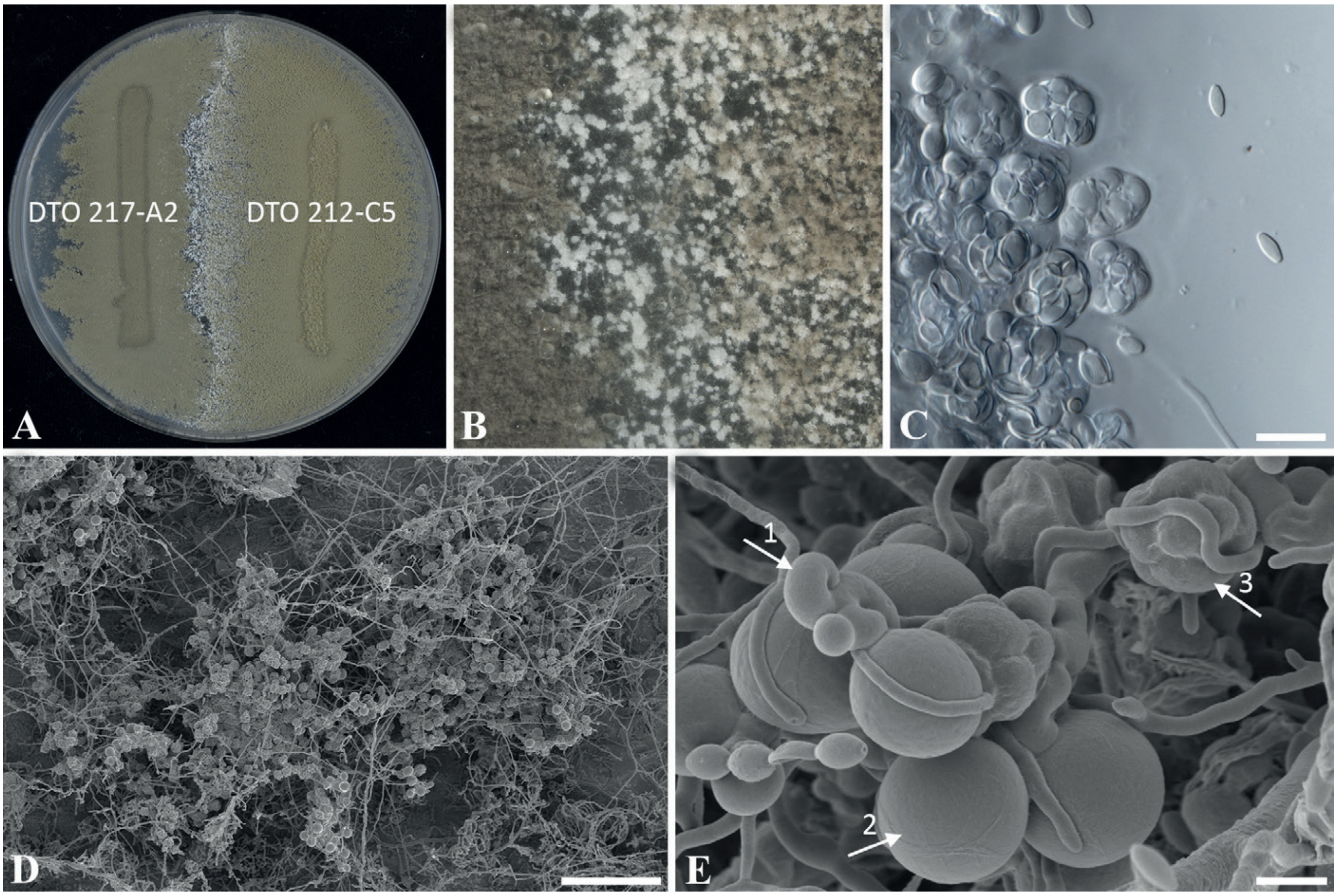

Fig. 67. Sexual reproduction of *Paec. variotii* (Van den Brule 2022). **A.** Two strains with compatible mating types, DTO 217-A2 and DTO 212-C5 (grown for 6 wk on potato dextrose agar at 30 °C). **B.** Magnification of the area between the two strains by stereo microscopy. Asci form between the colonies resulting in typically white ascomata. **C.** Light microscopy of asci, each containing 8 ascospores. **D.** Cryo-SEM image of grouped asci. **E.** Cryo-SEM image of ascogenous cell (1) forming young asci; (2) the membrane of the asci shrinks when asci mature, revealing its individual ascospores (3). Scale bars: C = 10 µm; D = 100 µm; E = 5 µm.

Ecological and economic significance

Biotechnology

Paecilomyces variotii is known to produce metabolites (Dai *et al.* 2020; many metabolites mentioned in this publication are related to species that do not belong to the genus *Paecilomyces*, such as *Purpureocillium lilacinus*) and enzymes (Herrera Bravo de Laguna *et al.* 2015). *Paecilomyces variotii s. lat.* and *Paec. fulvus* are reported as producers of the mycotoxin patulin (Escoula 1975a, b, Percebois *et al*. 1975, Rice *et al*. 1977). However, in the revision of the genus, Samson *et al*. (2009) showed that patulin production is restricted to *Paec. dactylethromorphus* and *Paec. niveus*.

Ecology

Paecilomyces species are ubiquitous, saprobic and isolated from soil, decaying vegetation, wood, acetic acid, air, human and extreme environments. Species can grow under extreme conditions, such as high temperatures (thermotolerant), low oxygen levels, low pH levels and high concentrations of metals.

Clinical impact

Paecilomyces species are potential human pathogens in immunocompromised individuals with *Paec. variotii* and *Paec. formosus* most frequently reported from clinical samples (Houbraken *et al.* 2010, Sprute *et al.* 2021). The genus may also be a source of allergens (Pfeiffer *et al.* 2021).

Plant diseases and food spoilage

Paecilomyces species can be causal agents of tree dieback diseases, such as pistachio dieback in Iran (Heidarian *et al.* 2018). They can also cause economic losses due to spoilage of (pasteurised) foods, such as margarine, fruit juices and rye bread. *Paecilomyces niveus* (as *Byssochlamys nivea*) was described in pasteurised strawberries in 1933 as the first example of a so-called heat-resistant fungus.

Heat resistance and stress resistance

Several *Paecilomyces* species produce smooth-walled ascospores that can withstand high temperatures (*e.g.*, pasteurisation). *Paecilomyces niveus* and *Paec. fulvus* produce these spores in a homothallic fashion, while *Paec. variotii* produces heterothallic ascospores. These ascospores (*e.g.*, Beuchat 1979) have been compared to other heat-resistant fungi within *Eurotiales* as within the genera *Talaromyces*, *Aspergillus* (mostly the *Neosartorya* morph), *Thermoascus* and *Hamigera* (Wyatt *et al.* 2015, Dijksterhuis 2019). Ascospores of *Paec. niveus* are relatively less resistant to sanitisers compared to other heat-resistant fungi (Dijksterhuis *et al*. 2018). The ascospores of *Paec. variotii* are potentially more resistant than ascospores of the related heat-resistant moulds *Paec. niveus* and *Paec. fulvus* (Beuchat & Rice 1979).

Entomopathogenicity

Most of this literature is related to the entomopathogen *Purpureocillium*

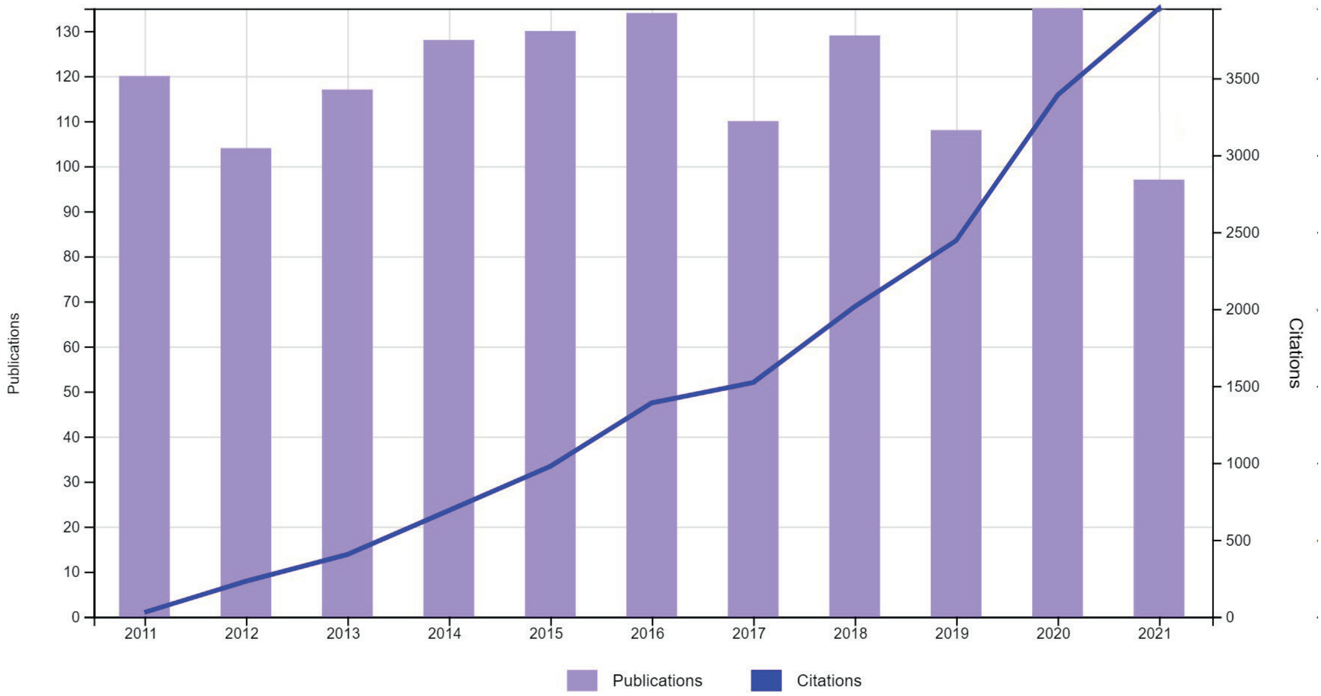

Fig. 68. Trends in research of *Paecilomyces* in the period 2011–2021.

Table 45. Top 10 cited articles related to *Paecilomyces* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Phylogeny of *Penicillium* and the segregation of *Trichocomaceae* into three families	316	Houbraken & Samson (2011)
2	ESCMID and ECMM joint guidelines on diagnosis and management of hyalohyphomycosis: *Fusarium* spp., *Scedosporium* spp. and others	271	Tortorano *et al.* (2014)
3	GH11 xylanases: Structure/function/properties relationships and applications	251	Paes *et al.* (2012)
4	Endophytic fungal association via gibberellins and indole acetic acid can improve plant growth under abiotic stress: an example of *Paecilomyces formosus* LHL10	162	Kahn *et al.* (2012)
5	Rhizosphere bacteria and fungi associated with plant growth in soils of three replanted apple orchards	130	Franke-Whittle *et al.* (2015)
6	Classification of *Aspergillus*, *Penicillium*, *Talaromyces* and related genera (*Eurotiales*): An overview of families, genera, subgenera, sections, series and species	126	Houbraken *et al.* (2020)
7	Plant-extract-assisted green synthesis of silver nanoparticles using *Origanum vulgare* L. extract and their microbicidal activities	109	Shaik *et al.* (2018)
8	Comparison of *in vitro* antifungal activities of Efinaconazole and currently available antifungal agents against a variety of pathogenic fungi associated with onychomycosis	106	Jo *et al.* (2013)
9	Bacterial and fungal taxon changes in soil microbial community composition induced by short-term biochar amendment in red oxidized loam soil	83	Hu *et al.* (2014a)
10	Filamentous fungal diversity and community structure associated with the solid state fermentation of Chinese Maotai-flavor liquor	81	Chen *et al.* (2014a)

lilacinus formerly known as *Peac. lilacinus.* In addition, the entomopathogenic species *Paec. farinosus* and *Peac. fumosoroseus* have been reclassified as *Cordyceps farinosa* and *C. fumosorosea* (Kepler *et al.* 2017) and literature using the old nomenclature will add to a false number of citations to *Paecilomyces*.

Research interests

There are 1 312 publications and 16 324 citations from 2011–2021 in the Web of Science (Fig. 68), with the top 10 most cited articles listed in Table 45. Most publications are related to biotechnology and food science (enzyme production and food spoilage).

Taxonomy and phylogeny

The taxonomy of *Paecilomyces* is well-studied and 12 species are currently accepted in the genus (Crous *et al.* 2020b, Houbraken *et al.* 2020, Spetik *et al.* 2022). These species can be identified using partial beta-tubulin (*BenA*) or calmodulin (*CaM*) gene sequences. Phylogenetic analysis showed that *Paec. formosus* consists of three clades and may represent a species complex. The taxonomic

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10	Filamentous fungal diversity and community structure associated with the solid state fermentation of Chinese Maotai-flavor liquor	81	Chen *et al.* (2014a)

status of *Paec. formosus* needs attention because the name is based on the invalidly described species *Monilia formosa* (*nom. inval*., Art. 36.1) (Houbraken *et al*. 2020).

Authors: T. van den Brule, J. Houbraken and J. Dijksterhuis

40. *Trichosporon* Behrend (1890) Berliner Klin. Wochenschr. 27: 464. 1890; **and related trichosporonoid yeasts**: *Apiotrichum*, *Cutaneotrichosporon*, *Effuseotrichosporon*, *Haglerozyma*, and *Pascua*

Type species: *Trichosporon ovoides* Behrend
Apiotrichum porosum Stautz
Cutaneotrichosporon cutaneum (Beurmann *et al.*) X.Z. Liu *et al.*
Effuseotrichosporon vanderwaltii (Motaung *et al.*) A.M. Yurkov *et al.*
Haglerozyma chiarellii (Pagnocca *et al.*) A. M. Yurkov *et al.*
Pascua guehoae (Middelhoven *et al.*) Takashima *et al.*

Classification: *Basidiomycota*, *Agaricomycotina*, *Tremellomycetes*, *Trichosporonales*, *Trichosporonaceae.*

Background

The genus *Trichosporon* has a secular and controversial history. The first description of its microscopic structures was made by visualisation of nodules causing infection of hair of a wig, which could not be removed by the usual cleaning process (Beigel 1865). On that occasion, based on findings and comments of authorities on microscopic fungal taxonomy, the organism was found to be related to a new species *Pleurococcus beigelii* (Rabenhorst 1867). Some original specimens were sent to the Pharmaceutical Institute of the Friedrich Schiller University Jena (Germany), and despite a good morphological description (Beigel 1869), no material is known to be preserved. In 1890, the generic name *Trichosporon* [from the Greek: *Trichos* (hair) and *sporon* (spores)] was introduced by Behrend to characterise a similar organism as observed by Beigel and that caused white piedra on a man’s beard (Behrend 1890). This organism was named *Trichosporon ovoides*, but no material was preserved. Later, European and Colombian white piedra specimens yielded two new *Trichosporon* species, *Tr. ovale* and *Tr. giganteum* (Unna 1896). Vuillemin (1902) transferred *Pleu. beigelii* to *Trichosporon*, considering all initial taxa to represent *Tr. beigelii* with the previous ones being a variant of the species described by Küchenmeister & Rabenhorst. It has been suggested that the material analysed by Vuillemin that led to the first reclassification of these isolates originated from a case of black piedra (piedra hortae), but no proof of this hypothesis was provided (Guého *et al.* 1992a, Vuillemin 1901).

The generic name *Trichosporon* was later reconsidered and further species were described and contested (Yamada *et al.* 1882, Castellani 1908, Ota 1926, 1928, Dodge 1935, Carmo-Sousa 1970). The genus name was frequently mixed up and no type material was preserved for a long time. A dimorphic isolate obtained from a pruritic skin, named *Oidium cutaneum* (De Beurmann *et al.* 1909), was later transferred to *Trichosporon* (Ota 1926). This likely authentic strain described by Beurmann was selected as neotype CBS 2466 *Tr. cutaneum* (De Beurmann *et al.* 1909) var. *cutaneum* (Guého *et al.* 1992b, Diddens & Lodder 1942). Later, a strain from a case of human white piedra exhibiting similar characteristics to those described by Behrend (1890) was selected as neotype CBS 7566 *Tr. ovoides* (Lasagni & Ermacora 1977, Guého *et al.* 1992b). Both species show differences in their ecological and biological characteristics (Guého *et al.* 1992b), and CBS 2466 is recognised as *Cutaneotrichosporon cutaneum* (Liu *et al.* 2015d). The reference strain CBS 7566 *Tr. ovoides* remains the current neotype of *Trichosporon*.

Up to 2015, over 50 *Trichosporon* species had been described. Based on their phenotypical, biochemical, and correlated taxonomic molecular characteristics, these species were distributed in five clades: *cutaneum*, *ovoides*, *brassicae*, *gracile*, and *porosum*

(Sugita *et al.* 2002, Middelhoven *et al.* 2004). Considering the results of phylogenetic analyses from a seven-gene dataset, Liu *et al.* (2015c) proposed a reclassification of families and genera assigned to *Tremellomycetes* that impacted the *Trichosporon* species classification. Thus, the *Trichosporonaceae* family was emended to accommodate the monophyletic lineages comprising the *brassicae*/*gracile*, *cutaneum*, *haglerorum*, *porosum*, *Trichosporon*, and *Vanrija* clades, and four single-species lineages comprising three *Cryptococcus* and one *Trichosporon* species as recognised in these multigene phylogenies. Consequently, five genera were proposed to accommodate trichosporonoid yeasts: *Apiotrichum emend*., *Cutaneotrichosporon*, *Effuseotrichosporon*, and *Haglerozyma. Trichosporon* was re-defined to accommodate only species of the *Trichosporon* clade as recognised in the seven-genes phylogeny.

Based on comparative genomics data, a new delimitation of the *Trichosporonales* was performed and the genus *Pascua* was created to accommodate a single species *P. guehoae*, a species formerly assigned to *Cutaneotrichosporon* (Takashima *et al.* 2019).

Ecological and economic significance

Basidiomycetous trichosporonoid yeasts that as far as we know only reproduce asexually and mainly by arthroconidia, are widely distributed in the environment, such as soil, air, decomposing wood, fresh water, rivers, seawater, scarab beetles, cheese, bats, bird droppings, pigeons, and cattle (Fell *et al.* 2006, Colombo *et al.* 2011a). *Trichosporon* species are part of the human microbiota, and transitory colonise the gastrointestinal tract and skin (Francisco *et al.* 2016). Species from the genera *Trichosporon*, *Cutaneotrichosporon,* and *Apiotrichum* have been isolated from clinical specimens, such as superficial mycosis, bronchial secretions, deep-seated infections, and from the houses of summer-type hypersensitivity pneumonitis patients (Nishiura *et al.* 1997, Sugita *et al.* 2001, 2004, Nakajima *et al.* 2013). The origin of strains as given in the 5th edition of "*The Yeasts, a Taxonomic Study*" (TYTS), also include nails of a psoriasis patient, axillary white piedra, human skin lesions, human urine and faeces, snail droppings, cheese, cabbage, activated sludge, mushroom, moist humus around roots, reptile, wood pulp, cow mastitis, and exudate of English yew (*Taxus baccata*) (Sugita *et al*. 2011).

Trichosporon and related trichosporonoid yeasts are known for their ability to hydrolyse urea (Liu et al. 2015d). They assimilate several carbohydrates and other carbon sources, but they are non-fermentative. According to the 5th edition of TYTS, these species exhibit the capability to use a broad range of substrates, especially aromatic compounds, aliphatic lipids, amines, and complex nitrogenous compounds as sole sources of carbon and energy, including uric acid, ethylamine, hydroxyproline, tyramine, and L-phenylamine (Middelhoven *et al.* 2004), but they also assimilate aromatic compounds, but not nitrate, and require thiamine, but not biotin, for growth.

Trichosporon asahii produces β-glucosidases with optimum pH and temperatures ranging from 5.5 to 6.0, and 50 to 70 °C, respectively (Wang *et al.* 2011c). These enzymes have been used to improve the quality and aroma of young red wine (Wang *et al.* 2012h). *Trichosporon asteroides* produces a 37kDa lipase showing optimal activity at pH 5 and 60 °C, which can be used in the production process of polyunsaturated fatty acids (Dharmsthiti & Ammaranond 1997).

Apiotrichum brassicae can be isolated from cabbage (Nakase 1971), salami (Aquilanti *et al.* 2007), and milk derivates, such as yogurt, and cheese (Mihyar *et al.* 1997). The species exhibits potential use as a microbial sensor of volatile compounds, such as ethyl alcohol and acetic acid (Karube *et al.* 1980), and can catalyse the hydrolysis of ketoprofen ethyl ester by its esterase (Shen *et al.* 2001). *Apiotrichum dulcitum* can degrade high levels of phenol at low temperatures (Margesin *et al.* 2005). The reference strain *A. montevideense* produces high quantities of cytochrome P450 after cultivation in a glucose-peptone medium (Stündl *et al.* 2000).

Cutaneotrichosporon cutaneum was found in the cloacae of migratory birds (Cafarchia *et al.* 2006) and has been isolated from milk and cheese (Mihyar *et al.* 1997, Corbo *et al.* 2001). This species has been used as an interface bioreactor for the degradation of (RS)-ibuprofen (Tanaka *et al.* 2001), as a biochemical oxygen demand (BOD) biosensor (Suriyawattanakul *et al.* 2002, Jia *et al.* 2003), as a biodegrader of lignocellulose compounds (Chen, *et al.* 2009), and as an efficient simultaneous consumer of glucose and xylose (Hu *et al.* 2011a). *Cutaneotrichosporon mucoides* can cleave the aromatic structure of the dioxin-like compound dibenzofuran (Hammer *et al.* 1998) and can hydroxylate biphenyl, thus biotransforming this compound into a less toxic one (Sietmann *et al.* 2000). *Cutaneotrichosporon jirovecii* can detect a low amount of L-cysteine (1 µg/L; Hassan *et al.* 2007), and mediate the synthesis of cadmium sulfide nanoparticles by producing hydrogen sulfide on cysteine containing medium (El-Baz *et al.* 2016). *Cutaneotrichosporon moniliiforme* produces the volatiles 2-methyl butanol, 3-methyl butanol, methanethiol, S-methyl thioacetate, dimethyl sulfide, dimethyl disulfide, dimethyl trisulfide, dihydro-2-methyl-3(2H)-thiophenone and 3-(methylthio)-1-propanol (MTP) (Buzzini *et al.* 2005). It also produces a salicylic acid decarboxylase able to catalyse the decarboxylation of salicylic acid to phenol, the carboxylation of phenol to form salicylic acid without any by-products (Kirimura *et al.* 2010), and demonstrated potential to be used in crude glycerol bioreactors and for bioremediation processes (Duarte *et al.* 2016). *Cutaneotrichosporon dermatis* can be useful for biodiesel production as is able to perform the bioconversion of wastewater from butanol fermentation to microbial oil (Peng *et al.* 2013). *Cutaneotrichosporon oleoginosus* presents several attributes that make this yeast a promising sustainable bioagent for oils and fuel production. The species exhibits upregulation in genes involved in amino acid and ammonium transport, and the ability to metabolise a broad spectrum of monosaccharides (Kourist *et al*. 2015). In a nitrogen limiting medium, *C. oleoginosus* can accumulate ~90 % w/w of triacylglyceride that conventionally resembles cocoa butter (Bracharz *et al*. 2017a, Wei *et al*. 2017). Inhibition of the target of rapamycin complexes is the current pathway associated with this yeast to enhance their lipid content (Bracharz *et al*. 2017b). The use of traditional physiological and biochemical characteristics as identification methods must be carefully considered as they do not provide enough discriminatory power to distinguish *Trichosporon* and related trichosporonoid yeasts. Accurate species identification is based on sequencing the IGS1 ribosomal DNA locus (Sugita *et al*. 2002, Liu *et al.* 2015c, d, Chen *et al.* 2021b). MALDI-TOF MS is a useful tool for the identification of *Trichosporon* and related trichosporonoid yeasts using a modulated database that needs to be updated further (Kolecka *et al*. 2013, De Almeida *et al*. 2014). MALDI Biotyper® (Bruker Daltonics Inc., Germany) and VITEK® MS (bioMerieux, France) exhibited similar results in the species identification when using an extended library (De Almeida *et al*. 2017, Guo *et al*. 2019b, Ahangarkani *et al*. 2021). Due to the lack of inclusion of Main Spectrum Profile (MSPs) of all clinically relevant *Trichosporon* and other trichosporonoid species, misidentification of closely related species might occur. Hence, the global guideline

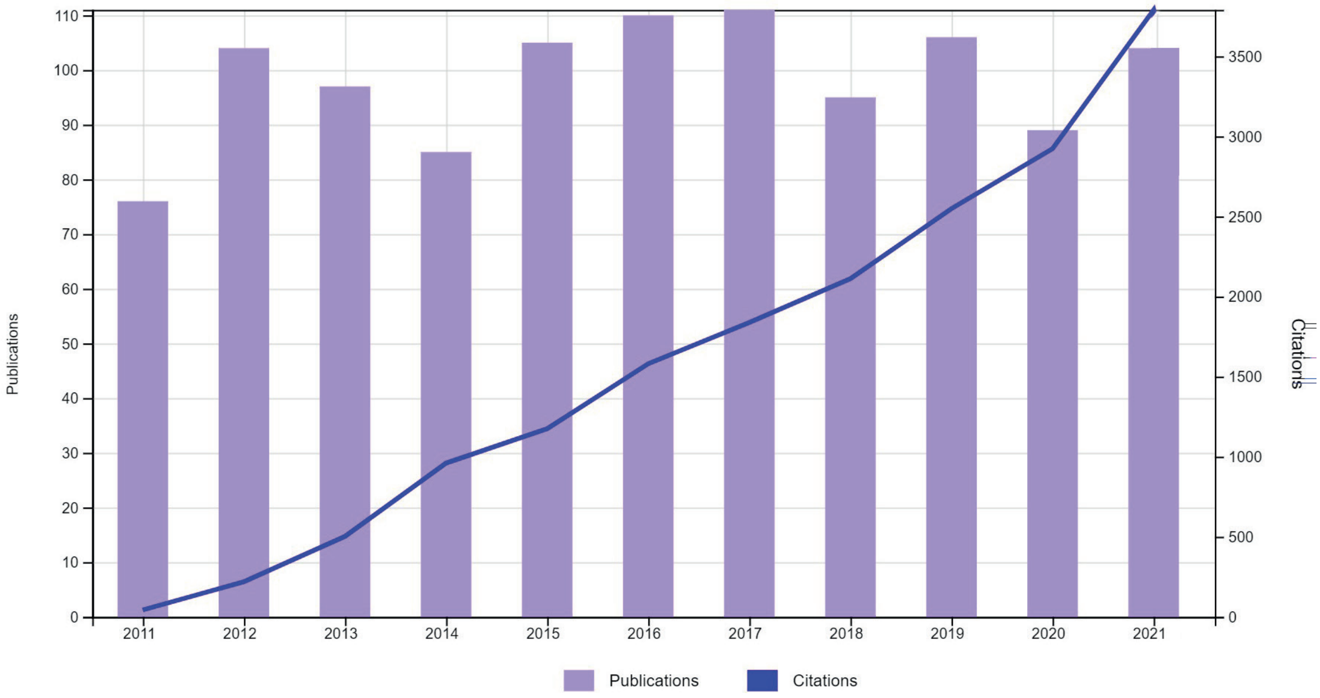

Fig. 69. Trends in research of *Trichosporon* and related trichosporonoid yeasts in the period 2011–2021.

Table 46. Top 10 cited articles related to *Trichosporon* and related trichosporonoid yeasts published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Oil production by the yeast *Trichosporon dermatis* cultured in enzymatic hydrolysates of corncobs	81	Huang *et al.* (2012)
2	The antifungal effect of silver nanoparticles on *Trichosporon asahii*	79	Xia *et al.* (2016)
3	Simultaneous saccharification and microbial lipid fermentation of corn stover by oleaginous yeast *Trichosporon cutaneum*	61	Liu *et al.* (2012c)
4	Evaluating the effect of medium composition and fermentation condition on the microbial oil production by *Trichosporon cutaneum* on corncob acid hydrolysate	56	Chen *et al.* (2013d)
5	Multiple species of *Trichosporon* produce biofilms highly resistant to Triazoles and Amphotericin B	55	Iturrieta- González *et al.* (2015)
6	Lipid fermentation of corncob residues hydrolysate by oleaginous yeast *Trichosporon cutaneum*	54	Gao *et al.* (2014)
7	Inhibitor degradation and lipid accumulation potentials of oleaginous yeast *Trichosporon cutaneum* using lignocellulose feedstock	54	Wang *et al.* (2016)
8	Genomics and transcriptomics analyses of the oil-accumulating basidiomycete yeast *Trichosporon oleaginosus*: Insights into substrate utilization and alternative evolutionary trajectories of fungal mating systems	49	Kourist *et al.* (2015)
9	*Trichosporon asahii* causing nosocomial urinary tract infections in intensive care unit patients: genotypes, virulence factors and antifungal susceptibility testing	47	Sun *et al.* (2012)
10	*In vitro* interactions between non-steroidal anti-inflammatory drugs and antifungal agents against planktonic and biofilm forms of *Trichosporon asahii*	35	Yang *et al.* (2016a)

for diagnosis and management of rare yeast infections caused by trichosporonoid yeasts only moderately supports the use of this tool for identification of these yeasts at the species level (Chen *et al.* 2021b).

Research interests

There are 1 082 publications and 15 922 citations from 2011–2021 in the Web of Science (Fig. 69), with the top 10 most cited articles listed in Table 46. Due to medical and industrial interest, published research on *Trichosporon* and related trichosporonoid yeasts during the past decade has focused on epidemiology, species distribution, antifungal susceptibility profiles, and biotechnologically interesting features. The top 10 papers related to these yeasts dealt with findings in oil and lipid production, acid hydrolysation, biofilm production, and the production of bio compounds (Table 46). Aspects included the oil production from lignocellulosic biomass; a description of the significant inhibitory effect on the growth of *Tr. asahii* by silver nanoparticles that damage the cell wall, cell membrane, and cellular compounds; practical and efficient way for lipid production from lignocellulose material; optimal conditions for lipid accumulation by *C. cutuneum* and its potential feedstock for biodiesel production. The gene content and expression of *C. oleaginosus* indicated it is well adapted to the use of chitin-rich biomass, while transcriptome data showed peculiarities in the lipid and nitrogen metabolism under nitrogen limitation resulting in the accumulation of fatty acids.

From a clinical perspective, the main results showed that for different species biofilm-forming cells are more resistant to antifungals than planktonic cells; hemolysin activity and the biofilm formation may be the main virulence factors in the development of nosocomial urinary tract infections in intensive care unit patients; and drug-drug combinations as a potential beneficial effect against this species.

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41. ***Malassezia*** Baill., Traité Bot. Méd. Crypt.: 234. 1889.

Type species: *Malassezia furfur* (C.P. Robin) Baill.

Classification: *Basidiomycota*, *Ustilaginomycotina*, *Malasseziomycetes*, *Malasseziales*, *Malasseziaceae.*

Background

Malassezia was first identified by Eichstedt in 1846 in relation to the human skin disease pityriasis versicolor (PV), but the organism was first named by Robin as *Microsporon furfur* in 1853, and later renamed by Baillon in 1889, when he created a new genus *Malassezia*, with only one species, *Malassezia furfur*. The second described *Malassezia* species was isolated from captive Indian rhinoceros, and originally described as *Pityrosporum pachydermatis* by Weidman in 1925, and later transferred to the genus *Malassezia* by Dodge in 1935 (Hay & Midgley 2010). For over five decades, the genus consisted of only these two species, until in 1990 *Malassezia sympodialis* was added (Simmons & Guého 1990). In 1996, four more species (*Ma. globosa*, *Ma. obtusa*, *Ma. restricta*, *Ma. slooffiae*) were described, for the first time by applying sequencing technology to distinguish species in this genus (Guého *et al*. 1996). To date, 18 species have been described in the genus *Malassezia*.

Malassezia are basidiomycetous yeasts, recently assigned to the class *Malasseziomycetes*, and are phylogenetically positioned in the *Ustilaginomycotina*, together with primarily plant pathogenic fungi (Wang *et al*. 2014d, 2015b). As they are lipid-dependent, their culture medium requires lipid supplementation for growth, except for *Ma. pachydermatis*, which is also able to grow on Sabouraud dextrose agar (SDA) due to the presence of short chain fatty acids in that medium. The optimal growth temperature for most species is 30–33 °C, with few exceptions (Guého-Kellermann *et al.* 2010). Comparative genomics showed a genus-wide expansion of lipid hydrolases and loss of genes coding for enzymes involved in lipid and carbohydrate metabolism, explaining its lipid dependence, and suggesting an early evolutionary host adaptation from plant to animal skin (Wu *et al*. 2015c).

Malassezia yeasts reside on human and animal skin as commensals, but under certain conditions, they may also cause various skin diseases, such as dandruff/seborrheic dermatitis (SD), PV, psoriasis, *Malassezia* folliculitis, and atopic dermatitis (AD) in humans; and otitis and dermatitis in cats, dogs and a variety of other animals (Bond *et al*. 2010, Gaitanis *et al*. 2012). In immunocompromised individuals and neonates, some species may also cause bloodstream infections (Gaitanis *et al*. 2012, Rhimi *et al*. 2020). Instigated by increased direct sequencing efforts and boosted attention for the fungal component in microbiome studies, it became clear that *Malassezia* not only is the most predominant fungal component of the human skin microbiome but may also play a role in other body sites, *e.g*., in human gut health and disease (Spatz & Richard 2020). With the application of fungal barcoding approaches, *Malassezia* presence has also been observed in a wide variety of environmental ecologies (Amend 2014).

Clinical and economic significance

Scientific literature dealing with *Malassezia*, historically mainly focused on its involvement in skin diseases in humans and a variety of animals. Here we present some of the most common skin diseases and their impact on human health. Though skin diseases involving *Malassezia* are not life-threatening, it is important to also consider the negative social and psychological effects of these diseases.

Dandruff/Seborrheic Dermatitis (D/SD)

Dandruff and Seborrheic Dermatitis (SD) are both skin diseases in the same spectrum, affecting the sebaceous areas such as the scalp, midface, chest, and back; only differing in locality and severity. Dandruff is limited to the scalp and involves itchy, flaking skin without visible inflammation. Seborrheic Dermatitis involves flaking, scaling, an itchy sensation, and also inflammation (Park *et al*. 2012b, Borda & Wikramanayake 2015, Saunte *et al*. 2020). Multiple factors may contribute to the pathogenesis of D/SD, such as host susceptibility, sebaceous activity and *Malassezia* (Borda & Wikramanayake 2015). Seborrheic Dermatitis affects 1–3 % of the general population, prevalence increases with age and men are affected more frequently. Seborrheic Dermatitis significantly increases in immune-compromised individuals, such as HIV/AIDS patients, with incidence ranging from 30 to 83 %. Dandruff is much more common, affecting approximately 50 % of adults worldwide, but varying between different ethnic groups. The economic burden from dandruff was estimated at 300 million US dollars annually for over-the-counter products in the USA alone and the total direct annual costs of SD were estimated at 179 US dollars, and an additional 51 million US dollars indirect costs as a result of lost working days. Due to the location of the affected skin areas, the disease has a significant negative impact on the patient's quality of life (Borda & Wikramanayake 2015).

Pityriasis versicolor (PV)

Pityriasis versicolor (PV) is a common skin infection, caused by *Malassezia*, and is characterised by hypo- or hyperpigmented plaques, covered by scales, mainly on the back, chest, and neck. Interestingly, there is a high correlation between PV and the occurrence of hyphae on the skin of patients (Gaitanis *et al*. 2012, Saunte *et al*. 2020). The disease occurs in a variety of geographies and age categories, but peak prevalence in more temperate climates is lower and between 20–40-yr-old adults, whereas in more tropical climates, peak prevalence is between 10–30-yr-old. Prevalence rates as low as 0.5 % have been observed in Sweden (Gaitanis *et al*. 2012), up to 22.5 % in a large student population in Vietnam (Nguyen *et al.* 2020), and 40 % of the population in some areas in Brazil (Saunte *et al*. 2020). Treatment may be topical or with oral antifungals in more severe cases, but disease recurrence is not uncommon and pigmentation normalisation may take up to

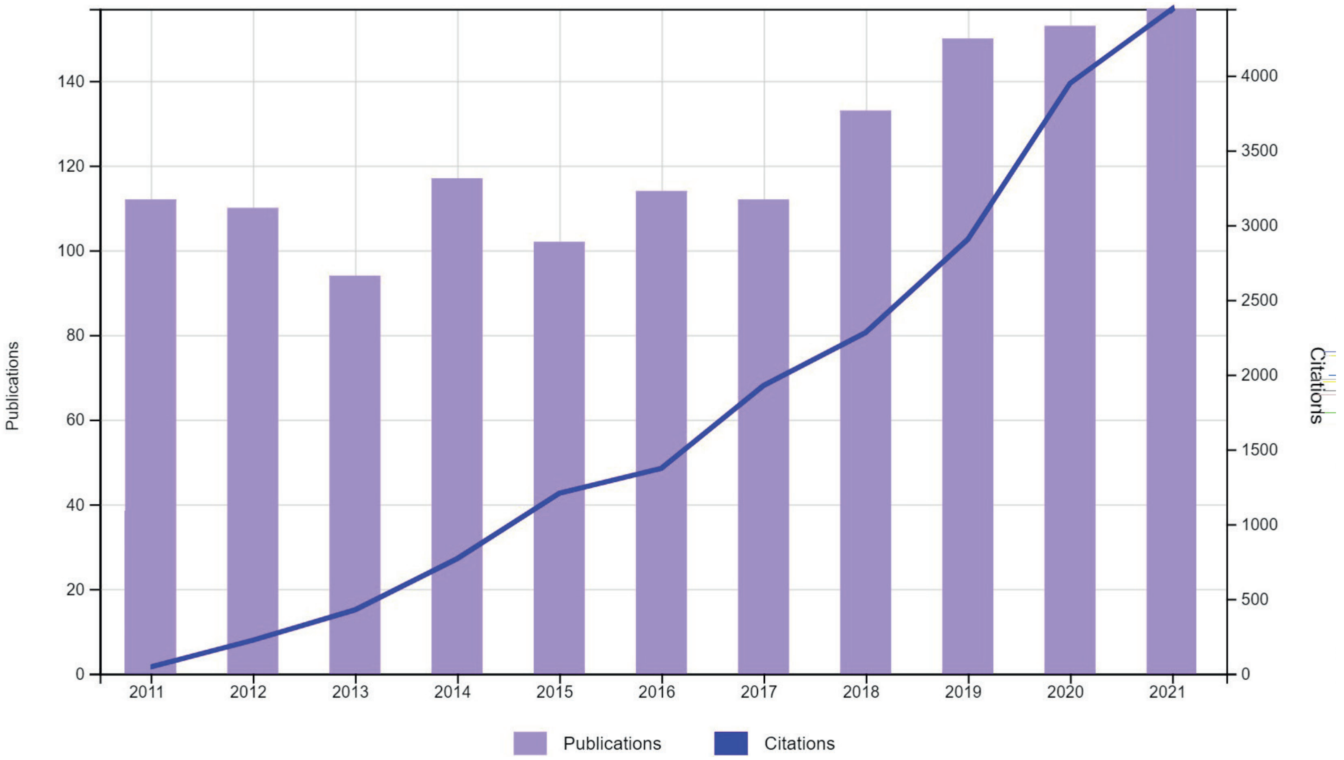

Fig. 70. Trends in research of *Malassezia* in the period 2011–2021.

several months after ending treatment (Gaitanis *et al*. 2012, Saunte *et al*. 2020). Information regarding economic burden is not known, but considering the very high prevalence in tropical regions and its impact on quality of life, it likely is substantial.

Research interests

There are 1 354 publications and 15 632 citations from 2011–2021 in the Web of Science (Fig. 70), with the top 10 most cited articles listed in Table 47. When exploring citations for *Malassezia*, it is relevant to distinguish two main categories: one where *Malassezia* is the "direct" focal point, mostly dealing with aspects of more traditionally associated skin diseases, modes of pathogenicity, and evolutionary and biological features; and a second category, where broader studies, not set out to focus on *Malassezia*, observe signals in their data, pointing towards previously unknown aspects of this genus. These categories are not mutually exclusive but stimulate one another towards a more holistic understanding of various ecosystems and the complex roles that *Malassezia* may play in them. Below, a few important developments for each category will be summarised.

Malassezia as a direct focal point

Diagnostic and disease management challenges

Its unique lipid requirement for growth is one of the challenges for epidemiology studies as is the diagnosis of *Malassezia* as a causative agent for disease, especially for bloodstream infections (BSIs). Lack of lipid supplementation in standard culture media in clinics results in under-diagnosis and therefore *Malassezia* may play a larger role than thus far believed (Iatta *et al*. 2014a, Rhimi *et al*. 2020). *Malassezia* BSIs especially affect immunocompromised patients and neonates, receiving intravenous (lipid-rich) nutrition (Gaitanis *et al*. 2012, Rhimi *et al*. 2020). An increasing number of studies describe *Malassezia* BSIs as an emerging phenomenon, possibly because of factors such as the growing numbers of immunocompromised patients and selective pressure of frequently applied prophylactic fluconazole, for which the most frequently observed BSI-related *Malassezia* species, *Ma. furfur*, is often less susceptible (Miceli *et al*. 2011, Iatta *et al*. 2014b, Chen *et al*. 2019a, Rhimi *et al*. 2021). So far, only two species have mainly been implicated in BSIs, *Ma. furfur* and *Ma. pachydermatis*, and a few additional cases of *Ma. sympodialis* (Rhimi *et al*. 2020). A general future disease management hurdle for *Malassezia*-related diseases may be a trend towards reduced antifungal susceptibility (Pedrosa *et al*. 2019, Rhimi *et al*. 2021, Peano *et al*. 2020), and the lack of standardised testing protocols (Arendrup *et al*. 2014, Rhimi *et al*. 2020). The omnipresence of *Malassezia* as a commensal on healthy skin poses a challenge in determining its role in disease but many contemporary advances have been made towards unravelling relevant factors driving host-microbe interactions, as is illustrated below.

Modes of pathogenicity

Whether *Malassezia* acts as an innocent commensal or harmful pathogen on the skin, seems to be the complex combined result of virulence determinants of the yeast, host susceptibility, and environmental factors such as temperature and humidity. In the case of PV, excess yeast proliferation is involved, which is not necessarily the case with D/SD or AD (Theelen *et al*. 2018). Two not mutually exclusive disease induction mechanisms were described: direct irritant pathways as with D/SD, and indirect allergic pathways as with AD (Grice & Dawson 2017, Theelen *et al*. 2018). In addition to virulence factors such as a high lipid content of the cell wall, lipolytic enzyme production, hyphae and biofilm formation (Hort & Mayser 2011), several studies further characterised previously identified allergens (Gaitanis *et al*. 2012, Gioti *et al*. 2013), and identified allergen-carrying extracellular vesicles which are released by *Malassezia* cells and that interact

Table 47. Top 10 cited articles related to *Malassezia* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Topographic diversity of fungal and bacterial communities in human skin	615	Findley *et al.* (2013)
2	Emerging opportunistic yeast infections	530	Miceli *et al.* (2011)
3	The *Malassezia* genus in skin and systemic diseases	325	Gaitanis *et al.* (2012)
4	ESCMID and ECMM joint clinical guidelines for the diagnosis and management of rare invasive yeast infections	305	Arendrup *et al.* (2014)
5	The gut mycobiome of the human microbiome project healthy cohort	286	Nash *et al.* (2017)
6	Characterization of the fungal microbiota (mycobiome) in healthy and dandruff-afflicted human scalps	250	Park *et al.* (2012b)
7	Adaptation of the human aryl hydrocarbon receptor to sense microbiota-derived indoles	166	Hubbard *et al.* (2015)
8	Mycology - an update. Part 1: Dermatomycoses: causative agents, epidemiology and pathogenesis	162	Nenoff *et al.* (2014)
9	Bacterial, fungal and protozoan carbonic anhydrases as drug targets	146	Capasso & Supuran (2015)
10	Identification of distinct ligands for the c-type lectin receptors mincle and dectin-2 in the pathogenic fungus *Malassezia*	138	Ishikawa *et al.* (2013)

with human skin cells (Gehrmann *et al*. 2011, Johansson *et al*. 2018). One additional feature of *Malassezia* worth mentioning is its ability to metabolise tryptophan, resulting in the production of several indolic compounds that may serve as potent ligands of the aryl hydrocarbon receptor (AhR). Recent studies have revealed a diverse number of roles of AhR in skin homeostasis and disease, including inflammation, melanogenesis, and cancer (Gaitanis *et al*. 2012, Furue *et al*. 2014, Hubbard *et al*. 2015, Szelest *et al*. 2021). A study comparing healthy and diseased skin found an increased presence of AhR ligands in scales from diseased skin *vs* healthy skin, and *Ma*. *furfur* species isolated from diseased skin showed a significantly higher AhR ligand production, compared to *Ma*. *furfur* isolates from healthy skin, confirming their status as virulence factors (Magiatis *et al*. 2013). A role for *Malassezia* in skin cancer (basal cell carcinoma) has been suggested via a number of AhR ligand mediated tumour promoting pathways (Gaitanis *et al*. 2011, 2012). Finally, there is increasing evidence that microbiota derived AhR ligands also play an important role in host-microbiota communication in the gastrointestinal tract, modulating physiology, and are possibly involved in etiology or progression of inflammatory bowel disease (IBD) (Dong & Perdew 2020).

The first *Malassezia* genome sequences (*Ma*. *globosa* and *Ma*. *restricta*) were published in 2007 (Xu, 2007), while during the following decade, genomes for 15 of the 18 described species were published and utilised as a resource for exploring aspects related to evolution and virulence traits (Xu *et al*. 2007, Gioti *et al*. 2013, Wu *et al*. 2015c, Zhu *et al*. 2017, Lorch *et al*. 2018). The genomes revealed the presence of mating-type genes, suggesting that sexual reproduction may be possible (Xu *et al*. 2007, Gioti *et al*. 2013, Wu *et al*. 2015c, Zhu *et al*. 2017). Additionally, in *Ma*. *furfur*, evidence was found for the presence of hybrids (Wu *et al*. 2015c, Theelen *et al*. 2022), an increasingly observed phenomenon, and frequently linked to the emergence of new pathogens (Mixão & Gabaldón 2018). Many questions remain regarding the complex role and pathogenicity modes of *Malassezia*. In addition to recent genomics advancements, the development of various model systems for host-pathogen interaction studies (Sparber & LeibundGut-Landmann 2019, Torres *et al*. 2020), and the establishment of tools for genetic manipulation in *Malassezia* (Ianiri *et al*. 2016, Celis *et al*. 2017, Ianiri *et al*. 2019), make way for answering many of the open questions.

Other perspectives on *Malassezia*

Microbiome

For many years, microbiome studies focused mainly on bacteria and only in the last decade it became clear that the long overlooked fungal kingdom might play a pivotal role in various aspects of human health and disease. For the first time, Findley *et al*. (2013) evaluated the microbial communities of various human skin sites, considering both bacterial and fungal microbiota, and found that *Malassezia* was the dominating fungal component on 11 core body sites of healthy adults. Many studies followed, exploring the human microbiome, now also considering fungi. Previously believed to predominantly be of relevance on human skin only, multiple studies found evidence for significant *Malassezia* presence in other human body sites as well. The yeast was found to be a member of the human oral mycobiome (Dupuy *et al*. 2014), and multiple studies also implicated *Malassezia* as a frequent resident of the human gut (Nash *et al*. 2017, Sokol *et al*. 2016, Spatz & Richard 2020). Comparing fungal gut microbiota from healthy individuals and Crohn's disease patients, fungi with increased abundance in patients were identified, of which *Ma*. *restricta* was linked to an IBD-associated polymorphism in the gene for CARD9 (a signalling adaptor important for antifungal defence), evoking an innate inflammatory response in a CARD9-dependent manner, and the yeast was also shown to aggravate colitis in mouse models (Limon *et al*. 2019). Another study implicated the fungal mycobiome in the pathogenesis of pancreatic cancer, with the fungal community being considerably enriched for *Ma*. *globosa*. Removal of the mycobiome was protective against tumour growth and repopulation only with *Ma*. *globosa* accelerated tumour growth in mice (Aykut *et al*. 2019). These and other findings, implicating a role for *Malassezia* on the skin and beyond, will likely incite many future studies that will further unravel the complex role of *Malassezia* in the human body.

Ecology

The direct sequencing approach to scan for microbial community compositions was not only applied to the human body but various studies also considered other ecologies and found *Malassezia* presence in a variety of different environments, such as terrestrial and marine ecosystems (Lai *et al*. 2007, Le Calvez *et al*. 2009), Antarctic soils (Arenz *et al*. 2006, Fell *et al*. 2006), corals (Amend *et al*. 2012), and sponges (Gao *et al*. 2008). Based on ribosomal sequence comparison, both sequences similar and distant to known *Malassezia* species were found. *Malassezia* has not yet been successfully cultured from any of these ecosystems and much about its broad presence is still puzzling, but it is becoming increasingly clear that *Malassezia* is ecologically very diverse (Amend 2014). Future comparison of malassezia-like isolates from these different environments with known strains/species may provide interesting new insights into the evolution of this unique genus.

Authors: B. Theelen and T. Boekhout

42. ***Phoma*** Sacc., Michelia 2(no. 6): 4. 1880.

Type species: *Phoma herbarum* Westend.

Classification: *Ascomycota*, *Pezizomycotina*, *Dothideomycetes*, *Pleosporales*, *Didymellaceae.*

Background

Phoma is a ubiquitous and widely distributed genus within *Pleosporales* (*Dothideomycetes*). Around 3 000 taxa have been described and approximately 110 taxa were reported as pathogenic on plants, animals and humans in different ecosystems (Aveskamp *et al.* 2008, Rai *et al.* 2014, Chen *et al.* 2015c, Bennett *et al.* 2018, Deb *et al.* 2020). *Phoma* species can change from opportunistic to pathogenic life mode when in contact with susceptible hosts (both animals and humans) (Aveskamp *et al.* 2008, Bennett *et al. 2018). Phoma* species primarily infect plant hosts through wounds, stomata and directly through the epidermis. Fungal hyphae then grow intercellularly through plant tissues and become necrotrophic (Aveskamp *et al.* 2008). After lesions production, dark-coloured conidiomata can be often seen and, occasionally, extra dermal mycelium is formed. Conidia or mycelial fragments can disperse by water-splash, misting or wind to infect new hosts (Aveskamp *et al*. 2008). Birds and insects can act as vectors of *Phoma* infections (Aveskamp *et al*. 2008). If the spores do not contact suitable hosts, they mostly persist as saprobes on decaying organic material in the soil (Aveskamp *et al.* 2008, Bennett *et al.* 2018). Saprobic *Phoma* species occur on inorganic materials while other species are found on fungi, humans and plant materials (Hutchison *et al.* 1994, Sullivan & White 2000, Aveskamp *et al.* 2008, Deb *et al.* 2020).

Phoma is an asexual genus and was formally introduced by Saccardo (1880) for plant stem pathogens. The genus was considered to be a pycnidial forming filamentous fungal genus with aseptate and hyaline conidia associated with plant stems (Saccardo 1884, Aveskamp *et al.* 2008, De Gruyter 2012, Bennett *et al.* 2018, Deb *et al.* 2020). Boerema & Bollen (1975) provided updates for the definition and classification of the genus. Taxonomically, *Phoma* is polyphyletic with indistinguishable species boundaries (Bennett *et al.* 2018, Deb *et al.* 2020).

Identification of *Phoma* species was previously mainly based on the host and the shape, the size of pycnidia and pycnidiospores (Rai *et al.* 2014, Hou *et al.* 2020). The "*Phoma* Identification Manual" by Boerema *et al.* (2004) described over 220 recognised taxa based on morphological characteristics. The key characters of *Phoma* asexual morphs are pseudoparenchymatous or scleroplectenchymatous pycnidia, ampulliform to doliiform, phialidic conidiogenous cells and initially unicellular, hyaline conidia that become septate with age (De Gruyter *et al.* 2010). Conidiogenesis cells were considered a significant morphological character in hyphomycete identification and was applied to all conidial fungi including asexual *Phoma* (Sutton 1964, Hughes 1953, Aveskamp *et al.* 2008). Other asexual characters, such as the formation of conidia, pycnidia, and chlamydospores, vegetative cells within hyphae or at hyphal tips can also be considered (Boerema *et al.* 2004, Guégan *et al.* 2016, Bennett *et al.* 2018). However, morphology-based identification has its limitations as several taxa exhibit characters that are shared between different *Phoma* genera (Aveskamp *et al.* 2009, Deb *et al.* 2020). Also, some characters overlap within and between other genera of coelomycetous fungi such as *Phyllostictoides* (producing similar pycnidia with unicellular conidia on natural substrate) and *Pilosa* (producing pseudoparenchymatous pycnidia and unicellular conidia) (De Gruyter *et al.* 2010, Deb *et al.* 2020). Currently, *Boeremia*, *Didymella* and *Pyrenochaeta* are often incorrectly used synonymously with *Phoma* (Blancard 2012, Duarte & Barreto 2015, Deb *et al.* 2020). With the advent of nucleotide sequence data, phylogenetic analyses greatly advanced *Phoma* taxonomy by adding novel taxa and delimitating unclear placements (Aveskamp *et al.* 2008). Similar to previous analyses, in the recent analysis of Deb *et al.* (2020), the type species *Phoma herbarum* represented a monophyletic lineage as *Phoma s. str.* in *Didymellaceae*. The species complex of *Phoma s. lat.* is highly polyphyletic and many species boundaries are unclear (Aveskamp *et al.* 2008, 2010, Zimowska *et al.* 2017, Deb *et al.* 2020).

Ecological and economic significance

Phoma species occur on economically important crops causing devastating plant diseases (Deb *et al.* 2020). Some *Phoma* taxa cause serious yield losses (Chen *et al.* 2015d, 2017, Fitt *et al.* 2006, Deb *et al.* 2020). *Phoma betae*, *Ph. clematidina*, *Ph. complanata*, *Ph. cucurbitacearum*, *Ph. destructive*, *Ph. dictamnicola*, *Ph. eupyrena*, *Ph. exigua*, *Ph. glycinicola*, *Ph. hedericola*, *Ph. herbarum*, *Ph. glomerata*, *Ph. macdonaldii*, *Ph. macrostoma*, *Ph. medicaginis*, *Ph. multirostrata*, *Ph. narcissi*, *Ph. negriana*, *Ph. koolunga*, *Ph. labilis*, *Ph. lingam*, *Ph. sambuci-nigrae*, *Ph. sambuci-nigrae*, *Ph. sclerotioides*, *Ph. sorghina* and *Ph. tracheiphila* are known as important plant pathogens (Boerema *et al*. 2004, Deb *et al.* 2020).

Phoma infections have been recorded in animals and humans (Aveskamp *et al.* 2008). In 1973, the first confirmed human case was reported of pathogenic *Phoma* spp. in a subcutaneous lesion of a post-renal transplant patient (Young *et al. 1973,* Bennett *et al.* 2018). Subsequently, a number of human pathogens were reported by Zaitz *et al.* (1997), De Hoog *et al.* (2000) and Balis *et al.* (2006). With the increase of immunosuppression in patients and the advancement of medicines, *Phoma i*nfections have gradually increased (Bennett *et al.* 2018). Bovine mycotic mastitis and fish-mycosis in salmon and trout are severe vertebrate diseases caused by *Phoma* species (Costa *et al.* 1993, Faisal *et al.* 2007, Aveskamp *et al.* 2008). Arthropods and nematodes can be also infected by *Phoma species* (Chen *et al.* 1996, Aveskamp *et al.* 2008). Other fungal taxa, oomycetes and lichens (lichenicolous) with associated *Phoma* species have been recorded (Hutchinson *et al.* 1994, Sullivan & White 2000, Hawksworth & Cole 2004, Aveskamp *et al.* 2008),

Some *Phoma* species play a beneficial role as biocontrol agents of weeds and plant pathogens (Aveskamp *et al.* 2008). *Phoma exigua*, *Ph. herbarum* and *Ph. macrostoma* have been used as bioherbicides and are effective against broadleaf weeds (dandelion, chickweed, clematis, salal species) (Aveskamp *et al.* 2008). *Phoma glomerata* has been reported as a causal agent for the synthesis of silver nanoparticles (Birla *et al.* 2009, Fabrega *et al.* 2011). Several *Phoma* species such as *Ph. eupyrena*, *Ph. glomerata*, *Ph. herbarum* and *Ph. pomorum* var. *pomorum* have been recorded on asbestos, cement, oil-paint, plaster, crockery and many other inorganic substrates (Aveskamp *et al.* 2008). These taxa play an important role in the degradation of organic materials. Also, *Phoma* species were reported from public bathrooms, swimming pools, air and food (Bennett *et al.* 2018).

Research interests

There are 1 277 publications and 15 402 citations from 2011–2021 in the Web of Science (Fig. 71), with the top 10 most cited articles listed in Table 48. The majority of the publications focused on advantageous biological activities (Li *et al.* 2012a, Wang *et al.* 2012c, Waqas *et al.* 2012, Gade *et al.* 2014), pathogenic lifestyles (Xu *et al.* 2012b) and resolving the phylogeny of phoma-like genera (De Gruyter *et al.* 2013, Chen *et al.* 2015c, Ertz *et al.* 2015, Valenzuela-Lopez *et al.* 2018).

Biological activities

Li *et al.* (2012a) investigated the diversity and heavy metal tolerance of endophytic *Phoma* from plants in a lead-zinc mine wasteland in China. *Phoma* species were identified as more sensitive isolates to Zn^{2+} than isolates of *Alternaria* and *Peyronellaea*. Pb^{2+} sensitivity of the isolates was not significantly different among *Phoma*, *Alternaria* and *Peyronellaea* (Li *et al.* 2012a). Waqas *et al.* (2012) examined

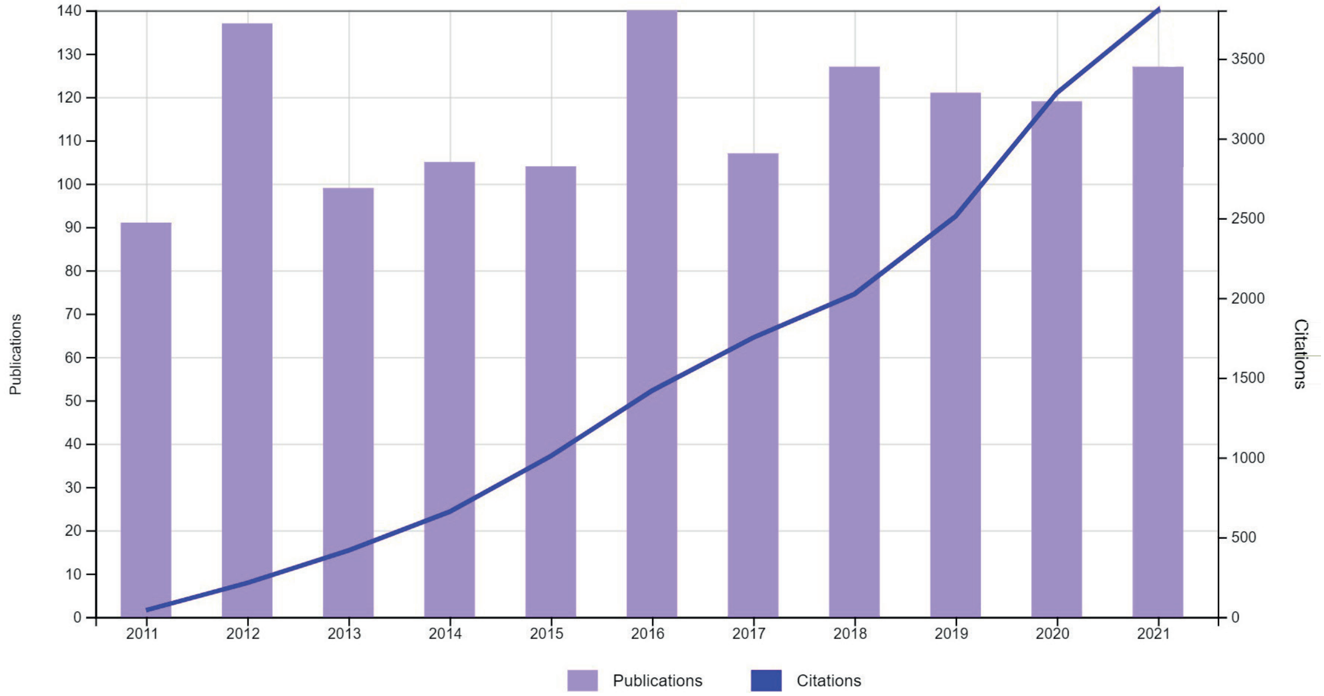

Fig. 71. Trends in research of *Phoma* in the period 2011–2021.

Table 48. Top 10 cited articles related to *Phoma* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Endophytic fungi produce gibberellins and indoleacetic acid and promotes host-plant growth during stress	234	Waqas *et al.* (2012)
2	Redisposition of phoma-like anamorphs in *Pleosporales*	221	De Gruyter *et al.* (2013)
3	Resolving the *Phoma enigma*	199	Chen *et al.* (2015c)
4	Antiviral activity of mycosynthesized silver nanoparticles against herpes simplex virus and human parainfluenza virus type 3	192	Gaikwad *et al.* (2013)
5	Soil fungal community structure along a soil health gradient in pea fields examined using deep amplicon sequencing	138	Xu *et al.* (2012a)
6	Coelomycetous dothideomycetes with emphasis on the families *Cucurbitariaceae* and *Didymellaceae*	90	Valenzuela-Lopez *et al.* (2018)
7	Bioactive metabolites from *Phoma* species, an endophytic fungus from the Chinese medicinal plant *Arisaema erubescens*	79	Wang *et al.* (2012)
8	Green synthesis of silver nanoparticles by *Phoma glomerata*	79	Gade *et al.* (2014)
9	Diversity and heavy metal tolerance of endophytic fungi from six dominant plant species in a Pb-Zn mine wasteland in China	69	Li *et al.* (2012a)
10	Phylogenetic insights resolve *Dacampiaceae* (*Pleosporales*) as polyphyletic: *Didymocyrtis* (*Pleosporales*, *Phaeosphaeriaceae*) with phoma-like anamorphs resurrected and segregated from *Polycoccum* (*Trypetheliales*, *Polycoccaceae fam. nov.*)	61	Ertz *et al.* (2015)

the endophytic *Phoma glomerata* LWL2 strain and identified indoleacetic acid (IAA) in the cultures.

Biologically active metabolites which showed antifungal and anti-tumour activities were identified from endophytic *Phoma* cultures, from the tuber of *Arisaema erubescens*, a medicinal plant in China (Wang *et al.* 2012c). (3S)-3,6,7-trihydroxy-α-tetralone, a new metabolite with antifungal activity was identified as the first report of the α-tetralone derivative from *Phoma*. Also, cercosporamide and β-sitosterol compounds were obtained from *Phoma* species for the first time.

Xu *et al.* (2012a) studied the structures of soil fungal communities with the soil health gradient in pea fields. *Phoma* was identified as an abundant fungal colony in soils with diseased plants (Rajak *et al.* 1982, Kövics *et al.* 2005, Rai *et al.* 2014). Gaikwad *et al.* (2013) investigated the biological synthesis of silver nanoparticles using *Phoma* species based on the colour change of the fungal cell filtrate from yellowish or colourless to yellowish brown with aqueous $AgNO_3$. Silver nanoparticles produced by *Phoma* species in the 7–20 nm range were identified with less antiviral activity and larger particle size. Gade *et al.* (2014) reported the extracellular synthesis of silver nanoparticles by *Ph. glomerata* (MTCC-2210) with rapid synthesis in bright sunlight.

Taxonomy and phylogeny

De Gruyter (2012) studied the taxonomy of excluded *Phoma* species that were classified in sections *Plenodomus*, *Heterospora* and *Pilosa*. Several species of *Leptosphaeria* and *Phoma* section *Plenodomus* were reclassified into *Plenodomus*, *Subplenodomus*, *Leptosphaeria* and *Paraleptosphaeria* based on the ITS and LSU phylogeny (De Gruyter 2012). Morphologically, *Ascochyta* and *Phoma* are difficult to distinguish, and species of these genera have been linked to *Didymella* sexual morphs in the past. The morphological observations and multi-locus phylogenetic analyses performed by Chen *et al.* (2015c) revealed that *Phoma* was delineated as a distinct genus with *Ascochyta* and *Didymella*. Ertz *et al.* (2015) included species of *Polycoccum s. lat.* in *Pleosporales* and they were closely related to lichenicolous phoma-like species in *Phaeosphaeriaceae*. *Didymocyrtis* was resurrected for these species and for lichenicolous species that were classified into *Diederichia*, *Diederichomyces*, *Leptosphaeria* and *Phoma*. Some of the sexual and asexual linkages were resolved by Ertz *et al.* (2015) such as *Didymocyrtis ramalinae*–*Phoma ficuzzae* and *D. consimilis*–*Ph. caloplacae* based on phylogenetic analyses.

Hou *et al.* (2020) revised the poly- and paraphyletic genera *Ascochyta*, *Didymella* and *Phoma*. By employing a DNA phylogeny of four gene loci (ITS, LSU, *rpb2*, *tub2*), they were able to delineate 36 well-supported monophyletic clades, representing 36 phoma-like genera. However, further research is still needed to resolve the phylogeny of several old generic names that still lack cultures and DNA data (Chethana *et al.* 2021b).

Author: S.N Wijesinghe

43. ***Thermomyces*** Tsikl., Ann. Inst. Pasteur, Paris 13: 500. 1899.

Type species: *Thermomyces lanuginosus* Tsikl.

Classification: *Ascomycota*, *Pezizomycotina*, *Eurotiomycetes*, *Eurotiales*, *Trichocomaceae.*

Background

Thermomyces was introduced in 1899 when P. Tsiklinsky reported the accidental discovery of a thermophilic hyphomycete on a potato inoculated with garden soil; he typified the genus with *Thermomyces lanuginosus* (Tsiklinsky 1899). *Thermomyces* belongs to the family *Trichocomaceae* (*Eurotiales*) and is phylogenetically sister of the monotypic genus *Ascospirella* (*Ascospirella lutea*, syn. *Talaromyces luteus*). These two genera differ in their thermophilicity: *Thermomyces* contains thermophilic species, while the sole species in *Ascospirella* is a mesophile (Houbraken *et al*. 2020). Seven species are described in the genus, and phylogenetic studies have shown that these species belong to different families. The thermophilicity of the species reflects their different evolutionary histories. Two species are accepted in *Thermomyces*: *Th. lanuginosus* (syn. *Th. ibadanensis*, *Humicola lanuginosa*) and *Th. dupontii* (syn. *Th. thermophilus*, *Talaromyces thermophilus*) (Houbraken *et al*. 2020). The mesophile *Thermomyces verrucosus* was combined in *Botryotrichum* (*Chaetomiaceae*) as *B. verrucosum* (Wang *et al*. 2019e), the thermotolerant *Th. stellatus* phylogenetically belongs to *Microascaceae* (Morgenstern *et al*. 2012, Houbraken *et al*. 2014) and the taxonomic position of *Th. piriformis* remains unresolved. Both *Th. lanuginosus* and *Th. dupontii* can grow at high temperatures but differ phenotypically and in reproductive behaviour. The presence of similar chlamydospores in both species suggests a common ancestor (Houbraken *et al*. 2014, 2020).

The genomes of *Th. lanuginosus* strains SSBP and ATCC 200065 were sequenced and are 19.2 and 19.9 Mb in size with an estimate of 6 241 and 8 129 protein-coding genes, respectively. The genome of *Th. dupontii* NRRL 2155 is similar in size (19.8 Mb) and the number of protein-coding genes is 7 560 (Mchunu *et al*. 2013, https://mycocosm.jgi.doe.gov/Thermophilic_ Fungi/Thermophilic_Fungi.info.html). These genome sequences will be studied further to identify and characterise genes responsible for the production of various industrially important enzymes.

Ecological and economic importance

Thermomyces species are thermophilic, and strains generally can grow between 20 and 60 °C, with an optimum growth temperature between 45 and 50 °C. Thermophilic fungi are commonly found in soil, compost, and other organic materials, especially those that have been subjected to high temperatures. *Thermomyces* as a genus of thermophilic fungal species has received considerable interest in biotechnology as a producer of enzymes with activity at higher temperatures, but also in processes such as composting. A search for patents using *Thermomyces* as a search term in Google patents yielded 76 011 hits, hence there is considerable commercial interest in the enzymes produced by species of the genus.

Research interests

There are 854 publications and 15 013 citations from 2011–2021 in the Web of Science (Fig. 72), with the top 10 most cited articles listed in Table 49. Most highly cited publications on the genus *Thermomyces* deal with enzymatic properties of *Th. lanuginosus*, such as lipases, lipolase, xylanases, and hemicellulase (Adlercreutz 2013, Chandra *et al.* 2020) and its biochemical, chemical and biotechnological applications (Cowan & Fernandez-Lafuente 2011, Deive *et al. 2011,* Manoel *et al*. 2015, Cipolatti *et al.* 2016). A major review describing the enzymes of *Th. lanuginosus* (Singh *et al.* 2003) focused on the biotechnological properties of xylanases and other hemicellulase. The lipase of *Th. lanuginosus*

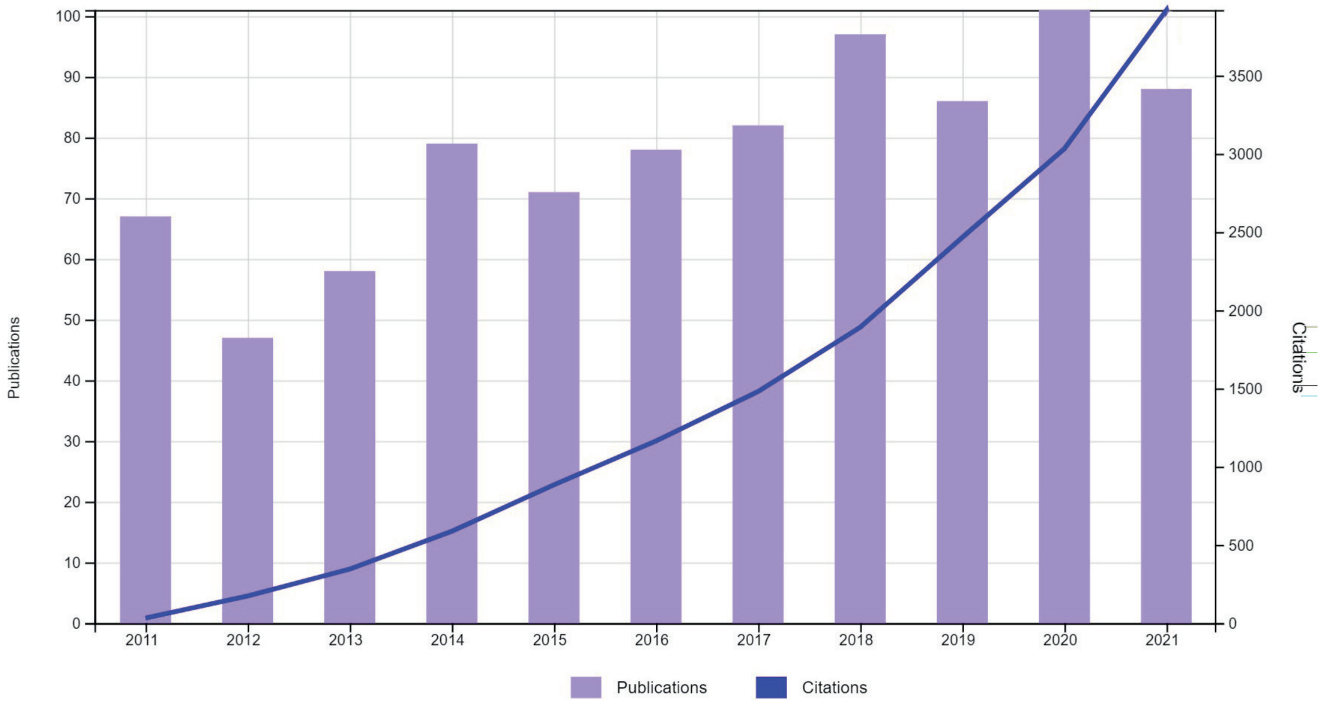

Fig. 72. Trends in research of *Thermomyces* between 2011–2021.

Table 49. Top 10 cited articles related to *Thermomyces* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Immobilisation and application of lipases in organic media	608	Adlercreutz (2013)
2	Immobilization of lipases on hydrophobic supports involves the open form of the enzyme	383	Manoel *et al.* (2015)
3	Nanomaterials for biocatalyst immobilization - state of the art and future trends	230	Cipolatti *et al.* (2016)
4	Microbial lipases and their industrial applications: a comprehensive review	220	Chandra *et al.* (2020)
5	Changes in bacterial and fungal communities across compost recipes, preparation methods, and composting times	194	Neher *et al.* (2013)
6	Modern taxonomy of biotechnologically important *Aspergillus* and *Penicillium* species	137	Houbraken *et al.* (2014)
7	SiO_2 microparticles with carbon nanotube-derived mesopores as an efficient support for enzyme immobilization	128	Kumar *et al.* (2019)
8	Classification of *Aspergillus*, *Penicillium*, *Talaromyces* and related genera (*Eurotiales*): An overview of families, genera, subgenera, sections, series and species	126	Houbraken *et al.* (2020)
9	Dynamic changes of the dominant functioning microbial community in the compost of a 90-m^3 aerobic solid state fermentor revealed by integrated meta-omics	126	Zhang *et al.* (2006)
10	Enzyme immobilisation on amino-functionalised multi-walled carbon nanotubes: structural and biocatalytic characterisation	120	Verma *et al.* (2013a)

is used as a model enzyme to study biocatalysis using immobilised enzymes on substrates such as aldehyde resins, multiwalled carbon nanotubules, octyl-glyoxyl agarose beads, poly-methacrylate particles, Fe_3O_4-chitosan magnetic particles, and siliciumoxide microparticles (Mendes *et al.* 2011, Verma *et al.* 2013a, Rueda *et al.* 2015, Wang *et al.* 2015h, Lage *et al.* 2016). The immobilised enzyme on the carbon nanotubules showed a broader pH range and improved thermal stability and could be used for up to 10 cycles (Verma *et al*. 2013a). The thermostability of a xylanase of *Th. lanuginosus* increased significantly by adding a disulfide bridge in the enzyme with the optimal temperature increasing from 10–75 °C (Wang *et al.* 2012f).

Thermomyces species, especially *Th. lanuginosus*, play an important role during composting as it is a major hemicellulose degrader and can withstand higher temperatures. A dominance of *Thermomyces* spp. in hay-based compost was observed together with species of *Epicoccum*, *Eurotium*, *Arthrobotrys*, and *Myriococcum* (Neher *et al.* 2013). *Thermomyces* species were found to be dominant after the thermophilic phase in windrow compost and became less dominant thereafter, whereas vermicompost contained equal abundances of species belonging to *Pezizaceae*, *Galactomyces*, and *Lecanoromycetes* (Neher *et al.* 2013). Another microbial ecological study on composting identified *Thermobifida*, *Bacillus*, *Thermomyces* and *Aspergillus* as the most important fungal genera, in which *Thermomyces* together with *Aspergillus* species degraded hemicellulose (Zhang *et al.* 2016c). In a compost made of spent mushroom substrate and rice husks, with and without treatment of pig manure, *Thermomyces* abundance was found to be higher in the spent mushroom-based compost without manure (Meng *et al.* 2018). *Thermomyces lanuginosus* was found to be the dominant species in maize straw compost (Zhang *et al.* 2015b).

Authors: J. Houbraken and T. Boekhout

44. **Lentinus** Fr., Elench. Fung. 1: 45. 1828.

Type species: *Lentinus crinitus* (L.) Fr.

Classification: *Basidiomycota*, *Agaricomycotina*, *Agaricomycetes*, *Polyporales*, *Polyporaceae.*

Background

Lentinus is a genus of agaricoid mushrooms in the family *Polyporaceae* (He *et al.* 2019b). A major monograph was published by Pegler (1983b). MycoBank holds over 500 species names, but currently only 55 species are accepted (He *et al.* 2019b). Several genera are congeneric, namely *Lentodiellum*, *Lentodium*, *Leucoporus*, and *Polyporellus* (He *et al*. 2019b). The sporocarps are usually stipitate, omphaloid, and lamellate, but secocioid forms also occur. The caps are usually thick-fleshed, firm, and usually with a depressed centre with somewhat inflexed margins, and a scaly to fibrillose surface. The hyphal system is dimitic. The genome sizes of an agaricoid and a secotioid strain of *Lentinus tigrinus* were 39.53–39.88 Mb with 15 380–15 581 genes (Wu *et al.* 2018a). *Lentinus* species occur globally, but many occur in (sub)-tropical regions. The species cause wood rot and are gregarious or solitary on living or dead trunks, stumps, and branches of both deciduous and coniferous trees. Some species are edible and are considered of medicinal importance (see below).

Ecological and economic importance

Lentinus species cause white rot and play an important role in the decomposition of wood (Wu *et al.* 2018a). In depth investigation of the wood degrading physiology of *Lentinus squarrosulus* showed activities of several lignocellulolytic enzymes, such as laccase, peroxidase, CMCase, and xylanase. The species is a good producer of exopolysaccharides and prefers hemicellulose over cellulose and might find application in the industrial pre-treatment and biodelignification of lignocellulosic biomass (Isikhuemhen *et al.* 2012). Field observations made in the Colombian Amazon on the rapid appearance of *Lentinus* spp. after primary forest trees were cut down for slash-and-burn agriculture, suggests that they might occur as endophytes in tree trunks (López-Quintero *et al.* 2012). The endophytic nature of *Lentinus* species was confirmed by observations made in Malaysia (Maadon *et al.* 2018). *Lentinus* species are considered “medicinal mushrooms” but are also biotechnologically important. Aspects of cultivation, biologically active compounds and nutritional values have been reviewed (Phonemany *et al.* 2021). Various *Lentinus* species are consumed in Southeast Asia (*e.g.*, Laos, Malaysia, Philippines, Thailand, Vietnam) and parts of Africa (Phonemany *et al.* 2021).

Research interests

There are 892 publications and 13 964 citations from 2011–2021 in the Web of Science (Fig. 73), with the top 10 most cited articles listed in Table 50. Most highly cited publications on *Lentinus* deal with reviews on medicinal aspects of various mushrooms, such as immunomodulatory, anti-tumoural, antiviral, anti-bacterial, and antihyperlipidemic effects (Wasser 2011, Alves *et al.* 2012, Chang &

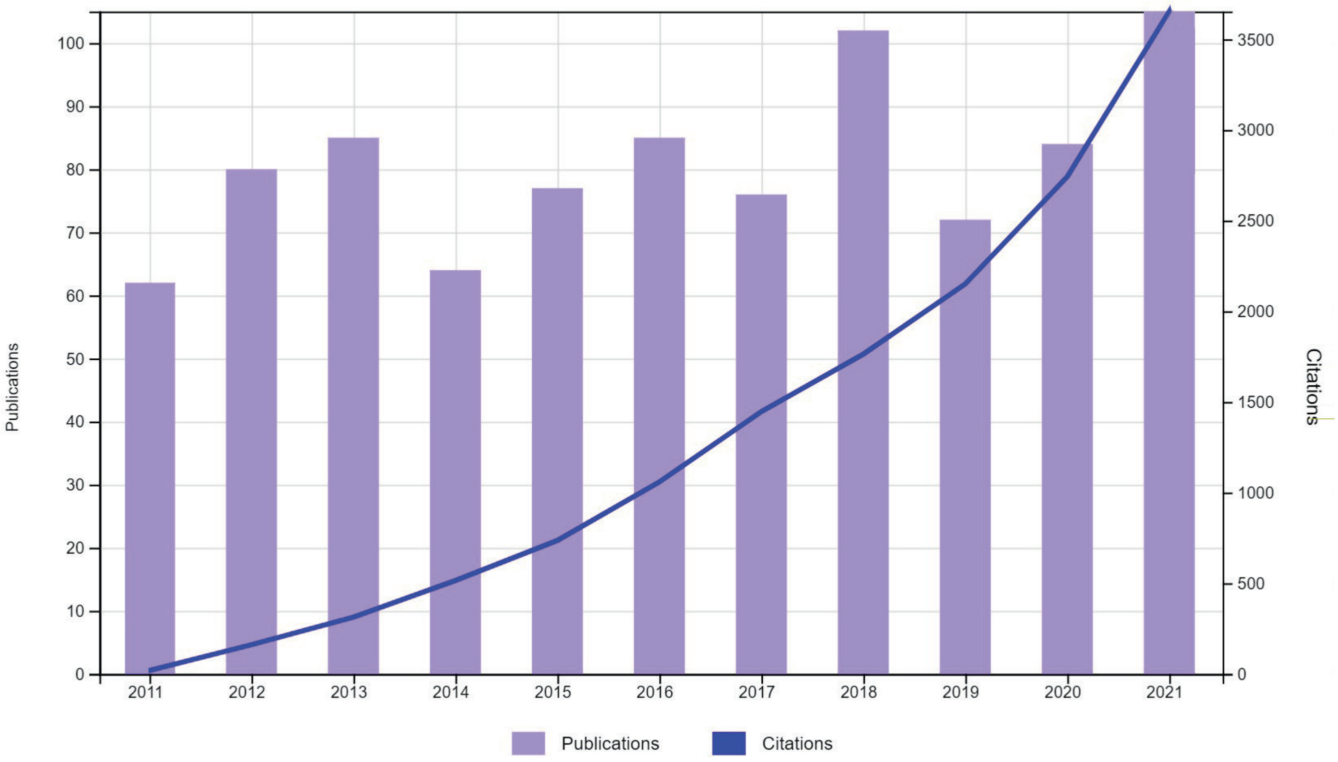

Fig. 73. Trends in research of *Lentinus* between 2011–2021.

Table 50. Top 10 cited articles related to *Lentinus* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	The role of culinary-medicinal mushrooms on human welfare with a pyramid model for human health	341	Chang & Wasser (2012)
2	Current findings, future trends, and unsolved problems in studies of medicinal mushrooms	267	Wasser (2011)
3	Advances in lentinan: Isolation, structure, chain conformation and bioactivities	260	Zhang *et al.* (2011c)
4	Bioactive fungal polysaccharides as potential functional ingredients in food and nutraceuticals	222	Giavasis (2014)
5	A review on antimicrobial activity of mushroom (basidiomycetes) extracts and isolated compounds	197	Alves *et al.* (2012)
6	Mushroom immunomodulators: unique molecules with unlimited applications	165	El Enshasy & Hatti-Kaul (2013)
7	Comparative assessment of bioremediation approaches to highly recalcitrant PAH degradation in a real industrial polluted soil	79	Lladó *et al.* (2013)
8	Anti-inflammatory potential of mushroom extracts and isolated metabolites	75	Taofiq *et al.* (2016)
9	Extraction of polysaccharides from edible mushrooms: Emerging technologies and recent advances	69	Leong *et al.* (2021)
10	Anticancer and other therapeutic relevance of mushroom polysaccharides: A holistic appraisal	64	Kothari *et al.* (2018)

Wasser 2012, El Enshasy & Hatti-Kaul 2013), aspects of functional molecules, such as lentinan (Zhang *et al.* 2011c, Giavasis 2014), and new species descriptions or new species records (Li *et al.* 2016a, Tibpromma *et al.* 2017). *Lentinula* (formerly classified as *Lentinus*) *edodes* or shiitake, a highly praised edible mushroom, is the most studied species with a broad antimicrobial action against both gram-positive and gram-negative bacteria (Alves *et al.* 2012) but is phylogenetically distinct from the genus *Lentinus* as it belongs to a different family, namely *Omphalotaceae* (Hibbett *et al.* 1993, 1998, Matheny *et al.* 2006, He *et al.* 2019b).

Author: T. Boekhout

45. ***Mortierella*** Coem., Bull. Acad. R. Sci. Belg., Cl. Sci., sér. 2 15: 536. 1863.

Type species: *Mortierella polycephala* Coem.

Classification: *Mucoromycota*, *Mortierellomycotina*, *Mortierellomycetes*, *Mortierellales*, *Mortierellaceae.*

Background

Mortierella species are mostly saprobic soil-inhabiting fungi and some are isolated from dead or dying plant tissues, animal carcasses or occasionally from freshwater habitats (Hyde *et al.* 2016, Nguyen *et al.* 2019, Karunarathna *et al.* 2020). *Mortierella* was introduced in 1863 with *Mor. polycephala* as the type species, and it is the largest genus in the family with approximately 112 accepted species (Wijayawardene *et al.* 2020). *Mortierella* is characterised by simple or branched sporangiophores terminating with sporangia or sometimes with a swelling at the base, and globose, multi-, few- or uni-spored sporangia (Hyde *et al.* 2016). The zygospores of *Mortierella* are homo- and heterothallic, which has been confirmed for about 28 species (Takashima *et al.* 2018). In morphology-based taxonomy, nine sections were distinguished in *Mortierella* (Gams 1977). However, a phylogenetic analysis based on LSU sequence dataset revealed seven distinct groups, and Wagner *et al.* (2013) indicated that the morphology of *Mortierella* is likely to depend on culture conditions. Identification of *Mortierella* is mostly based on LSU and ITS sequence data in recent phylogenetic analyses (Wagner *et al*. 2013, Hyde *et al.* 2016, Karunarathna *et al*. 2020). Karunarathna *et al*. (2020) utilised SEM to demonstrate the microstructures of *Mortierella* species. Several species that lack DNA sequence data and distinguishable morphology, remain doubtful and may be excluded from the genus when isolates are available.

Ecological and economic significance

Mortierella species catalyse the formation of rare fatty acids, which is promising for application in industry. They also cause serious diseases in animals.

Agricultural application

Phosphate fixation causes serious problems in agriculture, which may lead to a production reduction. *Mortierella* species can desorb phosphate from soil samples by producing oxalic acid (Osorio & Habte 2014). *Mortierella capitata* promotes crop growth by increasing biomass, chlorophyll and gibberellic acid (Li *et al*. 2020b). Zhang *et al*. (2020b) demonstrated that *Mor. elongata* increases plant biomass among non-leguminous crop species.

Application and disease management

The ability of *Mortierella* to catalyse the formation of rare fatty acids is promising and may improve human health or lead to the development of new chemical materials. Bioremediation may reduce environmental stress caused by organic pesticides from agriculture or chemical plants. However, control of diseases caused by *Mortierella* is challenging and requires more knowledge of the interaction of fungi and their hosts.

Animal pathogen

Mortierella wolfii is reported as a common cause of mycotic abortion and pneumonia in cattle (Neilan *et al*. 1982, Seviour *et al*.

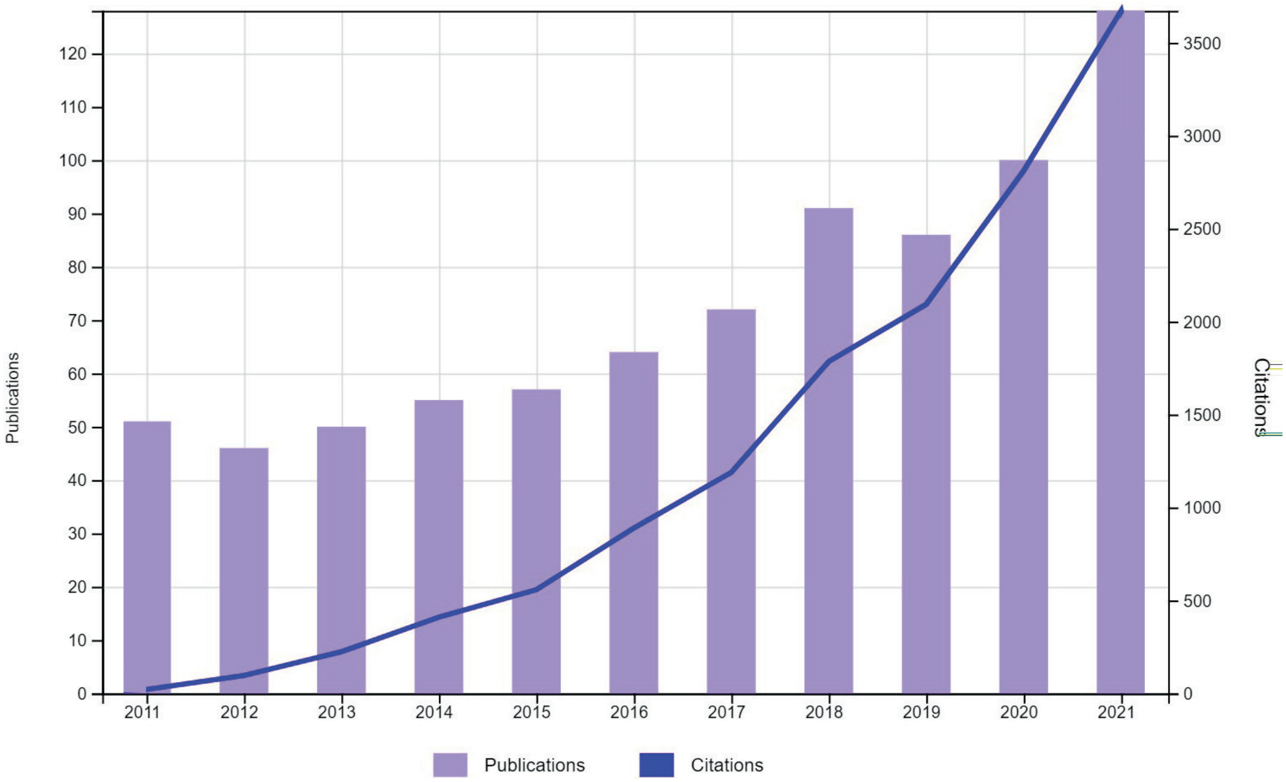

Fig. 74. Trends in research of *Mortierella* in the period 2011–2021.

Table 51. Top 10 cited articles related to *Mortierella* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Advancing oleaginous microorganisms to produce lipid via metabolic engineering technology	248	Liang & Jiang (2013)
2	Microbial degradation and deterioration of polyethylene – A review	231	Restrepo-Flórez *et al.* (2014)
3	Microbial oils as food additives: recent approaches for improving microbial oil production and its polyunsaturated fatty acid content	184	Bellou *et al.* (2016)
4	Soil pH is a key determinant of soil fungal community composition in the Ny-Alesund region, Svalbard (High Arctic)	183	Zhang *et al.* (2016e)
5	Microbial lipid-based lignocellulosic biorefinery: feasibility and challenges	180	Jin *et al.* (2015)
6	Single cell oil production from rice hulls hydrolysate	155	Economou *et al.* (2011)
7	Fungal pathogen accumulation at the expense of plant-beneficial fungi as a consequence of consecutive peanut monoculturing	140	Li *et al.* (2014f)
8	Distinct roles for soil fungal and bacterial communities associated with the suppression of vanilla Fusarium wilt disease	136	Xiong *et al.* (2017)
9	Ice nucleation by water-soluble macromolecules	125	Pummer *et al.* (2015)
10	Soil sickness of peanuts is attributable to modifications in soil microbes induced by peanut root exudates rather than to direct allelopathy	112	Li *et al.* (2014e)

1987). Karunarathna *et al*. (2020) reported three novel *Mortierella* species isolated from bat carcasses. They are likely to be saprobic or opportunistic pathogens but this needs to be confirmed.

Research interests

There are 800 publications and 12 787 citations from 2011–2021 in the Web of Science (Fig. 74), with the top 10 most cited articles listed in Table 51. Most of the publications focused on taxonomy and light industrial applications (producers of polyunsaturated fatty acids and bioremediation).

Taxonomy and phylogeny

The application of *Mortierella* has been intensively studied, but the identification of species was often overlooked and isolates were referred to as *Mortierella* sp. (Kataoka *et al*. 2010, Ellegaard-Jensen *et al*. 2013, Osorio & Habte 2014, Tamayo-Vélez & Osorio 2018). Accurate identification is especially important for those species that are human pathogens, while the taxonomic utility of old names is hampered by a lack of type specimens, representative cultures, or DNA sequence data. However, the taxonomy and phylogeny of *Mortierella* have received great attention in recent years (Hyde *et al*. 2012, 2017, Ariyawansa *et al.* 2015a, Li *et al.* 2016a).

Producers of PUFAs

Many *Mortierella* species have shown potential as producers of polyunsaturated fatty acids (PUFAs). Ogawa *et al.* (2012) concluded that *Mortierella* species are good fermentative producers of several useful single-cell oils, *e.g.*, *Mor. alpina* and its mutants and transformants are useful as producers of PUFAs and they exhibit the ability to produce new oils containing rare PUFAs such as *n*–9, *n*–7, *n*–4 and *n*–1.

Bioremediation

Two *Mortierella* strains, W8 and Cm1-45, isolated from soil have the potential for the bioremediation of contaminated sites with endosulfan. They degraded *α* and *β*-endosulfan by more than 70 % and 50 % in the liquid cultures, respectively, over 28 d at 25 °C, which indicated that *Mortierella* species are likely to play a major role in the formation of hydroxylated metabolites (Kataoka *et al.* 2010). Ellegaard-Jensen *et al*. (2013) clarified the ability of *Mortierella* species to degrade the phenylurea herbicide diuron, and the degradation of diuron was fastest in carbon and nitrogen-rich media. Restrepo-Flórez *et al*. (2014) reviewed recent hypotheses and experimental findings regarding the biodegradation of polyethylene, and described the effects of these microorganisms on the physiochemical properties of this polymer including changes in crystallinity, molecular weight, the topography of samples and the functional groups found on the surface. *Mortierella* species also decompose leaf litter to improve soil fertility, which is a major process in nutrient recycling (Tamayo-Vélez & Osorio 2018).

Author: W. Dong

46. ***Debaryomyces*** Lodder & Kreger-van Rij, in Kreger-van Rij, Yeasts, a taxonomic study, 3rd Edn (Amsterdam): 130, 145. 1984.

Type species: *Debaryomyces hansenii* (Zopf) Lodder & Kreger-van Rij

Classification: *Ascomycota*, *Saccharomycotina*, *Pichiomycetes*, *Serinales*, *Debaryomycetaceae.*

Background

Debaryomyces species are widespread and have been isolated from many sources (Kurtzman *et al*. 2011) such as fruit, soil, air, insects, plants and human tissue (Nishikawa *et al*. 1996, Pfaller *et al*. 2005, De Hoog *et al*. 2020), but most frequently from processed food products (Fröhlich-Wyder 2003, Samelis & Sofos 2003). *Debaryomyces* was established with the description of *De. globosus* (Klöcker 1909) after which various species were described using morphological characteristics that include the presence of spherical cells and spherical, warty ascospores. Lodder & Kreger-van Rij (1952) drew attention to the heterogeneity among species to ferment different carbon sources, therefore, the strongly fermenting species, such as *De. globosus*, were transferred to *Saccharomyces* and the weakly- or non-fermenting species remained in *Debaryomyces*, with *De. hansenii* as the type species.

The currently used method to describe novelties and distinguish among species of this genus is by sequence analysis of the D1/D2 domains of LSU gene and ITS regions (Kurtzman & Robnett 1998, Kurtzman *et al*. 2011). Sequencing analyses using the D1/D2 domains and the SSU genes showed that *Debaryomyces* species are polyphyletic and segregated into three genera, *Debaryomyces*, *Schwanniomyces* (*emend.*) and *Priceomyces* (Kurtzman & Suzuki 2010). The currently described *Debaryomyces* species include *De. coudertii*, *De. fabryi*, *De. hansenii*, *De. mycophilus*, *De. macquariensis*, *De. marama*, *De. nepalensis*, *De. prosopidis*, *De. psychrosporus*, *De. renaii*, *De. robertsiae*, *De. singareniensis*, *De. subglobosus*, *De. udenii. Debaryomyces vietnamensis* and *De. vindobonensis* (Lee *et al*. 2009, Kurtzman *et al.* 2011, Dlauchy *et al*. 2011, Lopandic *et al.* 2013). *Candida psychrophilla*, although not yet proposed as a new combination within *Debaryomyces*, clusters with the rest of the *Debaryomyces* species in phylogenetic studies. *Debaryomyces hansenii* is the most abundantly isolated, used and studied *Debaryomyces* species. However, as *Debaryomyces* species are phenotypically difficult to separate it is likely that strains assessed in earlier studies have been misidentified.

Debaryomyces species are commonly found in natural sources, like fruit, air, fresh and salt water, soil and phylloplane of different plant species, but what makes this genus very interesting is that it was found to play an important role in the production processes as a natural or added inhabitant of many food products, in particular dairy products (Fröhlich-Wyder 2003), meat and sausages (Samelis & Sofos 2003), and also in fermented soy products sake-moto, wine, tobacco, coffee beans, brines. Many of the products listed are high in salt and this is why the osmo-, halo- and xero-tolerant capabilities of *Debaryomyces* species (Breuer & Harms 2006, Ramos-Moreno *et al.* 2021) play a significant role.

Economical and medical significance

Food and food safety

Debaryomyces species, in particular, *De. hansenii*, is commonly found in dairy products such as cheeses (soft cheeses, semi-hard and hard cheeses, brines and cheese quark), yoghurt, fruit, meat (mostly sausages and dry-meat products) as well as fermented olives, cucumbers and *Fuzhuan* brick-tea (Fleet 1987, Seiler 1991, Viljoen & Greyling 1995, Deak & Beuchat 1996, Boekhout & Robert 2003, Breuer & Harms 2006, Flores & Toldra *et al*. 2011, Xu *et al.* 2011a, Gori *et al*. 2012, Bokulich & Mills 2013, Chen *et al*. 2021a, reviewed in Ramos-Moreno *et al*. 2021).

The occurrence and growth of *Debaryomyces* species in dairy products are favored by their ability to ferment lactose, produce proteolytic and lipolytic enzymes that can metabolise milk proteins and fat, and their capacity to grow at low temperatures, high salt concentrations and low water activities (aw) (Besancon *et al*. 1992, Roostita & Fleet 1996, Wyder & Puhan 1999). The ability of *De. hansenii* to produce branched-chain aldehydes and alcohols contributes to the final cheese flavour and influences the sensory properties of cheeses. In addition, the metabolic activities of *De. hansenii* modify the micro-environment in cheese to the benefit of some desired microorganisms such as *Penicillium roqueforti* (Besancon *et al.* 1992, Roostita & Fleet 1996). However, under uncontrolled conditions in the production of semi-soft and soft cheeses, yeast spoilage, that most likely also include *Debaryomyces* spp., causes off-flavours, softening, gas production, discoloration, and swollen packages, so although mostly known for its beneficial effect in the production of dairy products this genus can also have detrimental effects on the end products (Boekhout & Robert 2003).

The involvement of *Debaryomyces* spp. in meat fermentation has been known since the 1960s (Rankine 1964). However, the precise effect *Debaryomyces* species have on the final product is not known. Individual *Debaryomyces* strains supposedly contribute to the final organoleptic characteristics of meat and therefore have a positive effect with respect to aroma and flavour. These strains were found to have an increased ability to ferment carbohydrates and catabolised amino acids, increasing therefore the production of volatile and aromatic compounds (Flores & Toldra *et al*. 2011, reviewed in Ramos-Moreno *et al*. 2021).

If cereal grains containing *De. hansenii*, were used as animal feed it acted as a stimulating factor for the growth of animals and this species can also induce an immune response in gilt-head sea bream if orally applied to the fish (Reyes-Becerril *et al*. 2008, Medina-Cordova *et al*. 2016).

Biological control agent

Debaryomyces hansenii has applicability as a biological control agent against fungal spoilage in dairy products, processed meats, fruits and cereals (Gori *et al.* 2012, reviewed in Median-Cordova *et al.* 2018, Huang *et al*. 2021a, reviewed in Ramos-Moreno *et al*. 2021,) due to its antagonistic effects against specific contaminating fungi. *Debaryomyces* spp. are not only beneficiary for enhancing the flavour of cheese but they can outcompete undesirable organisms such as *Clostridium* spp. for nutrients and can produce antimicrobial metabolites that inhibit the growth of these organisms in cheese brines (Gori *et al.* 2012). *Debaryomyces* spp. have been proposed to be biocontrol agents in meat products as they contribute to the inhibition of the growth of aflatoxin producing (such as *Aspergillus flavus* and *A. parasiticus*) and ochratoxin producing fungi (such as *Penicillium nordicum*, *P. verrucosum* and *A. westerdijkiae*) (reviewed in Ramos-Moreno *et al*. 2021).

Debaryomyces hansenii is an excellent coloniser of damaged citrus fruits and grows rapidly in wounds on the fruit surface, protecting it against spoilage fungi. It is clear that *Debaryomyces* spp. have great potential in biological control, and cereal grains used as animal feed and can act as a stimulating factor for the growth of animals feeding on the grain (Reyes-Becerril *et al*. 2008, Medina-Cordova *et al*. 2016). However, it should be kept in mind that some clinical isolates of *Debaryomyces* species have been observed, although the species that are commonly associated with the food industry, *De. hansenii* and *De. fabryi* do not seem to be associated with disease in healthy humans and belong to the generally regarded as safe category (Jacques & Casaregola 2008).

Medical importance

Strains of *De. hansenii*, *De. fabryi* and *De. marama* have been reported from human tissue (Kurtzman *et al*. 2011) and although *De. hansenii* has been reported as an emergent pathogen, no clear clinical significance has been documented that this species is responsible for problems in healthy individuals.

Some *Debaryomyces* species tested for antifungal drug resistance (Desnos-Ollivier *et al*. 2012) showed high minimum inhibitory concentrations to some antifungals. These included *De. hansenii*, *De. fabryi*, *De. nepalensis*, *De. marama* to Amphotericin B; *De. prosopidis* to Terbinafin; *De. nepalensis* to Posaconazole; *De. nepalensis*, *De. prosopidis*, *De. udenii*, *De. singareniensis* to Voriconazole; *De. nepalensis*, *De. prosopidis* to Itraconazole and *De. nepalensis*, *De. prosopidis*, *De. udenii*, *De. singareniensis* to Fluconazole. This data concluded that the species isolated from patients, *De. hansenii*, *De. fabryi* and *De. marama*, have no resistance to most of the antifungals tested. However, *De. nepalensis* and *De. prosopidis*, resistant to four and five of the antifungals, respectively, may be potential risks for immunocompromised patients, especially *De. prosopidis* that can also grow at 37 °C.

Research interests

There are 861 publications and 12 476 citations from 2011–2021 in the Web of Science (Fig. 75), with the top 10 most cited articles listed in Table 52. There is an increased interest in *Debaryomyces* spp. as they are known to be extremophilic yeasts, due to their osmo-, halo-, xero- and cryotolerant capabilities (Breuer & Harms

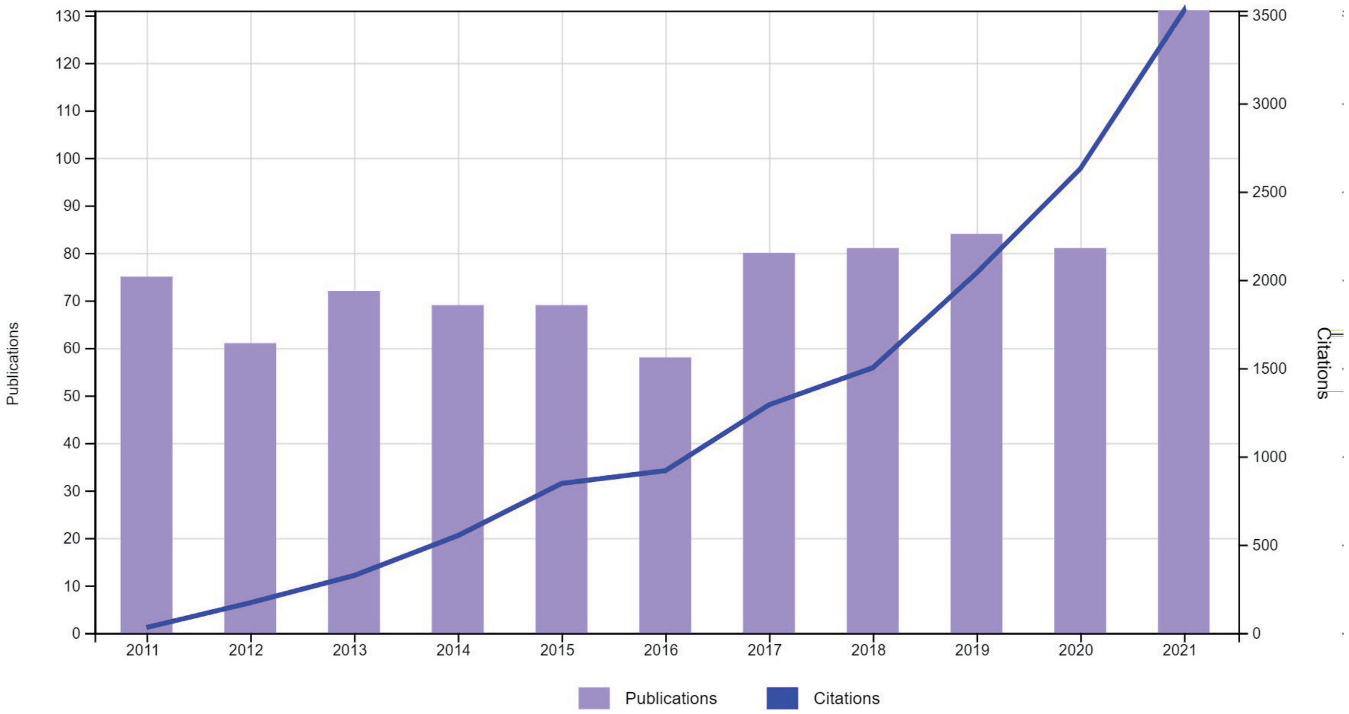

Fig. 75. Trends in research of *Debaryomyces* in the period 2011–2021.

Table 52. Top 10 cited articles related to *Debaryomyces* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Genetic control of biosynthesis and transport of riboflavin and flavin nucleotides and construction of robust biotechnological producers	192	Abbas *et al.* (2011)
2	Fungi in the healthy human gastrointestinal tract	171	Hallen-Adams & Suhr (2017)
3	Brewer's spent grain: A review of its potentials and applications	168	Aliyu & Bala (2011)
4	Facility-specific house microbiome drives microbial landscapes of artisan cheesemaking plants	154	Bokulich & Mills (2013)
5	Antimicrobial activity of lactic acid bacteria against pathogenic and spoilage microorganism isolated from food and their control in wheat bread	147	Cizeikiene *et al.* (2013)
6	Rewiring yeast sugar transporter preference through modifying a conserved protein motif	114	Young *et al.* (2013b)
7	Selection of non-*Saccharomyces* yeast strains for reducing alcohol levels in wine by sugar respiration	111	Quiros *et al.* (2014)
8	Fungal community associated with fermentation and storage of Fuzhuan brick-tea	105	Xu *et al.* (2011a)
9	Functional survey for heterologous sugar transport proteins, using *Saccharomyces cerevisiae* as a host	99	Young *et al.* (2011a)
10	Microbial enzymatic activities for improved fermented meats	95	Flores & Toldra *et al.* (2011)

2006, Ramos-Moreno *et al.* 2021). They have proved on various levels to have considerable biotechnological promise to be used in food production and commercial processes (Ratledge & Tan 1990, Baronian 2004, Breuer & Harms 2006).

Industry

This metabolically versatile non-pathogenic, extremophilic and oleaginous genus represents an attractive target for fundamental and applied biotechnological research in the manufacture of various foods and heterologous synthesis of a range of fine chemicals. As already mentioned, *Debaryomyces* spp. are very important for the food industry and play a role in the production of a variety of cheese and dairy products as well as the fermentation of meat products. They also have great potential as biological control agents and are used as bio-preservatives against fungal spoilage in food products (Reyes-Becerril *et al.* 2016). As an oleaginous yeast, *Debaryomyces* has the ability to synthesise, accumulate and store industrial useful lipids (*e.g.*, sophortose) *Debaryomyces* strains can be induced or manipulated to produce such lipids cost-effectively and could be commercially competitive. Additional industrial interesting compounds to look at for biotechnological production are riboflavin (vitamin B2), o-arabinitol, xylitol, lipases and exopeptidases, termophilic B-glucosidase bioconversion of xylose into the sweetener xylitol, and potential synthesis of arabinitol, pyruvic acid and lytic enzymes (Charoenchai *et al*. 1997, review Breuer & Harms 2006, Satyanarayana & Kunze 2009, Abbas *et al*. 2011, Flores & Toldra 2011).

Biotechnology and future research

As a metabolically versatile, non-pathogenic, extremophilic and oleaginous genus, *Debaryomyces* represents an attractive target for fundamental and applied biotechnological research in the manufacture of various foods, and heterologous synthesis of a range of valuable fine chemicals and polysaccharides (Charoenchai *et al*. 1997, Breuer & Harms 2006, Satyanarayana & Kunze 2009, Abbas *et al*. 2011, Flores & Toldra 2011). This provides great possibilities for alternative biological compounds to be used in food processing, the production of fuel alcohol, the bio-industry and medicine rather than existing chemical processes or to enter new applications in these industries (Satyanarayana & Kunze 2009). It is however essential that these products should be produced competitively with regards to current chemical syntheses to be attractive alternatives that will be further explored in future research. It is suggested that the next biotechnology trends will be to use antagonistic *Debaryomyces* strains to manage fungal diseases and to be integrated into pathogen management in fruits, meat, dairy products and cereal grains while at the same time having the ability to act as probiotics for animals and humans (Reyes-Becerril *et al*. 2016). Therefore, it is likely that this genus will be further explored to be used in above mentioned industrial significant areas in the future (Ratledge & Tan 1990, Baronian 2004, Breuer & Harms 2006).

Author: M. Groenewald

47. ***Metschnikowia*** T. Kamieński, Trudy Imp. S.-Peterburgsk. Obshch. Estestvoisp. 30: 364. 1900.

Type: *Metschnikowia bicuspidata* ((Metschn.) T. Kamieński

Classification: *Ascomycota*, *Saccharomycotina*, *Pichiomycetes*, *Serinales*, *Metschnikowiaceae.*

Background

Metschnikowia lasted six decades as a monotypic genus with only the species used by Eli Metschnikoff (1884) to demonstrate phagocytosis as an immune defense mechanism. Since the re-definition of the genus by Van Uden (1962) membership has grown to well over 70 described species, prompting some to reiterate an urge to divide the genus into smaller units (Kurtzman *et al*. 2018). Having survived potential renaming (Doweld 2015), *Metschnikowia* remains one of the most cohesive genera in the *Saccharomycetes*, as most species share the unique characteristic of forming exactly two aciculate ascospores in elongate to sphaeropedunculate asci. As is typical in biology, exceptions exist, such as the single-spored flexuous asci of *Mets. caudata* (De Vega *et al*. 2014) or the ovopedunculate ascospores of *Mets. lachancei* (Giménez-Jurado *et al*. 2003). Variations in ascus size are extreme, from slightly above 5 µm in *Mets. kunwiensis* to nearly 250 µm in *Mets. hawaiiensis*

(Lachance 2011a). Half the species form a clade (Guzmán *et al*. 2013) consisting exclusively of haplontic, heterothallic species where conjugation often leads to the formation of larger ascospores, up to 50 times the length of typical budding cells. These are primarily associated with floricolous beetles or other insects and are distributed along strong biogeographic lines (Lachance *et al*. 2016). The remaining species exist mostly in the diploid state, where sporulation is environmentally triggered and sometimes preceded by the formation of lipoferous chlamydospores that can give rise to asci (Lachance 2011a).

Ascus formation from chlamydospores can be induced in the laboratory by culturing on diluted V8 agar, a condition that is almost exclusive to those yeast species. Among the diplontic species are several noteworthy subclades (Guzmán *et al*. 2013). One consists of closely related, chlamydospore-forming species capable of producing the iron-rich pigment pulcherrimin, exemplified by *Mets. pulcherrima*; these are often fruit associated. Another subclade consists of mostly marine, invertebrate pathogens that include the type species, *Mets. bicuspidata*. Other chlamydospore formers, although not part of a monophyletic assemblage, have a strong association with nectar, as typified by *Mets. reukaufii*. Responses to growth tests are remarkably similar across the genus. Well-utilised carbon sources include, among others, sucrose, trehalose, β-glucosides, L-sorbose, and N-acetyl-D-glucosamine. Few species grow at 37 °C or in the presence of 10 ppm cycloheximide, but most tolerate the presence of 10 ppm CTAB in growth media, which may facilitate their isolation from natural substrates. *Metschnikowia* shares membership in the family *Metschnikowiaceae* with the smaller genus *Clavispora* as well as a disparate collection of species temporarily assigned to *Candida* while awaiting placement in better-defined genera, which is expected to arise from the determination of genome sequences for all species as well as progress in obtaining ascus formation. Among the *Candida* species, *C. auris* is an important emerging pathogen. Members of the family share the same unique mating locus structure (Lee *et al*. 2018). The *Metschnikowiaceae* together with the *Debaryomycetaceae* constitute the CUG-Ser1 clade, a relatively large collection of yeasts that share the use of an alternative codon usage where the CUG codon is associated with serine instead of leucine (Shen *et al*. 2019).

Ecological and economic significance

***Metschnikowia pulcherrima* is gaining popularity in vinification** due to its β-glucosidase and α-L-rhamnosidase activities, a relatively low H_2S production, and its "killer" activity, which is likely a reference to the production of pulcherriminic acid and its strong inhibitory effect on other microorganisms due to iron sequestration (Comitini *et al*. 2011, Padilla *et al.* 2016b). In co-culture with *Mets. pulcherrima*, *S. cerevisiae* retains its vigour, and the resulting wines are of excellent quality. The yeast does cause a reduction in fermentation rate and ethanol yields, however (Sadoudi *et al*. 2012), but the volatile acidity is low. Reductions in ethanol can be regarded as desirable (Contreras *et al*. 2014) as high ethanol may reduce the quality of wines or interfere with the perception of other aromas. Interestingly, *Mets. pulcherrima* can be supplanted by *S. cerevisiae* by the end of the fermentation due to the better ability of the latter to thrive in the near absence of oxygen (Sadoudi *et al*. 2012). There is a strong synergistic effect in the production of aromatic compounds such as fatty acids and esters, and the modification of the terpenol profile is not biomass dependent, indicating that the interaction itself is a major factor. Barata *et al*. (2012) assigned microbial species encountered in vinification to three categories, oligotrophs, strongly fermentative copiotrophs, and oxidative or moderately fermentative copiotrophs, *Mets. pulcherrima* belonging to the last category. The species is thought to be vectored around the vineyard by *Drosophila*, as opposed to bees or wasps, which are also important parts of this ecosystem. Vicente *et al.* (2020) added *Mets. fructicola* and *Mets. viticola* to the list of species of oenological interest. Four commercial preparations based on *Mets. pulcherrima* or *Mets. fructicola* are used in oenology, either for the prevention of mould damage or as a fermentation adjunct aimed at controlling other microorganisms and enhancing organoleptic properties of the wine.

Biocontrol of fungal damage to crops by species of the *Mets. pulcherrima* clade is now a reality. Fruit crops undergo losses approaching 50 % in some countries (Liu *et al.* 2013c). The causative agents are often moulds that compete with yeasts for nutrients in nature. Antagonistic yeasts can be used as agents of environmentally friendly biocontrol. A small number of diverse yeast species have been studied for their potential. The most efficacious are members of the *Mets. pulcherrima* clade, including *Mets. fructicola* and *Mets. andauensis*. Sipiczki (2006) provided strong evidence that these yeasts act through the depletion of iron caused by the excretion of pulcherriminic acid, which combines with ferric ions, rendering them inaccessible to neighbouring species. He also questioned whether the distinct status accorded to these species is warranted (Sipiczki 2020). It is not entirely inconceivable that economic gain might have played a role in the proliferation of specific epithets. The phylogenetic discontinuity that one would expect between independently evolving populations is difficult to detect in the three aforementioned species as well as *Mets. chrysoperlae*, *Mets. leonuri*, *Mets. rubicola*, *Mets. shanxiensis*, *Mets. sinensis*, and *Mets. zizyphicola*. In addition, GenBank is rife with sequences attached to related but unassigned strains queueing for eventual naming. Following a careful examination of the available data, and having demonstrated unusually high variability in barcode sequences even within individual strains, Sipiczki (2022) reduced nine named species (but not *Mets. chrysoperlae*) to synonymy with *Mets. pulcherrima*. For the sake of clarity, the names used in the original publications are retained in the present discussion. A commercial yeast biocontrol product consisting of a dried culture of *Mets. fructicola* has been developed, first under the name "Shemer", but now to be licensed under the name "Noli" by Koppert Biological Systems. Six such yeast-based products have been developed (Spadaro & Droby 2016). Pulcherrimin formation appears to be the most efficient of several mechanisms by which yeasts exercise interference competition (Liu *et al.* 2013c). Other processes include the production of chitinases, glucanases, or proteases and the induction of plant defences, the first and last of which have been demonstrated in *Mets. fructicola* and *Mets. pulcherrima*. Also important is the ability of biocontrol agents to resist plant defences. *Metschnikowia fructicola* has been shown to be affected, for example, by reactive oxygen species put out on plant surfaces. Lytic enzymes, volatile organic compounds, biofilm formation, fruit wound colonisation, and *in situ* competition also contribute to yeast antagonism, as shown for *Botrytis cinerea* by Parafati *et al*. (2015). Although lytic enzyme activity has not been detected in *Mets. pulcherrima*, the species rates well in all other attributes and is the only one among the species tested that is capable of iron scavenging, which gives it a strong advantage over other species.

The functional and evolutionary genetics of pulcherrimin metabolism in yeasts make for a fascinating story. Krause *et al*. (2018), through a truly Holmesian genome dissection of pulcherrimin-producing yeasts (*Kluyveromyces lactis*, *Mets. fructicola*, and *Zygosaccharomyces mrakii*), showed that these species share a cluster of four genes, two of which code for enzymes that catalyse, respectively, the dimerisation of leucine to cyclo-leucyl-leucine and its isomerisation to pulcherriminic acid. A third gene regulates the process. Pulcherriminic acid spontaneously complexes with ferric ions to form pulcherrimin, a low solubility, ochre pigment that may then be transported to the cytoplasm via the product of a fourth gene. All four genes were found in pulcherrimin-positive strains, but the presence of all four genes does not guarantee pigment production, as for example in *Candida auris*. Pulcherriminic acid production may in some cases benefit other species by recruiting rare iron, which is then taken up in the complexed form by yeasts such as most *Saccharomyces* species, by virtue of the presence of the *PUL4* gene in their genome.

Oil from *Mets. pulcherrima* is the goal set by Abeln & Chuck (2019). The species offers a number of advantages over other oleaginous yeasts such as *Rhodosporidium toruloides* and *Yarrowia lipolytica*, in particular the potential for non-aseptic growth conditions. However, optimal growth and oil generation conditions in *Mets. pulcherrima* do not yet rival those of these other species.

***Metschnikowia reukaufii* is the dominant yeast in the nectar** of many plants. It is vectored mostly by insects, including bees (Brysch-Herzberg 2004, Herrera *et al*. 2009). *Metschnikowia reukaufii* is thought to influence plant fitness in many ways, positive or negative. For example, nectar fermentation can generate enough heat to warm up flowers by several degrees, assisting in their maturation in cold environments (Herrera & Pozo 2010). Microorganisms also alter the nature of mutualistic interactions between plants and their pollinators. However, in an experimental study of the hummingbird-pollinated shrub *Mimulus aurantiacus*, Vannette *et al*. (2013) determined that bacteria of the genus *Gluconobacter*, and not the yeast *Mets. reukaufii*, were responsible for interfering with the bird-plant mutualism by modifying nectar chemistry.

***Metschnikowia bicuspidata* features in a predator-prey model system** centred on water fleas in the genus *Daphnia*. *Metschnikowia* species are often encountered as insect symbionts, but the nature of their interaction with the host is often not clear. In contrast, the *Daphnia* system (McLean & Duffy 2020) involves an eclectic collection of organisms that include vertebrates, crustaceans, algae, bacteria (in particular *Pasteuria ramosa*), viruses, oomycetes, microsporidians, protozoa, and, not least, *Mets. bicuspidata*. Although of theoretical interest, some of these interactions are also of economic importance, as most recently reported by Bao *et al*. (2021) and Zhang *et al*. (2021a), where the yeast causes significant mortality in farmed Chinese mitten crab. Although the crab is a local delicacy of high economic value, it has become an invasive pest in other world regions. A better knowledge of its interaction with *Mets. bicuspidata* may one day provide solutions to both problems.

Research interests

There are 674 publications and 11 995 citations from 2011–2021 in the Web of Science (Fig. 76), with the top 10 most cited articles listed in Table 53. Citation records are often driven by economic impact or model organism status, as is the case for much of the literature in Table 53. But a robust Metschnikowian connection is not always so clear, however. The article by Cray *et al.* (2013) makes the case that yeasts and other microorganisms may be adapted to invade and dominate diverse, open habitats, in contrast to others that are greatly specialised. *Metschnikowia pulcherrima* is given as an example of the former, with *Mets. orientalis* as a counter-example. A justification for this conclusion in the literature, however, is lacking. A simple reference to the article describing *Mets. orientalis* (Lachance *et al*. 2006) would have doubled its (non-

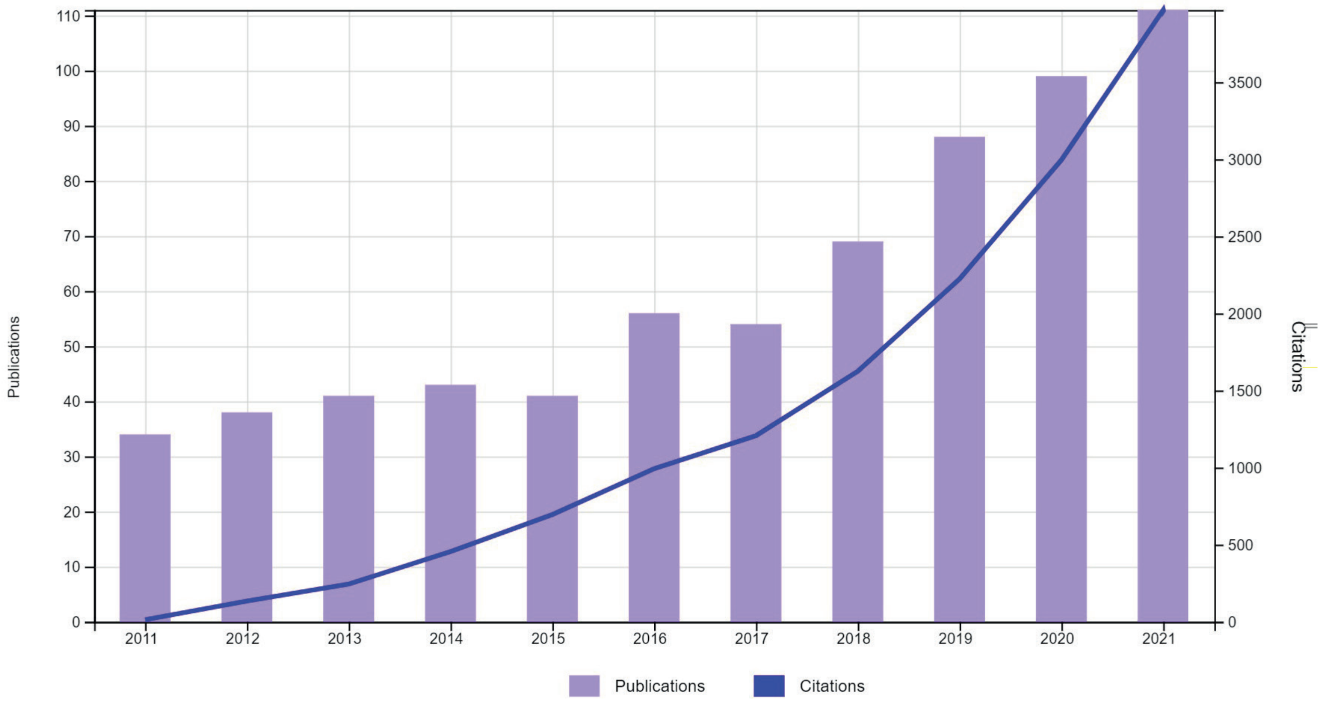

Fig. 76. Trends in research of *Metschnikowia* in the period 2011–2021.

Table 53. Top 10 cited articles related to *Metschnikowia* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Not your ordinary yeast: non-*Saccharomyces* yeasts in wine production uncovered	465	Jolly *et al.* (2014)
2	Selected non-*Saccharomyces* wine yeasts in controlled multistarter fermentations with *Saccharomyces cerevisiae*	366	Comitini *et al.* (2011)
3	The microbial ecology of wine grape berries	360	Barata *et al*. (2012)
4	Development of biocontrol products for postharvest diseases of fruit: The importance of elucidating the mechanisms of action of yeast antagonists	276	Spadaro & Droby (2016)
5	Review: Utilization of antagonistic yeasts to manage postharvest fungal diseases of fruit	273	Liu *et al*. (2013c)
6	Yeast-yeast interactions revealed by aromatic profile analysis of Sauvignon Blanc wine fermented by single or co-culture of non-*Saccharomyces* and *Saccharomyces* yeasts	236	Sadoudi *et al.* (2012)
7	Evaluation of non-*Saccharomyces* yeasts for the reduction of alcohol content in wine	191	Contreras *et al.* (2014)
8	Biocontrol ability and action mechanism of food-isolated yeast strains against *Botrytis cinerea* causing post-harvest bunch rot of table grape	181	Parafati *et al.* (2015)
9	The biology of habitat dominance; can microbes behave as weeds?	159	Cray *et al.* (2013)
10	Nectar bacteria, but not yeast, weaken a plant - pollinator mutualism	142	Vannette *et al*. (2013)

self) citation record. Species descriptions rarely join the citation hall of fame. Of the over 70 *Metschnikowia* currently accepted species, nearly two dozen have been described in the last decade, but few of the articles have rated more than a dozen citations. The 160 citations associated with *Mets. colchici* are therefore in sharp contrast to this but are easily explained by the fact that the description was part of a multi-authored paper (Crous *et al*. 2015) that bundled together 50 short entries. The entry concerning *Mets. colchici* did not make a particularly strong case for its separate status from *Mets. henanensis* from mating experiments, a distinct phylogenetic placement, or a distinct D1/D2 barcode sequence (three substitutions), but the proposed species was reported to assimilate starch, nitrate, and nitrite, each of which on its own would be unprecedented in the genus *Metschnikowia*. In the past, equally startling reports of β-galactosidase activity in *Mets. corniflorae* (Nguyen *et al*. 2006) or the absence of pulcherrimin in *Mets. fructicola* (Kurtzman & Droby 2001) were later found to be mistaken (Lachance 2011a). With that in mind, the author of this review re-evaluated the unexpected assimilations on the type strains of *Mets. colchici* and *Mets. henanensis*. Neither strain utilized nitrate or nitrite. A delayed utilization of dextrin (Difco) was observed in both strains. *Metschnikowia colchici* gave a delayed growth response on 2 % whole potato starch, but not on 2 % soluble starch (both Sigma) or starch at the recommended concentration (0.5 %) for standard growth tests.

Unculturable yeasts

Unlikely to climb to the top of the citation chart is the nonetheless intriguing matter of unculturable yeasts. The paucity of diagnostic morphological features makes yeast identification by microscopy difficult at best. The quintessential example is *Coccidiascus legeri*, known only from morphology. Electron micrographs (Lushbaugh *et al*. 1976) suggest a metschnikowia-like morphology but also hint at a prokaryotic structure. Reports of unculturable *Metschnikowia* species in the gut of beetles have featured daring assertions on their identity and status based on low-definition light micrographs or electron micrographs that fail to capture the gestalt of the material. Weiser *et al*. (2003) described the unculturable species *Mets. typographi* from such images. Recent progress (Kleespies *et al*. 2017) arose when DNA amplified from material containing an uncultured yeast from the gut of Austrian pine bark beetles, circumstantially identified as *Metschnikowia cf. typographi*, showed a strong affinity to *Mets. agaves*, a species found in insect-damaged agave tissue. Whole genome approaches might in the future provide information that will enable researchers to grow these organisms or at least understand why it has hitherto not been possible to culture them.

Author: M.A. Lachance

48. ***Talaromyces*** C.R. Benj., Mycologia 47: 681. 1955.

Type species: *Talaromyces flavus* (Klöcker) Stolk & Samson

Classification: *Ascomycota*, *Pezizomycotina*, *Eurotiomycetes*, *Eurotiales*, *Trichocomaceae.*

Background

Talaromyces was introduced with *Ta. vermiculatus* (syn. *Ta. flavus*) as the generic type characterised by typically yellow cleistothecia having soft walls of interwoven hyphae and ovate to subglobose ascospores with spiny walls (Benjamin 1955). The asexual morphs were commonly classified in *Penicillium* subgenus *Biverticillium* and together were known to form a clade distinct from the main *Penicillium* clade (Berbee *et al.* 1995, Houbraken & Samson 2011). Samson *et al.* (2011) reviewed the taxonomy of *Talaromyces* based on a multigene phylogeny and considered *Penicillium* subg. *Biverticillium*, *Penicillium* subg. *Biverticillata-Symmetrica*, *Erythrogymnotheca*, *Paratalaromyces* and *Sagenoma* as synonyms, while providing new *Talaromyces* combinations for most of these names. A monograph adopting a polyphasic approach was subsequently published with 88 species accepted within seven sections (Yilmaz *et al.* 2014). Similar to *Penicillium*, beta-tubulin was proposed as the sequence marker for species identification. Many new *Talaromyces* species were subsequently introduced. Houbraken *et al.* (2020) reviewed the taxonomy and nomenclature of *Eurotiales,* including an updated species list for *Talaromyces* where 171 species were accepted. More recently, Visagie *et al.* (2024) provided an update, which brought the number to 203 accepted species in *Talaromyces* (currently 218).

Ecological and economic significance

Food mycology and ecology

Talaromyces species are commonly distributed in a wide range of substrates, although mostly in soil. However, new species have been isolated from indoor air, dust, clinical samples, plants, seeds, leaf litter, honey, pollen and stingless bee nests. The main interest of food mycologists lies in their production of heat resistant ascospores and their association with spoilage of pasteurised fruit juices and fruit-based products. The most isolated heat-resistant species include *Ta. bacilisporus*, *Ta. helicus*, *Ta. macrosporus*, *Ta. stipitatus* and *Ta. trachyspermus* (Pitt & Hocking 2009, Yilmaz *et al.* 2014). *Talaromyces trachyspermus* or *Ta. bacillisporus* were recently found in low levels as contaminants of raw material (< 100 CFU/kg) for the food industry, and a traditional pasteurisation process would be insufficient to avoid potential spoilage problems (Tranquillini *et al.* 2017). In addition, *Ta. flavus*, *Ta. funiculosus*, *Ta. pinophilus*, *Ta. purpurogenus*, *Ta. rugulosus* and *Ta. wortmannii* have been found quite frequently in food, including fruit, nuts and cereals (Pitt & Hocking 2009). *Talaromyces islandicus* can cause yellowing of stored rice and has been reported from *e.g.*, flour, peanuts, pecans, soybeans and maize (Sakai *et al.* 2005, Oh *et al.* 2008). Several species have been proven effective biocontrol agents against soil-borne pathogens. *Talaromyces flavus* suppresses *Verticillium* wilt of tomato, eggplant and potato (Marois *et al.* 1984, Fahima & Henis 1995). *Talaromyces* species have been used to parasitise and rot the hyphae and/or sclerotia of *Botrytis cinerea*, *Rhizopus oryzae*, *Pythium graminicola*, *Gibberella fujikuroi*, *Sclerotium rolfsii,* and *Verticillium dahliae* (Naraghi *et al*. 2010, 2012). A marine-derived species *Ta. tratensis* KUFA 0091 proved significant in reducing rice brown spots and dirty panicle disease (Dethoup *et al*. 2018). *Talaromyces* species may have multiple mechanisms to control plant diseases. They were demonstrated to be better adapted than *Trichoderma* to paddy soil and could be developed as eco-friendly BCAs to parasitise the hyphae and sclerotia of *R. solani*, to promote rice growth and yield, and to protect rice crops against rice sheath blight (Abbas *et al.* 2021). Interestingly for food and industry, *Talaromyces* produce a broad range of colours of high industrial relevance. They produce high pigment yields with high stability, and some of the pigments are added-value compounds with bioactive properties (Morales-Oyervides *et al.* 2020). *Talaromyces*, like also *Aspergillus* and *Penicillium*, are ubiquitous fungi and possess the robust metabolic plasticity to interact with hash environmental factors either abiotic or biotic. In this respect, two new marine-derived strains of *Ta. zhenhaiensis* and *Ta. haitouensis,* not taxonomically distinct from their terrestrial counterparts, were recovered from marine habitats while they rare or difficult to find in terrestrial sites (Han *et al.* 2021). Their wide ecological adaptation and distribution in nature render *Talaromyces* species as excellent enzyme producers for plant biomass applications. Their cellulases were recently reviewed (Vaishnav *et al.* 2018), and many strains produce the enzymatic arsenal required to degrade the heterogeneous plant hemicelluloses (Yoon *et al.* 2007, Lee *et al.* 2012). Méndez-Líter *et al.* (2021) reviewed the enzymatic properties of *Penicillium* and *Talaromyces* evidencing the ecological ability of several species, as a response to different lignocellulosic substrates, to produce xylanases, feruloyl esterases, β-xylosidases and arabinofuranosidases. From an industrial perspective, some strains of *Ta. emersonii* and *Ta. thermophilus* produce thermostable endoxylanases, β-xylosidases and xylanolytic auxiliary enzymes (Méndez-Líter *et al.* 2021). Recently, its endophytic role has been evidenced with 46 *Talaromyces* species found associated with 281 plant species belonging to 108 families (Nicoletti *et al.* 2023).

Research interests

There are 1 147 publications and 11 976 citations from 2011–2021 in the Web of Science (Fig. 77), with the top 10 most cited articles included in Table 54. Most publications focused on taxonomy, diseases and secondary metabolites associated with *Talaromyces*.

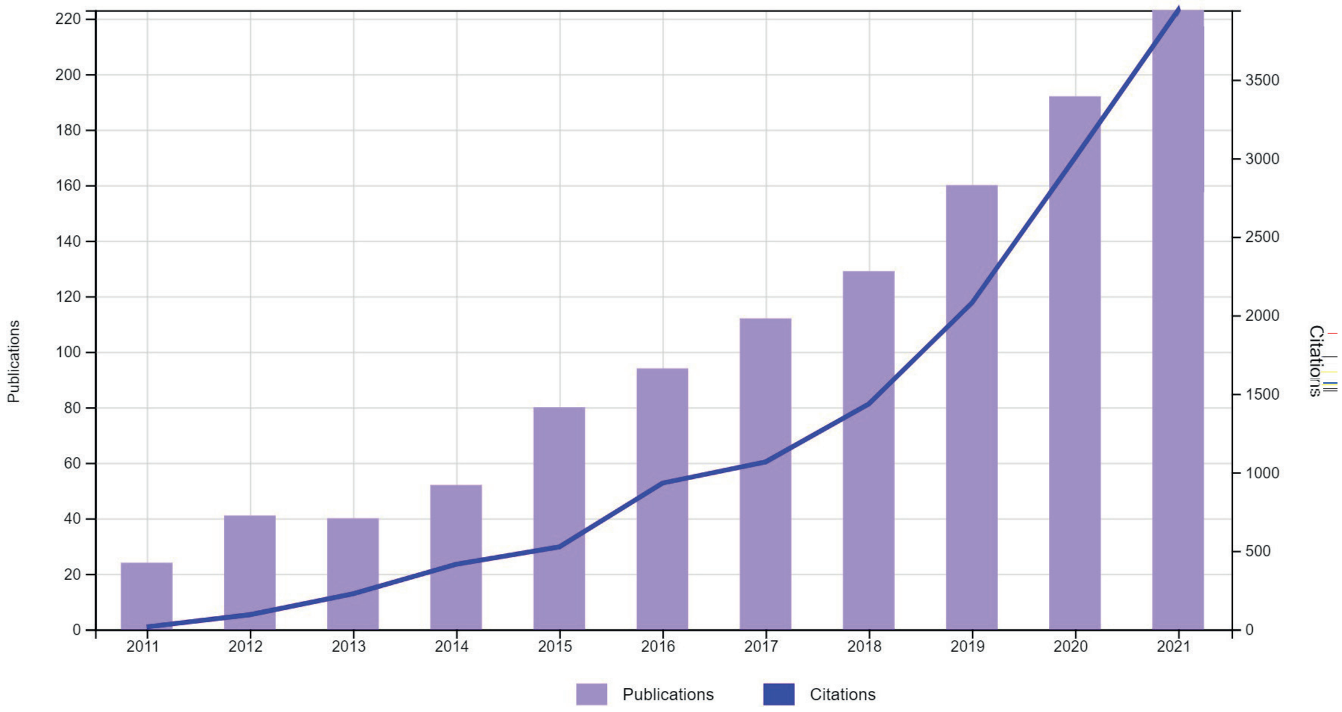

Fig. 77. Trends in research of *Talaromyces* in the period 2011–2021.

Table 54. Top 10 cited articles related to *Talaromyces* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Phylogeny of *Penicillium* and the segregation of *Trichocomaceae* into three families	316	Houbraken & Samson (2011)
2	Phylogeny and nomenclature of the genus *Talaromyces* and taxa accommodated in *Penicillium* subgenus *Biverticillium*	253	Samson *et al*. (2011)
3	Polyphasic taxonomy of the genus *Talaromyces*	202	Yilmaz *et al*. (2014)
4	Fungal infections in HIV/AIDS	175	Limper *et al*. (2017)
5	*Aspergillus*, *Penicillium* and *Talaromyces* isolated from house dust samples collected around the world	148	Visagie *et al*. (2014a)
6	*Penicillium marneffei* infection: An emerging disease in mainland China	143	Hu *et al*. (2013a)
7	*Talaromyces* (*Penicillium*) *marneffei* infection in non-HIV-infected patients	135	Chan *et al*. (2016)
8	Classification of *Aspergillus*, *Penicillium*, *Talaromyces* and related genera (*Eurotiales*): An overview of families, genera, subgenera, sections, series and species	126	Houbraken *et al*. (2020)
9	*Rasamsonia*, a new genus comprising thermotolerant and thermophilic *Talaromyces* and *Geosmithia* species	124	Houbraken *et al*. (2012)
10	Cytotoxic norsesquiterpene peroxides from the endophytic fungus *Talaromyces flavus* isolated from the mangrove plant *Sonneratia apetala*	107	Li *et al*. (2011a)

Extrolites

Being competition selected fungi, *Talaromyces* can produce a very large number of small molecule extrolites (Frisvad *et al*. 1990, Samson *et al*. 2011, Yilmaz *et al*. 2014, Frisvad 2015), but they share few of these with *Aspergillus* and *Penicillium*. Important drugs or promising drug lead candidates produced by *Talaromyces* species include wortmannin a potential anticancer drug (Kornienko et *al*. 2015, Gambardelli *et al*. 2021) and the anticancerogenic rubratoxin A (Wada *et al.* 2010). Many other promising bioactive secondary metabolites have been found in *Talaromyces* species (Nicoletti & Trincone 2016). Mycotoxins produced by *Talaromyces* species include the hepatotoxin rubratoxin B produced by *Ta. purpureogenus* (Yilmaz *et al*. 2012), rugulosin produced by *Ta. islandicus*, *Ta. rugulosus* and other *Talaromyces* species in section *Islandici* (Yilmaz *et al*. 2016), and cyclochlorotin and luteoskyrin from *Ta. islandicus* (Uraguchi *et al*. 1972).

Authors: G. Perrone, C.M. Visagie, J.C. Frisvad and N. Yilmaz

49. ***Geotrichum*** Link, Mag. Gesell. Naturf. Freunde, Berlin 3(1–2): 17. 1809.

Type species: *Geotrichum candidum* Link

Classification: *Ascomycota*, *Saccharomycotina*, *Dipodascomycetes*, *Dipodascales*, *Dipodascaceae.*

Background

Geotrichum is a ubiquitous filamentous yeast-like fungus, which is commonly isolated from soil, air, water, milk, silage, plant tissues, and they can also be pathogenic causing skin disease in humans and animals (Dolensek *et al.* 1977, Chahota *et al.* 2001, Pottier *et al.* 2008, Miceli *et al.* 2011). *Geotrichum* is generally characterised by the presence of arthroconidia with schizolytic conidial secession in a random order, and the conidial septal walls are perforated by micropores (De Hoog & Smith 2004). The taxonomy of this genus has been continuously studied in recent decades (Butler 1960, De Hoog *et al.* 1986, Guého *et al.* 1987, Smith *et al.* 2000b). Phylogenetic analyses showed that *Geotrichum* species, as well as their sexual morphs, formed several divergent groups with remarkable diversity in the ITS sequence, which resulted in the modifications of the sexual/asexual genera (De Hoog & Smith 2004). The sexual morphs *Dipodascus* and *Galactomyces* have been linked with *Geotrichum* based on 18S, 26S and ITS sequence data (De Hoog & Smith 2004).

Ecological and economic significance

Geotrichum species have attractive benefits for humans because of their great biotechnological potential such as improving cheese flavour in the food industry, and biodegradation and decolourisation in the environmental protection industry. They are however also pathogenic, causing fungal infections in plants, humans and other mammals. For example, *Geotrichum candidum* is an important post-harvest pathogen which causes sour rot in ripe and over-ripe fruits such as citrus, kiwifruit, loquat, mulberry, peach and strawberry (Hafeez *et al.* 2015, Alonzo *et al.* 2020, Cheng *et al.* 2021a, Lu *et al.* 2021). Infection detracts from the quality of fresh fruits during harvesting, storage, transportation and marketing operations, leading to great economic losses (Zhang *et al.* 2018b).

Research interests

There are 794 publications and 11 900 citations from 2011–2021 in the Web of Science (Fig. 78), with the top 10 most cited articles listed in Table 55. Most publications focused on disease infections and management (pathogens of humans, biological control of postharvest diseases on citrus and other fruits), application (cheese products, biodegradation and decolourisation), as well as taxonomy.

Pathogens of humans

Geotrichum candidum can colonise human skin, respiratory tract and gastrointestinal tract. The pathogenicity of *Geotrichum* species to humans should not be underestimated, especially in the immunocompromised population (*e.g.*, HIV, alcoholism, critical illness, immunosuppressant use, diabetes mellitus). For example,

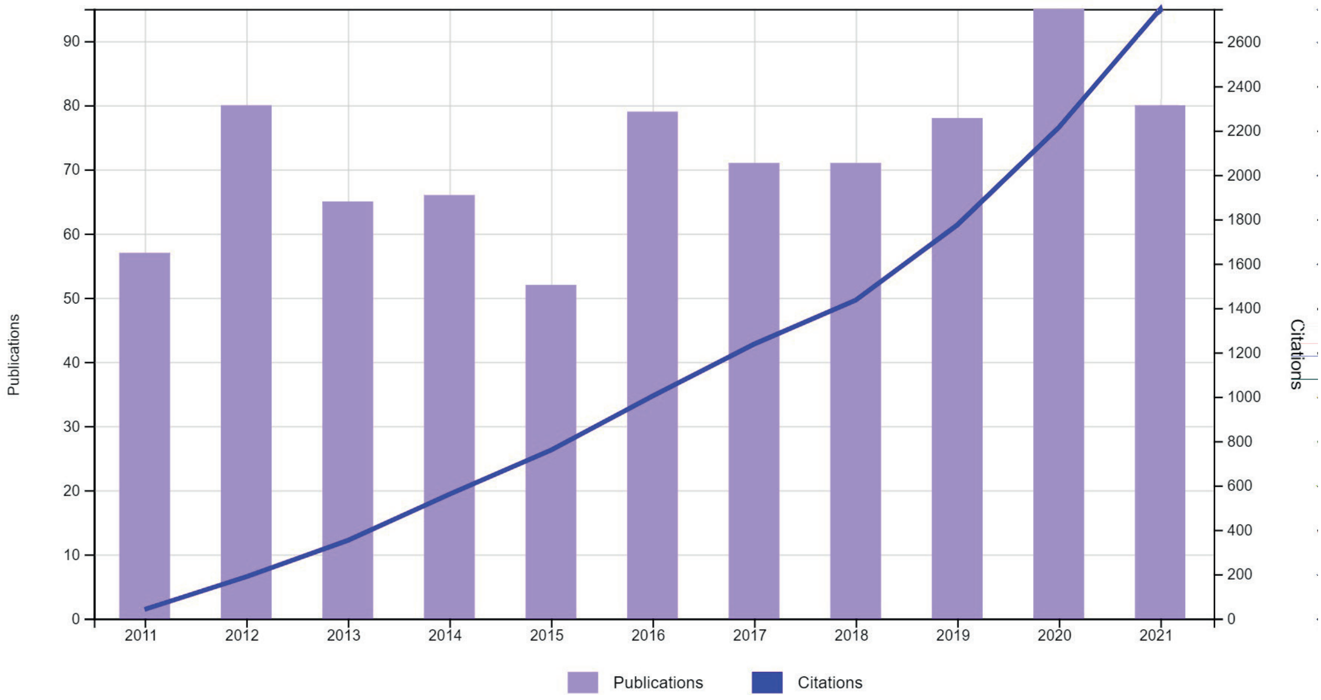

Fig. 78. Trends in research of *Geotrichum* in the period 2011–2021.

Kassamali *et al.* (1987) reported one patient with acute leukaemia who was infected by *Ge. candidum*, which indicated the potential virulence of the fungus in such patient population. Heinic *et al.* (1992) reported a *Ge. candidum* infection associated with human immunodeficiency virus (HIV) infection. The patient responded well after treatment with nystatin tablets. Prakash *et al.* (2012) reported a case of renal fungal bezoar caused by *Ge. candidum* in a female patient in the postpartum period. Bilman & Yetik (2017) detected *Ge. candidum* reproduction in urinary tract infection in a 74-yr-old man who developed severe pain in the lumbar region. Keene *et al.* (2019) reported the first case of cutaneous geotrichosis by *Ge. candidum* infection in a patient with severe thermal burns. Antifungal resistance and breakthrough disease are an ongoing concern due to the increasing number of at-risk patients and the use of routine mould prophylaxis (Keene *et al.* 2019). Enhanced knowledge of *Geotrichum* infection in immunocompromised patients with accurate and rapid identification is crucial to improve diagnosis and contribute toward their effective antifungal therapy.

Biological control of postharvest diseases on citrus and other fruits

Geotrichum candidum and *Ge. citri-aurantii* are the major causal agents of postharvest sour rot in citrus and other fruits worldwide. They have therefore received great attention and scientific interest in disease management and antifungal activities. Salts and food additives have been used for the control of citrus post-harvest diseases (El-Mougy *et al.* 2008, Talibi *et al.* 2014). Soto-Muñoz *et al.* (2022) found that two edible coating emulsions based on potato starch formulated with 2 % w/w sodium benzoate significantly reduced sour rot incidence and severity compared to uncoated control samples on lemons incubated at 28 °C for 4 and 7 d. The use of natural plant-derived compounds is an interesting useful alternative approach for disease control. Talibi *et al.* (2012) determined the antifungal activity of some Moroccan plants against *Ge. candidum* postharvest citrus fungal pathogens. Among the 43 plant species tested *Cistus villosus*, *Halimium antiatlanticum*, *H. umbellatum*, *Pistacia lentiscus* and *Inula viscosa* showed

Table 55. Top 10 cited articles related to *Geotrichum* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Emerging opportunistic yeast infections	530	Miceli *et al.* (2011)
2	ESCMID and ECMM joint clinical guidelines for the diagnosis and management of rare invasive yeast infections	305	Arendrup *et al.* (2014)
3	Isavuconazole: A new broad-spectrum Triazole antifungal agent	177	Miceli *et al.* (2015)
4	Fungi in the healthy human gastrointestinal tract	171	Hallen-Adams *et al.* (2017)
5	Fabrication of fungus/attapulgite composites and their removal of U(VI) from aqueous solution	115	Cheng *et al.* (2015)
6	Alternative methods for the control of postharvest citrus diseases	114	Talibi *et al.* (2014)
7	Antifungal activity of citral, octanal and alpha-terpineol against *Geotrichum citri-aurantii*	99	Zhou *et al.* (2014a)
8	Filamentous fungi and mycotoxins in cheese: A review	97	Hymery *et al.* (2014)
9	Anti yeast activities of some essential oils in growth medium, fruit juices and milk	90	Tserennadmid *et al.* (2011)
10	Microbial community dynamics during fermentation of doenjang-meju, traditional Korean fermented soybean	82	Jung *et al.* (2014)

high antifungal activities against *Ge. candidum* both *in vitro* and *in vivo*. Zhou *et al.* (2014a) found that three volatile compounds (citral, octanal, and a-terpineol) exhibited strong antifungal activity against *Ge. citri-aurantii*, with minimum inhibitory concentration and minimum fungicidal concentration of 0.50 µL/mL and 1.00 µL/mL, 0.50 µL/mL and 2.00 µL/mL, and 2.00 µL/mL and 4.00 µL/mL, respectively. Management of postharvest diseases using microbial antagonists, which are generally recognised as safe compounds and natural plant-derived products are suitable alternative methods to replace synthetic fungicides because of their antifungal activity, biodegradability, nonphytotoxicity and systemicity (Talibi *et al.* 2014). Therefore, the development of appropriate tools to effectively implement these alternative methods is necessary to provide more effective disease control for commercial citrus and other fruit production.

Cheese products

There has been a lot of interest in making cheese with *Geotrichum candidum* due to its many different metabolic pathways (Jollivet *et al.* 1994, Boutrou & Guéguen 2005, Sacristán *et al.* 2013, Lessard *et al.* 2014, Jaster *et al.* 2019). *Geotrichum candidum* can contribute to the maturation of cheese, as well as ripening and flavour formation and its application in the dairy industry was reviewed by Boutrou & Guéguen (2005).

Biodegradation and decolourisation

Geotrichum candidum is very efficient in the decolourisation of fresh and stored black olive mill wastewater, textile effluent, acid scarlet and molasses (Kim & Shoda 1999, Assas *et al.* 2000, Govindwar *et al.* 2014, Guo *et al.* 2019a, Ahmed & Sohail 2020). Borja *et al.* (1993a, b) reported that *Ge. candidum* was capable of removing phenolic compounds from molasses and distillery wastewater. FitzGibbon *et al.* (1998) showed that *Ge. candidum* was efficient for the biodegradation of distillery wastewater with evidence of fungal growth rates increasing in the presence of gallic acid. Kim & Shoda (1999) showed that *Ge. candidum* successfully decolourised molasses and an anthraquinone dye in shaken flasks after 12 and 7 d of cultivation, respectively. Interest in studying biodegradation and decolourisation by *Geotrichum* species, as well as its relatives, is increasing (Dieuleveux *et al.* 1998, Assas *et al.* 2000, 2002, Jadhav *et al.* 2008a, b, Govindwar *et al.* 2014, Guo *et al.* 2019a).

Taxonomy and phylogeny

Gente *et al.* (2006) proposed a standardised protocol for the identification of *Geotrichum candidum* at the species and strain level with primers M13 and GATA4. The current classification of *Geotrichum* and its sexual morph *Galactomyces* is based on morphology, ecology, biochemistry, DNA-DNA reassociation comparisons, gene sequencing, phylogenetic analyses and mating compatibility (Groenewald *et al.* 2012). More work is needed for a standard systematic classification.

Author: M. Doilom

50. ***Pestalotiopsis*** Steyaert, Bull. Jard. Bot. État Bruxelles 19: 300. 1949.

Type species: *Pestalotiopsis maculans* (Corda) Nag Raj

Classification: *Ascomycota*, *Pezizomycotina*, *Sordariomycetes*, *Xylariales*, *Sporocadaceae.*

Background

Pestalotiopsis is an appendage-bearing conidial form of Sporocadaceae with many species (Liu et al. 2019a). The genus was erected by Steyaert (1949) to describe the species Pes. guepinii. However, Nag Raj (1985) pointed out that the use of Pes. guepinii as the generic type of the genus Pestalotiopsis is contentious. He regarded Pes. maculans as the generic type of Pestalotiopsis and as the correct, older name for Pes. guepinii with Pes. guepinii as a synonym. According to Index Fungorum (2024), there are 406 names, while in MycoBank there are 377 names. Many of these names have traditionally been applied according to their host association (Tejesvi et al. 2009). However, sequence data has shown that host association and geographical location are less informative in their classification (Maharachchikumbura et al. 2012). The sexual morph of Pestalotiopsis is recognised as Pestalosphaeria M.E. Barr. Since Pestalotiopsis is the oldest and most commonly used name, Maharachchikumbura et al. (2011) suggested that this name be adopted for the sexual and asexual forms.

Pestalotiopsis comprises complexes of morphologically indistinguishable species that are closely related to each other. Maharachchikumbura *et al.* (2012) evaluated three ribosomal RNA regions and seven protein-coding markers for suitability in resolving species in *Pestalotiopsis*. Because of greater amplification and high-resolution power, ITS, *tub* and *tef1* proved to be better markers. Conidial morphology, such as the colour of the median cells, is a widely used character in *Pestalotiopsis* taxonomy. Considering conidial pigmentation, conidiophores character and sequence data, Maharachchikumbura *et al.* (2014) segregated *Pestalotiopsis* into three genera: *Neopestalotiopsis*, *Pseudopestalotiopsis* and *Pestalotiopsis*. *Pestalotiopsis* is characterised by septate conidiophores that are unbranched and often reduced to conidiogenous cells. The conidiogenous cells are ampulliform to lageniform or cylindrical to subcylindrical phialides, and the conidia have concolourous median cells. *Neopestalotioposis* conidiophores are indistinct, and median cells are versicolourous, while *Pseudopestalotiopsis* is characterised by indistinct conidiophores and median cells are generally dark-coloured and concolourous. These genera can be approximately assigned to separate groups based on the ITS region.

Ecological and economic significance

Plant pathogens

Pestalotiopsis species have a cosmopolitan distribution and accommodate mostly terrestrial taxa, although several can be found in aquatic environments (Maharachchikumbura *et al*. 2011). They are common phytopathogens that cause a variety of diseases, decrease production and cause economic loss in apple, blueberry, chestnut, grapevine, guava, mango, orchid, peach, rambutan, strawberries and tea (Sun & Cao 1990, Sangchote *et al.* 1998, Keith *et al.* 2006, Ismail *et al.* 2013a, Maharachchikumbura *et al.* 2013a, b, 2016, Jayawardena *et al.* 2015, 2022, Morales-Mora *et al.* 2019, Silva *et al.* 2020a). It has been estimated that in southern India, grey blight disease of tea caused by pestalotiopsis-like taxa resulted in 17 % yield loss (Joshi *et al.* 2009) and 10–20 % yield decline in Japan (Horikawa 1986). Some species cause human and animal infections. Pestalotiopsis-like taxa have been isolated from the human sinuses, fingernails, a bronchial biopsy, eyes, scalp and feet with corneal abrasions (Sutton 1999, Monden *et al.* 2013).

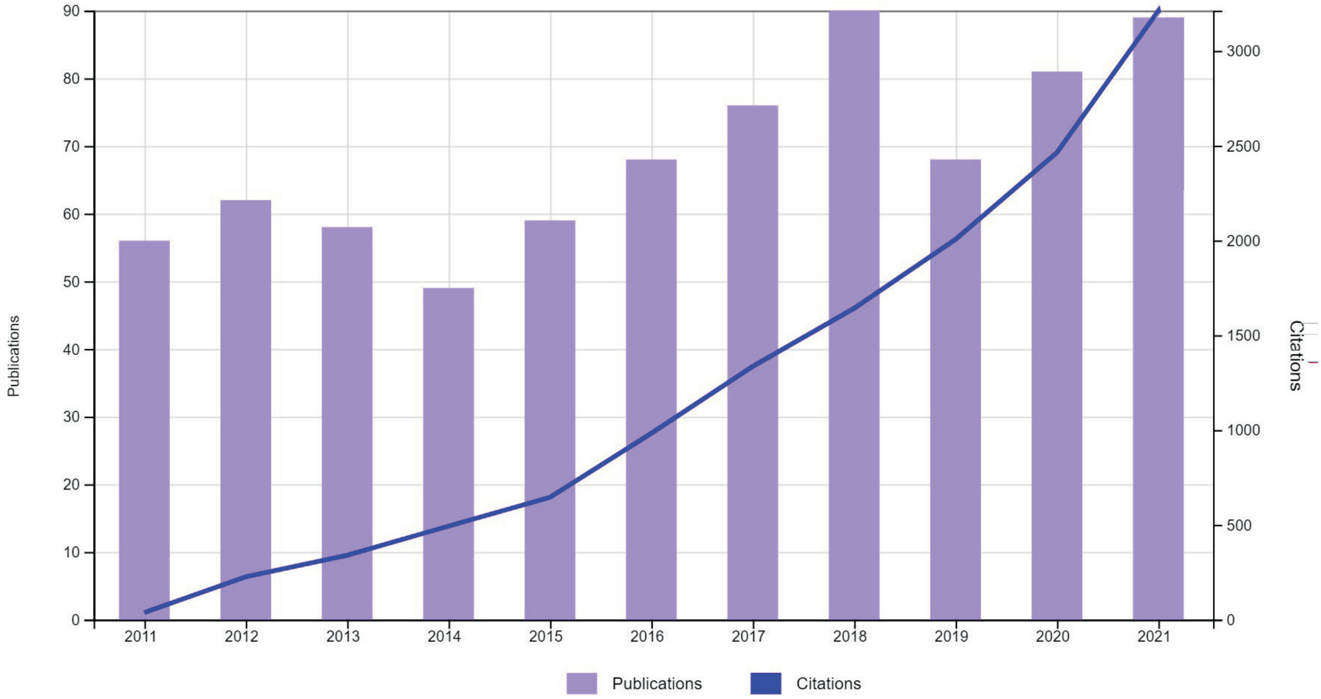

Fig. 79. Trends in research of *Pestalotiopsis* in the period 2011–2021.

Secondary metabolites producers

Species of *Pestalotiopsis* are frequently isolated as endophytes that reside in plants without causing apparent symptoms of disease or occur as saprobes (Xu *et al.* 2010, Tian *et al.* 2022, Samaradiwakara *et al.* 2023). There are numerous reports that these endophytes have an enormous potential to produce active compounds constituting a new way to obtain various precursors or novel molecules useful in agriculture, medicine, and industrial applications (Xu *et al.* 2010, 2014). Chemical exploration of endophytic *Pestalotiopsis* subsequently increased exponentially, and these genera are the most studied fungal group for secondary metabolic products in the preceding 15 years. Xu *et al.* (2010, 2014) reviewed 130 and 160 different compounds, respectively, isolated from species of pestalotiopsis-like taxa. These included bioactive alkaloids, terpenoids, isocoumarin derivatives, coumarins, chromones, quinones, semiquinones, peptides, xanthones, xanthone derivatives, phenols, phenolic acids, and lactones with a range of antifungal, antimicrobial, and antitumor activities.

Research interests

There are 759 publications and 11 758 citations from 2011–2021 in the Web of Science (Fig. 79), with the top 10 most cited articles listed in Table 56. Most publications focused on taxonomy, phylogeny, description of new species, biochemistry and bioactive metabolites from endophytic *Pestalotiopsis*.

Table 56. Top 10 cited articles related to *Pestalotiopsis* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	*Pestalotiopsis* revisited	242	Maharachchikumbura *et al.* (2014)
2	One stop shop: backbones trees for important phytopathogenic genera: I (2014)	235	Hyde *et al.* (2014)
3	Biodegradation of polyester polyurethane by endophytic fungi	201	Russell *et al.* (2011)
4	Towards unraveling relationships in *Xylariomycetidae* (*Sordariomycetes*)	173	Senanayake *et al.* (2015)
5	*Pestalotiopsis*—morphology, phylogeny, biochemistry and diversity	172	Maharachchikumbura *et al.* (2011)
6	A multi-locus backbone tree for *Pestalotiopsis*, with a polyphasic characterisation of 14 new species	167	Maharachchikumbura *et al.* (2012)
7	Endophytic fungi from medicinal plants: a treasure hunt for bioactive metabolites	154	Kaul *et al.* (2012)
8	Species delimitation in fungal endophyte diversity studies and its implications in ecological and biogeographic inferences	149	Gazis *et al.* (2011)
9	Characterization of fungal pathogens associated with grapevine trunk diseases in Arkansas and Missouri	106	Urbez-Torres *et al.* (2012)
10	The taxonomy, biology and chemistry of the fungal *Pestalotiopsis* genus	87	Yang *et al.* (2012e)

Emerging fungal pathogens

Pestalotiopsis is reported to cause various new diseases globally and to have expanded way beyond its natural host range in the recent past. *Pestalotiopsis* species described initially as endophytes may adapt to a new host and alter their life modes becoming plant pathogens and causing different novel diseases. Early diagnosis of these cryptic pathogens and understanding pathogen-host interactions will enable the development of a comprehensive set of measures to control diseases.

Secondary metabolites

Pestalotiopsis is one of the most biologically diverse groups of fungi that have great potential to produce new active compounds (Xu *et al*. 2010). The secondary metabolites of *Pestalotiopsis* species are highly diverse and synthesised through various biosynthetic pathways (Helaly *et al*. 2018). However, exploration of secondary metabolites is limited because of a lack of detection methods and culture conditions (Bills *et al.* 2013). Therefore, in further research, new methods and detection techniques should be developed. Furthermore, isolating new substances may be achieved by activation of weakened or dormant gene clusters that encode the formation of previously unknown secondary metabolites. These predominantly endophytic organisms have a fascinating ecology that makes them highly suitable as candidate organisms for biocontrol.

Taxonomy and phylogeny

The identification of *Pestalotiopsis* species only on a morphological basis is often difficult (Maharachchikumbura *et al.* 2011, 2014). For this reason, the use of molecular data for the identification of species has increased rapidly. However, the available gene regions lack species level resolution for several cryptic species complexes in *Pestalotiopsis*. Therefore, it is essential to utilise additional loci in future studies to identify cryptic species in *Pestalotiopsis*.

Author: S.S.N. Maharachchikumbura

51. ***Microsporum*** Gruby, C. R. Hebd. Séanc. Acad. Sci., Paris 17: 302. 1843.

Type species: *Microsporum audouinii* Gruby

Classification: *Ascomycota*, *Pezizomycotina*, *Eurotiomycetes*, *Onygenales*, *Arthrodermataceae.*

Background

Microsporum is a name that until recently was applied to a phylogenetically diverse group of fungi in the family *Arthrodermataceae.* This family lies within the protein-loving order *Onygenales*, which contains many of the best-known fungal pathogens infecting humans, other mammals, birds and reptiles. After phylogenetic analysis (De Hoog *et al.* 2017), *Microsporum* was restricted to three closely related species. The most common is *Microsporum canis*, a cosmopolitan zoophilic dermatophyte ("zoophilic" = an ecological class for skin pathogens with non-human mammalian primary population hosts). In addition, *Mi. canis* has engendered two anthropophilic (specifically human-adapted) unifactorial radiate lineages (Summerbell 2002), type species *Mi. audouinii* and the uncommon and likely endangered *Mi. ferrugineum*. Among the prominent species recently removed from *Microsporum* are the geophilic dermatophytes (potentially human- and animal-infecting but primarily saprobic and soil-associated) in the *Nannizzia gypsea* multi-species complex and the associated *N. persicolor*, as well as the poultry- and occasionally human-infecting *Lophophyton gallinae*, and the geophilic non-pathogen *Paraphyton cookei*.

Microsporum was introduced by physician David Gruby in 1843 as a concept encompassing a disease presentation, namely, the appearance of masses of small spores coating the hair shafts of children with *Microsporum audouinii* scalp infections (Sabouraud 1910). It was not reliably described from culture until some years later by Raymond Sabouraud. *Microsporum canis*, at first mainly observed from infected dogs and cats, was first named as a variety of *Mi. audouinii* by Eugène Bodin in 1900 but shortly thereafter in 1902 was upgraded to species status by the same author (Sabouraud 1910, De Hoog *et al.* 2017). The third currently phylogenetically sanctioned member of the genus, *Mi. ferrugineum*, was described by Masao Ota and Maurice Langeron in 1921 based on human hair and skin infections studied by the former in Japanese-occupied Manchuria (Kitamura 1957).

The relationship between the three *Microsporum* species is unusual. *Microsporum canis*, clearly the ancestral species, is known from a worldwide near-clonal lineage of "minus" mating type established as a skin-infecting population on cats and less commonly on horses, as well as from a single phylogenetically distant isolate representing the "plus" mating type (Kaszubiak *et al.* 2004). The main population crosses over to infect various other species, including humans, but infections and outbreaks in these occasional hosts are usually self-limiting, and a permanent population is not known to be established. The species' derivative based on a fully successful host-jump to humans, *Mi. audouinii*, is a product of the ancestral "plus" mating type and is much more closely related to CBS 495.86, the "plus" mating type tester strain of *Mi. canis*, than to the cosmopolitan 'minus' cat lineage of that species. *Microsporum ferrugineum* appears to constitute an independent host-jump to humans, though also derived from the "plus" mating type. The mating-type relations outlined here can be confirmed both by analysis of *MAT* mating type idiomorph as well as, in some isolates, by the long-standing technique of mating with testers of *Trichophyton simii* (Kosanke *et al.* 2018, Stockdale 1968).

Microsporum species on the host appear only as mycelium or substrate-arthroconidia; the latter, historically called "arthrospores", are infectious elements that appear mostly on the surfaces of infected scalp hairs. They have some ability to disarticulate rhexolytically, but otherwise have no perceptible ontogenetic relation with the rhexolytically dehiscing macro- and micro- aleuriocondia that form in culture. In appearance, they resemble typical fungal chlamydospores. Growth of *Mi. canis* in culture is distinguished by formation of two types of aerial aleurioconidia (rhexolytically dehiscing specialised side-branches formed only above the substrate line): macroconidia, which are fusoid in shape, beaked at the apex, superficially encrusted with rough material, 40–150 × 8–20 µm and 7–16-celled; and microconidia, which are small (3–5 µm long), unicellular, droplet-shaped and smooth-walled.

Conidiation in derivative species and some atypical isolates is not as regular as in typical *Mi. canis* isolates. *Microsporum* is affected by the common trend among dermatophytes for conidiation to become reduced or atypical in lineages that have hosts whose ecologies do not provide hair-rich soil as an alternative growth site (Summerbell 2000). Thus, *Mi. audouinii* makes only infrequent, poorly formed *Mi. canis*-like macroconidia, often lacking most internal septa; many isolates make no macroconidia at all, and some also make no microconidia. *Microsporum ferrugineum* has essentially completely lost aerial conidiation, although a few conidium-like structures have rarely been induced. Even within

Mi. canis, a form previously known as the variety "*distortum*" (now with no separate taxonomic status) produces only highly irregular macroconidia, while lineages in the now synonymised horse population formerly called *Mi. equinum*, when they can be induced to produce macroconidia on special media, form structures that are only 2–4 cells long (occasionally to 8 cells), 18–60 × 5–13 µm (Kane *et al.* 1982).

When the "plus" and "minus" forms of *Mi. canis* are mated, spherical ascomata 280–700 µm in diameter are formed with loosely interwoven, branching, echinulate peridial hyphae bearing straight to spiralling, terminal, spiny protective appendages up to 150 µm long. Ascospores are formed in rounded, 8-spored, evanescent asci and are smooth and lenticular, 2.5–4.8 × 2–2.5 µm. These ascomata in the pre-2013 era of dual fungal nomenclature at first bore the name *Nannizzia otae,* later recombined as *Arthroderma otae*. Both generic names, *Nannizzia* and *Arthroderma* are currently validly applied to other clades in phylogenetic systematics.

Ecological (including medical and veterinary) and economic significance

Microsporum canis is primarily an agent of subclinical skin infection in cats that live in groups, such as the common feral cats of the Mediterranean area (often seen in restaurant patios), barn cats, and cats raised in breeding catteries (Nenoff *et al.* 2014). Though often causing minimal symptomatology, the infection is easily detected in the clinic, since infecting elements of *Mi. canis* fluoresce yellow-green in a Wood's Lamp (ultraviolet at ~ 365 nm). Economic interest in *Mi. canis* derives in large part from its common occurrence in the human scalp and upper-body skin infections (face, trunk, arms) based almost entirely on recent contact with infected cats. In many parts of the world, it has proliferated as the most common cause of tinea capitis (dermatophytic scalp infection) (Rodríguez-Cerdeira *et al.* 2020) and upper-body dermatophytosis (tinea corporis) in general. It is especially prominent in Europe, North Africa, China, New Zealand and Mexico (Rodríguez-Cerdeira *et al.* 2020, Xiao *et al.* 2022). In urban areas worldwide influenced by recent immigration from Africa, the anthropophilic *Mi. audouinii* may become more common than *Mi. canis* as a scalp ringworm fungus (Rodríguez-Cerdeira *et al.* 2020), although it grows almost exclusively in children (Borman & Summerbell 2019). In North American cities and the Caribbean, *Trichophyton tonsurans* predominates as the main childhood tinea capitis agent, while in Africa, *T. soudanense*, *Mi. audouinii*, *T. violaceum* and *Mi. canis* each predominates in partially overlapping regions (Rodríguez-Cerdeira *et al.* 2020).

Microsporum ferrugineum is seen uncommonly in a few scattered areas of continued endemicity, such as parts of China, southern Ethiopia, and parts of Macedonia, and like the more frequently seen *Mi. audouinii*, is occasionally brought into western Europe via immigration (Nenoff *et al.* 2020).

Research interests

There are 1 176 publications and 11 474 citations from 2011–2021 in the Web of Science (Fig. 80), with the top 10 most cited articles listed in Table 57. Three of the five most cited publications focused on molecular biosystematics or genomic research shedding insight into relationships and mechanisms of pathogenicity. Three of the top ten publications, including two of the top five, were clinical reviews focused towards updating physicians on some or all of the common topics of practical interest: biosystematics/nomenclature, epidemiology, pathogenesis and therapy. A similar review, also in the top ten, was directed at veterinarians. Of the three non-DNA-based experimental studies in the top ten, one investigated the susceptibility to a novel commercially marketed antifungal agent, one investigated a novel approach to laboratory species identification with MALDI-TOF spectroscopy, and one investigated the inhibitory effects of some natural plant extracts. The array of topics considered in the top 10 publications gives an excellent overview of current topics of activity by researchers investigating *Microsporum*. Four relatively prominent topics abstracted from those mentioned above are commented on further below.

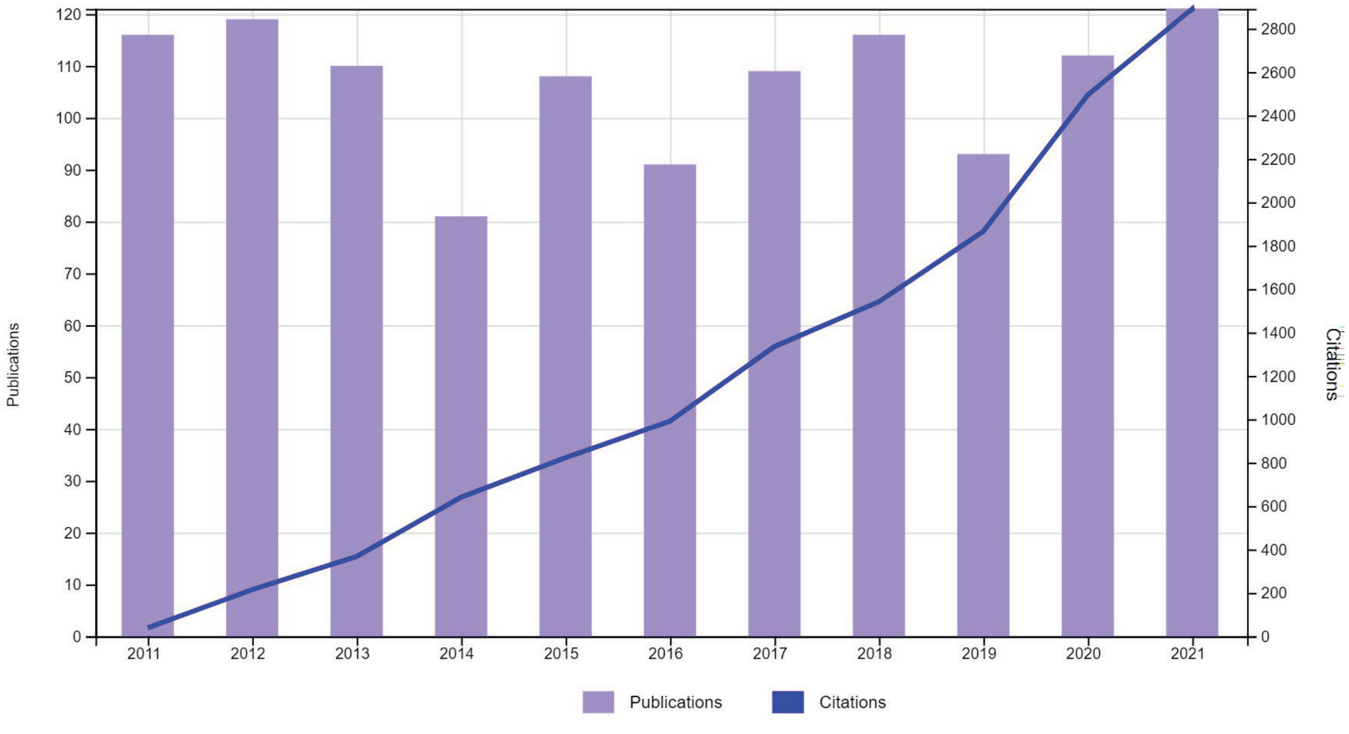

Fig. 80. Trends in research of *Microsporum* in the period 2011–2021.

Table 57. Top 10 cited articles related to *Microsporum* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Toward a novel multilocus phylogenetic taxonomy for the dermatophytes	264	De Hoog *et al.* (2017)
2	Mycology - an update. Part 1: dermatomycoses: causative agents, epidemiology and pathogenesis	162	Nenoff *et al.* (2014)
3	Comparative genome analysis of *Trichophyton rubrum* and related dermatophytes reveals candidate genes involved in infection	150	Martinez *et al.* (2012)
4	Comparative and functional genomics provide insights into the pathogenicity of dermatophytic fungi	137	Burmester *et al.* (2011)
5	The changing face of dermatophytic infections worldwide	123	Zhan *et al.* (2017)
6	Comparison of *in vitro* antifungal activities of efinaconazole and currently available antifungal agents against a variety of pathogenic fungi associated with onychomycosis	106	Jo Siu *et al.* (2013)
7	Diagnosis and treatment of dermatophytosis in dogs and cats. Clinical Consensus Guidelines of the World Association for Veterinary Dermatology	103	Moriello *et al.* (2017)
8	Antimicrobial activity of southern African medicinal plants with dermatological relevance: From an ethnopharmacological screening approach, to combination studies and the isolation of a bioactive compound	100	Mabona *et al.* (2013)
9	MALDI-TOF mass spectrometry - a rapid method for the identification of dermatophyte species	95	Nenoff *et al.* (2013)
10	British Association of Dermatologists' guidelines for the management of tinea capitis	87	Fuller *et al.* (2014)

Biosystematics

With only three *Microsporum* species to work with, ongoing research in biosystematics tends to focus on the infraspecific distinction of strain types, along with the connection of these types to patterns in epidemiology (*e.g.*, Mochizuki *et al.* 2022).

Pathogenesis

No *Microsporum* species has yet been the principal focus of a major comparative genomics study analysing patterns of virulence factors, but *Mi. canis* has been used as a comparator in initial whole genome surveys with other dermatophytes such as *Trichophyton rubrum*, as well as related non-pathogens such as *Arthroderma uncinatum* (Martinez *et al.* 2012, Zheng *et al.* 2020). Individual pathogenicity factors, especially proteases responsible for binding *Mi. canis* to human and animal cells have come under investigation. The protease subtilisin, variant sub3, from *Mi. canis* was the first protease secreted by a dermatophyte for which *in vivo* production during skin infection was clearly demonstrated, and was also found to be necessary for the adherence of *Mi. canis* to both feline and human epidermis (Băguţ *et al.* 2012). An overlapping topic of interest is gene expression studies on proteolytic enzymes produced under different conditions and by different strains in *Mi. canis* pathogenicity (Mathy *et al.* 2010). Complementary studies on host responses to *Mi. canis* pathogenicity factors are likewise in progress (Cambier *et al.* 2016).

Susceptibility and treatment

Microsporum infections tend to be susceptible to existing antidermatophytic therapies and are not at the forefront of major research into new drugs or strategies against resistance. Nonetheless, there are numerous studies such as that of Mabona *et al.* (2013) from Table 57 and Giordani *et al.* (2022), where natural products are explored for inhibitory properties against *Mi. canis*, among other pathogenic fungi.

This is an unusual area of research, in that these studies probably often re-investigate natural materials that were screened by multinational pharmaceutical companies in previous years, perhaps decades ago, but for which there is no public record of the results obtained. The research is thus, even setting aside the economic situations of the researchers currently doing the studies, exquisitely unlikely to become connected to the heavily privately funded networks of chemical refinements and clinical trials that lead to licensed conventional medical therapies. This area of study, then, adds to our knowledge of antifungal chemistry more as a theoretical discipline than as the applied discipline it seems to be at first glance. It may also connect to sociological considerations by validating traditional folk remedies and could, in principle, supply new materials to alternative medicine.

Conservatively approximating the strength of this natural inhibitory products research front, a search in Web of Science from 2011 through 2021 on "*Microsporum* inhibit* extract*" yields 174 results, making this area account for almost 15 % of publications on *Microsporum*.

Epidemiology and unusual cases

Describing and analysing outbreaks and unusual cases make up a substantial amount of research activity in *Microsporum*. For example, the recent rise to prominence, through immigration from Africa, of *Mi. audouinii* in childhood tinea capitis in Belgium has been well documented (Sacheli *et al.* 2020, 2021, Lecerf *et al.* 2022). *Microsporum ferrugineum*, found in Germany to be infecting two immigrant children from Russia who participated in a sports wrestling club, raised concerns about "tinea gladiatorum", a frequently seen pattern of contagious ringworm outbreaks among child and adolescent wrestlers. However, in contrast to the pattern that would be expected with the notorious *Trichophyton tonsurans*, the *Microsporum* inoculum turned out not to have been communicated to other children in the club (Nenoff *et al.* 2020). It is important for physicians and health authorities to be able to use such findings to predict the risk to social contacts entailed by dermatophytosis cases, especially in children.

Author: R. Summerbell

52. ***Curvularia*** Boedijn, Bull. Jard. Bot. Buitenzorg, 3 Sér. 13(1): 123. 1933.

Type species: *Curvularia lunata* (Wakker) Boedijn

Classification: *Ascomycota*, *Pezizomycotina*, *Dothideomycetes*, *Pleosporales*, *Pleosporaceae.*

Background

The globally distributed genus *Curvularia,* includes pathogens or saprobes of a wide range of plant hosts, especially members of *Poaceae* (Marin-Felix *et al.* 2017a, Ferdinandez *et al.* 2023). It also includes emerging opportunistic human pathogens which can cause superficial to deep infections (De Hoog *et al.* 2011b). Species of this genus can also be found in other substrates, *i.e.*, aquatic environments (Verma *et al.* 2013b), air (Manamgoda *et al.* 2015) and soil (Marin-Felix *et al.* 2017a, Tan *et al.* 2018).

Curvularia is the largest genus of helminthosporioid fungi with 222 species epithets listed in Index Fungorum (2022). However, only 143 species are accepted based on DNA sequence data (Raza *et al.* 2019, Song *et al.* 2019a, Crous *et al.* 2020a, Iturrieta-González *et al.* 2020, Marin-Felix *et al.* 2020a, Safi *et al.* 2020, Zhang *et al.* 2020e). This genus is characterised by the production of brown distoseptate conidia, usually with paler terminal cells and inordinately enlarged intermediate cells. Similar conidia are observed in the other helminthosporioid genera *Bipolaris*, *Exserohilum*, *Johnalcornia* and *Pyrenophora*, which led to the wrong identification of species in these genera (Manamgoda *et al.* 2012, 2014, Tan *et al.* 2014, Hernández-Restrepo *et al.* 2018, Marin-Felix *et al.* 2019b, 2020). *Exserohilum* can be easily distinguished by the production of conidia with distinctly protruding hila, but similar structures have also been observed in *Curvularia* (Hernández-Restrepo *et al.* 2018). *Pyrenophora* differs by its muriform septate ascospores. In *Curvularia*, the sexual morph was known as *Cochliobolus*, which is now synonymised to *Bipolaris*, and is characterised by brown or black, globose ascomata, bitunicate, cylindrical asci and filiform or flagelliform, hyaline ascospores, which are loosely arranged into a helix or in a parallel arrangement (Manamgoda *et al.* 2012). However, the asexual morph of *Pyrenophora* is similar to *Curvularia*, which also leads to wrong identifications (Marin-Felix *et al.* 2019b). *Johnalcornia* can be distinguished from the other helminthosporioid genera by the presence of a second conidial septum in the apical cell and distinctive conidia-like chlamydospores (Tan *et al.* 2014). *Curvularia* and *Bipolaris* can be distinguished by the curvature of their conidia, being throughout the length of the conidium in *Bipolaris*, while in *Curvularia*, it is generally restricted to the middle due to its inordinately enlarged intermediate cells (Marin-Felix *et al.* 2017a, b). The sexual morphs are similar, with the only difference being the presence of stromata in some *Curvularia* species, a feature not observed in *Bipolaris*, but it is of limited value since the sexual stage is rarely found in nature and difficult to induce in culture (Manamgoda *et al.* 2012). Moreover, *Curvularia* shows a wider host range and geographic distribution than *Bipolaris* (Marin-Felix *et al.* 2017b). Therefore, molecular data of the ITS, *gapdh* and *tef1* sequences are required for accurate species delimitation in all these genera due to the similarity and overlapping dimensions between their species (Manamgoda *et al.* 2014, Hernández-Restrepo *et al.* 2018, Marin-Felix *et al.* 2019b, 2020).

Ecological and economic significance

Diseases in plants and animals caused by *Curvularia* and *Bipolaris* species amount to an estimated annual loss of 10 billion US dollars worldwide (Bengyella *et al.* 2019). Species of *Curvularia* occur mainly on *Poaceae* and represent important pathogens of grasses and staple crops, including rice, maize, wheat and sorghum (Marin-Felix *et al.* 2017a). Other hosts are members of the families *Actinidiaceae*, *Aizoaceae*, *Caricaceae*, *Convolvulaceae*, *Fabaceae*, *Iridaceae*, *Lamiaceae*, *Lythraceae*, *Oleaceae*, *Polygonaceae* and *Rubiaceae* (Sivanesan 1987, Manamgoda *et al.* 2015, Marin-Felix *et al.* 2017a, b, Tan *et al.* 2018). A prominent example of an economically significant disease caused by *Curvularia* species is a leaf spot of maize, with maize being the third most cultivated crop in the world (Ahmad *et al.* 2020). This disease is characterised by brownish leaf lesions and is produced by different species, *e.g.*, *Cur. australiensis* in China (Chang *et al.* 2016), *Cur. chiangmaiensis* in Thailand (Marin-Felix *et al.* 2017b) and *Cur. lunata* in the USA (Garcia-Aroca *et al.* 2018). Diseases in rice caused by *Curvularia* species also lead to yield losses, with rice being a major staple crop that provides more than 20 % of calories for more than half of the human population (Gutaker *et al.* 2020). Different symptoms or diseases are observed in this crop, *e.g.*, black kernel disease (Bengyella *et al.* 2018) and leaf spots observed for example in Cambodia, Malaysia and Pakistan (Kusai *et al.* 2016, Majeed *et al.* 2016, Tann & Soytong 2017), all caused by *Cur. lunata*. Other examples of diseases are leaf spots of sorghum in China and Pakistan (Akram *et al.* 2014, Tong *et al.* 2016), the foliar necrosis of potatoes in India (Louis *et al.* 2013), and stem blight disease of cassava in West Africa (Msikita *et al.* 2007), all caused by *Cur. lunata.*

Curvularia species are also emerging opportunistic pathogens of humans, causing respiratory tract, cerebral, cutaneous and corneal infections, as well as deep and disseminated infections, in both immunocompetent and immunocompromised patients (Krizsán *et al.* 2016). The most common disease caused by *Curvularia* is keratitis, being extensively reported in India, *e.g.*, the two recently described species *Cur. coimbatorensis* and *Cur. tamilnaduensis* (Kiss *et al.* 2020), with 97 cases reported from 2012 to 2018 in only one tertiary eye care centre (Khurana *et al.* 2020). *Curvularia* species also commonly cause respiratory tract infections (Cruz *et al.* 2013, Cavanna *et al.* 2014, Chowdhary *et al.* 2014a), with sinusitis being the second most common human infection caused by this genus (Krizsán *et al.* 2016). Both cutaneous and subcutaneous phaeohyphomycoses skin infections are known (Moody *et al.* 2012, Gunathilake *et al.* 2013, Vásquez-del-Mercado *et al.* 2013, Requena López *et al.* 2020). *Curvularia* species have also been reported to cause deep infections such as cerebral phaeohyphomycosis (Rosow *et al.* 2011, Gongidi *et al.* 2013, Wang *et al.* 2014f), and even human disseminated phaeohyphomycosis (Revankar *et al.* 2002, Kobayashi *et al.* 2008, Vasikasin *et al.* 2019). Different antifungals have been applied as a treatment for the diseases produced by *Curvularia*, but differences in the susceptibility of different species and isolates have been observed (Krizsán *et al.* 2016). Da Cunha *et al.* (2013) studied the *in vitro* susceptibility of 99 clinical isolates belonging to 14 different species, concluding that the most active drugs were amphotericin B, echinocandins and posaconazole, while voriconazole and itraconazole showed poor activity. However, itraconazole was highly effective in two different studies, one including 25 isolates belonging to seven different species (Guarro *et al.* 1999), and the other including 30 isolates from keratitis belonging to four different species (Krizsán *et al.* 2015).

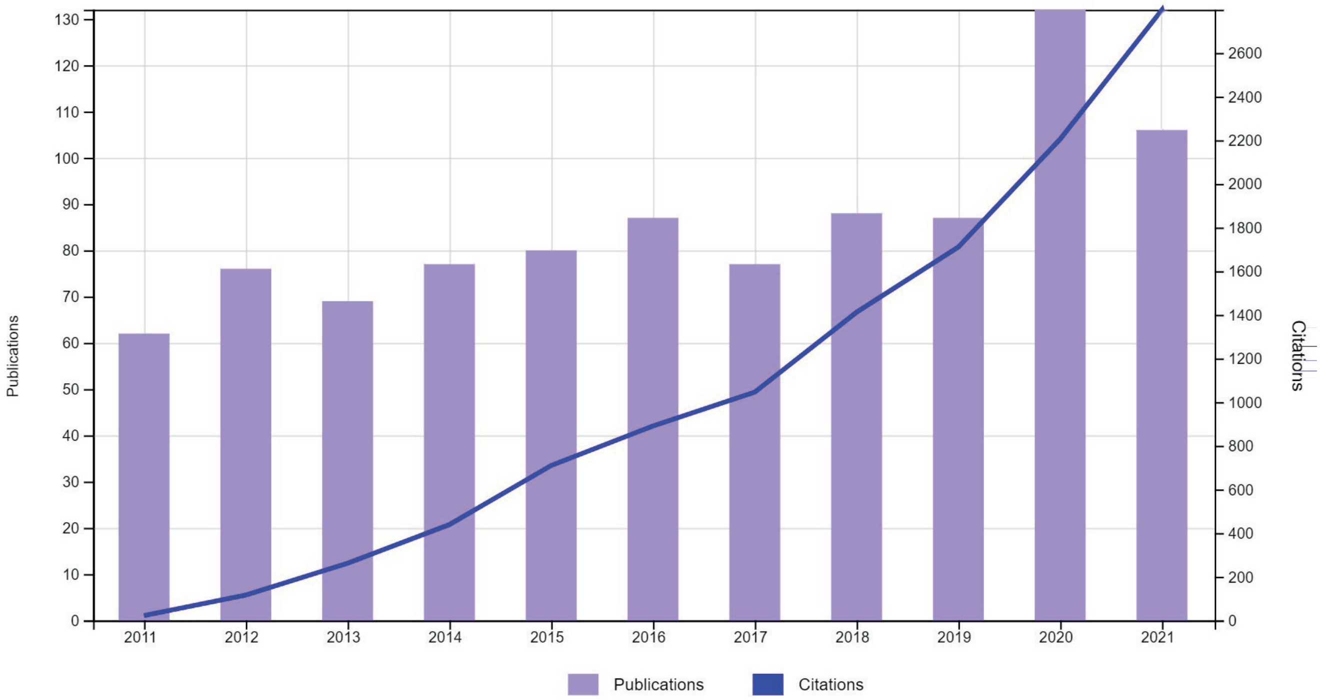

Fig. 81. Trends in research of *Curvularia* in the period 2011–2021.

Research interests

There are 941 publications and 11 008 citations from 2011–2021 in the Web of Science (Fig. 81), with the top 10 most cited articles listed in Table 58. Most publications focused on the plant and human diseases caused by *Curvularia* species (see above for more details), their taxonomy and phylogeny, as well as their biotechnological application as producers of compounds with antimicrobial properties or beneficial to the environment.

Taxonomy and phylogeny

Species delimitation in *Curvularia* based only on morphology is problematic since many species share similar characters with overlapping dimensions. Therefore, phylogenetic studies using ITS, *gapdh* and *tef*1 sequences are necessary for proper delimitation and identification (Manamgoda *et al.* 2012, 2015, Tan *et al.* 2014, 2018, Marin-Felix *et al.* 2017a, b, 2020, Raza *et al.* 2019). Many species were described before the DNA era and were based only on morphology. The lack of molecular data is causing many of these species to be ignored by the scientific community. Thus, one of the objectives addressed in the last years is to provide sequence data of the main markers used in molecular studies of *Curvularia* and to determine the taxonomic position of many of these previously described species (Marin-Felix *et al.* 2020a).

Biotechnological application

In the last years, the study of *Curvularia* for biotechnological applications in medicine, global agriculture and eco-system

Table 58. Top 10 cited articles related to *Curvularia* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Fungi and allergic lower respiratory tract diseases	305	Knutsen *et al.* (2012)
2	One stop shop: backbones trees for important phytopathogenic genera: I (2014)	235	Hyde *et al.* (2014)
3	Optimization for rapid synthesis of silver nanoparticles and its effect on phytopathogenic fungi	202	Krishnaraj *et al.* (2012)
4	Genera of phytopathogenic fungi: GOPHY 1	185	Marin-Felix *et al.* (2017a)
5	*In vitro* antifungal efficacy of copper nanoparticles against selected crop pathogenic fungi	178	Kanhed *et al.* (2014)
6	A phylogenetic and taxonomic re-evaluation of the *Bipolaris* – *Cochliobolus* – *Curvularia* complex	169	Manamgoda *et al.* (2012)
7	Antimicrobial enzymes: an emerging strategy to fight microbes and microbial biofilms	163	Thallinger *et al.* (2013)
8	The genus *Bipolaris*	146	Manamgoda *et al.* (2014)
9	Allergic bronchopulmonary mycosis due to fungi other than *Aspergillus*: a global overview	120	Chowdhary *et al.* (2014a)
10	*Cochliobolus*: an overview and current status of species	118	Manamgoda *et al.* (2011)

clean-up has increased (Bengyella *et al.* 2019). Different strains of *Curvularia* species have been subjected for screening to produce bioactive compounds. These studies demonstrated that *Curvularia* species are prolific producers of antimicrobial secondary metabolites, with potential uses in the pharmacological industry. Examples of antifungal compounds are moriniafungin E, which is a sordarin tetracyclic diterpene glycoside isolated from *Cur. hawaiiensis* (Zhang *et al.* 2019b), and curvularide B, which is a hybrid peptide-polyketide isolated from *Cur. geniculata* with activity against *Candida albicans* and synergistic activity with fluconazole drug (Chomcheon *et al.* 2010). Antibiotic compounds have also been isolated from *Curvularia* species, such as curvulamine, which showed strong activity against the human pathogens *Actinomyces israelii*, *Streptococcus* sp., *Peptostreptococcus* sp. and *Bacteroides vulgatus* (Han *et al.* 2014), and 4-epiradicinol, which inhibited the growth of *Bacillus subtilis*, *Escherichia coli*, *Salmonella choleraesuis* and *Staphylococcus aureus* (Varma *et al.* 2006). Other bioactive secondary metabolites isolated from *Curvularia* are pyrenolide A, which showed strong motility impairing activity against zoospores of the oomycete *Phytophthora capsici* (Mondol *et al.* 2017), and curindoziline, which displays an anti-inflammatory action representing a possible solution for managing inflammation-derived diseases (Han *et al.* 2016b). Cytotoxic compounds, which can hold great potential for cancer treatment, have been found in *Curvularia*, *e.g.*, pyrenocine J isolated from *Cur. affinis*, which showed activity against human hepatic cancer cell line HepG2 (Zhang *et al.* 2012a), and a polyketide isolated from *Cur. trifolii*, which showed cytotoxic activity against five different cancer cell lines (Samanthi *et al.* 2015).

Curvularia spp. have been demonstrated to provide potential solutions for environmental and agricultural problems. For example, phytotoxic compounds produced by *Curvularia*, could be used as eco-friendly mycoherbicides, *e.g.*, phthalic acid butyl isobutyl ester and radicinin, which showed significant phytotoxic activity against the radical growth of *Echinochloa crusgalli* (Zhang *et al.* 2011d), and zeaenol, isolated from *Cur. crepinii*, which possessed herbicidal activity against *Echinochloa crusgalli* (Yin *et al.* 2018a). Bioremediation using *Curvularia* species is also an increasing field of study. For example, Senthilkumar *et al.* (2012) demonstrated that a strain of *Curvularia* was able to uptake Reactive Red 195 in dye wastewater, suggesting its potential to decolourise wastewater of textile industries. *Curvularia lunata* was found to have the ability to biodegrade crude oil (Al-Nasrawi 2012), as well as chrysene, which is a polycyclic aromatic hydrocarbon (Bhatt *et al.* 2014). The potential use of *Curvularia* in bioremediation processes was also observed in a strain of *Cur. geniculata* that was able to remove 100 % of mercury from a culture medium and promoted the growth of *Aeschynomene fluminensis* and *Zea mays* in substrates containing this metal (Pietro-Souza *et al.* 2020). Other uses could be cleaning industrial metallic wastewater since Abu-Elreesh & Abd-El-Haleem (2014) demonstrated that cell debris of *Curvularia* sp. removed 85 % of Cd and 15 % of Zn after 1 h contact time in solution. Species of *Curvularia* have a great impact on industrial enzyme production, such as the laccases produced by *Cur. kusanoi.* Vazquez *et al.* (2020) demonstrated that these enzymes decreased the fibre content and increased *in vitro* digestibility of sugarcane bagasse; therefore, it could represent a novel tool for improving the nutritional quality of fibrous sources for animal feed.

Author: Y. Marin-Felix

53. ***Rhizomucor*** Lucet & Costantin, Rev. Gén. Bot. 12: 92. 1900.

Type species: *Rhizomucor pusillus* (Lindt) Schipper

Classification: *Mucoromycota*, *Mucoromycotina*, *Mucoromycetes*, *Mucorales*, *Lichtheimiaceae.*

Background

Rhizomucor was established by Lucet & Costantin in 1900. It is classified in *Rhizomucoraceae* and has 15 epithets (Zhao *et al.* 2023). In recent publications, the number of accepted species is not congruent. Wijayawardene *et al.* (2018a) list four species, Walther *et al.* (2019) accept two species, and Wijayawardene *et al.* (2020) list six species. The genus exclusively comprises thermophilic species that can grow at temperatures above 50 °C. All mesophilic species such as *Rhi. chlamydosporus* and *Rhi. endophyticus* were transferred to *Mucor*. Hence in the current classification scheme, *Rhizomucor* comprises *Rhi. miehei*, *Rhi. pusillus*, *Rhi. nainitalensis*, and *Rhi. pakistanicus*. However, for *Rhi. nainitalensis*, and *Rhi. pakistanicus* no strains, DNA sequence data, or reports are available, and it may be that they represent synonyms of *Rhi. pusillus* or *Rhi. miehei*. Species of *Rhizomucor* account for 5 % of mucormycosis worldwide. They mainly cause pulmonary, cutaneous infections or rhino-orbital-cerebral manifestations (Walther *et al.* 2019).

Rhizomucor shares several morphological similarities with *Mucor*. One of the key characteristics used to differentiate these two genera was the presence of rhizoids in the species of *Rhizomucor* and the absence in *Mucor*. However, recent studies revealed that some *Mucor* species do produce rhizoids under certain conditions. In literature, another difference used to segregate *Mucor* from *Rhizomucor* was the production of stolons in the latter. Route of infection can also be taxonomically informative to differentiate among *Mucorales* genera. *Rhizopus* and *Rhizomucor* are primarily airborne while *Mucor* and *Lichtheimia* usually infect their host by contact (Nicolás *et al.* 2020). This preference in the mode of infection is reflected in the intergeneric sporangial differences. *Rhizomucor* and *Rhizopus* species usually have dry sporangia on thin and long sporangiophores which are fully adapted for spore release in the air. *Mucor* and *Lichtheimia* typically have wet sporangia and release spores in small droplets when several sporangia stick together which may explain why *Mucor* and *Lichtheimia* infect burn wounds and trauma injuries (Nicolás *et al.* 2020). Intrageneric delimitations usually consider the colour of the colonies, the origin of rhizoids, the appearance of the sporangiophores (length, branching, diameter), the size of the columella, spores, and sporangium, or the presence or absence of a collar (Zheng *et al.* 2009).

Ecological and economic significance

Production of ester compound using lipase

Esters of long-chain fatty acids and polyhydric alcohols such as glycerol, sorbitol, and other carbohydrates have an array of uses in the food and pharmaceutical industries. They are important aroma compounds and oleochemicals that can be used as lubricants and anti-static reagents. Esterification catalysed by lipase has been used to produce esters of glycerol, aliphatic, and terpene alcohols. In this sense, lipase derived from *Rhizomucor miehei* has a wide range of applications such as in hydrolysing oils into free fatty acids and glycerol and esterification processes (Hari Krishna *et al.* 2000).

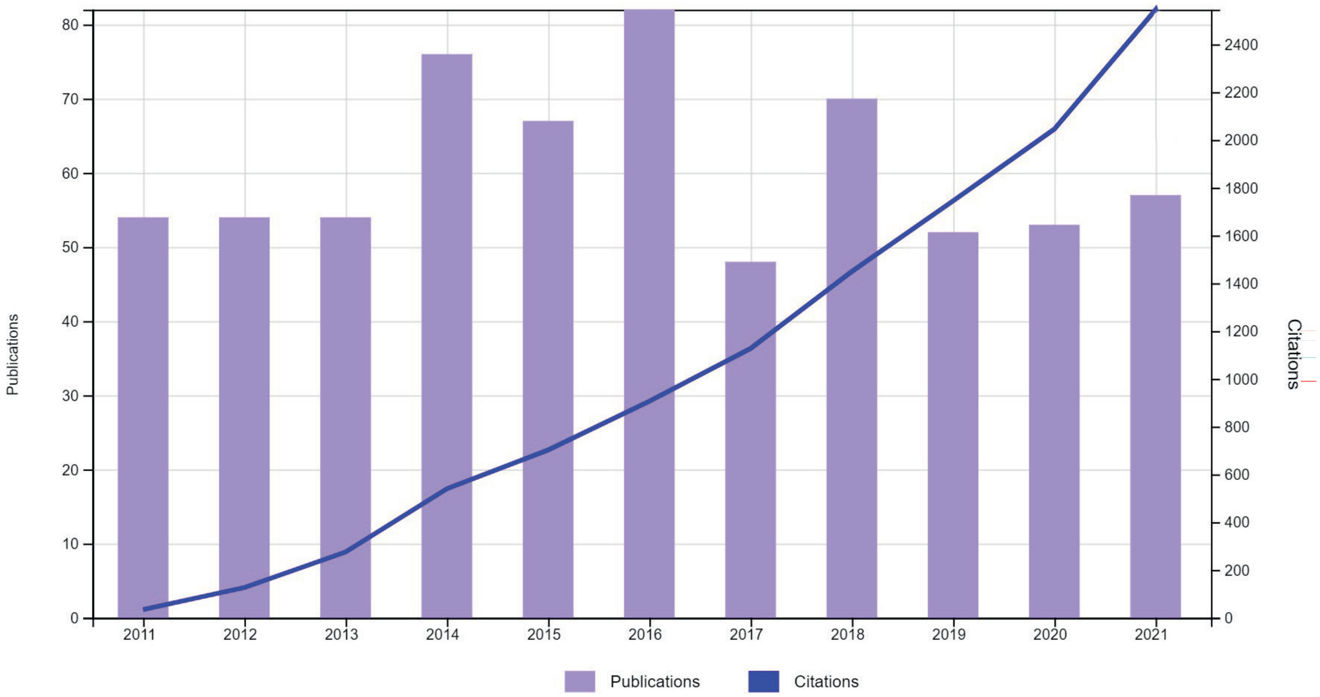

Fig. 82. Trends in research of *Rhizomucor* in the period 2011–2021.

In several studies, *Rhi. miehei* lipase has been used to produce esters. The enzyme is known for its ability to efficiently synthesise esters with high yields and broad substrate specificity ranging from low to high molecular weight acids, alcohol to amines, and amino acids (Hari Krishna *et al.* 2000, Rodrigues & Fernandez-Lafuente 2010).

Hydrolysis of oil

The partial hydrolysis of glycerides in oil can help to modify the specific properties of the oil. Several studies focus on the hydrolysis of commercially available oils such as soybean oil and peanut oil. *Rhizomucor miehei* lipase can selectively hydrolyse saturated fatty acids in soybean oil. For example, the removal of saturated fatty acids from epoxidised soybean oil allows for the processing of the oil for polymer synthesis applications (Rodrigues & Fernandez-Lafuente 2010).

Research interests

There are 667 publications and 10 915 citations from 2011 to 2021 in the Web of Science (Fig. 82), with the top 10 most cited articles listed in Table 59. Most publications are related to the taxonomy of *Rhizomucor* to produce enzymes, and human pathogenicity (mucormycosis).

Clinical importance

Similar to *Mucor* and *Lichtheimia*, *Rhizomucor* is also known to cause mucormycosis. One of the species known to cause

Table 59. Top 10 cited articles related to *Rhizomucor* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	A global analysis of Mucormycosis in France: The RetroZygo study (2005–2007)	271	Lanternier *et al.* (2012)
2	Mucormycosis caused by unusual mucormycetes, non-*Rhizopus*, -*Mucor*, and -*Lichtheimia* species	224	Gomes *et al.* (2011)
3	DNA barcoding in *Mucorales*: an inventory of biodiversity	176	Walther *et al.* (2013)
4	Daqu - A traditional Chinese liquor fermentation starter	173	Zheng *et al.* (2011b)
5	Complex microbiota of a Chinese “Fen” liquor fermentation starter (Fen-Daqu), revealed by culture-dependent and culture-independent methods	148	Zheng *et al.* (2012)
6	Quantitative Polymerase Chain Reaction detection of circulating DNA in serum for early diagnosis of Mucormycosis in immunocompromised patients	123	Millon *et al.* (2013)
7	Biodiesel production from *Acrocomia aculeata* acid oil by (enzyme/enzyme) hydroesterification process: Use of vegetable lipase and fermented solid as low-cost biocatalysts	106	Aguieiras *et al.* (2014)
8	Improved performance of lipases immobilized on heterofunctional octyl-glyoxyl agarose beads	105	Rueda *et al.* (2015)
9	Fungal community associated with fermentation and storage of Fuzhuan brick-tea	105	Xu *et al.* (2011a)
10	The family structure of the *Mucorales*: a synoptic revision based on comprehensive multigene-genealogies	104	Hoffmann *et al.* (2013)

mucormycosis is *Rhi. pusillus*. The pathogen is usually transmitted by inhalation of the spores, percutaneously and mainly affects immunocompromised patients. Like all species in the genus, the fungus is thermophilic and usually isolated as a saprobe (Menzinger *et al.* 2019). Twenty-two cases of mucormycosis caused by *Rhi. pusillus* were recorded before 2013 worldwide (Menzinger *et al.* 2019). *Rhizomucor pusillus* can lead to rhinoorbito-cerebral mucormycosis which occurs in 9 % of cases (Bala *et al.* 2014). Similar to other agents of mucormycosis, the fungus mainly affects people with haematological disorders (Zhao *et al.* 2009, Bala *et al.* 2014). The pathogenicity of the species is associated with its angioinvasive nature and thermotolerance (Bala *et al.* 2014). There has been a recent case of *Rhi. pusillus* causing mucormycosis in Magellanic penguins. The bird exhibited acute neurologic symptoms. Further examination showed the presence of congested, oedematous lungs and intracranial haemorrhage (Reed *et al.* 2021).

Industrial applications

Several studies on *Rhizomucor* revolve around its industrial applications (De Oliveira *et al.* 2019). These include the production of enzymes such as proteases and lipases which have an array of applications in various industries (Dhake *et al.* 2013, Wang *et al.* 2020). For example, *Rhi. pusillus* is commonly used to produce industrial enzymes by solid-state fermentation. *Rhizomucor miehei* is commonly used in industries such as cheese making. Proteases produced by *Rhi. miehei* are commonly used as a substitute for calf rennet. This enzyme can split peptide bonds in kappa-casein similar to rennet obtained from calves, and has high milk coagulating activity, similar calcium content, and low incidence of the bitter taste of the curds produced (Aljammas *et al.* 2018).

Author: V.G. Hurdeal

54. ***Pyricularia*** (Sacc.) Sacc., Syll. Fung. (Abellini) 4: 217. 1886.

Type species: *Pyricularia grisea* Cooke *ex* Sacc.

Classification: *Ascomycota*, *Pezizomycotina*, *Sordariomycetes*, *Magnaporthales*, *Pyriculariaceae.*

Background

Pyricularia is one of the most important genera of plant pathogenic hyphomycetes (Ellis 1971, 1976, Bussaban *et al.* 2003, Hirata *et al.* 2007, Klaubauf *et al.* 2014) More than 60 species of *Pyricularia* are listed in Index Fungorum (2022), but only nine species are validated (Klaubauf *et al.* 2014, Marin-Felix *et al.* 2019a, Pordel *et al.* 2019). *Pyricularia* species are the causal agents of blast and leaf spot diseases on many monocotyledonous species in *Poaceae*, *Musaceae*, and *Zingiberaceae* (Bussaban *et al.* 2005, Murata *et al.* 2014, Zhong *et al.* 2016, Marin-Felix *et al.* 2019a). *Pyricularia* species attack all aerial parts of host plants (Igarashi 1986, Wilson & Talbot 2009, Saleh *et al.* 2014, Reges *et al.* 2016, Crous *et al.* 2016). Tropical and subtropical regions with high humidity and warm conditions are ideal for *Pyricularia* species to infect and appear on host plants (Couch & Kohn 2002, Bussaban *et al.* 2003, Ganesan *et al.* 2017). *Pyricularia oryzae* is the causal agent of rice, wheat, and maize blast disease worldwide (Couch & Kohn, 2002, Bussaban *et al.* 2005, Islam *et al.* 2016, Pordel *et al.* 2021). This fungus produces several secondary metabolites in pathogenicity mechanisms; for example, pyriculols, a salicylaldehyde polyketide, have been produced in culture medium and nature (Narayana & Suryanarayanan 1974). In light conditions, application of the pyriculols on a rice leaf made necrotic lesions and caused inhibition of the growth of shoots, roots, and seedlings (Iwasaki *et al.* 1973, Narayana & Suryanarayanan 1974, Kono *et al.* 1991, Kim *et al.* 1998).

Pyricularia species are favoured by high air temperatures, and relative humidity (Male 2011, Cruz & Valent 2017, Ganesan *et al*. 2017, Kastsantonis *et al*. 2017). They are distributed readily by natural dispersion of spores and seed transmission by humans and equipment (Saleh *et al.* 2014). The diseases cause large lesions on the stem, leaves, neck, glume, panicle, spike, and fruits. In general, the symptoms initially formed are small water-soaked or chlorotic lesions and gradually enlarge. The centre of the spots is usually grey or white, and the margins are reddish brown or yellow (Wilson & Talbot 2009, Male 2011, Pordel *et al.* 2016, Cruz & Valent 2017). Lesions have grey centres during sporulation and white to tan centres after spore release (Igarashi 1986, Wilson & Talbot 2009, Male 2011, Pordel *et al.* 2016, Cruz & Valent 2017).

In 1880, Saccardo coined the generic name *Pyricularia* based on the asexual form *Pyr. grisea* isolated from *Digitaria sanguinalis* (Couch & Kohn 2002). Ellis (1971) described *Pyricularia*, which is similar to some species of *Dactylaria* with polyblastic, integrated and sympodial, geniculate, thin-walled conidiophores that have cylindrical denticles and solitary, dry, acropleurogenous, obpyriform, obturbinate or obclavate, hyaline to pale olivaceous brown, conidia with a protuberant hilum (Ellis 1976, Goh & Hyde 1997, Bussaban *et al.* 2003). Some species described initially in *Pyricularia* have been synonymised or transferred to other genera (Ingold 1943, Ellis 1971, 1976). Multigene-based phylogenetic analyses resulted in establishing the *Pyriculariaceae* to accommodate the genus *Pyricularia* (Klaubauf *et al*. 2014). The study was based on partial sequences of the ITS regions with the 5.8S nuclear ribosomal RNA gene (ITS-rDNA), LSU, and several protein-encoding genes, including the *rpb1*, *act*, and *cal*. The *Magnaporthales* now contain three families, *Magnaporthaceae*, *Pyriculariaceae*, and *Ophioceraceae* (Klaubauf *et al.* 2014, Luo *et al.* 2015). *Pyriculariaceae* (type genus: *Pyricularia*) has nine genera divided from *Pyricularia s. lat.* (Klaubauf *et al*. 2014).

Ecological and economic significance

Pyricularia oryzae causes annual destruction of rice, wheat, and foxtail millets, which supply millions of people with food (Pennisi 2010, Liu *et al.* 2004). It also has an economic impact through the cost of control methods to prevent or limit epidemics on golf courses (Uddin *et al.* 1999).

Blast disease of rice, wheat, and maize caused by *Pyricularia oryzae* (sexual morph *Magnaporthe oryzae*), the causal agent of rice, wheat, and maize blast disease, is one of the most widely distributed diseases of these crops and is highly destructive on rice leading to up to 30 % yield loss worldwide (Skamnioti & Gurr 2009, Islam *et al.* 2016, Castroagudín *et al.* 2016) at the cost of around 66 billion US dollars (Pennisi 2010, Nalley *et al.* 2016). The notorious wheat blast disease leads to 40–100 % yield losses in some extreme conditions (Skamnioti & Gurr 2009, Inoue *et al.* 2017). Blast disease has spread in all rice and some wheat-growing areas globally (Couch *et al*. 2005, Pennisi 2010, Murata *et al*. 2014, Islam *et al*. 2016). *Pyricularia oryzae* expends its host range from barnyard grass to maize in Iran (Pordel *et al*. 2021). Host resistance is the most economically viable and environmentally friendly way to manage this disease (Ou 1980, Zeigler *et al.* 1994); nearly 100 different resistance genes and > 350 QTLs, of which 23 resistance genes have been identified, mapped and cloned, and functionally validated to find suitable rice cultivars against *Pyr. oryzae* (Fukuoka *et al.* 2014). To achieve rice with a high resistance response to the pathogen, horizon, and vertical resistance are applied in the new races (Liu *et al.* 2004). Some fungicides with high application for the control of blast disease include probenazole, tricyclazole, azoxystrobin, isoprothiolane, and propiconazole (Rijal & Devkota 2020). High genetic variability, polycyclic nature, and sporulation by the fungus quickly overcome host and fungicide resistance, and cultivars and fungicides typically become ineffective (Dean *et al.* 2012, Rijal & Devkota 2020).

Blast disease on leaves and heads of *Triticum aestivum*, *Hordeum vulgare*, and *Urochloa brizantha* caused *Pyricularia urashimae*. Reges *et al.* (2016) sampled *Poaceae* species infected with blast disease by *Pyr. pennisetigena*, Pyr. zingibericola, *Pyr. grisea*, and *Pyr. oryzae.* They proved that *Pyr. pennisetigena* and Pyr. zingibericola can attack barley and wheat with varying aggressiveness levels. Phylogenetic analysis showed that *Pyr. zingibericola* isolates are close to *Pyr. oryzae* isolates (Reges *et al.* 2016). Following the revision of *Pyricularia*, Pyr. zingibericola isolates were re-described under a new name, *Pyr. urashimae* (Castroagudín *et al*. 2016, Crous *et al*. 2016, Reges *et al.* 2016). Some species of *Pyricularia* such as *Pyr*. *penniseticola*, *Pyr. pennisetigena*, *Pyr. grisea* and *Pyr. setariae* (used as a bioherbicide agent for control of green foxtail (*Setaria viridis*)) infect weed plants, especially in *Poaceae* (Peng *et al.* 2004, Klaubauf *et al.* 2014, Peng & Byer 2017). *Pyricularia ctenantheicola* and *Pyr. zingibericola* were isolated from the ornamental *Ctenanthe oppenheimiana* and medicinal plant *Zingiber officinale*, respectively (Klaubauf *et al.* 2014).

Blast and pitting disease of banana caused by *P. angulata*

Pitting disease on bananas caused by *Pyricularia* sp. was reported as early as 1931 on fruit shipped from Brazil to England (Tomkins 1931), and subsequently reported from other countries where banana is cultivated (Hoette 1963, Meredith 1962, Hashioka 1971, Ganesan *et al*. 2017). *Pyricularia angulata* causes symptoms in the young and mature parts of the banana (Ganesan *et al.* 2017). Blast lesions appear on leaves, stems and pitting symptoms appear on fruits (Ganesan *et al.* 2017). Severe pitting symptoms on fruit require heavy rain with high humidity (Shafaullah *et al.* 2011, Ganesan *et al.* 2017).

Research interests

There are 1 038 publications and 10 856 citations from 2011–2021 in the Web of Science (Fig. 83), with the top 10 most cited articles listed in Table 60. Most publications focused on the pathogenicity mechanism (*in vitro*, host-species interaction) and the economic importance of the blast pathogen.

Disease management

Efforts to breed cultivars with improved resistance have been constant against some *Pyricularia* spp., especially to control wheat and rice blast (Lenné *et al.* 2007, Zhan *et al.* 2008, Tagle *et al.* 2015, Islam *et al.* 2020). However, resistant cultivars proved to be susceptible when deployed across different geographical regions (Urashima *et al*. 2004a, b, Rijal & Devkota 2020, Volante *et al*. 2020). Researchers and farmers use many methods for the management of *Pyricularia* species on crop plants, including cultural and sanitary methods, host nutrition, biological and chemical management (Urashima & Kato 1998, Laker-Ojok *et al.* 2005, Varma & Santhakumari 2012, Magar *et al.* 2015, Castroagudın *et al.* 2016). Nowadays, farmers prefer to control blast disease on wheat, rice, and foxtail millet using chemical compounds (Rijal & Devkota

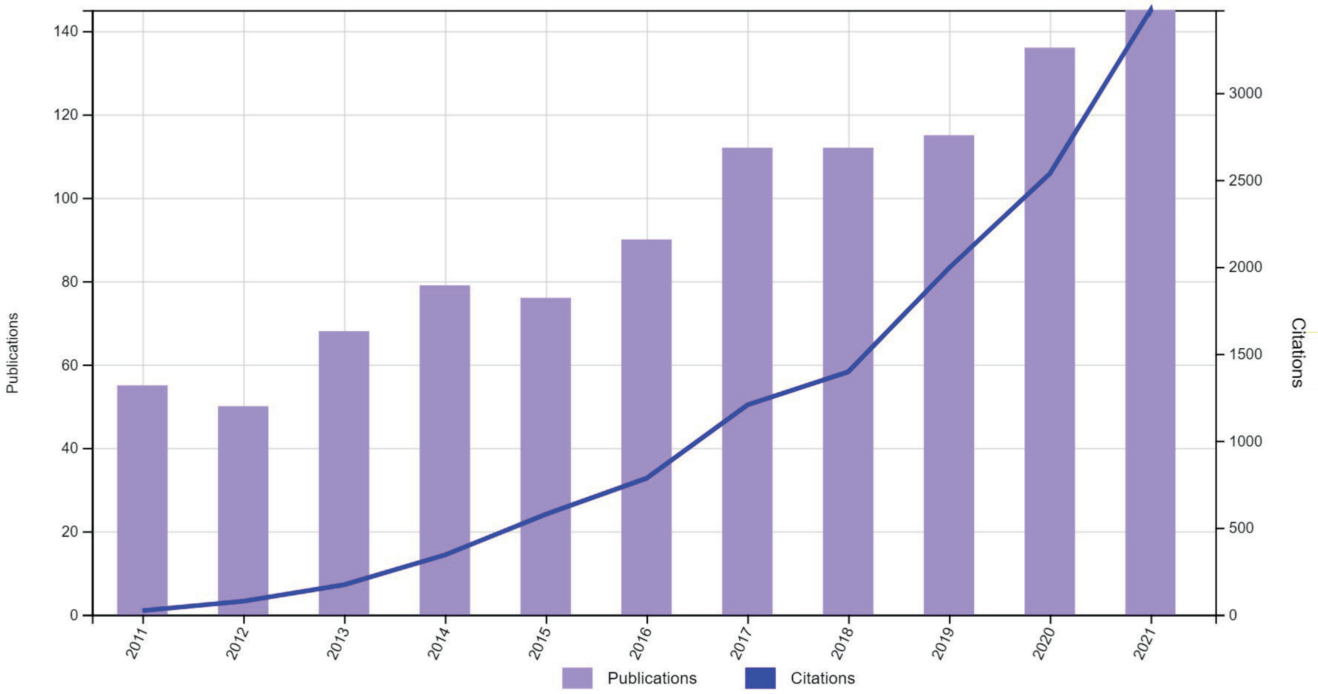

Fig. 83. Trends in research of *Pyricularia* in the period 2011–2021.

Table 60. Top 10 cited articles related to *Pyricularia* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	The top 10 fungal pathogens in molecular plant pathology	1 769	Dean *et al.* (2012)
2	Fungal effectors and plant susceptibility	383	Lo Presti *et al.* (2015)
3	Genome evolution in filamentous plant pathogens: why bigger can be better	361	Raffaele & Kamoun (2012)
4	Effector-mediated suppression of chitin-triggered immunity by *Magnaporthe oryzae* is necessary for rice blast disease	253	Mentlak *et al.* (2012)
5	Plant cell wall-degrading enzymes and their secretion in plant-pathogenic fungi	222	Kubicek *et al.* (2014)
6	One-step hydrothermal approach to fabricate carbon dots from apple juice for imaging of mycobacterium and fungal cells	206	Mehta *et al.* (2015)
7	The *Magnaporthe oryzae* effector AvrPiz-t targets the RING E3 ubiquitin ligase APIP6 to suppress pathogen-associated molecular pattern-triggered immunity in rice	205	Park *et al.* (2012a)
8	The rice resistance protein pair RGA4/RGA5 recognizes the *Magnaporthe oryzae* effectors AVR-Pia and AVR1-CO39 by direct binding	203	Cesari *et al.* (2013)
9	The bZIP transcription factor MoAP1 mediates the oxidative stress response and is critical for pathogenicity of the rice blast fungus *Magnaporthe oryzae*	172	Guo *et al.* (2011)
10	A multifaceted genomics approach allows the isolation of the rice Pia-blast resistance gene consisting of two adjacent NBS-LRR protein genes	164	Okuyama *et al.* (2011)

2020). However, the efficacy of fungicides has been continuously marred by the emergence of resistant strains after repeated and widespread use of the same fungicide classes (Ceresini *et al.* 2018). New cultivars and fungicide applications provide a good strategy in the integrated management of *Pyricularia* disease.

Toxins

Secondary metabolites produced by *Pyricularia* isolates have also been examined. Some *Pyricularia* isolates induce necrosis on rice and wheat as well as cause chlorosis on oat leaves (Iwasaki *et al.* 1973, Tsurushima *et al.* 2010, Castroagudín *et al.* 2016). Pyriculol and epipyriculol have been detected as the main necrosis-inducing factors produced by *Pyr. oryzae*. However, they are thought to be non-specific, as most *Pyricularia* isolates from graminaceous plants produce these compounds in culture (Tsurushima *et al.* 2010). *Pyricularia oryzae* infecting rice leaves produced non-host selective toxins such as pyricularin, pyriculol, epipyriculol, tenuazonic acid, and picolinic acid (Iwasaki *et al.* 1973, Tsurushima *et al.* 2010). Several studies demonstrated the importance of tenuazonic acid and picolinic acid in the development of the characteristic symptoms of the blast (Umetsu *et al.* 1972). Pyrichalasin H has been detected from *Pyricularia grisea* infecting *Digitaria* (Nukina 1987). Pyrichalasin H increases the ability of a *Pyricularia* isolate to infect *Digitaria* plants (Tsurushima *et al.* 2010).

Taxonomy and phylogeny

In general, to identify the phylogenetic placement of *Pyricularia* among other *Pyriculariaceae* genera, LSU has been supplemented with *rpb*1 data (Klaubauf *et al.* 2014, Pordel *et al.* 2016, 2021). To improve the resolution of the placement of *Pyricularia* species, *act* or *cal* supplemented by ITS and *rpb1* are strong candidates for species delimitation (Klaubauf *et al.* 2014, Pordel *et al.* 2016, 2021).

Author: A. Pordel

55. ***Parastagonospora*** Quaedvl. *et al.*, Stud. Mycol. 75: 362. 2013.

Type species: *Parastagonospora nodorum* (Berk.) Quaedvlieg *et al.*

Classification: *Ascomycota*, *Pezizomycotina*, *Dothideomycetes*, *Pleosporales*, *Phaeosphaeriaceae.*

Background

Parastagonospora was introduced by Quaedvlieg *et al*. (2013) to accommodate several important plant pathogenic fungi. The genus comprises 20 species (Index Fungorum 2022) and many species were previously accommodated in *Leptosphaeria*, *Phaeosphaeria*, *Septoria* or *Stagonospora* (Ghaderi *et al*. 2017, Goonasekara *et al*. 2019). *Parastagonospora* was originally introduced as *Septoria* (Weber 1922) and later assigned to *Stagonospora* based on the asexual morph while the sexual morph was recognised in *Phaeosphaeria* (Weber 1922). However, based on the International Code of Nomenclature for Algae, Fungi and Plants (ICNafp), along with molecular support, these genera were further confined to a newly introduced genus *Parastagonospora* (Quaedvlieg *et al*. 2013). *Parastagonospora* mainly differs from *Stagonospora* in its sexual morph, as *Parastagonospora* are phaeosphaeria-like whereas *Stagonospora* are didymella-like (Quaedvlieg *et al*. 2013, Marin-Felix *et al*. 2019a, Bhagya *et al*. 2024). The sexual morph is characterised by immersed ascocarps, papillate ostiole, clavate, cylindrical or curved, short-stipitate asci, fusoid, subhyaline to pale brown, transversely euseptate ascospores, while the asexual morph produces pycnidial conidiomata, phialidic and hyaline conidiogenous cells, and cylindrical, granular to multi-guttulate, hyaline conidia (Quaedvlieg *et al*. 2013, Li *et al*. 2015c, Thambugala *et al*. 2017).

Parastagonospora comprises many cereal pathogens, including cultivated and wild plants recorded around the world (Quaedvlieg *et al*. 2013, Ghaderi *et al*. 2017, Thambugala *et al*. 2017). They can also be saprobes on grasses (Marin-Felix *et al*. 2019a). These species can infect various hosts and are responsible for significant annual production losses for economically important major crops such as wheat, barley and rye. *Parastagonospora nodorum* and *Paras. pseudonodorum* cause significant yield losses in global wheat

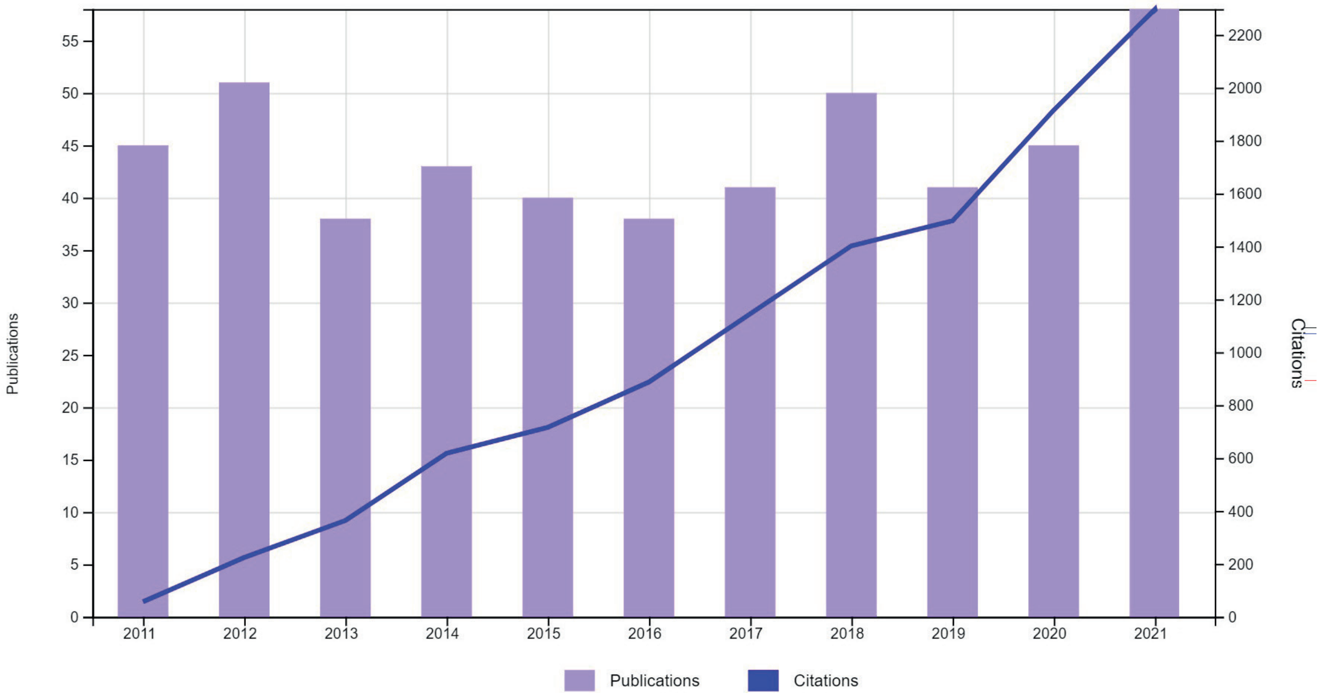

Fig. 84. Trends in research of *Parastagonospora* in the period 2011–2021.

production (Richards *et al*. 2019). The diseased plant presents with mainly node spots on leaves and glumes (Marin-Felix *et al*. 2019a).

The taxa of *Parastagonospora* are delimited largely based on molecular approaches due to overlapping morphological characteristics with related genera (Ghaderi *et al*. 2017). In taxonomic literature, several pathogenic *Parastagonospora* species have been classified into different groups due to a lack of supporting morphological characteristics such as *Paras. nodorum* placed in *Leptosphaeria*, *Septoria* and *Stagonospora* (McDonald *et al*. 2012). However, the increased use of multigene phylogenetic analysis has led to significant clarification within the taxonomy (McDonald *et al*. 2012, Ghaderi *et al*. 2017). Researchers have used different molecular gene markers, such as ITS sequences (Ueng *et al*. 1998), *tub* (Malkus *et al*. 2005), glucosidase (*bgl*1) (Reszka *et al*. 2005), *rpb*2 (Arkadiusz *et al*. 2006), histidine synthase (*his*) (Wang *et al*. 2007) and mating-type loci (Bennett *et al*. 2003, Ueng *et al*. 2003).

Ecological and economic significance

Parastagonospora species are responsible for numerous economically important plant diseases, two of which are discussed below.

***Parastagonospora nodorum* leaf blotch and glume blotch on *Triticum aestivum* (wheat)** also known as septoria-like blotch caused by *Paras. nodorum* is a major pathogen in wheat and other cereals (Oliver *et al*. 2012) that was originally described as

Table 61. Top 10 cited articles related to *Parastagonospora* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Finished genome of the fungal wheat pathogen *Mycosphaerella graminicola* reveals dispensome structure, chromosome plasticity, and stealth pathogenesis	360	Goodwin *et al.* (2011)
2	Sizing up *Septoria*	223	Quaedvlieg *et al.* (2013)
3	When and how to kill a plant cell: infection strategies of plant pathogenic fungi	209	Horbach *et al.* (2011)
4	Disease impact on wheat yield potential and prospects of genetic control	185	Singh *et al.* (2016b)
5	The cysteine rich necrotrophic effector SnTox1 produced by *Stagonospora nodorum* triggers susceptibility of wheat lines harboring *Snn1*	139	Liu *et al.* (2012d)
6	Revision of *Phaeosphaeriaceae*	135	Phookamsak *et al.* (2014)
7	*Stagonospora nodorum*: from pathology to genomics and host resistance	121	Oliver *et al.* (2012)
8	Comparative pathogenomics reveals horizontally acquired novel virulence genes in fungi infecting cereal hosts	118	Gardiner *et al.* (2012)
9	Horizontal gene and chromosome transfer in plant pathogenic fungi affecting host range	106	Mehrabi *et al.* (2011)
10	Genome-wide association study reveals novel quantitative trait loci associated with resistance to multiple leaf spot diseases of spring wheat	103	Gurung *et al.* (2014)

Depazea nodorum from wheat collected in the UK (Croll *et al*. 2021). The disease was reported to cause 31 % loss of yield in Australia (Bhathal *et al*. 2003). This pathogen commonly occurs in northern latitudes (Leath *et al*. 1993). The sexual morph of this species was initially described on wheat as *Leptosphaeria nodorum* (Muller 1952) but later transferred to *Phaeosphaeria* (Hedjaroude 1968). The primary dispersal is via air and during the winter, and ascospores are released while the secondary dispersal occurs through splash-dispersed conidia (Solomon *et al*. 2006). Leaf blotch primarily affects leaves, while glume blotch affects leaves, glumes and nodes. Wet leaf surface facilitates the germination of spores and the development of fungal hyphae, and later the penetration can occur through stromata or cuticles (Solomon *et al*. 2006). At the initial stage, the infected host shows water-soaked and small chlorotic lesions on the lower leaves of the plant that become yellow and eventually red-brown. At the mature stage, the lesions become lens shaped without a distinct yellow border (McMullen & Adhikari 2009). *Parastagonospora avenae* leaf blotch is also recorded from wheat, but it has a lower impact than *Paras. nodorum* (Van Ginkel *et al*. 1999). *Parastagonospora nodorum* glume blotch and *Paras. nodorum* leaf blotch (SNLB) are important disease in wheat and grains (Friesen *et al*. 2008).

***Parastagonospora* leaf blotch of barley and rye** caused by *Parastagonospora avenae f. sp. triticea.* This species also occurs as a pathogen on wheat, oats, rye and various grasses (Johnson 1947). At the initial stage, an off-white centre with a narrow brown edge can be observed, later becoming yellow-brown lesions on barley (Cunfer 2000), while small brown spots with yellow halos and necrotic spots were observed in oats (Shearer *et al*. 1978). Brown with off-white centres before coalescing to cause necrotic areas with a brown margin was observed in rye (Shearer *et al*. 1978, Cunfer 2000).

Research interests

There are 490 publications and 10 146 citations from 2011–2021 in the Web of Science (Fig. 84), with the top 10 most cited articles included in Table 61. Most publications focused on disease management (disease resistance, quantitative trait loci, sensitivity genes) and research on pathogenic *Parastagonospora nodorum* (winter wheat, *Stagonospora nodurum* blotch, host selective toxins) as well as identification.

Disease management

Parastagonospora nodorum blotch (SNB) is a major disease worldwide and commonly controlled by crop rotation, tillage, growth of resistant cultivars, fungicide-treated seeds and foliar fungicide (Krupinsky *et al*. 2007). However, these cultural practices and chemical methods are ineffective, as widespread airborne ascospores can develop without wheat residue (Cowger & Silva-Rojas 2006). Resistant cultivar and pathogenicity of the fungus determined the spread of SNB. Pre-planting decision management tools have also been found to be effective for controlling *Paras. nodorum* (Mehra *et al*. 2016). Cultivar resistance levels vary; cultivars with low resistance have a high risk of susceptibility and adapted, highly resistant cultivars are not available (Milus & Chalkley 1997). Some cultivars can be resistant to foliar infection, but seed-transmitted inoculum could trigger an epidemic (Shah *et al*. 2000). Hyperspectral imaging techniques with a molecular approach have also been used for early detection of *Parastagonospora nodorum* on leaves of durum wheat (Iori *et al*. 2015). Percentage of necrotic leaf area or pycnidial density have been conducted by visual or microscopic examination but they are not accurate; thus, enzyme-linked immunosorbent assay is an accurate alternative method to detect pathogens in plants (Tian *et al*. 2005). Restriction fragment length polymorphisms (RFLPs) (McDonald *et al*. 1994), amplified fragment length polymorphisms (AFLPs) (Bennett *et al*. 2005), microsatellites or simple sequence repeats or SSRs (Stukenbrock *et al*. 2005), single nucleotide polymorphisms from entire genome sequences (Richards *et al*. 2019, Pereira *et al*. 2020) and single nucleotide polymorphism (SNP) have been used to identify the genetic structure of *Paras. nodorum* (Gao et *al*. 2016a).

Toxins

Three types of proteinaceous host-selective toxins (HST) (SnToxA, SnTox1, and SnTox3) have been identified in *Paras. nodorum* (Friesen *et al*. 2008), and these necrotrophic effectors facilitate the infection process (Friesen *et al*. 2008). These necrotrophic effectors are small and secreted proteins that infect hosts by triggering programmed cell death (PCD), resulting in NE-triggered susceptibility (Richards *et al*. 2019).

Taxonomy and phylogeny

Parastagonospora is well established within *Phaeosphaeriaceae* and found to be a separate clade from other cereal pathogens (Quaedvlieg *et al*. 2013). Combined multigene phylogenetic analyses of ITS, LSU, SSU, *tef*1, *rpb*2 and *tub* are commonly used in the taxonomy (Quaedvlieg *et al*. 2013, Li *et al*. 2015c, Thambugala *et al*. 2017).

Author: D.N. Wanasinghe

56. ***Monascus*** Tiegh., Bull. Soc. Bot. France 31: 226. 1884.

Type species: *Monascus ruber* Tiegh.

Classification: *Ascomycota*, *Pezizomycotina*, *Eurotiomycetes*, *Eurotiales*, *Aspergillaceae.*

Background

Monascus is an important genus in *Eurotiales* due to its application in several industrial segments, such as food colorants. Red pigments are of particular interest, as red is the most popular food colour but true natural pigments suitable for applications in food industries are difficult to obtain. *Monascus* species commonly exist in soil, starch, grain, mouldy feed and more recently in stingless bee substrates and colonies (Stchigel *et al.* 2015, Barbosa *et al.* 2017). Most species show osmophilic affinity (Pitt & Hocking 1985). *Monascus* was introduced by Van Tieghem (1884) to accommodate two species, *Mo. ruber* and *Mo. mucoroides* that produce non-ostiolate ascomata. In the past, the position of *Monascus* in *Aspergillaceae* (*Eurotiales*) was the subject of discussion (Benny & Kimbrough 1980, Von Arx 1987), but its placement was confirmed by several phylogenetic analyses (Berbee *et al.* 1995, Ogawa *et al.* 1997, Ogawa & Sugiyama 2000, Peterson 2008, Houbraken & Samson 2011, Houbraken *et al.* 2020). The identification and classification of *Monascus* have long been based on macro- and microscopic features, such as pigmentation of the cleistothecial walls and conidia, as well as the growth rates on agar media. The number of *Monascus* species increased with the description of *Mo. albidulus*, *Mo. argentinensis*, *Mo. aurantiacus*, *Mo. eremophilus*, *Mo. floridanus*, *Mo. fumeus*, *Mo. lunisporas*, *Mo. pallens*, *Mo.*

rutilus and *Mo. sanguineus*. However, the genus became morphologically and physiologically more diverse, and many of the species are now considered to be synonyms (Shao *et al.* 2011). The genus *Basipetospora* has been linked to *Monascus* for many years, however with the introduction of "One Fungus = One Name" nomenclature system, *Monascus* has taken precedence over *Basipetospora* (Rossman *et al.* 2016). Barbosa *et al.* (2017) conducted a comprehensive polyphasic examination of *Monascus* based on a multi-locus DNA sequence dataset (ITS, *tub*, *cal*, LSU and *rpb2*), morphology and extrolites analysis. They resolved *Monascus* into nine species (*Monascus argentinensis*, *Mo. flavipigmentosus*, *Mo. floridanus*, *Mo. lunisporas*, *Mo. mellicola*, *Mo. pallens*, *Mo. purpureus*, *Mo. recifensis* and *Mo. ruber*) and two sections (sect. *Floridani* containing seven species and sect. *Rubri* with three species). These findings led to the conclusion that a polyphasic approach is the best route for the delimitation of *Monascus* species (Barbosa *et al.* 2017).

Ecological and economic significance

***Monascus* may have an ecological value** for native bees, as it has been reported as closely associated with bees (Menezes *et al.* 2015, Barbosa *et al.* 2017). However, this aspect deserves to be better evaluated.

***Monascus* species produce yellow, orange, and red pigments**, which have been used as natural food colouring in Asian fermented foods, particularly red rice. Red rice is of particular interest because of its health-promoting effects (Lee & Pan 2011, 2012, Hsu & Pan 2012, Shi & Pan 2012). *Monascus* pigments have been used to colour food for centuries and the traditional method of pigment production involves the growth of the fungus on a solid medium such as steamed rice (Manan *et al.* 2017).

Several *Monascus* species, mainly *Mo. ruber* can produce heat-resistant ascospores, which survive thermal pasteurisation, and this has been a methodological challenge for the food industry, which has increasingly investigated different techniques for food and feed preservation. Fungal spoilage of products imposes significant annual global revenue losses, and *Mo. ruber* has contributed to this spoiling of food, feed products and silage, and is well documented (*e.g.*, Panagou *et al.* 2005, Cappato *et al.* 2018, Rico-Munoz *et al.* 2019).

Derivatives of *Monascus* pigments also have importance in health promotion due to the production of compounds with anti-bacterial properties and cholesterol-lowering statins. Several companies (especially in China) are working to produce *Monascus* products containing lovastatin (Monacolin K = mevinolin = lovastatin) used to reduce cholesterol levels (Srianta *et al.* 2014). Lovastatin is the first reported in *Mo. ruber* and works by competitively inhibiting HMG Co-A reductase. Monacolin M, a specific inhibitor of cholesterol biosynthesis structurally related to monacolin K is produced by *Monascus* (Seenivasan *et al.* 2008, Vendruscolo *et al.* 2016). The antimicrobial activity of *Monascus* pigments has been a focus of research. Wong & Koehler (1981) studied the antibiotic effect of *Mo. purpureus* N11S against *Bacillus subtilis*. The pigments from *Mo. ruber* strain CCT 3802 showed antimicrobial activity against *Staphylococcus aureus* ATCC 25923 and *Escherichia coli* ATCC 25922 (Vendruscolo *et al.* 2014), revealing their antibacterial potential for use in the food and pharmaceutical industry. *Monascus* products have been used for the treatment of dengue virus infection (Triyono *et al.* 2020).

Mycotoxin production can be observed in several species. *Monascus purpureus* and *Mo. ruber* have been reported to produce the mycotoxin citrinin (Barbosa *et al.* 2017), and the presence of this mycotoxin in food, including red rice, should be avoided. Wang *et al.* (2005b) also reported citrinin production by *Mo. floridanus*, *Mo. lunisporas* and *Mo. pallens*, but this has not been confirmed by other authors working on citrinin and *Monascus*.

In humans, *Monascus* can be pathogenic in several ways, for example, allergy and anaphylaxis in response to red yeast rice have

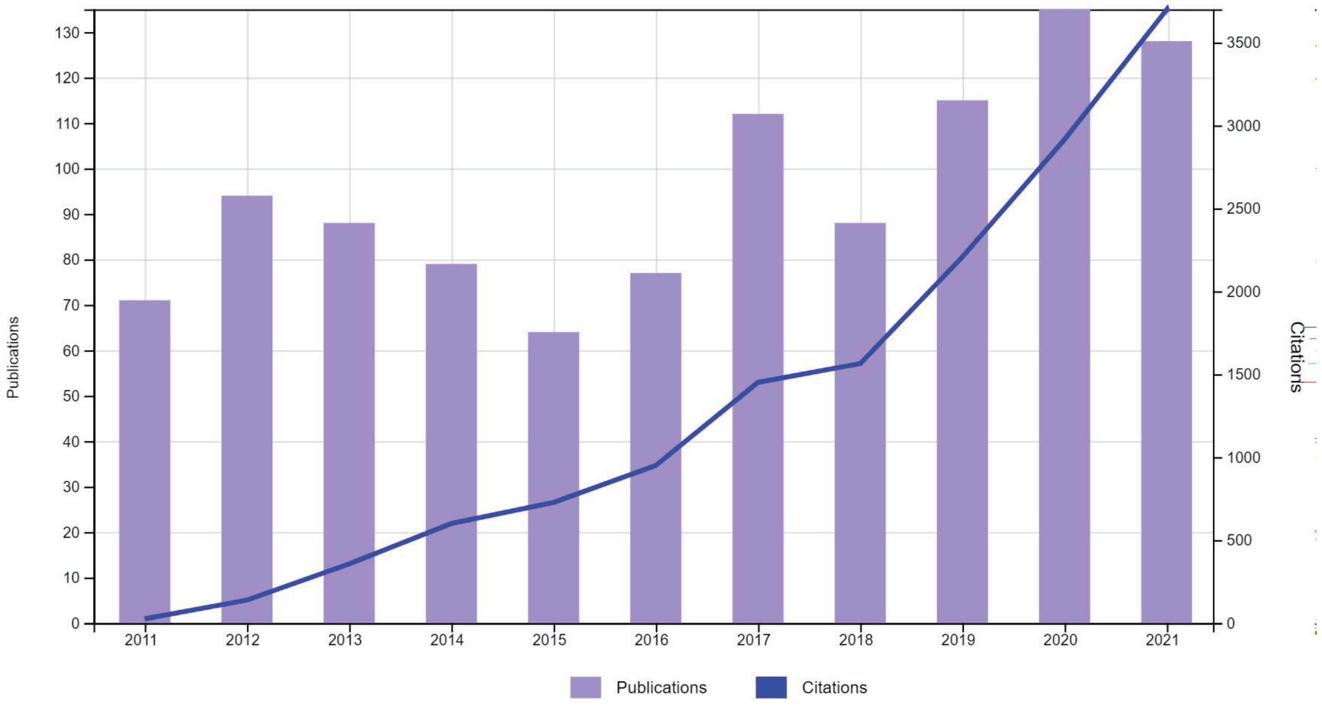

Fig. 85. Trends in research of *Monascus* in the period 2011–2021.

Table 62. Top 10 cited articles related to *Monascus* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	*Monascus* pigments	213	Feng *et al.* (2012)
2	*Monascus* secondary metabolites: production and biological activity	167	Patakova (2013)
3	Density functional theory study on the electronic structure of *Monascus* dyes as photosensitizer for dye-sensitized solar cells	153	Sang-aroon *et al.* (2012)
4	Orange, red, yellow: biosynthesis of azaphilone pigments in *Monascus* fungi	124	Chen *et al.* (2017d)
5	Edible filamentous fungi from the species *Monascus*: early traditional fermentations, modern molecular biology, and future genomics	102	Chen *et al.* (2015e)
6	Genetic localization and *in vivo* characterization of a *Monascus* azaphilone pigment biosynthetic gene cluster	87	Balakrishnan *et al.* (2013)
7	Purification and characterization of a new red pigment from *Monascus purpureus* in submerged fermentation	75	Mukherjee *et al.* (2011)
8	Production of citrinin-free *Monascus* pigments by submerged culture at low pH	72	Kang *et al.* (2014)
9	Beneficial effects of *Monascus purpureus* NTU 568-fermented products: a review	71	Shi *et al.* (2011)
10	Perstraction of intracellular pigments by submerged cultivation of *Monascus* in nonionic surfactant micelle aqueous solution	62	Hu *et al.* (2012)

been described, due to an immediate sensitivity to *Mo. purpureus* (Hipler *et al.* 2002). Citrinin is a nephrohepatotoxic agent deserving attention when present in contaminated food (Krejci *et al.* 2002). Renal infection after surgery due to *Mo. ruber* was described in a 70-yr-old patient with multiple kidney stones (Sigler *et al.* 1999), and an invasive gastric infection was observed in a patient with gastric adenocarcinoma by the consumption of *Mo. ruber* contaminated food (Iriart *et al.* 2010).

Research interests

There are 1 051 publications and 10 083 citations from 2011–2021 in the Web of Science (Fig. 85), with the top 10 most cited articles included in Table 62. Most publications focused on *Monascus* secondary metabolites including pigments and fermented products. A few papers focused on the taxonomy and phylogeny of *Monascus*.

Monascus pigments

Monascus pigments are widely used in the food industry as a colour intensifier, food additive and nitrite substitute in meat products. The pigments also have potential for therapeutic uses, and as a dye in cosmetic and textile industries (Agboyibor *et al.* 2018). However, the production of the nephrotoxic and hepatotoxic citrinin limits the wide application of *Monascus* related products (Blanc *et al.* 1995). The six primary pigments produced by *Monascus* are the colours yellow (angkak flavin, monascine), orange (rubropunctatin, monascorubrine) and red (rubropuntantamine, monascorubramine) (Meinicke *et al.* 2012). The orange pigments possess antibiotic activities against bacteria, yeast, and filamentous fungi and inhibit the growth of *Bacillus subtilis* and *Candida pseudotropicalis*. Yellow pigments such as monascin and ankaflavin have immunosuppressive activities against mouse T splenocytes (Martinkova *et al.* 1999). The red pigment is the most common and suitable for food use (Chen & Johns 1993).

Monascus-fermented products

Monascus purpureus, *Mo. pilosus*, *Mo. anka* and *Mo. ruber* can be used for fermentation. The first product, which has been consumed over centuries in Asian countries, is *Monascus*-fermented rice (angkak, anka, beni koji, red yeast rice). The red yeast rice contains the compound monacolin K, the same active ingredient found in prescription cholesterol-lowering medications like lovastatin. The red pigment produced in rice also possesses antioxidant properties, immunosuppressive properties, teratogenicity, and antimicrobial, cytotoxic and anti-tumour activities (Lin *et al.* 2008).

Taxonomy and phylogeny

Barbosa *et al.* (2017) revealed that the *BenA* gene has strong power for species delimitation in *Monascus* when supplemented with ITS and *cmd*. LSU has limited resolving power and *rpb2* is recommended only in phylogenetic studies (Barbosa *et al.* 2017). These authors considered nine species to belong to the genus (*Mo. argentinensis*, *Mo. flavipigmentosus*, *Mo. floridanus*, *Mo. lunisporas*, *Mo. mellicola*, *Mo. pallens*, *Mo. purpureus*, *Mo. recifensis* and *Mo. ruber*). He *et al.* (2020b) studied the morphological characteristics and analysed sequences of seven genes (ITS, *tub*, *cal*, LSU, *rpb2*, β-ketoacyl synthase, and mating-type locus 1-1) of 15 *Monascus* strains, including sequencing of multiple clones of five protein genes in four *Mo. sanguineus* strains. They observed two types of haplotypes in the five protein genes of *Mo. sanguineus*. One haplotype was closely related to *Mo. ruber*, and the other may be derived from an unknown *Monascus* species. Thus, the authors suggested that *Mo. sanguineus* including type strains may be a natural species, and that its genome must be analysed for a better understanding.

Author: R.N. Barbosa, C.M. Souza-Motta and J. Houbraken

57. ***Hanseniaspora*** Zikes *ex* Klöcker, Centbl. Bakt. ParasitKde, Abt. II 35: 385. 1912.

Type species: *Hanseniaspora valbyensis* Klöcker

Classification: *Ascomycota*, *Saccharomycotina*, *Saccharomycetes*, *Saccharomycodales*, *Saccharomycodaceae.*

Background

Hanseniaspora is a genus of ascomycetous yeasts that are morphologically characterised as apiculate yeasts with bipolar budding and are phylogenetically placed at the base of the *Saccharomycetaceae*. Currently, there are 22 species recognised. Recently, according to the new rules of nomenclature (Shenzen Code; Turland *et al.* 2018), three asexual species that were assigned to the asexual counterpart *Kloeckera* have been transferred to the sexual genus *Hanseniaspora* (Čadež *et al.* 2019). As their primary habitat, *Hanseniaspora* spp. are abundant on various fruits, and also on flowers and bark (Saubin *et al.* 2020). Insects can serve as their dispersal vectors (Hamby *et al.* 2012), and their presence in the upper layers of soil suggests that this acts as their reservoir (Maksimova & Chernov 2004, Kachalkin *et al.* 2015). As predominant inhabitants on the surface of various fruit, and mostly on grapes, they contribute to the starting phases of various spontaneous food fermentation processes. In this context, *Hanseniaspora* spp. have been intensively studied to determine their potential to improve the sensorial complexity of fermented products (Steensels & Verstrepen 2014).

An extensive study on the evolutionary diversification of budding yeasts was published recently (Shen *et al.* 2018). This was followed by the study of Steenwyck *et al.* (2019) that focused on the evolution of *Hanseniaspora* spp. Through analysis of their genomes, Steenwyck *et al.* (2019) showed that the origin of *Hanseniaspora* spp. coincides with the origin of flowering plants with fruit, where simple sugars were available as a food source only once a year. They reported that ancient *Hanseniaspora* spp. lost numerous genes associated with metabolism, the cell cycle and DNA repair processes. This most likely provided *Hanseniaspora* spp. with a burst of accelerated evolution and adaptation to the grape environment, which was followed by a reduction in the pace of their sequence evolution. Compared to *Saccharomyces cerevisiae*, the most abundant *Hanseniaspora* spp. on grapes, *Hanseniaspora uvarum*, has a lower fermentative capacity due to reduced glycolytic enzyme activities, which can be correlated with its Crabtree-negative phenotype (Langenberg *et al.* 2017). Further, *Hanseniaspora* spp. have the lowest GC content, and the smallest genomes and gene numbers in the entire subphylum *Saccharomycotina* (Riley *et al.* 2016, Shen *et al.* 2018). The mitochondrial DNA of *H. uvarum* was shown to be in the form of a very compact linear molecule that contains the shortest functional region found in fungi (Pramateftaki *et al.* 2006). These evolutionary and functional studies have shown that the genus *Hanseniaspora* represents enigmatic fungi, with many questions on its biology remaining unanswered.

Reess (1870) first described apiculate yeasts and considered them members of the genus *Saccharomyces* because they fermented grape juice. He classified them into the single species *Saccharomyces apiculatus*. The name *Hanseniaspora* was proposed by Zikes (1911), but did not include a generic concept. For this reason, Klöcker (1912) was the first who placed sporogenous apiculate yeasts in the genus *Hanseniaspora*. Subsequent studies on the classification of apiculate yeast have provided an extensive bibliography, with their generic concept based on their ability (or not) to form ascospores, and their various reported forms have contributed to much confusion (Phaff 1979). It was not until the introduction of molecular taxonomy of the genus *Hanseniaspora* by Meyer *et al.* (1978) that the status of the various *Hanseniaspora* spp. became established through DNA-DNA reassociation studies, with *Hanseniaspora* sexual morphs correlated with *Kloeckera* asexual morphs.

However, with the introduction of phylogenetic analysis (Yamada *et al.* 1992), the generic concept of *Hanseniaspora* was again revised, mainly because of the high sequence divergence between two groups of *Hanseniaspora* species. Nevertheless, Boekhout *et al.* (1994) argued against splitting the genus solely on the basis of genetic divergence, because the two species groups share many similarities in morphology, physiology and ecology. As the ribosomal gene regions of *Hanseniaspora* are unusually conservative for reliable species phylogeny, it was necessary to include multi-locus DNA sequence datasets (Čadež *et al.* 2006), or to resolve the relationships between species using a genome-scale phylogeny (Steenwyk *et al.* 2019). Later, the long-standing puzzle of the long branches was solved from an evolutionary perspective, with the delimitation into two lineages within the genus (*i.e.*, FEL, SEL lines). This was probably due to the loss of many genes associated with DNA repair and maintenance, which resulted in a hypermutator phenotype.

Ecological and economic significance

Hanseniaspora spp. have significant roles in food fermentations through the production of enzymes and aroma compounds. The aroma compounds can also be exploited in biocontrol against pests.

Increased flavour complexity of wine

Hanseniaspora spp. can provide increased complexity of the flavours of wines when they are added as co-starter cultures in wine fermentation. Indeed, in recent years, this has been shown to be the preferred practice over wines produced by monocultures of *S. cerevisiae* (for reviews, see Jolly *et al.* 2013, Martin *et al.* 2018). As the most abundant *Hanseniaspora* spp. on grapes, those that are most commonly associated with wine fermentation are *H. vineae* (Medina *et al.* 2013), *H. osmophila* (Viana *et al.* 2009), *H. uvarum* (Hu *et al.* 2018a) and *H. opuntiae* (Luan *et al.* 2018). However, their effects on wine aromas appear to be a strain-specific trait, as only certain *Hanseniaspora* strains result in wines with increased levels of acetate esters, such as 2-phenyl acetate and ethyl acetate, which are associated with fruity and floral aroma descriptors of wines (Viana *et al.* 2009, Martin *et al.* 2018). In addition to metabolic activity, selected strains of apiculate yeasts have high β-glucosidase activity, which can free volatile compounds from glycosides in grapes, and thus produce typical varietal aromas (Hu *et al.* 2018a).

On the other hand, apiculate yeasts are also known to be high producers of acetic acid and ethyl esters, which at higher levels can contribute negatively to wine quality (Zironi *et al.* 1993, Rojas *et al.* 2003) or limit nutrient availability to *S. cerevisiae,* which can lead to stuck fermentations (Medina *et al.* 2012). Nevertheless, with novel technological advances and controlled fermentation processes, *Hanseniaspora* yeasts continue to gain importance in winemaking.

As indicated, most of the properties of apiculate yeasts in wine making are strain dependent, and therefore several studies have been aimed at the characterisation of genetic variability among the populations of *Hanseniaspora* spp. However, population structure based on geographic or substrate origins has been very difficult to establish, most probably due to their highly dynamic genomic structure (Albertin *et al.* 2016, Saubin *et al.* 2020). Furthermore, the first interspecific hybrids were found between *H. opuntiae* and *H. pseudoguilliermondii* (Saubin *et al.* 2020).

Bioflavouring of fermented foods

As the dominant species of spontaneous fermentations, the bioflavouring of various foods by *Hanseniaspora* spp. has recently gained attention, particularly as spontaneous processes generally yield products of inconsistent quality, and starter cultures with only one species provide a limited flavour spectrum (Steensels & Verstrepen 2014). *Hanseniaspora opuntiae* has been suggested as a starter culture for cocoa fermentation because it produces high

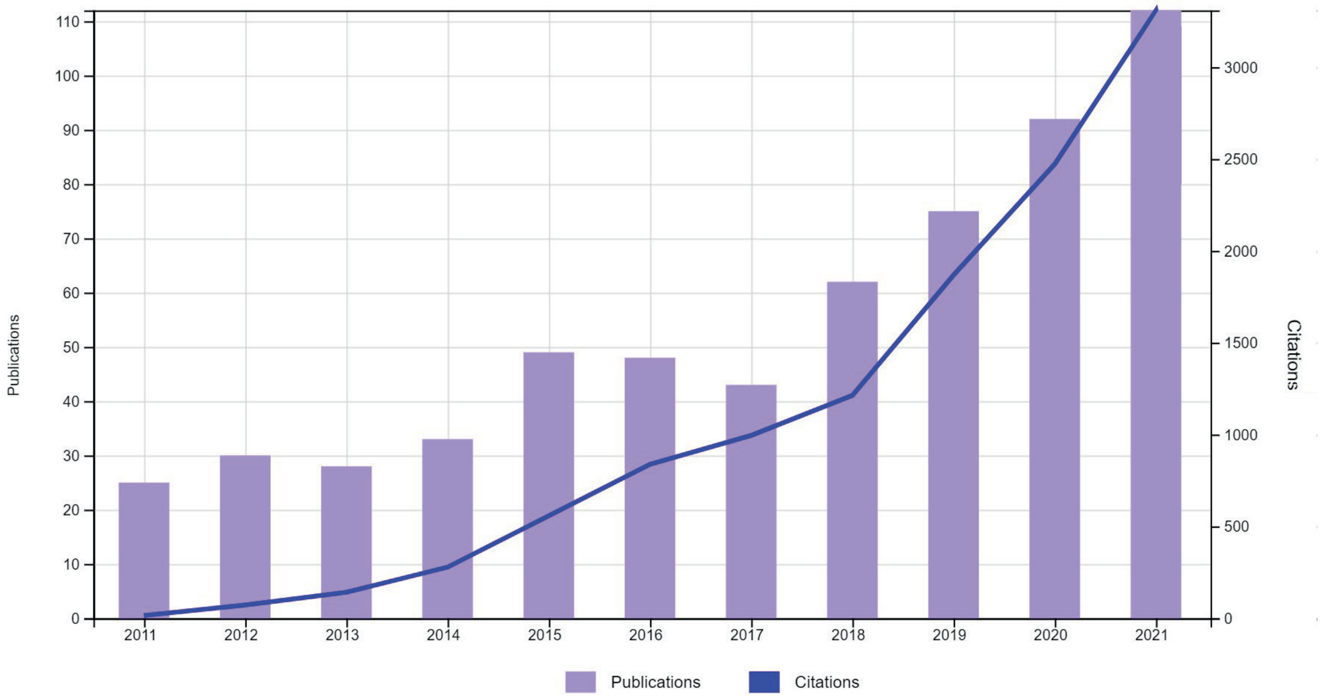

Fig. 86. Trends in research of *Hanseniaspora* in the period 2011–2021.

levels of aromatic compounds (Mota-Gutierrez *et al.* 2018) and pectinases (Verce *et al.* 2021). *Hanseniaspora guilliermondii* and *H. opuntiae* have also been defined for beer fermentation in mixed cultures with *S. cerevisiae*, because they improve the aroma profile of the beer, although they cannot assimilate maltose, as the main sugar of the wort (Bourbon-Melo *et al.* 2021).

Postharvest biocontrol of moulds

In the fruit industry, preharvest application of *Hanseniaspora* spp. for postharvest control of moulds is an alternative to the use of synthetic fungicides, as these pose health concerns. Most studies have reported on the use of *H. uvarum* with a bioactive compound, to augment its activity (Liu *et al.* 2010). By synthesising volatile organic compounds, *H. uvarum* can induce plant defence-related enzymes and inhibit spore germination, without affecting fruit quality. From this perspective, *Hanseniaspora* strains have great potential as an alternative method against postharvest moulds of various fruit (Li *et al.* 2016b, Qin *et al.* 2017, Ruiz-Moyano *et al.* 2020).

Nutritional ecology of insects

Drosophila have been well studied in terms of its nutritional ecology. *Hanseniaspora* yeasts have crucial roles in supplementing the sugar-rich diet of *Drosophila* with a source of dietary protein, which is needed for oviposition (Hamby *et al.* 2012). *Drosophila* are attracted to the CO_2 emitted by ripe fruit and to the volatile compounds produced by fermentative yeasts (*e.g.*, fruity esters, in particular), with feeding preferences shown towards *Hanseniaspora*

Table 63. Top 10 cited articles related to *Hanseniaspora* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Not your ordinary yeast: non-*Saccharomyces* yeasts in wine production uncovered	465	Jolly *et al.* (2014)
2	The microbial ecology of wine grape berries	360	Barata *et al.* (2012)
3	Yeast biodiversity from DOQ Priorat uninoculated fermentations	249	Padilla *et al.* (2016a)
4	Recent advances on the use of natural and safe alternatives to conventional methods to control postharvest gray mold of table grapes	169	Romanazzi *et al.* (2012)
5	Increased flavour diversity of Chardonnay wines by spontaneous fermentation and co-fermentation with *Hanseniaspora vineae*	153	Medina *et al.* (2013)
6	Taming wild yeast: potential of conventional and nonconventional yeasts in industrial fermentations	134	Steensels & Verstrepen (2014)
7	Outlining a future for non-*Saccharomyces* yeasts: selection of putative spoilage wine strains to be used in association with *Saccharomyces cerevisiae* for grape juice fermentation	131	Domizio *et al.* (2011)
8	Yeasts are essential for cocoa bean fermentation	129	Ho *et al.* (2014)
9	Microbial terroir and food innovation: the case of yeast biodiversity in wine	112	Capozzi *et al.* (2015)
10	Growth of non-*Saccharomyces* yeasts affects nutrient availability for *Saccharomyces cerevisiae* during wine fermentation	99	Medina *et al.* (2012)

spp. (Mori *et al.* 2017). In this regard, *Hanseniaspora* spp. might serve as attractive and selective bait for fruit fly pests, and thus contribute to sustainable insecticides (Jones *et al.* 2021).

Research interests

For *Hanseniaspora* spp., there were 597 publications and 9 891 citations from 2011–2021 in the Web of Science (Fig. 86), with the top 10 most-cited articles given in Table 63. Most of these publications have been focused on wine ecology (*e.g.*, grape microbiota, mixed wine fermentation, *Hanseniaspora* diversity), the ecology of other fermented foods, and research into biocontrol activities.

Wine ecology

Spontaneous wine fermentations are characterised by the presence of "wild" non-*Saccharomyces* yeasts that participate in a sequential manner, mostly in the early phases of grape must fermentation (Barata *et al.* 2012, Jolly *et al.* 2014). As the predominant species on grapes, *Hanseniaspora* spp. have important roles in the harmonisation of the aromatic profiles of wines, and at the same time, they are "compatible" with *S. cerevisiae* wine yeast, to finish the fermentation (Medina *et al.* 2013, Padilla *et al.* 2016b).

Postharvest control

The control of postharvest fruit decay is an important challenge for the fruit industry. As strong producers of volatile organic compounds, *Hanseniaspora* spp. are gaining attention as the predominant inhabitants of healthy fruit (Romanazzi *et al.* 2012).

Taxonomy and phylogeny

Since the introduction of DNA sequence analysis for species delineation, the number of newly described *Hanseniaspora* spp. has increased significantly (Jindamorakot *et al.* 2009, Chang *et al.* 2012, Čadež *et al.* 2014, 2019, Ouoba *et al.* 2015, Liu *et al.* 2021b). Currently, with the emergence of whole-genome sequencing, the reconstruction of more robust yeast phylogenies has recovered statistically well-supported phylogenetic trees that reflect the evolutionary relationships between species and genera. With the exploration of novel ecological niches, the genetic diversity and modes of speciation of this fascinating genus are being elucidated.

Author: N. Čadež

58. ***Paracoccidioides*** F.P. Almeida, Compt.-Rend. Hebd. Séances Mém. Soc. Biol. 105: 316. 1930.

Type species: *Paracoccidioides brasiliensis* (Splend.) F.P. Almeida

Classification: *Ascomycota*, *Pezizomycotina*, *Eurotiomycetes*, *Onygenales*, *Ajellomycetaceae.*

Background

Paracoccidioides is an ascomycete genus that belongs to the family *Ajellomycetaceae*, order *Onygenales*. It encompasses two species complexes, *Para. brasiliensis*, with at least five phylogenetic lineages, and *Para. lutzii*, known as the causative agent of paracoccidioidomycosis. Paracoccidioidomycosis (PCM) is the most relevant systemic mycosis in Latin America, described in 1908 from Brazil by Adolf Lutz (Lutz 1908). The first name proposed for the agent was *Zymonema brasiliensis* in 1912 by Splendore and only in 1930 Floriano de Almeida (De Almeida 1930) formally described the species as *Paracoccidioides brasiliensis*. *Paracoccidioides* species are thermal dimorphic fungi, with a mycelial phase at room temperature, or in a saprobic substrate, producing conidia that can be inhaled by humans and other vertebrate hosts, while at higher temperatures, growth converts to a multi-budding yeast phase. Once in pulmonary alveoli, *Paracoccidioides* yeasts disseminate to other organs and tissues. Chronic pulmonary or disseminated disease is the most common manifestation of PCM, which may mimic some clinical aspects of tuberculosis, causing severe disability (Bocca *et al.* 2013). The highest prevalence of PCM occurs in Brazil, where it is a serious public health issue, accounting for 50 % of deaths caused by systemic mycosis (Prado *et al.* 2009). Hospital admissions due to PCM is 7.99/1 000 (Giacomazzi *et al.* 2016), which is higher than other endemic mycoses. Due to *Paracoccidioides* spp. saprobic association with soil, PCM is predominant in rural areas, affecting socioeconomically vulnerable individuals (Griffiths *et al.* 2019, Nery *et al.* 2021). Its relevance in public health has led to great research efforts concerning diagnosis, immunological and other biological/ecological aspects and treatment of PCM in the last century.

Clinical significance

The main risk factors for being infected by *Paracoccidioides* species are the activities of soil management, such as earthworks, soil preparation, gardening, transportation of plant products, and others. Most PCM patients are exposed to the fungal agent in their first two decades of life, presenting the symptoms many years later, so some have already left the rural areas when clinical manifestation is presented. This long latency period (up to 50 years) makes identification of the exact local of fungal exposure impossible. Smoking and alcoholism are considered risk factors for disease development, but different from other systemic mycoses, such as cryptococcosis and disseminated histoplasmosis, PCM is not exclusively associated with immunosuppression (Shikanai-Yasuda *et al.* 2017).

In humans, PCM infection is usually asymptomatic or with non-specific symptoms. In those patients that exhibit PCM disease, there are two main clinical manifestations: acute or subacute manifestation, also known as juvenile, and the chronic or adult form. The acute or subacute form affects predominantly children and young adults, usually after a short period since fungus exposure, presenting the involvement of the phagocytic-mononuclear system, and having, as main symptoms, localised or generalised lymph adenomegaly and hepatosplenomegaly, in addition to digestive manifestations, accompanied by lesions in skin mucosa and bone. The chronic or adult form, which represents the majority of PCM cases (74–96 %), affects mainly adult men (there is 22:1 women:men ratio) over 30 yr old, after a long latency period. This clinical manifestation is usually characterised by lesions in the lungs and also in upper airways and oral mucosa and, in some cases, by fungal spread to other organs such as adrenals and the brain. In this manifestation, PCM may be misdiagnosed as tuberculosis, which severely compromises the disease prognostic (Bellíssimo-Rodrigues *et al.* 2013).

Paracoccidioides spp. also infect vertebrates other than humans. The most common accidental wild host of *Paracoccidioides* spp. are armadillos, mainly *Dasypus novemcinctus*, from which this fungus has been constantly isolated in endemic areas (Bagagli *et al.* 2003). Curiously, only species from the complex *Para. brasiliensis* have been isolated in culture from these mammals, although *Para.*

lutzii has been detected by molecular tools in soil from armadillo burrows (Arantes *et al.* 2017, Hrycyk *et al.* 2018). The occurrence of *Paracoccidioides* spp. in wild animals is not restricted to armadillos, since it was also detected in other wild mammals road killed, such as *Cavia aperea* ("guinea pig"), *Sphiggurus pinosus* ("porcupine"), *Gallictis vittata* ("grison") and *Procyon cancrivorus* ("raccoon") (Richini-Pereira *et al.* 2008). In addition to these, the manifestation of PCM disease has been confirmed in dogs (Ricci *et al.* 2004) and more recently in dolphins (Vilela *et al.* 2016). Although no fungal isolation from dolphin tissues was possible, the molecular phylogeny suggested this uncultivable *Paracoccidioides* belongs to the *Para. brasiliensis* complex.

Paracoccidioidomycosis have endemic areas well defined in Brazil, Colombia, Venezuela, Argentina and Ecuador but climate changes, as well as human migration to new territories, are known to influence PCM expansion to new regions, such as northern and centre-west regions of Brazil (Martinez 2017). Since most PCM cases are chronic and therefore present long latency periods, the definition of *Paracoccidioides* spp. occurrence in nature depends on their detection in the environment. The isolation of *Paracoccidioides* spp., in culture, from saprobic substrates, such as soil, is extremely rare (Bagagli *et al.* 2008) since it has fastidious growth requirements when compared to contaminant microorganisms. Nevertheless, molecular tools such as nested PCR (Theodoro *et al.* 2005, Arantes *et al.* 2013, Hrycyk *et al.* 2018), and *in situ* hybridisation techniques (Arantes *et al.* 2017), of multi-copy genomic targets such as ITS allowed mapping of the exact occurrence of these pathogens in the environment, which has been frequently related to armadillo burrows, mainly in sandy and disturbed soils, with medium to low concentrations of organic matter (Bagagli *et al.* 2003). Also, Geographic Information System analysis indicates that moisture availability in soil plays an important role in PCM distribution (Barrozo *et al.* 2009). The strong relationship between *Para. brasiliensis* and armadillos reinforced the idea that soil is the environmental substrate for this fungus in nature and mapping positive armadillo burrows for the presence of these pathogens has become a great strategy for mapping areas of infection risk.

Concerning the immune response against *Paracoccidioides* spp., the Th1 response, mediated by T lymphocytes (T-helper type 1) plays a central role in those patients who do not develop PCM disease. This response is characterised by the synthesis of cytokines that activate macrophages and TCD4+ and TCD8+ lymphocytes, producing compact granulomas that contain fungal replication and spread. However, quiescent forms may persist in such granulomas and, eventually, in a weak Th1 response, give rise to PCM disease. In patients with symptomatic and severe forms, both from acute and chronic manifestations, the main immune response is the Th-2 and Th-9 type, with B lymphocytes producing high titres of specific antibodies (Benard *et al.* 2001, Benard, 2008, Oliveira *et al.* 2002, Castro *et al.* 2013).

Paracoccidioidomycosis is usually treated with the administration of itraconazole, co-trimoxazole (sulfamethoxazole/trimethoprim association) and amphotericin B, although many other antifungal drugs have proved to be effective in the treatment of different clinical forms of PCM, including azolic and sulfamid derivatives. Depending on the clinical manifestation, as well as the treatment drug choice, the management of PCM disease may last up to 24 mo (Shikanai-Yasuda *et al.* 2017). Besides the long treatment, many patients may present sequelae due to anatomical and functional changes caused by scars in several organs, mainly in the lungs, skin, larynx, trachea, adrenal glands, airway mucosa, upper limbs, central nervous system and lymphatic system (Shikanai-Yasuda *et al.* 2017). Thus, the disease itself as well as its post-treatment sequelae make PCM a serious disability disease, once its patients are in their most productive ages.

Research interests

There are 994 publications and 9 763 citations from 2011–2021 in the Web of Science (Fig. 87). The top 10 most cited articles are listed in Table 64. Most of the publications focused on fungal

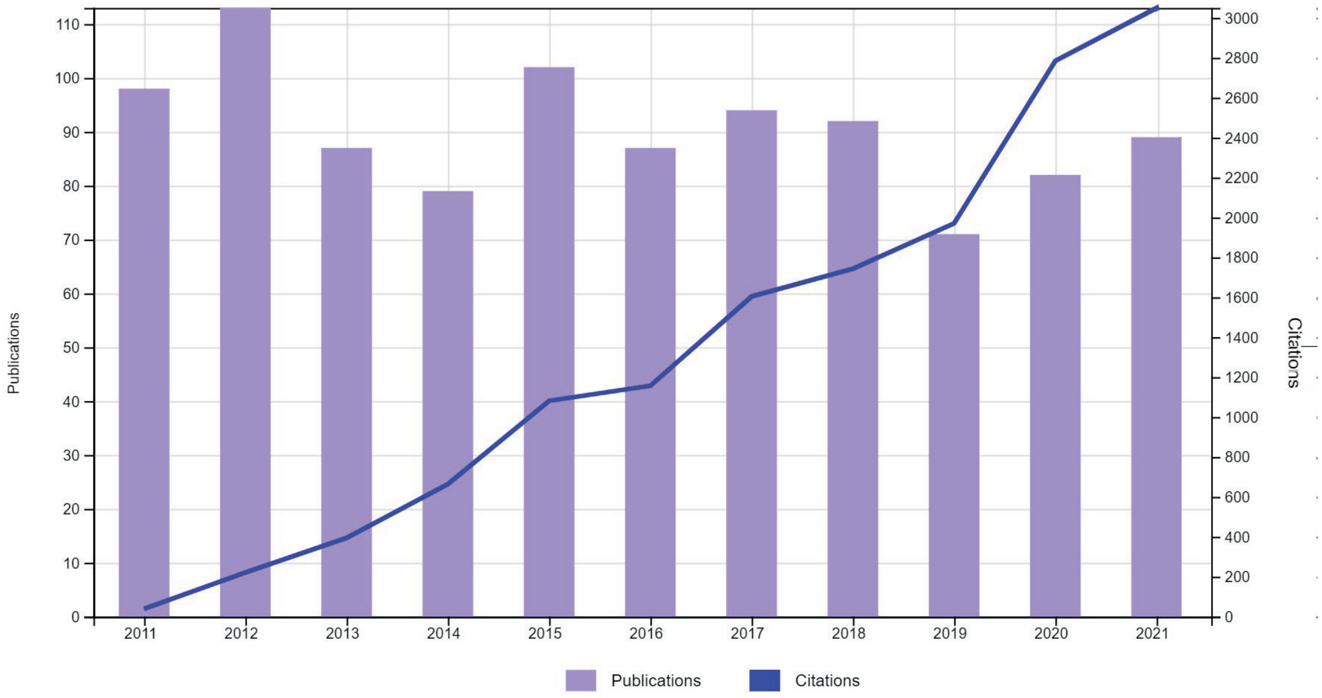

Fig. 87. Trends in research of *Paracoccidioides* in the period 2011–2021.

Table 64. Top 10 cited articles related to *Paracoccidioides* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Epidemiology of endemic systemic fungal infections in Latin America	213	Colombo *et al.* (2011b)
2	Brazilian guidelines for the clinical management of paracoccidioidomycosis	153	Shikanai-Yasuda *et al.* (2017)
3	New trends in paracoccidioidomycosis epidemiology	125	Martinez (2017)
4	Paracoccidioidomycosis: eco-epidemiology, taxonomy and clinical and therapeutic issues	118	Bocca *et al.* (2013)
5	The spectrum of fungi that infects humans	118	Köhler *et al.* (2015)
6	Vesicle and vesicle-free extracellular proteome of *Paracoccidioides brasiliensis*: Comparative analysis with other pathogenic fungi	118	Vallejo *et al.* (2012)
7	Extracellular vesicle-mediated export of fungal RNA	116	Peres da Silva *et al.* (2015)
8	Species boundaries in the human pathogen *Paracoccidioides*	116	Turissini *et al.* (2017)
9	Comparative genomic analysis of human fungal pathogens causing paracoccidioidomycosis	115	Desjardins *et al.* (2011)
10	Comparative genomics allowed the identification of drug targets against human fungal pathogens	73	Abadio *et al.* (2011)

taxonomy, concerning cryptic speciation in *Paracoccidioides* genus and their impact on diagnosis, epidemiology and management of PCM disease, studies of virulence factors and their immunogenicity.

Regarding species diversity since its formal description in 1930 until 2006, only one species, *Para. brasiliensis*, was known to belong to this genus, being the causative agent of PCM. However, Matute *et al.* (2006) identified three cryptic species, in what was known as *Para. brasiliensis*. They did not formally describe the species but identified them as clades S1, PS2 and PS3. Clades S1 and PS2 are sympatric in some regions of South America and PS3 is endemic in Colombia. Later, a new and very divergent clade was discovered and formally named *Para. lutzii* (Teixeira *et al.* 2009). In 2014 a new phylogenetic species, the Venezuelan clade PS4, was included in *Para. brasiliensis* complex (Teixeira *et al.* 2014). More recently S1, PS2, PS3, and PS4 were formally named *Para. brasiliensis s. str.*, *Para. americana*, *Para. restrepiensis*, and *Para. venezuelensis*, respectively (Turissini *et al.* 2017). Recently, the uncultivated *Paracoccidioides* sp. detected in dolphins was described as a new species, *Para. cetii* (Vilela *et al.* 2021).

Although clinical researchers have not observed any difference in PCM manifestations caused by the species described so far, their existence is impacting diagnosis because, whether it is histological, by culture isolation (gold standard method, despite taking more time), molecular or serologic, it should be capable of detecting all species causing PCM. For instance, serological diagnosis may result in false negative results when specific antigenic preparations derived from a single *Paracoccidioides* sp. are used (Queiroz Junior *et al.* 2014, Teixeira *et al.* 2014). Also, molecular detection needs primers or probes that hybridise with conservative genomic sequences among the species (Arantes *et al.* 2017).

According to a recent literature review, most molecular markers for species identification are ITS and the GP43 (glycoprotein 43) gene, although many other nuclear and mitochondrial genomic regions have been evaluated. Pinheiro *et al.* (2020) highlighted that most techniques do not accompany taxonomic updates, since some do not include *Para. lutzii* or do not consider species diversity in the *Para. brasiliensis* complex, and also highlighted the urgency for the development of point-of-care testing assays (POCT or bedside testing) to diagnose PCM at sites with limited infrastructure. Indeed, despite being affordable and simple, diagnosis by fungal isolation and identification in culture takes up to 30 d, which is too long, especially for patients presenting severe forms of PCM, that need treatment as soon as possible. On the other hand, molecular tools for diagnosis are still only applied for research and not in routine labs, since they are more expensive and demand equipment and trained professionals, which is not affordable in many developing countries, such as those where PCM is endemic.

To better understand the pathogenesis caused by *Paracoccidioides* species, numerous studies have focused on their virulence factors, which make possible fungal survival and dissemination in host tissues but are not essential for the growth of the yeast (parasitic phase) in culture (Mendes-Giannini *et al.* 2008). The main virulence factors studied in *Paracoccidioides*, and many other invasive fungi, are dimorphism and thermal tolerance, cell wall components, proteinases, lipases and phospholipases (Van Burik & Magee 2001). Many of these components are extracellular and function as adhesins, for instance, the enolase, 14-3-3 protein, fructose-1,6-bisphosphate aldolase, triose phosphate isomerase, glyceraldeyde-3-phosphate dehydrogenase, and glycoprotein gp43 (Santos *et al.* 2020). Among them, the gp43, a cell surface and exocellular glycoprotein with proteinase activity at acidic pH is considered the immune dominant antigen in PCM caused by *Para. brasiliensis* species complex, since it reacts with 100 % of patient sera in immunoblotting assays (Puccia & Travassos 1991). However, the same is not observed for patients infected with *Para. lutzii* whose gp43 is poorly expressed and have few common epitopes with *Para. brasiliensis*; this observation invalidates the use of this antigen for serological diagnosis of PCM caused by *Para. lutzii* (Leitão *et al.* 2014).

Other virulence factors are important intracellular proteins, such as α-(1,4)-amylase (AMY1), which is involved in the synthesis α-(1,3)-glucan in the cell wall, present in the parasitic yeast phase (Camacho *et al.* 2012) and HSP (heat shock proteins), which are chaperones highly expressed during mycelia to yeast conversion in response to thermic and other environmental stresses (Cleare *et al.* 2017). For an in-depth review of *Paracoccidioides* virulence factors, we recommend the recent review from Santos *et al.* (2020), in which the most important virulence factors are revised as well as pointing out those that may be considered important therapeutic targets, such as gp43.

Author: R.C. Theodoro

59. *Schizophyllum* Fr., Syst. Mycol. 1: 330. 1821.

Type species: *Schizophyllum commune* Fr.

Classification: *Basidiomycota*, *Agaricomycotina*, *Agaricomycetes*, *Agaricales*, *Schizophyllaceae.*

Background

Schizophyllum is a basidiomycete that belongs to *Schizophyllaceae* of *Agaricales*. Its name originates from the Latin words *schizo*, which means split, and *phyllum*, which means lamella, which appropriately describes its unique characteristics and distinctive morphology (Cooke 1961, Guzmán 2004). It is commonly known as the split gill mushroom. It is an edible and medicinal mushroom, found on every continent except Antarctica (Imtiaj *et al*. 2008). There are 31 records with 20 species of *Schizophyllum* in Index Fungorum (2022). Linder (1933) recognised two groups within *Schizophyllum* and named them Stirps Commune subhymenium, including *Sch*. *commune*, *Sch*. *radiatum*, *Sch brevilamellatum* and *Sch*. *fasciatum*; and Stirps Umbrinum with subhymenium undifferentiated, including *Sch*. *umbrinum* and *Sch*. *leprieuri*. Based on observations by the authors, all species described in this treatment differ in their subhymenium, although this may not be obvious in all samples (Linder 1933, Raper & Miles 1958, Cooke 1961, Guzmán 2004). *Schizophyllum* is easily recognised based on its tiny basidiomes that lack stems, and they attach themselves like tiny bracket fungi on dead wood. The genus is characterised by basidiomes that are fan-shaped or resemble undulating waves; small hairs protect the upper surface, and when dry, are white to greyish or tan; the under surface has gill-like folds that are split down the centre; folds in the under surface are "split" or "doubled". *Schizophyllum* is able to survive harsh conditions as the sporophores are able to tolerate prolonged drought and the mycelium can grow on almost any organic matter while the sporophores have the ability to rebuild lost parts (Essig 2012).

Ecological and economic significance

Schizophyllum species are common in the tropics and temperate regions, spreading throughout North America and around the world. They are typically found in large numbers within small spaces on logs or trees, including *Aceraceae*, *Betulaceae*, *Fagaceae*, *Hippocastanaceae*, *Juglandaceae*, *Lauraceae*, *Leguminosae*, *Moraceae*, *Palmaceae*, *Pinaceae*, *Rosaceae*, *Rubiaceae*, *Rutaceae*, and *Tiliaceae* (Essig 2012). They are saprobic on dead wood or sometimes parasitic on living wood, some growing alone or more often in clumps on hardwood and rotten logs (Riley *et al*. 2014). The most common species, *Sch. commune* is used for food in southern parts of Asian countries such as Thailand, Taiwan, Malaysia, Vietnam and southern China (Imtiaj *et al*. 2008). *Schizophyllum* mushrooms have been used medicinally for a long time in China and Japan.

Research interests

There are 699 publications and 9 725 citations from 2011–2021 in the Web of Science (Fig. 88), with the top 10 most cited articles listed in Table 65. Most of the publications focused on the medicinal value (secondary metabolites, compounds, health-promoting properties), and taxonomy (physiological, genomes) of *Schizophyllum* species.

Medicinal value

Schizophyllum mushrooms are an important source of biologically active material that has medicinal value. They contain secondary metabolites, carbohydrates, minerals, proteins, fibres, vitamins, fats, and bioactive compounds such as phenolic, polysaccharide and b- glucan (Lindequist *et al*. 2005, Klaus *et al*. 2011, Joel & Bhimba 2013). Schizophyllan is a polysaccharide containing a 1,3-b-D-linked backbone of glucose residues with 1,6-b-D-glucosyl side groups (Kumari *et al*. 2008, Üstün *et al*. 2018).

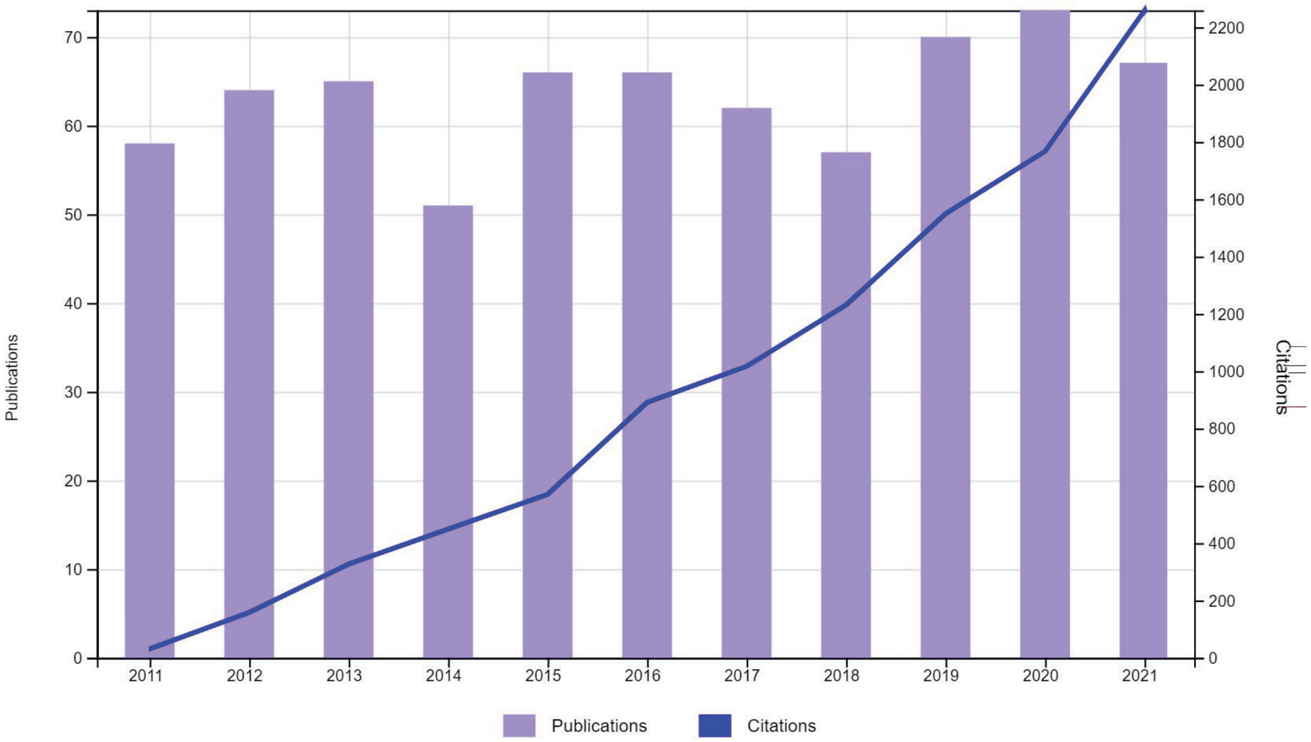

Fig. 88. Trends in research of *Schizophyllum* in the period 2011–2021.

Table 65. Top 10 cited articles related to *Schizophyllum* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Extensive sampling of basidiomycete genomes demonstrates inadequacy of the white-rot/brown-rot paradigm for wood decay fungi	422	Riley *et al*. (2014)
2	The plant cell wall–decomposing machinery underlies the functional diversity of forest fungi	366	Eastwood *et al*. (2011)
3	Genome sequence of the model mushroom *Schizophyllum commune*	295	Ohm *et al*. (2010)
4	Recent developments in mushrooms as anti-cancer therapeutics: a review	216	Patel & Goyal (2012)
5	Beta-glucans from edible and medicinal mushrooms: Characteristics, physicochemical and biological activities	138	Zhu *et al*. (2015)
6	Microsatellites in the genome of the edible mushroom, *Volvariella volvacea*	125	Wang *et al*. (2014g)
7	Allergic bronchopulmonary mycosis due to fungi other than *Aspergillus*: a global overview	120	Chowdhary *et al*. (2014a)
8	Characterization of fungal pathogens associated with grapevine trunk diseases in Arkansas and Missouri	106	Urbez-Torres *et al*. (2012)
9	Evolution of novel wood decay mechanisms in *Agaricales* revealed by the genome sequences of *Fistulina hepatica* and *Cylindrobasidium torrendii*	92	Floudas *et al*. (2015)
10	Transcription factor genes of *Schizophyllum commune* involved in regulation of mushroom formation	83	Ohm *et al*. (2011)

Mirfat *et al*. (2014) found that *Schizophyllum* extract had more effective anti-bacterial activity against Gram-positive bacteria than Gram-negative bacteria.

Taxonomy and phylogeny

The taxonomy of this genus was uncertain as the previous classification was based on morphological characters (Carreño-Ruiz *et al*. 2019). Molecular analyses based on ITS and LSU sequences have provided better resolution (Robledo *et al*. 2014). Genomic data has revealed that *Schizophyllum* contains six homeodomain genes *abq6* (HD1), *abr6* (HD2), *abs6* (HD1), *abt6* (HD1), *abu6* (HD1) and *abv6* (HD2) (Ohm *et al*. 2010). Therefore, the generation of additional taxonomic information for *Schizophyllum* species is important for their application and conservation.

Author: D. Gonkhom

60. ***Plasmopara*** J. Schröt., in Cohn, Krypt.-Fl. Schlesien 3.1: 236. 1886.

Type species: *Plasmopara nivea* (Unger) J. Schröt.

Classification: *Oomycota*, *Peronosporomycetes*, *Peronosporales*, *Peronosporaceae.*

Background

Plasmopara is the second largest genus of the downy mildews and belongs to the oomycetes, fungus-like organisms of the kingdom *Straminipila*, related to brown algae and diatoms (Beakes & Thines 2017). The genus contains about 150 species (Wijayawardene *et al.* 2022), which are all obligate biotrophic plant parasites of dicot hosts (Thines & Choi 2016). *Plasmopara* species can incite both systemic and local infections, resulting in typical downy mildew symptoms. In systemically infected hosts, these include stunting of the hosts and often smaller leaves and discolouration of the whole plant, local infections are characterised by often leaf-vein-delimited lesions that are yellow green (chlorotic) from above, sometimes reddening due to anthocyane accumulation and with sporangiophore outgrowth through the stomata on the lower surface, resulting in a felt-like covering with sporangiophores and sporangia. At later stages of infection, oospores, which are thick-walled resting spores, are formed in infected tissues that sometimes turn necrotic after the life cycle of the pathogen is concluded (Thines 2014). For sporulation humid conditions are required, with (almost) water-saturated air or leaf wetness for several hours. *Plasmopara* species have been found on all continents except Antarctica, but are particularly abundant in Northern America (Voglmayr *et al.* 2006).

Plasmopara was segregated from *Peronospora* by Schröter (1886) including downy mildews of dicots in which the sporangia germinate by the production of zoospores instead of a germ tube (Thines *et al.* 2009). In addition, the sporangiophores in *Plasmopara* are mostly clearly monopodial and have a branching pattern with close to rectangular angles, while species of *Peronospora* often have more acute branching angles (Constantinescu *et al.* 2005). Based on similarities in sporangiophore morphology, some conidial species were added to *Plasmopara*, while other species with a distinct sporangiophore morphology were excluded from the genus (*e.g.*, Wilson 1907, 1914, Skalický 1966, Constantinescu 1989). As a result, *Plasmopara* became rather heterogenous until it was revised to a monophyletic group after thorough morphological and molecular phylogenetic studies by Constantinescu (1989), Göker *et al.* (2003), Voglmayr *et al.* (2004), Constantinescu *et al.* (2005), Thines *et al.* (2007), Voglmayr & Constantinescu (2008), respectively segregating *Paraperonospora*, *Viennotia*, *Protobremia*, *Plasmoverna*, *Poakatesthia*, and *Novotelnova* from *Plasmopara*, and after Voglmayr & Thines (2007) merged the genus *Bremiella* with *Plasmopara*. As currently understood, *Plasmopara* contains downy mildews of eudicots other than *Ranunculales* that have hyaline sporangia that germinate by the (facultative) production of zoospores.

Species of *Plasmopara* are highly host-specific (Salgado-Salaza *et al.* 2023). Almost all species complexes that have been investigated in detail have shown host specificity below the host genus level (Voglmayr *et al.* 2006, Choi *et al.* 2007, 2020, Komjáti *et al.* 2007, Schröder *et al.* 2011, Thines 2011, Görg *et al.* 2017), but there are a few notable exceptions, such as the report of infection of *Ligularia fischeri* by *Pl. angustiterminalis*, a species otherwise infecting *Xanthium* species (Chen *et al.* 2018e).

Ecological and economic significance

Plasmopara species affect numerous economically important plants, and the most prominent diseases are listed below.

Downy mildew of grape (*Vitis vinifera*) is caused by *Plasmopara viticola* and remains one of the most destructive diseases of grapevine for almost 150 yr (Gobbin *et al.* 2006, Fontaine *et al.* 2013, 2021). Infection by *Plasmopara viticola* leads to direct loss of berries and indirect losses due to foliage damage and is difficult to control due to the airborne nature of the spores and rapid evolution of fungicide resistance (Gessler *et al.* 2011, Campbell *et al.* 2021). In addition to the high genetic variability and genetic recombination by sexual reproduction (Gobbin *et al.* 2006), it is noteworthy that several phylogenetically distinct lineages exist on other species of *Vitis* and allied genera, of which only *Pl. muralis* has been described so far as an independent species (Schröder *et al.* 2011, Thines 2011, Rouxel *et al.* 2014). Some of these are able to parasitise the alien host *Vitis vinifera*, but are yet restricted to North America (Schröder *et al.* 2010, Rouxel *et al.* 2014, Fontaine *et al.* 2021). An introduction of these lineages into Europe or other grape-producing areas could have a strong negative impact on grape production.

Downy mildew of sunflower (*Helianthus annuus*) is caused by *Plasmopara halstedii*, a pathogen which, like *Pl. viticola*, originates from North America (Cohen & Sackston 1974). *Plasmopara halstedii* was initially described from *Eupatorium rubrum* (Farlow 1883), so the assumption would be that based on the high degree of host specificity the pathogen of sunflower should be a species independent from *Pl. halstedii*. Based on this assumption and some morphological differences, Novotel’nova (1966) argued for recognising the species *Pl. helianthi* as the pathogen on sunflowers. However, this species name was not taken up widely (Spring 2019). In the absence of sequence data from the original type specimens of multiple recent specimens of the downy mildew of *Eupatorium rubrum* it remains unclear if the pathogens of *Eupatorium rubrum* and *Helianthus annuus* belong to different species, especially as morphological differences are rather minor and there are reports of host shifts (Thines 2019) in other species of *Plasmopara* affecting *Asteraceae* (Chen *et al.* 2018e).

Downy mildew of balsamines (*Impatiens* spp.) caused by *Plasmopara destructor* and *Pl. velutina* leads to defoliation and collapse of ornamental species of the genus *Impatiens*. While *Pl. obducens*, downy mildew of the wild species, *Impatiens noli-tangere*, was among the first *Plasmopara* species described in Europe (Schröter 1877), the downy mildew of ornamental *Impatiens* has been recorded widely only after the turn of the millennium (Wegulo *et al.* 2004, Lane *et al.* 2005), suggesting that the disease might be caused by an invading species. However, the species was generally reported as *Pl. obducens* (Wegulo *et al.* 2004, Lane *et al.* 2005, Cunnington *et al.* 2008) until detailed phylogenetic and morphological investigations revealed that the downy mildew of buzzy lizzy is caused by a distinct species, *Pl. destructor*, while the downy mildew of lady slippers balsamine is caused by *Pl. velutina* (Görg *et al.* 2017). Thus, it seems likely that the downy mildew pathogens of cultivated impatiens were only recently imported to Europe, North America, and Australasia, possibly by infected seeds, which might also be the way of import for the sunflower downy mildew, *Pl. halstedii* (Döken 1989), as many downy mildew species are seed-borne (Thines & Choi 2016).

There are no immediate beneficial uses of *Plasmopara* species reported, but *Plasmopara* on *Ambrosia* has been suggested as a potential biocontrol agent for these often-noxious weeds (Choi *et al.* 2009).

Research interests

There are 813 publications on *Plasmopara* species with 9 535 citations from 2011–2021 in the Web of Science (Fig. 89), and the top 10 most cited articles are given in Table 66. Most of the publications focused on the management of downy mildew of grapes, including fungicide sensitivity, disease forecasting, virulence, and resistance. However, especially species boundaries

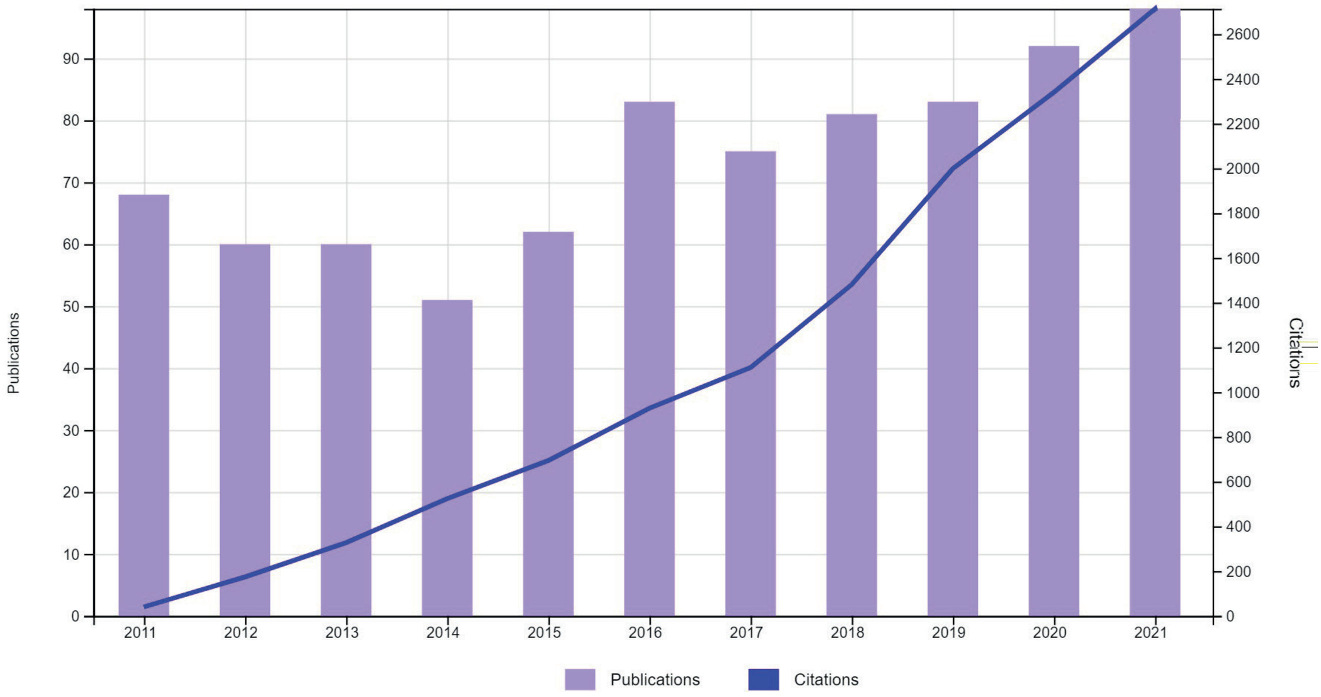

Fig. 89. Trends in research of *Plasmopara* in the period 2011–2021.

Table 66. Top 10 cited articles related to *Plasmopara* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	The top 10 oomycete pathogens in molecular plant pathology	383	Kamoun *et al.* (2015)
2	*Plasmopara viticola*: a review of knowledge on downy mildew of grapevine and effective disease management	274	Gessler *et al.* (2011)
3	Advanced knowledge of three important classes of grape phenolics: anthocyanins, stilbenes and flavonols	184	Flamini *et al.* (2011)
4	Carbohydrates in plant immunity and plant protection: roles and potential application as foliar sprays	161	Trouvelot *et al.* (2014)
5	Rpv10: a new locus from the Asian *Vitis* gene pool for pyramiding downy mildew resistance loci in grapevine	116	Schwander *et al.* (2012)
6	The SWEET family of sugar transporters in grapevine: VvSWEET4 is involved in the interaction with *Botrytis cinerea*	112	Chong *et al.* (2014)
7	*In planta* functional analysis and subcellular localization of the oomycete pathogen *Plasmopara viticola* candidate RXLR effector repertoire	97	Liu *et al.* (2018d)
8	Construction of a reference linkage map of *Vitis amurensis* and genetic mapping of *Rpv8*, a locus conferring resistance to grapevine downy mildew	93	Blasi *et al.* (2011)
9	Genetic dissection of a TIR-NB-LRR locus from the wild North American grapevine species *Muscadinia rotundifolia* identifies paralogous genes conferring resistance to major fungal and oomycete pathogens in cultivated grapevine	86	Feechan *et al.* (2013)
10	Genome analyses of the sunflower pathogen *Plasmopara halstedii* provide insights into effector evolution in downy mildews and *Phytophthora*	71	Sharma *et al.* (2015b)

for most *Plasmopara* species complexes, *i.e.*, *Plasmopara* species infecting the same plant family remain unresolved, foremost the *Plasmopara* pathogens affecting *Asteraceae*, which hampers an understanding of the evolution and potential risk of infections of weedy hosts for cultivated crops (Thines & Choi 2016).

Disease management

Disease control for downy mildew caused by *Plasmopara* species has mainly been by application of fungicides, but resistance against major fungicides used is widely reported (Corio-Costet *et al.* 2011, Sawant *et al.* 2017, Campbell *et al.* 2021), and the rapid emergence of fungicide-tolerant and fungicide-resistant strains is a major obstacle to sustainable control. For major crops affected by *Plasmopara*, such as grapes and sunflowers, extensive resistance breeding efforts have been carried out (Gessler *et al.* 2011, Sánchez-Mora *et al.* 2017, Trojanová *et al.* 2017). However, disease resistance is frequently overcome by more virulent strains, necessitating a continuous breeding effort (Viranyi *et al.* 2015, Spring & Zipper 2018, Sargolzaei *et al.* 2020).

Toxins

Downy mildews, like other oomycetes, do not produce known toxins.

Taxonomy and phylogeny

The phylogenetic relationships of most *Plasmopara* species remain unresolved, but the overall phylogeny of the genus has been addressed in several studies leading to major taxonomic rearrangements (Thines *et al.* 2009). For identification of species via barcoding, the otherwise frequently used nuclear ribosomal internal transcribed spacer (nrITS) is of limited use as in the nrITS region two tandem repeat regions that lead to nrITS lengths of well above 2 000 bp in many species are present, which complicates both PCR and sequencing (Thines *et al.* 2005, Thines 2007). Consequently, mitochondrial loci, in particular, *cox*2 sequences have been used for species delimitation (Choi *et al.* 2007, 2020, Görg *et al.* 2017), as they have the advantage that apart from high resolution, they are also readily amplifiable from herbarium material (Choi *et al.* 2015).

Author: M. Thines

61. ***Auricularia*** Bull., Herb. France (Paris) 3: pl. 290. 1780.

Type species: *Auricularia mesenterica* (Dicks.) Pers.

Classification: *Basidiomycota*, *Agaricomycotina*, *Agaricomycetes*, *Auriculariales*, *Auriculariaceae.*

Background

Auricularia is one of the most common gelatinous genera with nearly 200 species epithets listed in Index Fungorum (2022), and 37 recognised species in the world (Wu *et al.* 2021). Members of *Auricularia* play an important role in wood degradation in forest ecosystems, especially in tropical forests. Most *Auricularia* species inhabit angiosperm wood, such as dead standing trees, stumps, fallen trunks and branches, and rotten wood, but a few grow on gymnosperm wood (Sysouphanthong *et al.* 2010, Baldrian & Lindahl 2011, Wu *et al.* 2021). Some species of *Auricularia* are edible and medicinal mushrooms, and they are rich in nutrients including carbohydrate, protein, amino acid, mineral and bioactive compounds (Bandara *et al.* 2019, Huang *et al.* 2021b), and have properties of lowering blood sugar and fat, anti-tumour, antioxidant, and immunity enhancement (Zeng *et al.* 2012b, Li *et al.* 2013a, Su & Li 2020). Several *Auricularia* species are widely cultivated in China and other Asian countries, *e.g.*, *Au. heimuer* and *Au. cornea* (Dai *et al.* 2010b, Wu *et al.* 2019b). Active components and pharmacological effects of *Auricularia* have always been hot research topics (Zeng *et al.* 2012b, Su & Li 2020).

Auricularia was established by Bulliard in 1789 and is characterised by gelatinous, resupinate to substipitate basidiomata with hairs on the upper surface, cylindrical to clavate and transversely 3-septate basidia with guttules and hyaline, thin-walled and allantoid basidiospores (Lowy 1951, Duncan & Macdonald 1967, Kobayasi 1981, Montoya-Alvarez *et al.* 2011). Lowy (1952) and Kobayasi (1981) recorded 10 and 15 *Auricularia* species in the world, respectively, most were considered to have intercontinental to cosmopolitan distributions. Those species were described and identified only based on morphology before the 21st century, and some of them represent species complexes. Looney *et al.* (2013) evaluated and revised species concepts in *Auricularia* using phylogenetic and morphological methods, and indicated that *Au. delicata* was a species complex and they described two new species in this complex. With the implementation of molecular analyses, other species complexes were confirmed, and new species were derived from these complexes (Wu *et al.* 2014a, 2015a, b, Bandara *et al.* 2015). Wu *et al.* (2021) conducted a comprehensive morphological and molecular study of *Auricularia* worldwide based on multi-locus DNA sequence datasets (ITS, nLSU, *rpb1* and *rpb2* sequences), and they accepted 31 species. The 31 *Auricularia* species nested in three major clades in phylogenies based on the muti-locus datasets, while two morphological complexes (*Au. auricula-judae* complex and *Au. mesenterica* complex) independently occupied two major phylogenetic clades, and three other morphological complexes (*Au. cornea* complex, *Au. delicata* complex and *Au. fuscosuccinea* complex) nested in one major clade. Taxa in the species complexes of *Au. cornea*, *Au. delicata* and *Au. fuscosuccinea* were scattered in different subclades of major clades, and the morphological complexes did not fully correspond to the phylogenetic clades (Wu *et al.* 2021). Host and geographical distribution probably have an influence on the speciation of *Auricularia* according to previous studies (Wu *et al.* 2014a, 2015a, b, 2021).

Ecological and economic significance

Auricularia species cause white rot to degrade lignin, cellulose and hemicellulose, and they can be used as edible and medicinal mushrooms. Their properties are summarised below.

Auricularia species as white-rot fungi have an extracellular enzyme system, which includes ligninolytic enzymes (laccase, manganese peroxidase, lignin peroxidase, and versatile peroxidase) and cellulolytic enzymes (endo-glucanase, cellobiohydrolase, and betaglucosidase), esterases, oxidases/dehydrogenases, and oxygenases (Manavalan *et al.* 2015). The enzyme system can effectively degrade lignocellulosic biomasses (Manavalan *et al.* 2015) and has been used to remove many emerging contaminants that are difficult to decompose, such as dye-based industrial pollutants and endocrine-disrupting compounds (Kupski *et al.* 2019, Chang *et al.* 2021). The application of white-rot fungi and their derivatives for environmental pollutant bioremediation is a low-cost, effective, and eco-friendly strategy, which has received attention in recent years (Akhtar *et al.* 2020, Chang *et al.* 2021).

Auricularia species are utilised as nutrient-rich foods and medicinal resources, with particular prominence in traditional Asian medicine (Bandara *et al.* 2019). *Auricularia heimuer* was considered a delicacy of emperors in the Eastern Zhou Dynasty 2 000 years ago, and it has been cultivated for over 1 400 yr (Zhang & Chen 2015). Its production in China reached 7.1 billion kg (fresh weight) in 2019 and is worth more than 5.6 billion US dollars (Wu *et al.* 2021). *Auricularia cornea*, *Au. sinodelicata* and *Au. fibrillifera* have also been cultivated in China, and some other species have the potential for cultivation (Zhang *et al.* 2019d). Carbohydrates are the major nutritional constituent of edible *Auricularia* species, and polysaccharides are the major active compounds in *Auricularia* species (Bandara *et al.* 2019). On average, dried *Auricularia* basidiomata have a composition of 79.9–93.2 % carbohydrates, 6.5–13 % crude proteins, 9.9–17.9 % total soluble sugars, 0.48–4.5 % crude fat (lipid), and 3.5–12.5 % crude fibre (Bandara *et al.* 2017, 2019). *Auricularia* polysaccharides have anti-tumour, immunomodulatory, anti-bacterial, antiviral, antioxidant, hypoglycemic, and antihypercholesterolemic properties (Song & Du 2012, Bandara *et al.* 2019, Su & Li 2020). *Auricularia* species have also been used as biomass material, such as *Au. cornea* used as a carbon precursor (Long *et al.* 2015) and metal ions adsorption (Li *et al.* 2018d).

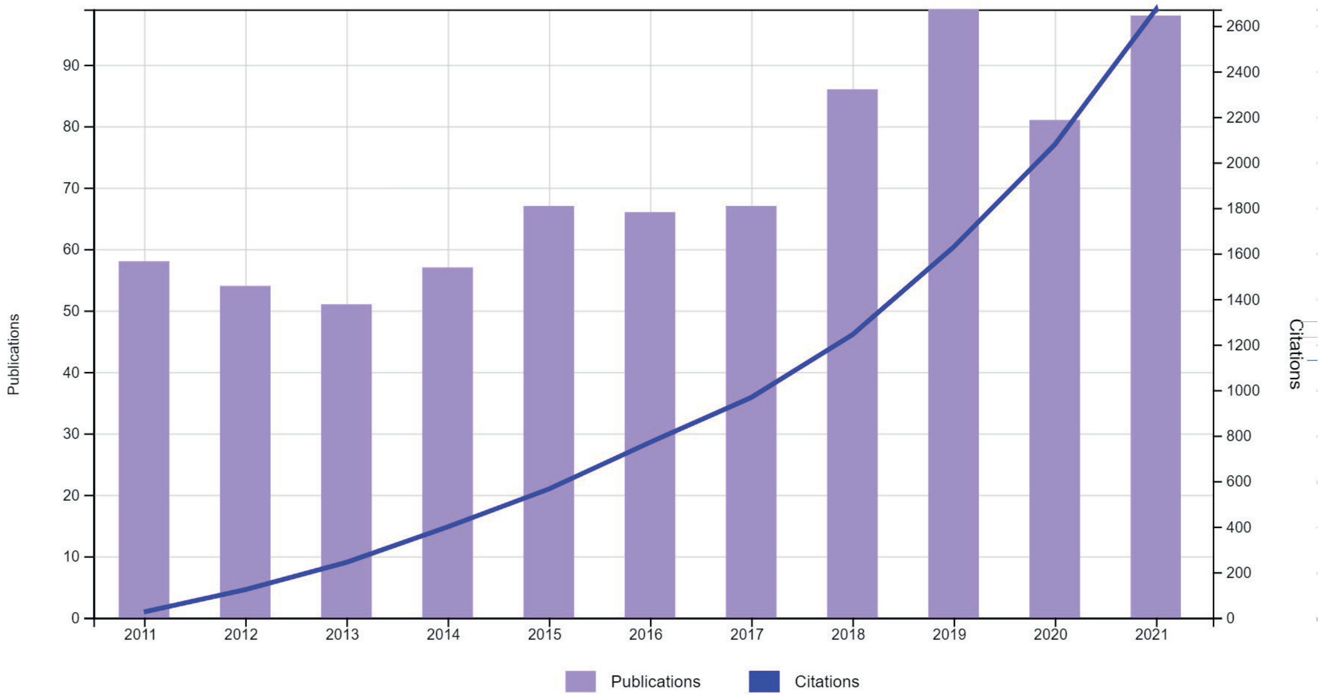

Fig. 90. Trends in research of *Auricularia* in the period 2011–2021.

Table 67. Top 10 cited articles related to *Auricularia* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Porous layer-stacking carbon derived from in-built template in biomass for high volumetric performance supercapacitors	426	Long *et al.* (2015)
2	Characterization of antioxidant polysaccharides from *Auricularia auricular* using microwave-assisted extraction	141	Zeng *et al.* (2012b)
3	Beta-glucans from edible and medicinal mushrooms: Characteristics, physicochemical and biological activities	138	Zhu *et al.* (2015)
4	Oxidoreductases on their way to industrial biotransformations	127	Martínez *et al.* (2017)
5	Contents of lovastatin, γ-aminobutyric acid and ergothioneine in mushroom fruiting bodies and mycelia	120	Chen *et al.* (2012a)
6	Construction of nitrogen-doped porous carbon buildings using interconnected ultra-small carbon nanosheets for ultra-high rate supercapacitors	115	Jiang *et al.* (2016)
7	Patterns of lignin degradation and oxidative enzyme secretion by different wood- and litter-colonizing basidiomycetes and ascomycetes grown on beech-wood	106	Liers *et al.* (2011)
8	Carboxymethylation of polysaccharides from *Auricularia auricula* and their antioxidant activities *in vitro*	96	Yang *et al.* (2011)
9	Effect of pig manure on the chemical composition and microbial diversity during co-composting with spent mushroom substrate and rice husks	90	Meng *et al.* (2018)
10	Structure characterization and antitumor activity of an alpha beta-glucan polysaccharide from *Auricularia polytricha*	79	Song *et al.* (2012)

Research interests

There are 784 publications and 9 237 citations from 2011–2021 in the Web of Science (Fig. 90), with the top 10 most cited articles listed in Table 67. Most of the publications focused on the characteristics, physicochemical and biological activities of *Auricularia* polysaccharides, and the application of extracellular enzymes, as well as porous carbon materials.

Auricularia polysaccharides

The structural characterisation and biological activities of *Auricularia* polysaccharides have been extensively studied, including the characterisation of antioxidant polysaccharides using different extraction methods (Zeng *et al.* 2012b), antitumor activities of the main active components Beta-glucans (Zhu *et al.* 2015, Song & Du 2012), antioxidant activities of different *Auricularia* species (Yang *et al*. 2011, Su & Li 2020). Yang *et al.* (2011) compared the antioxidant activities of three polysaccharides isolated from *Au. auricula* and found that the activity of one carboxymethylated polysaccharide (CMAAP22) was nearly twice that of the crude polysaccharide from *Au. auricula*. Zeng *et al.* (2012b) found that microwave-assisted extraction of antioxidant polysaccharides from *Au. auricula* had low molecular weight and remarkable antioxidant capability. The structural characterisation and antioxidant activities of four *Auricularia* polysaccharides indicated that they were mainly composed of mannose and galactose which jointly determined total antioxidant capacity (Su & Li 2020).

Application of enzymes

Auricularia species have valuable lignocellulolytic enzymes to degrade both lignin and cellulose biopolymers in lignocellulose biomass, and these have been employed in various industrial applications, especially in the pre-treatment and hydrolysis stages of biorefinery systems, industrial biotransformations, and removing endocrine-disrupting compounds (Liers *et al*. 2011, Manavalan *et al.* 2015, Martínez *et al.* 2017, Kupski *et al.* 2019). Oxidoreductases are the major enzymes isolated from *Auricularia* species, and typically include: (i) haem-containing peroxidases and peroxygenases, being activated by H_2O_2 as sole electron acceptor; (ii) flavin-containing oxidases and dehydrogenases, being activated by O_2 and other oxidants – such as Fe^{3+} and quinones – respectively; and (iii) copper-containing oxidases and monooxygenases, being activated by O_2, the latter with a more complicated activation mechanism (Martínez *et al.* 2017).

Porous carbon materials

Densely porous graphene-like carbon materials were greenly synthesised through hydrothermal treatment of *Auricularia* and the subsequent carbonisation process by Long *et al.* (2015). Jiang *et al.* (2016) demonstrated a facile one-step construction of a nitrogen-doped porous carbon building (N-PCB) using interconnected ultra-small carbon nanosheets through the carbonisation of *Auricularia* biomass using $ZnCl_2$ as the activating agent and NH_4Cl as the nitrogen source. These results suggest a low-cost and environmentally friendly design of electrode materials for high volumetric-performance supercapacitors (Long *et al.* 2015, Jiang *et al.* 2016).

Authors: Y.C. Dai and F. Wu

62. ***Russula*** Pers., Observ. Mycol. (Lipsiae) 1: 100. 1796.

Type species: *Russula emetica* (Schaeff.) Pers.

Classification: *Basidiomycota*, *Agaricomycotina*, *Agaricomycetes*, *Russulales*, *Russulaceae.*

Background

The genus *Russula*, introduced by Persoon (1796), is the type genus of *Russulaceae*, a family in which all agaricoid members are recognisable in the field because of their unique brittle context due to the predominant presence of large spherical cells, called sphaerocytes. Although the original concept of *Russula* could not be maintained (see below), this genus still resists the recent trend of splitting hyper-diverse genera, such as *Inocybe* (Matheny *et al.* 2020) or *Cortinarius* (Liimatainen *et al.* 2022) into a multitude of smaller satellite genera. Recent estimates of species numbers based on the number of sequenced OTUs in the Northern Hemisphere alone are already in excess of 1 000 (Looney 2016), but the total number of *Russula* species in the world has been estimated to be in excess of 3 000 (He *et al.* 2019b) and could even be quite higher. The great challenge for the future will be to document this incredible diversity that is vanishing very quickly due to the conversion of the natural environment for human activities. As a result, *Russula* now holds the record of being the most diverse ectomycorrhizal mushroom genus, and probably could be the most diverse mushroom genus in "all categories". The only other mushroom genus that outcompetes *Russula* in terms of diversity is *Entoloma s. lat*. (Noordeloos *et al.* 2022). The latter genus contains both saprotrophic and ectomycorrhizal species. It has been split on a morphological basis into many separate genera in the past, but a generic delimitation on a sound phylogenetic and ecological basis is needed (Bhunjun *et al.* 2022). With its 1 348 presently described species (Bhunjun *et al*. 2022), *Russula* also outnumbers by far the other genera in the family *Russulaceae*, three of which predominantly include agaricoid species, *viz*. *Lactarius* with 450 spp., *Lactifluus* with 207 spp. (He *et al.* 2019b) and *Multifurca* with 12 spp. (Wang *et al.* 2019b). *Russula* differs from these in the absence of a branching, lactiferous system that ends in pseudocystidia at the surface of pileus and hymenium (Buyck *et al.* 2008, 2020).

The most recent multilocus genus phylogeny (Buyck *et al.* 2023) divides the genus into nine subgenera of very unequal size, varying in number of species from hardly two or three (subgen. *Glutinosae* and *Crassotunicatae*) to more than 600 for subgen. *Russula*, which is the dominant subgenus in the Northern Hemisphere. The genus is also unique in the fact that the anatomy of the plant-symbiotic organs, the ectomycorrhiza, reflects the subgeneric phylogeny better than the features of the structures for sexual reproduction or basidiomata (Buyck *et al.* 2018). This ectomycorrhizal anatomy has also been used to explain different ecological roles and foraging strategies among *Russula* species (Agerer 2001, 2006, Beenken 2004). As an obligate ectomycorrhizal genus, *Russula* also lost the ability to reproduce asexually through the formation of conidia, and it is quasi-impossible to maintain species in culture, as sexual basidiospores do not germinate in normal culture conditions.

Both its attractive field appearance and its abundance in nearly every type of forested habitat on earth have resulted in a long-standing interest from both professional and amateur mycologists. *Russula* is certainly the most frequently monographed genus in Europe (for an overview see Romagnesi 1967, Sarnari 1998, 2005), but remains poorly known elsewhere, although this situation is rapidly changing in the past few years. The main game changer has been the important impact of the application of molecular tools on species concepts, descriptions of new species and fungal phylogenies. Between 11 and 115 new *Russula* species have been introduced on a yearly basis between 2011 and 2020 (Bhunjun *et al.* 2022).

As mentioned above, *Russula* has not maintained its original generic concept. Instead of being split into a number of smaller genera, the genus has "absorbed" several smaller polyphyletic genera with similar microscopic features but often very different field appearances, including tiny, pleurotoid species that are formed above the soil, often on wood or living parts of trees (*Pleurogala*), others with strongly reduced stipe and deformed hymenophore (*Elasmomyces*, *Macowanites*) to truffle-like and completely hypogeous taxa (*Cystangium*, *Gymnomyces*, *Martellia*). All these abandoned genera share with *Russula* the presence of gloeocystidia and an amyloid spore ornamentation, as well as being obligate ectomycorrhizal symbionts.

Ecological and economic significance

Russula harbours some economically important edible fungi, particularly in Asia (*e.g.*, Wang 2020) and Africa (*e.g.*, Buyck 1994, 2008, Härkönen *et al.* 1993). Apart from research papers and books focusing on the taxonomy and identification of these edible species (*e.g.*, Eyi Ndong *et al*. 2011, De Kesel *et al*. 2017), rather different aspects of this edibility constituted the subject of highly cited papers in *Russula* research. The ability of mushrooms to accumulate toxic metals that are present in the soil is certainly one

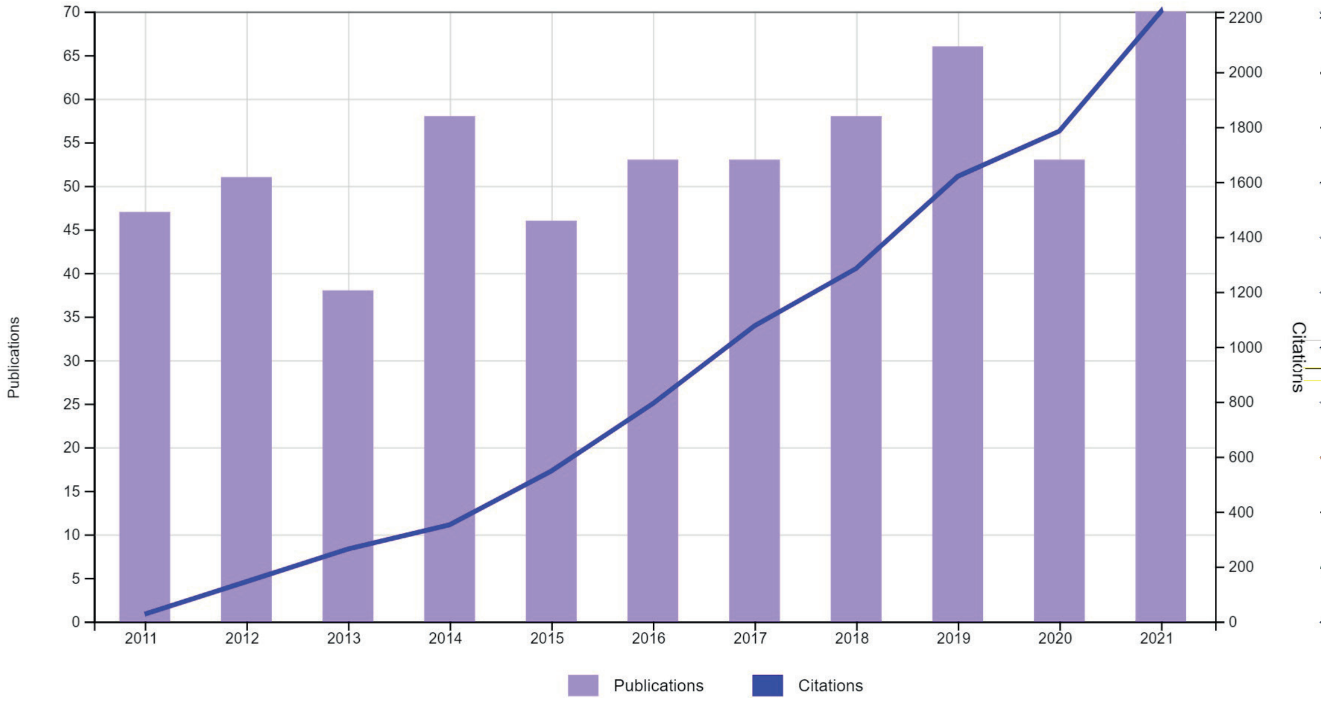

Fig. 91. Trends in research of *Russula* in the period 2011–2021.

Table 68. Top 10 cited articles related to *Russula* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Recent developments in mushrooms as anti-cancer therapeutics: a review	216	Patel & Goyal (2012)
2	Long-term experimental manipulation of climate alters the ectomycorrhizal community of *Betula nana* in Arctic tundra	141	Deslippe *et al*. (2011)
3	Long-term warming alters the composition of arctic soil microbial communities	141	Deslippe *et al.* (2012)
4	Shift in fungal communities and associated enzyme activities along an age gradient of managed *Pinus sylvestris* stands	126	Kyaschenko *et al.* (2017)
5	An arctic community of symbiotic fungi assembled by long-distance dispersers: phylogenetic diversity of ectomycorrhizal basidiomycetes in Svalbard based on soil and sporocarp DNA	121	Geml *et al*. (2012)
6	Ectomycorrhizal fungal diversity and community structure on three co-occurring leguminous canopy tree species in a Neotropical rainforest	114	Smith *et al.* (2011)
7	Soil bacterial community composition altered by increased nutrient availability in Arctic tundra soils	112	Koyama *et al.* (2014)
8	Assessment of heavy metals in some wild edible mushrooms collected from Yunnan Province, China	105	Zhu *et al.* (2011a)
9	Community composition of root-associated fungi in a Quercus-dominated temperate forest: “codominance” of mycorrhizal and root-endophytic fungi	80	Toju *et al.* (2013)
10	Trace metal contents in wild edible mushrooms growing on serpentine and volcanic soils on the island of Lesvos, Greece	79	Aloupi *et al.* (2012)

of these (Zhu *et al.* 2011a, Aloupi *et al.* 2012). Another highly cited topic relates to the search for medically or therapeutically important substances (Patel & Goyal 2012), as well as to the identification of toxic substances (Huang *et al.* 2023).

As one of the most diverse obligate root symbionts, *Russula* is a key lineage in ectomycorrhizal fungi and is highly cited in most papers that study fungal communities, ecosystem functions and global carbon sequestration. The genus represents one of the most important ectomycorrhizal partners in arctic-boreal, temperate and tropical ecosystems, associating mainly with *Pinaceae*, *Fagaceae* and *Betulaceae* in the Northern Hemisphere, with *Myrtaceae* and *Nothofagaceae* in the Southern Hemisphere, and with *Caesalpinioideae* and *Dipterocarpaceae* in the paleo- and neotropics. Ecological research papers focusing on fungal communities in one or more of these ecosystems figure among the top ten highly cited papers related to *Russula* (Geml *et al.* 2011, Smith *et al*. 2011, Toju *et al.* 2013), and frequently relate fungal community composition with forest age (Kyaschenko *et al.* 2017) or warming climate conditions (Deslippe *et al.* 2011, 2012). Interactions between *Russulaceae* and mammals or other animals that feed on them also have more profound consequences on the entire ecosystem (Elliott *et al.* 2022).

Some mycoheterotrophic *Orchidaceae* and species in *Ericaceae* subfamily *Monotropoideae* lack chlorophyll and obtain their organic carbon through a fungal link connecting the ectomycorrhizas of nearby autotrophic plants with their mycorrhizae. Species of *Russula* are well-known to constitute the privileged partner for this fungal link as well as very few *Lactarius*, but no *Lactifluus* nor *Multifurca* species (Bidartondo & Bruns 2001, 2005). However, whereas the fungus-tree host relationship involves many different fungal partners for a single tree individual, the mycoheterotrophic plants target frequently a single fungal individual (Bidartondo & Read 2008, Kong *et al.* 2015).

Research interests

There are 593 publications and 9 156 citations from 2011–2021 in the Web of Science (Fig. 91), with the top 10 most cited articles listed in Table 68. Most publications focused on taxonomy and phylogeny, but the most cited papers treat aspects of the ectomycorrhizal lifestyle and aspects related to the edibility or pharmaceutical potential of *Russula* species as discussed above.

Future perspectives

The description of new species and new infrageneric taxa takes a very important place in *Russula* research and this will remain the subject of many smaller contributions in the years to come, although rarely highly cited. For most of the accepted subsections of *Russula* in the northern hemisphere, the most recent estimates announce a 3–6-fold increase in the number of species (Bhunjun *et al.* 2022). More than 170 new *Russula* species have been described over the past two decennia from Asia, principally from India and China and this is just the beginning.

Seven out of the 10 most highly cited papers that mention *Russula* and were published between 2011 and 2021, have been discarded from the results in Table 68 because they all correspond to the “Fungal diversity notes” series, *i.e.*, taxonomic compilations of a large number (usually 100) of various new fungal taxa featuring between one and five new *Russula* species in each issue (Ariyawansa *et al.* 2015a, Liu *et al*. 2015b, Hyde *et al*. 2016, 2017, 2020, Li *et al.* 2016a, Tibpromma *et al*. 2017). The ITS region was frequently mentioned as most new species of *Russula* described during the past 10 years were supported by single gene phylogenies based on ITS sequences. In the coming years, it can be expected that combined phylogenetic analyses using several loci will become much more frequent.

When extending the top 10 to the top 50 of most cited papers, there are merely two papers entirely focused on *Russula*. The first (Looney *et al.* 2016) discusses host association and diversification of the genus at a world scale; the second is a purely taxonomic paper (Buyck *et al.* 2018) that discusses features of above- and below-ground organs in the context of a multi-locus phylogeny to propose a new infrageneric classification.

The biogeographic history and diversification of the genus certainly also remain a major research issue in the coming years, especially when sequences will become available for important key taxa in the Southern Hemisphere and tropical Asia and Africa. Looney *et al.* (2016) hypothesised that the agaricoid *Russulaceae* started to diversify between 55 and 61 MYA (45–74; 95 % highest posterior density interval) during the early Palaeogene when global climates underwent gradual cooling that continued through the ice ages of the late Pleistocene. But whether *Russula* originated in the temperate northern hemisphere *ca*. 44 MYA (33–56; 95 % highest posterior density interval) as hypothesised by Looney *et al.* (2016) or has a tropical African origin as concluded by Hackel *et al.* (2022) remains an open question.

All four genera that comprise agaricoid species in the family *Russulaceae* are ectomycorrhizal. However, the two corticioid and resupinate, small saprotrophic genera, *Boidinia* (12 accepted species) and *Gloeopeniophorella* (four species), are very closely related (Larsson & Larsson 2003) and placed in the same family. Consequently, the *Russulaceae*, and *Russula* in particular, are also a targeted model group for genomic approaches to better understand the saprotroph-ectotroph transition. The Mycorrhizal Genomics Initiative has already generated important discoveries including a pattern of convergent loss of some metabolic functions and the evolutionary development of effectors that interact with plant hosts to facilitate mutualistic interactions (Martin *et al.* 2016). *Russulaceae* are dominant producers of oxidative enzymes, including lignin peroxidases and laccases, indicating a white-rot ancestry and the potential ability to mobilise nutrients from lignin. These enzymes have been shown to be present, both at transcription levels and in enzymatic assays, in even greater abundance in *Russulaceae* than in many saprotrophic fungi (Luis *et al.* 2005). The specific roles of *Russula* in nutrient cycling and plant health will certainly remain a major focus in the *Russulaceae* Genome Initiative (RGI) project in the near future (Looney *et al.* 2018, 2021).

Author: B. Buyck

63. ***Zygosaccharomyces*** B.T.P. Barker, Phil. Trans. Roy. Soc. London, Ser. B, Biolog. Sci. 194: 482. 1901.

Type species: *Zygosaccharomyces rouxii* (Boutroux) Yarrow

Classification: *Ascomycota*, *Saccharomycotina*, *Saccharomycetes*, *Saccharomycetales*, *Saccharomycetaceae.*

Background

Zygosaccharomyces species are widely distributed and are often associated with food products with high sugar content, but strains can also be isolated from weak acid and alcohol-containing food or beverages (Boekhout & Robert 2003, Kurtzman *et al.* 2011). They exhibit remarkable tolerance to several stress conditions. *Zygosaccharomyces* species can convert highly concentrated sugars into ethanol, with a preference for fructose over glucose, a trait called fructophily. This characteristic together with their tolerance to severe stress conditions makes *Zygosaccharomyces* strains suitable for use in a wide range of industrial processes (reviewed by Solieri 2021).

The genus *Zygosaccharomyces* is morphologically, physiologically and phylogenetically related to *Saccharomyces* (Kurtzman *et al*. 2011). *Zygosaccharomyces* was introduced by Barker (1901), to accommodate yeasts that undergo conjugation prior to ascus formation but are otherwise similar to species of *Saccharomyces*. However, Stelling-Dekker (1931) observed that conjugation did not always occur prior to ascus formation, and could on occasion be lacking. As a result, *Zygosaccharomyces* was subsequently reduced to a subgenus of *Saccharomyces*. Only in the 1970s was this genus reinstated following studies by Van der Walt & Johannsen (1975). *Zygosaccharomyces barkeri* was originally designated as the type species, but with no existing type material and as *Z. barkeri* was believed to be a synonym of *Z. rouxii* (Lodder & Kreger-van Rij 1952, Yarrow 1984), Kurtzman (2003) proposed *Z. rouxii* as the neotype species of the genus.

Sequence analysis of the D1/D2 domains of the LSU gene, the ITS regions and SSU gene (Kurtzman & Robnett 1998, Kurtzman *et al.* 2011, Kurtzman & Robnett 2013) is used to describe novelties and distinguish among species of *Zygosaccharomyces*. The described *Zygosaccharomyces* species include *Z. bailii*, *Z. bisporus*, *Z. favii*, *Z. gambellarensis*, *Z. kombuchaensis*, *Z. lentus*, *Z. machadoi*, *Z. mellis*, *Z. osmophilus*, *Z. parabailii*, *Z. pseudobailii*, *Z. rouxii* (type species), *Z. sapae*, *Z. seidelii* and *Z. siamensis* (Kurtzman *et al.* 2011, Torriani *et al.* 2011, Saksinchai *et al.* 2012, Solieri *et al.* 2013, Suh *et al.* 2013, Čadež *et al.* 2015, Brysch-Herzberg *et al.* 2020, Matos *et al.* 2020).

Zygosaccharomyces species have been isolated from various habitats but are most commonly associated with food products (Kurtzman *et al.* 2011, Torriani *et al.* 2011, Solieri *et al.* 2013, Čadež *et al.* 2015). Most species are highly halotolerant and osmotolerant and some are even tolerant to weak organic acid preservatives *e.g*., acetic acid, benzoic acid or sorbic acid as well as dimithyldicarbonate (Steels *et al*. 1999, 2002, Deak 2008, Escott *et al.* 2018, reviewed by Solieri 2021). Dimithyldicarbonate is also used as a sterilant in beverage industries. These characteristics make *Zygosaccharomyces* species important food spoilage organisms, particularly food with low water activity, acidified preserved foods and beverages with a high concentration of fermentable sugars (Boekhout & Robert 2003, Deak 2008, Escott *et al.* 2018). On the other hand, their ability to cope with a wide range of process conditions makes these yeasts very attractive for converting various substrates that are not favourable for the growth of other microorganisms such as *Saccharomyces cerevisiae* that is already used in a vast number of industrial processes. *Zygosaccharomyces* yeasts live the transition from dangerous food spoilage agents to robust and stress-tolerant bio-catalysers exploitable in several bioprocesses other than food fermentation, such as bioethanol, chemicals, and enzyme production (reviewed by Solieri 2021).

Economic significance

Food and food safety

The physiological characteristics of many *Zygosaccharomyces* species indicate that they have remarkable tolerance to extreme environmental stress conditions (Steels *et al*. 1999, 2002, Deak 2008, Escott *et al.* 2018, reviewed by Solieri 2021), including high concentrations of organic acids, inorganic salts, weak acids (*e.g*., acetic and lactic acids), sugars, alcohol and also low pH and oxygen conditions (Jansen *et al.* 2003) as well as low water-activity (Stevenson *et al*. 2015). This genus, comprising halotolerant and osmotolerant strains in combination with resistance to heat and food preservatives, such as sorbic acid, benzoic acid, acetic acid, cinnamic acid and ethanol, is one of the major yeast genera responsible for causing food spoilage and plays a prominent role as a contaminant in preserved food and beverages. Food products and beverages prone to spoilage due to *Zygosaccharomyces* include juice concentrates, sugar syrups, honey and other bee hive material, jams, cane sugar, chocolate syrup, vinegar, pickled cucumbers, wine and other alcoholic beverages, salad dressing, tomato ketchup, tea beer fungus, carbonated soft drinks and dried fruit (Boekhout & Robert 2003, Fleet 2010, Kurtzman *et al*. 2011, Torriani *et al*. 2011, Saksinchai *et al.* 2012, Solieri *et al.* 2013, Čadež *et al.* 2015). The spoilage activities comprise mainly the production of excess carbon dioxide as well as the production of non-desired compounds such as ethanol and carbon esters. This undesirable fermentation also compromises the integrity of food packages as it can cause package expansion or the explosion of glass bottles (Solieri 2021). Due to their capacity to also grow at very low pH values, *Zygosaccharomyces* species are good candidates for spoilage of wines (Escott *et al*. 2018). Strains may cause re-fermentation and excessive CO_2 production in sweet wines. In wine fermentation, *Z. bailii* is conventionally associated with high production of volatile acidity and is considered a dangerous spoilage agent in several cases (Padilla *et al*. 2016b, Malfeito-Ferreira & Silva 2019).

Despite its non-desirable effects on food related products, *Zygosaccharomyces* species can also be used in the production of foodstuffs under controlled conditions and by selecting strains with desirable characteristics. The physiological characteristics of *Zygosaccharomyces* strains can vary, even among strains of the same species. The same abilities of *Zygosaccharomyces* species that make their presence in food products undesirable also give some strains the potential to be used as starter cultures as alternative and/or complementary to *Saccharomyces cerevisiae* (Domizio *et al.* 2011, Solieri 2021). Re-fermentation and excessive production of CO_2 in alcoholic beverages are mostly unwanted. However, for the production of sparkling wines, it is a desirable trait and *Z. bailii* was used as a mixed starter with *S. cerevisiae* to improve the production of ethyl esters and polysaccharides which remarkably contribute to wine aroma (Garavaglia *et al.* 2015) and enhance the wine taste and body (Domizio *et al.* 2011). The fructophilic characteristic is also used as an advantage and selected *Zygosaccharomyces* strains are included in the fermentation processes of grape musts from over-ripened grapes, therefore removing remaining sugar from Cabernet Sauvignon and Syrah sluggish fermentations. Maltose fermenting strains were successfully used in trials to produce ethanol-free beer (De Francesco *et al*. 2015). *Zygosaccharomyces* can assimilate ethanol under aerobic conditions and, at the same time, produce active flavour compounds that positively affect the beer aroma profile.

Zygosaccharomyces spp. can also play a role in the production of soy sauce and balsamic vinegar (Solieri *et al.* 2013), in traditional homemade fermented beverages such as the Chinese alcoholic beverage, Maotai-flavor liquor, and Kombucha tea. Maotai-flavor liquor fermentation (Wu *et al*. 2013b, Xu & Ji 2017) is produced by spontaneous and solid-state alcoholic fermentation of grains at high temperatures. *Zygosaccharomyces* strains isolated from this beverage are significant producers of higher alcohol acids, esters, ketones, and aldehydes, therefore greatly impacting the unique aroma of the end product (Wu *et al.* 2012a). Kombucha tea is a sugared tea that is a traditional homemade fermented drink that is popular and consumed worldwide for its refreshing and beneficial properties on human health (Jayabalan *et al.* 2014; Sreeramulu *et al.* 2000). Yeasts and bacteria in kombucha are involved in such metabolic activities that utilise substrates by different and in complementary ways. The micro-organisms present are usually mixed cultures of acetic acid bacteria and moulds with *Acetobacter* and *Zygosaccharomyces* the dominant genera (Marsh *et al*. 2014). The yeast species present hydrolyse sucrose into glucose and fructose and produce ethanol via glycolysis, with a preference for fructose as a substrate, making the fructophilic phenotype of *Zygosaccharomyces* spp. indispensable. Soy sauce is probably the main product produced on an industrial scale with the use of *Zygosaccharomyces* (Devanthi & Gkatzionis 2019). It contributes to flavour enhancement of the sauce during the production process, since this yeast can increase the concentration of various aromatic volatile compounds, due to the formation of larger amounts of isoamyl alcohol, amyl alcohol, acetoin and alcohol (Jansen *et al.* 2003). *Zygosaccharomyces rouxii*, is used industrially in the production of other salted condiments, such as balsamic vinegar (Solieri *et al.* 2007, Solieri & Giudici 2008).

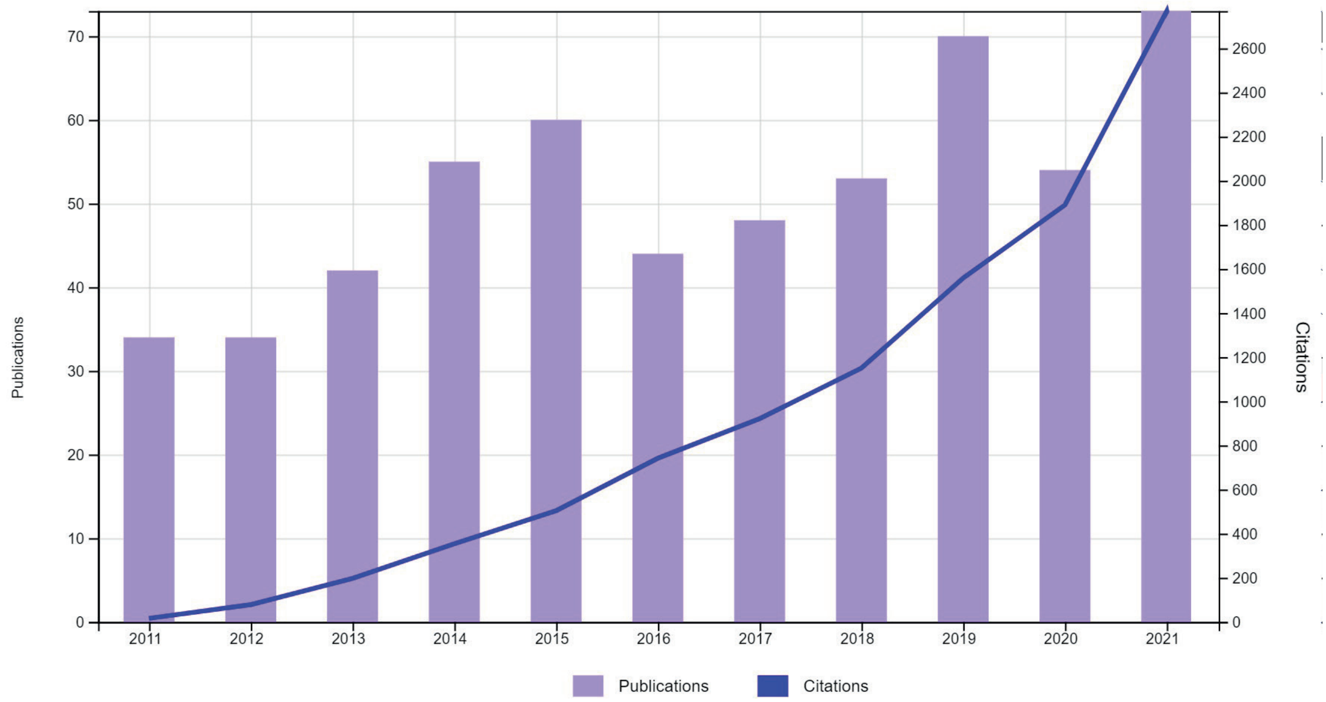

Fig. 92. Trends in research of *Zygosaccharomyces* in the period 2011–2021.

Table 69. Top 10 cited articles related to *Zygosaccharomyces* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	The microbial ecology of wine grape berries	360	Barata *et al.* (2012)
2	Yeast biodiversity from DOQ Priorat uninoculated fermentations	249	Padilla *et al.* (2016a)
3	Past and future of non-*Saccharomyces* yeasts: from spoilage microorganisms to biotechnological tools for improving wine aroma complexity	243	Padilla *et al.* (2016b)
4	Influence of surfactant charge on antimicrobial efficacy of surfactant-stabilized thyme oil nanoemulsions	162	Ziani *et al.* (2011)
5	Sequence-based analysis of the bacterial and fungal compositions of multiple kombucha (tea fungus) samples	160	Marsh *et al.* (2014)
6	Is there a common water-activity limit for the three domains of life?	151	Stevenson *et al.* (2015)
7	Physical properties and antimicrobial efficacy of thyme oil nanoemulsions: influence of ripening inhibitors	145	Chang *et al.* (2012)
8	Outlining a future for non-*Saccharomyces* yeasts: selection of putative spoilage wine strains to be used in association with *Saccharomyces cerevisiae* for grape juice fermentation	131	Domizio *et al.* (2011)
9	Molecular basis for the recognition of methylated adenines in RNA by the eukaryotic YTH domain	126	Luo *et al.* (2014)
10	Microbial terroir and food innovation: The case of yeast biodiversity in wine	112	Capozzi *et al.* (2015)

Industrial significance

In addition to the desirable effects that *Zygosaccharomyces* strains have on the industrial production of many food products and beverages, they also produce many other important compounds/ products used in various industries. These include antimicrobial agents, aroma-like molecules, antioxidants, food additives and compounds used in the pharmaceutical and cosmetics industries and the production of bioethanol (reviewed by Solieri 2021).

Zygocin is a killer toxin produced by some *Zygosaccharomyces* spp. (Schaffrath & Breunig 2000). It disrupts plasma membrane integrity and therefore has the potential to act as a natural antimicrobial in food and for biological control of plant pathogens. This killer phenotype exhibits a broad lethality activity upon many filamentous fungi and yeasts. Other antimicrobial compounds (reviewed by Solieri 2021) produced by *Zygosaccharomyces* species are L-glutaminase and 2-phenylethanol which have effects against Gram-negative bacteria and various filamentous fungi. 2-phenylethanol is not only a molecule that has antimicrobial abilities but is also a rose-honey-like aroma molecule that is utilised as an ingredient in cosmetics, perfumes, beer, olive oil, tea and coffee. *Zygosaccharomyces* spp. can also produce malic acid, which can be applied as an antioxidant, in the pharmaceutical and cosmetics industries and as a food additive. Malic acid-consuming *Zygosaccharomyces* spp. have been successfully used to stabilise the pH in fermenting musts with an excess of malic acid (reviewed by Vilela 2017). Another polyester compound produced by strains of *Zygosaccharomyces* is 4-hydroxy-2,5-dimethyl-3 (2H)-furanone which is used as a food additive with a caramel-like odour.

Zygosaccharomyces spp. are promising bioethanol-producing cell factories due to their suitability to metabolise pentoses and exhibit robustness towards multiple stresses during the production of bioethanol (reviewed by Solieri 2021). Also, their fructophilic behaviour increases ethanol yield from inulin-rich feedstocks such as tubers, bulbs and tuberous roots, as the fructose produced from inulin hydrolysis can be assimilated completely (Paixao *et al.* 2013, 2018).

Research interests

There are 567 publications and 9 140 citations from 2011–2021 in the Web of Science (Fig. 92), with the top 10 most cited articles listed in Table 69. Most of the publications focused on the bioindustry, genetic engineering and future processes.

(Bio-)industry

Zygosaccharomyces yeasts are living the transition from dangerous food spoilage agents to robust and stress tolerant bio-catalysers exploitable in several bioprocesses other than food fermentation, such as bioethanol, chemicals, and enzyme production (Paixao *et al.* 2013, 2018, reviewed by Solieri 2021). This is strongly dependent upon knowledge about the mechanisms whereby *Zygosaccharomyces* cells exhibit industrially relevant phenotypes in response to environmental stimuli. Although interesting relationships have been established among stress responses in *Zygosaccharomyces*, its fructophily characteristic and furanones production is still poorly understood and deserves further investigation. Current data comparison is suboptimal as information is often heterogenous and collected under diverse stress conditions and from strains that differ in ploidy and genetic make-up. Investigating and expanding the array of genes and increasing knowledge of the mechanisms involved in stress adaptation will be extremely helpful.

Although the presence of *Zygosaccharomyces* yeast strains in many food products may represent a quality control danger and negative economic impact, the controlled use of selected strains may positively contribute to the improvement of a particular range of products in the food/beverage industry. For example, the use of *Zygosaccharomyces* strains in winemaking is still controversial due to their high spoilage activity, but it might also be an alternative to current technologically challenging conditions to investigate further, especially in stuck fermentations or the use of high fructose-containing grape musts.

There are several natural compounds produced by *Zygosaccharomyces* strains that can provide valuable alternatives to chemical counterparts. Improving the production of these natural compounds by selecting strains with the most potential and optimal growth conditions will be of great value for future use of these compounds. The most interesting compounds currently studied are (reviewed by Solieri 2021) (i) 2-phenylethanol that can be used as an antimicrobial compound as well as enhance aroma and flavour of food and beverages; (ii) the chiral alcohols, providing chiral building blocks for the bio-synthesis of different pharmaceutical molecules and fine chemicals; (iii) L-glutaminase can be used in the pharmaceutical and food industries as flavour enhancer as well as a therapeutic agent against cancer and HIV (Kashyap *et al.* 2002, Amobonye *et al.* 2019); (iv) malic acid can replace chemically produced compounds now used as food additives, pharmaceuticals, cosmetics and has also potential to be used as antioxidants; and (v) xylitol produced from glucose via the d-arabitol route, is a five-carbon sugar alcohol, used as a natural food sweetener.

Genetic engineering and future processes

Lactic acid is an important chemical for food, pharmaceutical, bioplast and leather industries. Yeast cell factories expressing a bacterial gene encoding lactate dehydrogenase can produce optical pure lactic acid with less environmental impact than chemical synthesis. Attempts to engineer *S. cerevisiae* for this purpose were not very successful due to its sensitivity toward lactic acid at lower pH. Engineering *Zygosaccharomyces* strains (Bianchi *et al.* 2001, Won *et al*. 2017) for heterologous expression of lactic acid is well demonstrated due to its ability to tolerate lactic acid at low pH. It is, therefore, a useful host to further develop for heterologous production of lactic acid and equivalent compounds to be used for industrial purposes that are also cost-effective and have no or limited negative impact on the environment.

Different strategies are currently used to genetically improve *Zygosaccharomyces* cells. An overview of these strategies and the main applications in industrial microbiology and food biotechnology of *Zygosaccharomyces* yeasts, so-called ZygoFactory, is given by Solieri (2021). The idea is to establish a set of reference strains fully characterised by phenotype, genotype, transcriptomic, and proteomic traits. This will increase in-depth knowledge of the mechanism behind the production of the compounds of interest and select strains for specific processes as novel ZygoFactories. This will broaden the biotechnological opportunities to implement them in sustainable bioprocesses. Genome editing tools, the construction of a library of well-characterised bio-compounds and further studies on the DNA repair mechanisms in *Zygosaccharomyces* cells will be vital for the generation of industrially relevant compounds from natural sources and wastes and to make these technologies scalable and cost-effective.

Author: M. Groenewald

64. ***Torulaspora*** Lindner, Jahrb. Vereins Lehranst. Brauerei Berlin 7: 441. 1904.

Type species: *Torulaspora delbrueckii* (Lindner) E.K. Novák & Zsolt

Classification: *Ascomycota*, *Saccharomycotina*, *Saccharomycetes*, *Saccharomycetales*, *Saccharomycetaceae.*

Background

The genus *Torulaspora* was established by Lindner in 1904 with the type species *To. delbrueckii* formerly known as *Sacchromyces delbrueckii*. In the first edition of the "Yeasts: A taxonomic Study" (Lodder & Kreger-van Rij 1952), *Torulaspora* was merged with *Saccharomyces*, and also the genus *Zygosaccharomyces* was added. A further taxonomic revision (Van der Walt & Johansen 1975) restored the genera *Zygosaccharomyces* and *Torulaspora*, and the latter was enriched with all the *Debaryomyces* species and some species of *Pichia*. In a study by Kreger-van Rij in 1984, the closely related genera *Torulaspora*, *Saccharomyces*, *Zygosaccharomyces* and *Debaryomyces*, showing very similar phenotypic characteristics, were distinguished based on a few physiological and morphological features (ascosporulation, dominant haploid/diploid status, ascospore aspects, fermentation, coenzyme Q-9/Q-6). The four genera were definitively separated thanks to a first phylogenetic investigation of D1/D2 LSU rRNA gene sequences (Kurtzman & Robnett 1998), and a subsequent multigene analysis based on rRNA gene repeat, single copy nuclear genes, and mitochondrial encoded genes (Kurtzman 2003, Kurtzman & Robnett 2003). At present *Torulaspora* includes nine species: *To. delbrueckii*, *To. globosa*, *To. franciscae*, *To. microellipsoides*, *To. pretoriensis* (Kurtzman 2003), *T maleeae* (Limtong *et al.* 2008), *To. quercuum* (Wang *et al.* 2009), *To. indica* (Saluja *et al.* 2012), and *To. nypae* (Kaewwichian *et al.* 2020).

Torulaspora belongs to the order *Saccharomycetales*, family *Saccharomycetaceae* and the closest related genera are *Zygotorulaspora* and *Zygosaccharomyces*. The complete genome sequence of *To. delbrueckii* and *To. microellipsoides* was obtained in recent years (Gordon *et al.* 2011, Galeote *et al.* 2018). The cells are spherical to ellipsoidal and asexual reproduction occurs by multilateral budding. Poorly differentiated pseudohyphae may be present but true hyphae were not observed. Asci may be formed by conjugation between a cell and its bud or between independent cells; tapered protuberances are often observed though not involved in the conjugation process. Asci contain 1–4 spherical ascospores with smooth or roughened walls. Both homothallic and heterothallic species occur within the genus. Glucose is fermented by all the species while other sugars, such as galactose, maltose, sucrose, trehalose, and raffinose are fermented differently within the genus (Kurtzman 2003, Limtong *et al.* 2008, Wang *et al.* 2009, Saluja *et al.* 2012, Kaewwichian *et al.* 2020).

Torulaspora delbrueckii is the most studied species and has a large number of synonyms. It is a ubiquitous species isolated from various habitats (natural and anthropic) and countries. It was found in gummy material of a sugar refinery, honey bee gut, fermented beverages (brandy, sour milk, colonche, juice, wine, beer), plants (ragi, grapes, bark, sugarcane, phylloplane), foods (salads, dairy products, fermenting coffee beans), soil, wastewater treatment systems, and skin lesion (De Azeredo *et al.* 1998, Bhadra *et al.* 2008, Kurtzman 2011a, Yang *et al.* 2013, Limtong *et al.* 2014, De Carvalho Neto *et al.* 2017, Barry *et al.* 2018). *Torulaspora delbrueckii* exhibits polyextremophilic/extremotolerant aptitudes; osmophilic/osmotolerant, alkali-tolerant and halophilic/halotolerant strains, as well as strains with high freeze tolerance correlated to high resistance to lipid oxidative damage, have been isolated from different extreme habitats (Alves-Araujo *et al.* 2004, Rojo *et al.* 2017, Buzzini *et al.* 2018). The habitats of other species were mainly represented by soil, leaves or inflorescences, moss (*To. maleeae*), human oral cavity (*To. quercuum*) and fermented substrates (*To. pretoriensis* and *To. microellipsoides*). No pathogenic aptitude was shown (Kurtzman 2003, Limtong *et al.* 2008, Wang *et al.* 2009, Saluja *et al.* 2012, Kaewwichian *et al.* 2020).

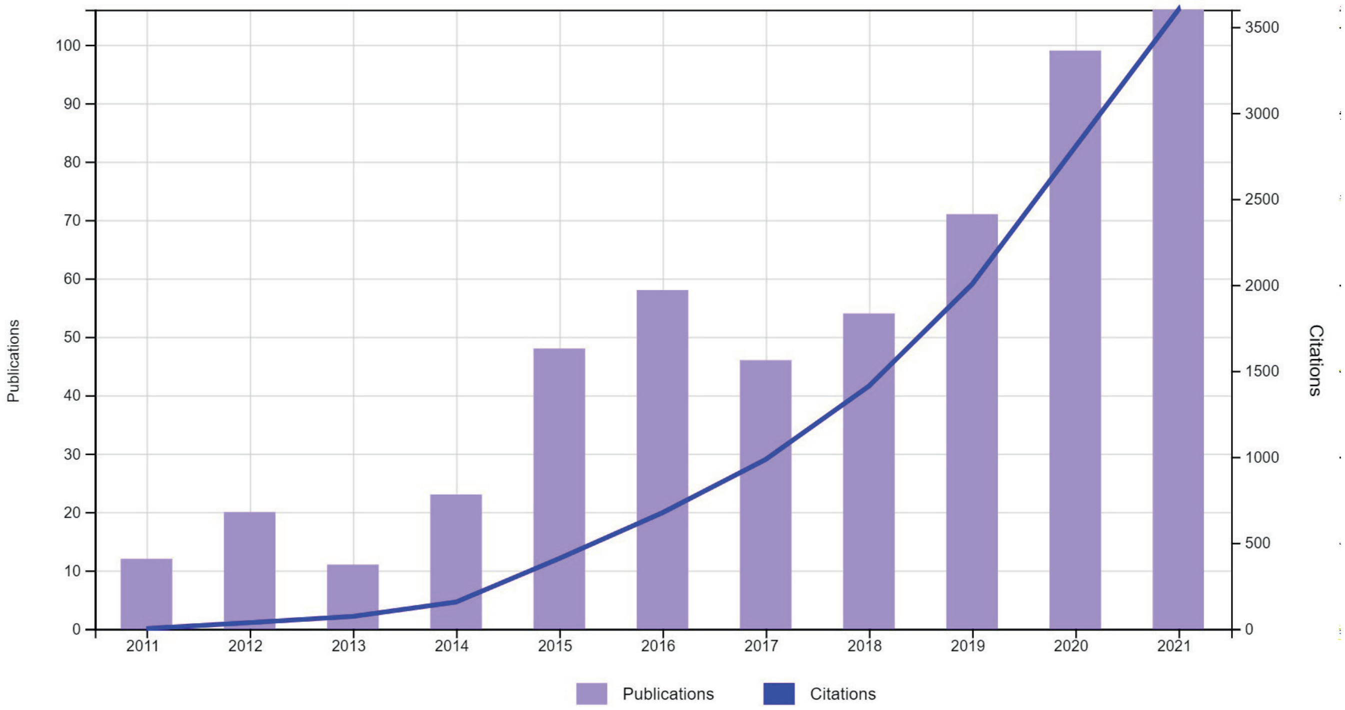

Fig. 93. Trends in research of *Torulaspora* in the period 2011–2021.

Ecological and economic significance

Torulaspora delbrueckii is the most studied of all species. It is one of the yeast species indigenous to grapes, an ecological niche mainly inhabited by non-*Saccharomyces* species. Although regarded as spoilage microorganisms in wine fermentations (Kurtzman 2011a), non-*Saccharomyces* species acquired the role of co-fermenters with *S. cerevisiae* due to their unique oenological traits which discontinue the wine uniform profiles deriving from the massive use of commercial starters. Publications relating to the role of *To. delbrueckii* as a selective starter in the fermentation of wine (some strains are currently on the market) have significantly increased in the last years (Mas *et al.* 2016, Benito 2018) (Fig. 93) and are mainly focused on its contribution to enhancing the organoleptic properties of wine, with strain dependant variability (Table 70).

Torulaspora delbrueckii resistance to ethanol is lower than that of *S. cerevisiae* but among non-*Saccharomyces* species *To. delbrueckii* shows one of the greatest fermenting abilities, reaching an ethanol concentration of 9.38 % (v/v) (Bely *et al.* 2008), enough to be defined as a relatively powerful fermenter. However, *To. delbrueckii* has never been proposed as a unique fermenting agent in high-alcohol beverages such as traditional wine, because it cannot

Table 70. Top 10 cited articles related to *Torulaspora* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Not your ordinary yeast: non-*Saccharomyces* yeasts in wine production uncovered	465	Jolly *et al.* (2014)
2	Selected non-*Saccharomyces* wine yeasts in controlled multistarter fermentations with *Saccharomyces cerevisiae*	366	Comitini *et al.* (2011)
3	The microbial ecology of wine grape berries	360	Barata *et al.* (2012)
4	Past and future of non-*Saccharomyces* yeasts: from spoilage microorganisms to biotechnological tools for improving wine aroma complexity	243	Padilla *et al.* (2016b)
5	Yeast-yeast interactions revealed by aromatic profile analysis of Sauvignon Blanc wine fermented by single or co-culture of non-*Saccharomyces* and *Saccharomyces* yeasts	236	Sadoudi *et al.* (2012)
6	Increase of fruity aroma during mixed *T. delbrueckii*/*S. cerevisiae* wine fermentation is linked to specific esters enhancement	134	Renault *et al.* (2015)
7	The impact of non-*Saccharomyces* yeasts in the production of alcoholic beverages	132	Varela (2016)
8	Dynamic analysis of physiological properties of *Torulaspora delbrueckii* in wine fermentations and its incidence on wine quality	112	Belda *et al.* (2015)
9	Microbial terroir and food innovation: the case of yeast biodiversity in wine	112	Capozzi *et al.* (2015)
10	The application of non-*Saccharomyces* yeast in fermentations with limited aeration as a strategy for the production of wine with reduced alcohol content	103	Contreras *et al.* (2015)

properly complete a fermentation process by itself. Its function has been shown to be essential in the first hours of spontaneous must fermentation when sugar concentration is elevated, as the cell abundance of *To. delbrueckii* is much higher than that of *S. cerevisiae*. Consequently, most studies in wine production involve *To. delbrueckii* in sequential fermentation before *S. cerevisiae*, in order to promote *To. delbrueckii* oenological features, minimising the competition with *S. cerevisiae* (Loira *et al.* 2014, González-Royo *et al.* 2015, Padilla *et al.* 2016b, Ramírez & Velazquez 2018). Sequential fermentations have also been tested for decreasing the content of alcohol in wine, compared to *S. cerevisiae* control, even if with variable results (decrease from 0 to 0.5 %) (Cus & Jenko 2013, Belda *et al.* 2015, 2017a, Renault *et al.* 2015, Puertas *et al.* 2017, Chen *et al.* 2018c).

Acetic acid and volatile acidity high concentration is the principal negative parameter in wine quality (vinegar character). *Torulaspora delbrueckii* has shown a significant reduction of acetic acid in pure and sequential fermentations compared to *S. cerevisiae* control (0.13–0.8 g/l depending on strain) (Ciani & Maccarelli 1998, Bely *et al.* 2008, Taillandier *et al.* 2014, Padilla *et al.* 2016a, Medina-Trujillo *et al.* 2017, Chen *et al.* 2018c).

This species plays an important role in producing esters and other volatile compounds which enhance the aroma complexity and intensity of wine and its fruity character. Some authors have reported an increase in esters (ethyl propanoate, ethyl isobutanoate, ethyl dihydrocinnamate, and isoamyl acetate) (Cordero-Bueso *et al.* 2013, Renault *et al.* 2015, Chen & Liu 2016, Belda *et al.* 2017a, Puertas *et al.* 2017), higher alcohols (Sadoudi *et al.* 2012, Azzolini *et al.* 2015, Belda *et al.* 2017a), 4-ethyl phenol (González-Royo *et al.* 2015), the typical grape derived volatile thiols (Swiegers *et al.* 2005, Swiegers & Pretorius 2007), and terpene compounds liberated by the action of β-D-glucosidase (such as α-terpineol, linalool, geraniol, trans-β-ocimene) (Hernández-Orte *et al.* 2008, Cus & Jenko 2013, Whitener *et al.* 2017) when *To. delbrueckii* is involved in most fermentation.

Some studies have described significant acid malic consumption of both pure and sequential fermentations with *To. delbrueckii*, thus contributing to the de-acidification of harsh wine typical of less sunny regions (Belda *et al.* 2015, Du Plessis *et al.* 2017, Chen *et al.* 2018c, Balmaseda *et al.* 2024).

Torulaspora delbrueckii was considered by several authors a notable producer of mannoproteins and polysaccharides, with production up to 25–50 % more than *S. cerevisiae* control. These compounds play an important role in increasing the sensory perception of properties such as mouthfeel, structure and overall impression of wine (Domizio *et al.* 2014, 2017, Belda *et al.* 2015, 2016, Garcia *et al.* 2017).

The contribution of *To. delbrueckii* in wine fermentation has also been studied for its nitrogen metabolism and the aptitude in the reduction of acetaldehyde content, and the increase of anthocyanins, phenolics, glycerol, and succinic acid (Ciani & Maccarelli 1998, Bely *et al.* 2008, González-Royo *et al.* 2015, Belda *et al.* 2016, 2017a, Puertas *et al.* 2017, Benito 2018, Chen *et al.* 2018c).

Research interests

There are 548 publications and 9 132 citations from 2011–2021 in the Web of Science (Fig. 93), with the top 10 most cited articles listed in Table 70. *Torulaspora* was considered in the past to be only an undesired or spoilage yeast of wine. Startford *et al.* (2000) listed *To. delbrueckii* and *To. microellipsoides* within the eleven most significant deteriorating yeasts in fruit juices and soft drinks. *Torulaspora delbrueckii* has also been isolated from spoiled dairy products, vegetable and meat salads (Kurtzman 2011a). The positive contribution of *Torulaspora* and in particular of *To. delbrueckii* to the enhancement of fermented food and beverage characteristics has been deeply investigated in the last 6 or 7 years, arousing the interests of a growing number of researchers and becoming the main topic of literature on this genus. Despite the traditional wine technology interest, several authors have suggested *To. delbrueckii* for sparkling base wine, cherry, lychee, mango, and durian wines, meads, but above all, for beer (Basso *et al.* 2016, Varela 2016, Canonico *et al.* 2017, Medina-Trujillo *et al.* 2017, Sottil *et al.* 2019, Fernandes *et al.* 2021), mainly because of the low alcohol and high volatile content production (Gamero *et al.* 2016, Varela 2016).

Various papers describe *To. delbrueckii* aptitude in the brewing industry, highlighting the typical strain variability. During wort fermentation, *To. delbrueckii* has shown synthesis of several esters (such as β- phenylethanol, n-propanol, iso-butanol, amyl alcohol, and ethyl acetate), and the ability to convert hop monoterpene alcohols into linalool, that defines hop aroma in beer (King & Dickinson 2000, Pires *et al.* 2014, Basso *et al.* 2016). Both pure cultures and mixed fermentations were tested obtaining beer with floral and fruity aromas and low-alcohol content (2.66–3.78 % v/v) in the first case, and a significant increment of esters, if compare with a *S. cerevisiae* control, in the second (Canonico *et al.* 2016, Michel *et al.* 2016, Toh *et al.* 2020).

The fermentation performance of *To. delbrueckii* has also been applied in the bakery industry and some strains are already on the market (Pech-Canul *et al.* 2019). Some tested strains of *To. delbrueckii* have shown a positive influence on the final quality of bread, combining satisfactory dough rheology, bread texture and volume, with rich flavour profiles that generate diversity when compared to the traditional *S. cerevisiae* (Wahyono *et al.* 2015, Aslankoohi *et al.* 2016). Some studies have described the low invertase activity and the slow rate of trehalose mobilisation of *To. delbrueckii*. These features are strictly related to the high tolerance to freeze-thaw and osmotic stress, which make *To. delbrueckii* suitable for frozen and sweet dough technology, respectively (Hernandez-Lopez *et al.* 2003, 2007, Pech-Canul *et al.* 2019).

Author: B. Turchetti

65. ***Boletus*** Fr., Syst. Mycol. 1: 385. 1821.

Type species: *Boletus edulis* Bull.

Classification: *Basidiomycota*, *Agaricomycotina*, *Agaricomycetes*, *Boletales*, *Boletaceae.*

Background

Boletus is likely the most famous genus of wild edible mushrooms with the type species *Boletus edulis* and its allies known as porcini, king bolete, noble mushroom, penny bun, ceps, borovik, or Karl Johan svamp. *Boletus* are some of the most popular and widely collected mushrooms having excellent taste, rich in valuable nutrients and biologically active substances which determine their high economic value (Arora 2008, Feng *et al.* 2012, Sitta & Davoli 2012, Cui *et al.* 2016b, Gelardi 2020).

The name *Boletus* has a long and complicated nomenclature history. Originally it was given by Carl Linnaeus in 1753 for all fungi having a tubular hymenophore. Later, starting from 1821 (Fries 1821, Gray 1821) to date, the genus has been repeatedly split with the separation of many genera. According to Kirk *et al.* (2008), *Boletus* comprises about 300 species. One of the first general research on the molecular phylogeny of *Boletales* (Binder & Hibbett 2006) presented data showing that relationships among genera are poorly resolved and most of the larger genera (*e.g.*, *Boletus*, *Tylopilus*, *Xerocomus*) are not monophyletic. Global multi-locus molecular phylogenetic work showed that *Boletus* should be reduced to *Boletus s. str.* (Nuhn *et al.* 2013). This was followed by many works confirming the segregation of several genera (Li et al. 2011e, Halling *et al.* 2012, Zeng et *al.* 2012a, Hosen *et al.* 2013, Arora & Frank 2014, Gelardi *et al.* 2014, Wu *et al.* 2014b, 2015d, 2016a, Zhao *et al.* 2014b, Gelardi *et al.* 2015). However, He *et al.* (2019b) accepted 350 species, while over 2 530 epithets are listed in Index Fungorum (2022). Gelardi (2020) provided a detailed and comprehensive list of 60 species of porcini fungi occurring in the world (including undescribed phylogenetic species). Each species listed by Gelardi (2020) was accompanied by a list of synonyms, pertinent geographic range, data on ecology and symbiotic partnerships, and relevant bibliography. Data of molecular phylogenies indicate that *Boletus s. str.* can be divided into five distinct lineages currently defined with provisional names: "porcini *s. str.*," "*Obtextiporus*," "*Inferiboletus*," "*Alloboletus*," and "*Orientiboletus*" (Dentinger *et al.* 2010, Feng *et al.* 2012, Cui *et al.* 2016b). The taxonomic rank of these informal groups is unclear and further analysis on a more inclusive number of taxa is required (Gelardi 2020).

Boletus s. str. species form characteristic fleshy medium-large sporocarps having a pileus, a stipe and pored hymenophore, also there are a few sequestrate species (He *et al.* 2019b, Gelardi 2020, Mao *et al.* 2023). The group can be characterised and separated from other boletes by the combination of some specific morphological features: white, mild-tasting flesh that does not change colour when exposed to air; stipe usually enlarged toward the base and more or less distinctly reticulate; a layer of tangled white hyphae that covers the pores of hymenophore similar to a partial veil (co-called "stuffed pores") in the first developmental stages; hymenophoral trama bilateral divergent of the "*Boletus* type" (Beugelsdijk *et al.* 2008, Dentinger *et al.* 2010, Halling *et al.* 2014, Cui *et al.* 2016b, Gelardi 2020). Most of these traits are not unique to porcini and can vary among individuals, however their combination usually quite surely leads to *Boletus s. str*. The feature "stuffed pores" is often considered a key character in the diagnosis of porcini (Dentinger *et al.* 2010, Cui *et al.* 2016b), however, sometimes it also has been reported from distantly related taxa including, for example, *Phlebopus beniensis* (Miller *et al.* 2000).

Species of *Boletus* are distributed mainly in the Northern Hemisphere but the genus is also reported from Australia, Malaysia, New Zealand, New Guinea, and South America (Muñoz 2005, Dentinger *et al.* 2010, Feng *et al.* 2012, Halling *et al.* 2014, Bessette *et al.* 2016, Noordeloos *et al.* 2018, Gelardi 2020). According to the current state of knowledge about 30 species are known only from eastern and southeastern Asia, 24 from North America, four from Europe and Western Asia, and only a few from Australasia; there are no endemic species described from South America (Gelardi 2020).

Ecological and economic significance

Boletus species form ectomycorrhiza with trees and shrubs of *Fagaceae*, *Betulaceae*, *Pinaceae*, *Dipterocarpaceae*, *Salicaceae*, *Tiliaceae*, *Cistaceae*, *Cupressaceae*, *Ericaceae*, *Myrtaceae*, and *Sapindaceae* (Dentinger *et al.* 2010, Gelardi 2020) inhabiting various types of forest communities from the tundra and taiga zone to the tropics. The significant diversity of this group, a wide circle of symbionts and high abundance throughout the world is evidence of their great ecological role in natural forest communities. Ectomycorrhizal species contribute to the successful development and sustainable existence of certain types of communities in which their symbiont tree dominates (Pérez-Moreno *et al.* 2021).

Porcini mushrooms are among the most highly-priced and widely appreciated forest-occurring fungi in the world. They are commonly used as an exquisite ingredient in a large variety of processed foods and their trade plays an important economic role as a source of income

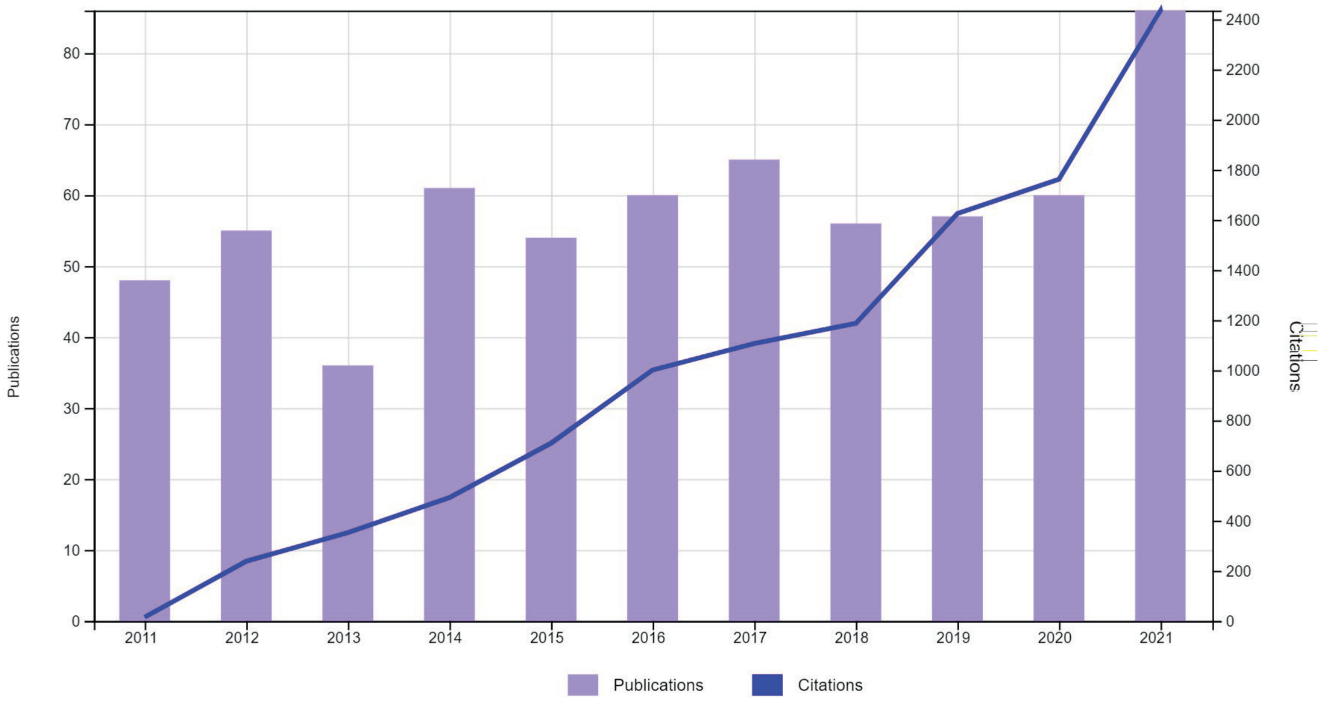

Fig. 94. Trends in research of *Boletus* in the period 2011–2021.

Table 71. Top 10 cited articles related to *Boletus* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	A review of chemical composition and nutritional value of wild-growing and cultivated mushrooms	322	Kalač (2013)
2	Antioxidant properties of phenolic compounds occurring in edible mushrooms	250	Palacios *et al*. (2011)
3	Macro and trace mineral constituents and radionuclides in mushrooms: health benefits and risks	238	Falandysz & Borovička (2013)
4	Molecular phylogenetic analyses redefine seven major clades and reveal 22 new generic clades in the fungal family *Boletaceae*	160	Wu *et al*. (2014b)
5	Chemical composition and non-volatile components of Croatian wild edible mushrooms	136	Beluhan & Ranogajec (2011)
6	Optimization of ultrasonic-assisted extraction of water-soluble polysaccharides from *Boletus edulis* mycelia using response surface methodology	128	Chen *et al*. (2012c)
7	Phylogenetic overview of the *Boletineae*	125	Nuhn *et al*. (2013)
8	Contents of lovastatin, γ-aminobutyric acid and ergothioneine in mushroom fruiting bodies and mycelia	120	Chen *et al*. (2012a)
9	Reactive oxygen species and antioxidant properties from mushrooms	119	Sánchez (2017)
10	Anti-inflammatory activity of methanolic extracts from edible mushrooms in LPS activated RAW 264.7 macrophages	113	Moro *et al*. (2012)

for local communities (Arora 2008, Mello 2012, Mortimer *et al.* 2012, Feng *et al.* 2012, Cui *et al.* 2016b, Gelardi 2020). The culture of use and trade of porcini dates back to the ancient Greeks and Romans (Buller 1914), and nowadays it has achieved a global scale (Sitta & Davoli 2012). Traditionally porcini mushrooms were harvested and consumed mainly by people in "mycophilic" Slavic or Romanic countries in Europe (Peintner *et al.* 2013) as well as some countries in eastern and southeastern Asia, especially China (Gelardi 2020). In North America as well as some northern European countries the collecting of porcini for food started at the beginning of the twentieth century (Arora 2008) and now is becoming a substantial economic resource. The total annual worldwide consumption of *Boletus edulis* and closely related species (*Bo. aereus*, *Bo. pinophilus*, and *Bo. reticulatus*) is estimated to be between 20 000 and 100 000 tons (Hall *et al.* 1998).

Primary and secondary metabolites of *Boletus* species have been reported to have many biological functions such as anticancer, antioxidant, anti-inflammatory, antimicrobial, antiviral and immunomodulatory effects which indicates the prospects for their use in medicine (see above).

Research interests

There are 638 publications and 9 078 citations from 2011–2021 in the Web of Science (Fig. 94), with the top 10 most cited articles listed in Table 71. Most publications focused on food science technology and biochemistry, also on environmental research, taxonomy, phylogeny, and ecological aspects. The publications are devoted to representatives of the genus *Boletus* both in the narrow and broad sense. A significant part of the highly cited works includes species of the genus as one of the objects of global research on fungi.

Food science technology and biochemistry

Many *Boletus* species are among the popular edible and valuable commercial wild mushrooms; therefore, many highly cited publications are devoted to the study of their nutritional value, chemical composition, and medicinal properties (Beluhan & Ranogajec 2011, Palacios *et al.* 2011, Falandysz & Borovička 2013, Kalač 2013, Heleno *et al.* 2015). Several publications were devoted to the different aspects of the chemical composition of *Boletus* species, especially, *Boletus edulis* (Falandysz *et al.* 2011, Zhang *et al.* 2018a). The analysis of primary metabolites revealed proteins, carbohydrates, fatty acids, mainly linoleic acid, sugars, mainly mannitol and trehalose, and vitamins (tocopherols and ascorbic acid). Secondary metabolites, such as phenolic acids, were also identified and correlated to *Boletus* antioxidant properties (Heleno *et al.* 2011). Ethanolic and methanolic extracts from different *Boletus* species demonstrate anti-inflammatory (Moro *et al*. 2012, Taofiq *et al.* 2015), antioxidant, and antimicrobial activities (Ozen *et al.* 2011, Vamanu & Nita 2013). Many studies deal with the antioxidant properties of *Boletus* (Guo *et al.* 2012, Novakovic *et al.* 2017, Sánchez 2017, Zhang *et al.* 2018a).

An object of special interest is the biological activity and medicinal properties of various chemical components of the *Boletus* species. Polysaccharides extracted from *Bo. edulis* have been reported to have many biological functions such as anticancer, antioxidant, anti-inflammatory, antiviral and immunomodulatory effects (Zhang *et al.* 2011a, 2014a, 2015a, Chen *et al.* 2012c, Santoyo *et al.* 2012, Wang *et al.* 2014b, Chroma *et al.* 2018). Lectins of porcini have also been the subject of study (Bovi *et al.* 2011, Singh *et al.* 2020). Lemieszek *et al.* (2017) showed that *Bo. edulis* RNA enhances natural killer cell activity and possesses immunomodulatory potential which suggests the possibility of their use in cancer treatment. Among wild species, *Bo. edulis* was reported with the highest content of ergosterol (Barreira *et al.* 2013), and γ-aminobutyric acid (Chen *et al.* 2012a).

Environmental studies

The ability of macrofungi to accumulate high concentrations of toxic metallic elements (Hg, Cd), toxic metalloids (As), essential and toxic nonmetal (Se), and other elements (Ag, Au, Cs, Rb, V, Zn), especially in contaminated areas, has led to many studies (Falandysz *et al.* 2011, 2014, Falandysz & Borovička 2013, Mleczek *et al.* 2013a, b, Wang *et al.* 2015f, Širić *et al.* 2016, Kavčič *et al.* 2019). In unpolluted areas species of *Boletus* are reported to accumulate manganese (Mn), mercury (Hg), rubidium (Rb) and selenium (Se) (Kalač 2013), with the content of elements differing in various parts of the sporocarp (Wang *et al.* 2015g).

Wild-grown mushrooms, including *Boletus* spp., are described as efficient accumulators of radionuclides and bioindicators of their environmental diffusion (Falandysz & Borovička 2013, Falandysz *et al.* 2015, Saniewski *et al.* 2016, Tucaković *et al.* 2018).

Taxonomy and phylogeny

Phylogenetic studies on *Boletus* were devoted to determining the number of species and position in *Boletaceae*. The global multi-locus molecular phylogenetic works specified a hierarchy of phylogenetic relationships between taxa within the *Boletaceae* and revealed that *Boletus* in the broad sense is polyphyletic, with species found throughout the phylogeny, and with most not closely related to the type species, *Boletus edulis* (Binder & Hibbett 2006, Nuhn *et al.* 2013, Wu *et al.* 2014b, 2016a). These studies were followed by the separation from *Boletus s. lat.* of several new genera (Li *et al.* 2011e, Halling *et al.* 2012, Zeng *et al.* 2012a, Hosen *et al.* 2013, Arora & Frank 2014a, Zhao *et al.* 2014b, Gelardi *et al.* 2015, Wu *et al.* 2015d, 2023, *etc.*). Several publications deal with *Boletus s. str.* (Beugelsdijk *et al.* 2008, Dentinger *et al.* 2010, Feng *et al.* 2012, Cui *et al.* 2016b), and *Boletus* species new to science were described within these frames (Arora & Frank 2014b, Halling *et al.* 2014, Zeng *et al.* 2014, Crous *et al.* 2019a), or with unresolved taxonomic position (Crous *et al.* 2019c).

Phylogenetic analyses support Eastern Asia as the centre of diversity for *Boletus*. Within this clade, most species are geographically restricted in distribution, and *Bo. edulis* is the only known holarctic species. Furthermore, molecular dating and geological evidence suggest that this group originated in Eastern Asia during the Eocene, and they then spread to other parts of Asia, Europe, and the Americas from the middle Miocene through the early Pliocene (Feng *et al.* 2012).

Ecology and conservation

Boletus edulis and related species are often found in works on ecology, productivity and conservation of the main edible mushrooms in different regions (Martínez-Peña *et al.* 2011, 2012, Mortimer *et al.* 2012, Tomao *et al.* 2017). *Boletus* spp. form ectomycorrhizal symbiotic relationships with both coniferous and deciduous trees and play an important role in the health of the trees and forest ecosystems. Thus, there are studies on different aspects of ectomycorrhiza, including the methods and the effect of inoculation of seedlings with EM fungi, especially with *Bo. edulis* and *Bo. reticulatus* (Endo *et al.* 2014, Mediavilla *et al.* 2016, Kayama, 2020, Chartier-Fitz Gerald *et al.* 2020).

Authors: O.V. Morozova and T.Y. Svetasheva

66. **_Botryosphaeria_** Ces. & De Not., Comment Soc. Crittog. Ital. 1(fasc. 4): 211. 1863.

Type species: *Botryosphaeria dothidea* (Moug.) Ces. & De Not.

Classification: *Ascomycota*, *Pezizomycotina*, *Dothideomycetes*, *Botryosphaeriales*, *Botryosphaeriaceae.*

Background

Cesati & De Notaris (1863) introduced *Botryosphaeria* with nine species and another six species which were not recombined. However, they did not introduce the type species for this genus. Since then, *Botryosphaeria* has undergone several revisions. Hypocreaceous species were removed from the genus by Saccardo (1877). Von Höhnel (1909) suggested *Bot. berengeriana* as the type species of *Botryosphaeria*, while Theissen & Sydow (1915) introduced *Bot. quercuum* as the type species. Neither of these species was in the original description of the genus. Barr (1972) suggested *Bot. dothidea* as a lectotype because it represents the original description of *Botryosphaeria* and this was accepted later. Slippers *et al.* (2004a) examined the type specimens and fresh specimens and provided a revised description. They also designed a neotype and epitype for *Bot. dothidea*.

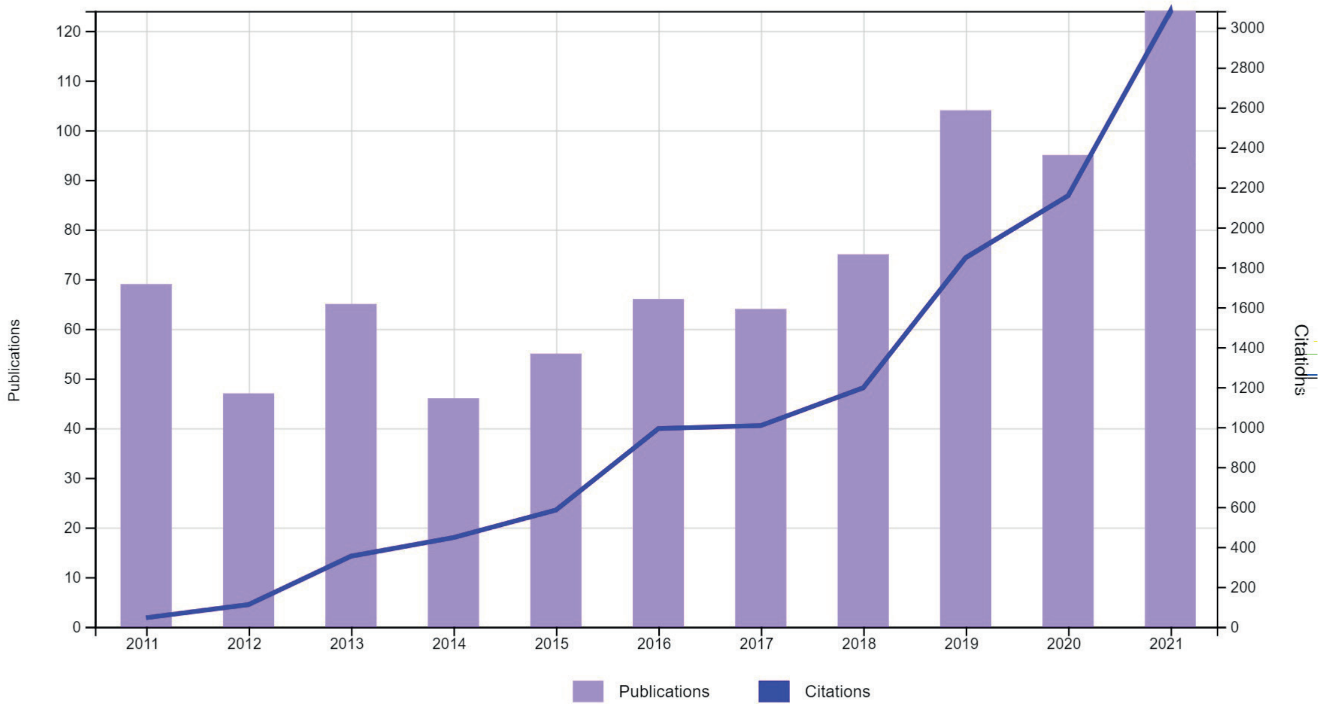

Fig. 95. Trends in research of *Botryosphaeria* in the period 2011–2021.

Table 72. Top 10 cited articles related to *Botryosphaeria* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	The *Botryosphaeriaceae*: genera and species known from culture	515	Phillips *et al.* (2013)
2	The status of *Botryosphaeriaceae* species infecting grapevines	238	Urbez-Torres (2011)
3	One stop shop: backbones trees for important phytopathogenic genera: I (2014)	235	Hyde *et al.* (2014)
4	Towards a natural classification of *Botryosphaeriales*	215	Liu *et al.* (2012b)
5	Phytotoxins produced by fungi associated with grapevine trunk diseases	125	Andolfi *et al.* (2011)
6	The endophytic mycota associated with *Vitis vinifera* in central Spain	123	González & Tello (2011)
7	Secondary metabolites from the endophytic *Botryosphaeria dothidea* of *Melia azedarach* and their antifungal, antibacterial, antioxidant, and cytotoxic activities	118	Xiao *et al.* (2014a)
8	*Botryosphaeria dothidea*: a latent pathogen of global importance to woody plant health	110	Marsberg *et al.* (2017)
9	*Botryosphaeriaceae*: Current status of genera and species	102	Dissanayake *et al.* (2016)
10	Species of *Botryosphaeriaceae* involved in grapevine dieback in China	75	Yan *et al.* (2013)

Most species of *Botryosphaeria* were described based on morphological characters. Von Arx and Müller (1954) studied 183 taxa and reduced them to 11 species and nine combinations. Most species were synonymised under *Bot*. *dothidea* and *Bot*. *quercuum* based on sexual morphological characters. However, these synonymies were not always accepted, as they did not consider the asexual morphological characters (Shoemaker 1964, Slippers *et al*. 2004a). *Botryosphaeria* is heterogeneous and currently over 250 epithets are included (Slippers *et al*. 2004a, Crous *et al*. 2006b, Phillips *et al.* 2008, 2013). According to a revision by Zhang *et al.* (2021d), eight species are accepted *i.e.*, *Bot. agaves*, *Bot. corticis*, *Bot. dothidea*, *Bot. fabicerciana*, *Bot. kuwatsukai*, *Bot. qingyuanensis*, *Bot. ramosa*, and *Bot. scharifii*. *Botryosphaeria* species have hyaline and aseptate ascospores that can become pale brown and septate with age (Phillips *et al*. 2013). Asexual morphs are characterised by hyaline, aseptate conidia and sometimes they also become pigmented with age (Phillips *et al*. 2013).

Ecological and economic significance

Botryosphaeria species are the most widespread and important canker and dieback pathogens worldwide.

Botryosphaeria species are common and widely distributed and have been reported as endophytes, pathogens and saprobes in the bark and leaves of trees (Pavlic *et al*. 2007, Jayawardena *et al*. 2018a, Hyde *et al.* 2020a, Hattori *et al*. 2021, Chethana *et al.* 2023). *Botryosphaeria dothidea* is one of the most important plant pathogenic species, occurring on a large number of hosts with a broad global distribution (Garcia *et al*. 2021a).

Botryosphaeria species use different mechanisms to enter their host. They use appressoria, enzymes and toxins for active mechanical penetration and natural openings, like stomata or lenticels for direct entry to the host. *Botryosphaeria* species then colonise host tissues and cause several diseases (Mancero-Castillo *et al*. 2018). *Botryosphaeria* species act as opportunistic pathogens and cause symptoms such as canker and die-back diseases on branches, twigs and trunks of trees, leaf diseases, seedling diseases and root cankers, shoot blights and even plant death (Pillay *et al*. 2013, Jayawardena *et al*. 2019)

Research interests

There are 810 publications and 9 058 citations from 2011–2021 in the Web of Science (Fig. 95), with the top 10 most cited articles listed in Table 72. Most studies focus on the pathogenicity of *Botryosphaeria* species, as well as its taxonomy. Although most studies focus on the pathogenicity of *Botryosphaeria* species there is also a need to focus on saprobic and endophytic taxa, as well as more taxonomic studies. This framework is essential to improve our understanding of how *Botryosphaeria* taxa switch their nutritional modes and how environmental changes affect these switches.

Pathogenicity of Botryosphaeria

Pathogenicity of *Botryosphaeria* species is often associated with environmental stress, such as drought, physical damage and frost (Marsberg *et al.* 2017, Bhunjun *et al.* 2021a).

Botryosphaeria species can severely affect *Eucalyptus* plantations, causing cankers and dieback diseases. Production of kino, dark red tree sap and even mortality of trees can occur in *Eucalyptus* due to this fungal infection (Darge & Woldemariam 2021). *Botryosphaeria* species also exist in healthy *Eucalyptus* leaves, twigs and stems as endophytes, without causing any disease. With environmental stress, these fungi become pathogens (Gezahgne *et al*. 2004, Pérez *et al*. 2008, 2010). *Botryosphaeria dothidea* is the main causal agent of band canker diseases of almonds (Holland *et al*. 2021). Ring rot disease is a serious disease of apples worldwide, and is caused by *Bot. dothidea* and *Bot*. *kuwatsukai* (Wang *et al*. 2018a). *Botryosphaeria dothidea* is pathogenic on grapevines causing bleaching of the outer bark, cracking of canes, dieback of shoots and bud mortality (Savocchia *et al*. 2007). Also, *Bot. stevensii* and *Bot. obtusa* act as wound pathogens, causing small lesions on grapevines (Savocchia *et al*. 2007).

Disease management

Apple ring rot disease, caused by *Bot. dothidea* has led to severe economic losses of Fuji apple cultivation in China. The disease can affect both before harvest and postharvest (Kexiang *et al*. 2002). The use of fungicides can cause serious environmental problems and, therefore, biological control using microorganisms has increased as an environmentally friendly and efficient method for the control of plant diseases (Fan *et al*. 2017). Fengycin is an antifungal lipopeptide complex produced by *Bacillus subtilis*, and fengycin plays an important role in biocontrol against apple ring rot disease (Fan *et al*. 2017). Therefore, *Bot. subtilis* is used to control apple ring rot disease (Fan *et al*. 2017). *Streptomyces rochei*, *Trichoderma harzianum* and *T. atroviride* also have antifungal activities against *Bot. dothidea* (Kexiang *et al.* 2002, Zhang *et al.* 2016d).

Taxonomy and phylogeny

DNA-based molecular techniques have been used to characterise and identify *Botryosphaeria* species (Slippers & Wingfield 2007, Phillips *et al*. 2013). Such techniques are applied to recent taxonomic studies of *Botryosphaeria* and have revealed phylogenetic relationships among *Botryosphaeria* species (Jayawardena *et al*. 2019, Hyde *et al.* 2020a, Chethana *et al.* 2023). The ITS and *tef1* genes are recommended molecular markers for species level identification (Jayawardena *et al*. 2019).

Author: A.R. Rathnayaka

67. **Cunninghamella** Matr., Ann. Mycol. 1(1): 46. 1903.

Type species: *Cunninghamella echinulata* (Thaxt.) Thaxt. *ex* Blakeslee

Classification: *Mucoromycota*, *Mucoromycotina*, *Mucoromycetes*, *Mucorales*, *Cunninghamellaceae.*

Background

The genus *Cunninghamella* proposed by Matruchot (1903) belongs to the phylum *Mucoromycota*, family *Mucoraceae*, order *Mucorales* (Wijayawardene *et al.* 2022). Species of this genus are morphologically characterised by producing erect sporophores, with a varied branching pattern, which can be monopodial, sympodial, verticillate, pseudoverticillate or with branches of different sizes appearing on the same sporophore. Sporophores end in a globose, subglobose, clavate or irregular vesicle with pedicellate unispored sporangiola. The reddish brown zygosporangia are formed between opposed suspensors that are more or less equal in size (Benny *et al.* 2005).

Traditionally, species of *Cunninghamella* have been delimited according to the maximum growth temperature, colour and texture of the colonies, sporophore branching pattern, shape and size of the vesicles, sporangiola, absence and/or presence of spines in the sporangiola, in addition to homothallic/heterothallic zygospore formation (Zycha 1935, Alcorn & Yeanger 1938, Naumov 1939, Cutter 1946, Mil'ko & Beljakova 1967, Samson 1969, Baijal & Mehrotra 1980). Zheng & Chen (2001) monographed this genus based on morphological characteristics, maximum growth temperature, mating experiments, as well as the length of the ITS region, delimiting 14 species and four varieties as follows: *Cu. bertholletiae*, *Cu. blakesleeana*, *Cu. binariae*, *Cu. clavata*, *Cu. echinulata* var. *antarctica*, *Cu. echinulata* var. *echinulata*, *Cu. echinulata* var. *nodosa*, *Cu. echinulata* var. *verticillata*, *Cu. elegans*, *Cu. homothallica*, *Cu. intermedia*, *Cu. multiverticillata*, *Cu. phaeospora* and *Cu. septata*. Molecular studies by Liu *et al*. (2001; ITS rDNA), Yu *et al.* (2014; ITS rDNA and *tef1*), Guo *et al*. (2015b; ITS, 28S rDNA and *tef1*), Hyde *et al*. (2016; ITS rDNA), Zhang *et al*. (2020j; ITS, 28S rDNA and *tef1*), Hallur *et al*. (2021; ITS, 28S rDNA and *tef1*), and Zhao *et al.* (2023; ITS rDNA), confirmed the species boundaries delimited by Zheng & Chen (2001) for the genus, except for *Cu. septata* that shared the clade with *Cu. echinulata* in the majority of these studies. As a result of some of these works, *Cu*. *bigelovii* (Guo *et al*. 2015b), *Cu*. *gigacellularis* (Hyde *et al*. 2016), *Cu. guizhouensis* (Zhang *et al.* 2020j), *Cu. arunalokei* (Hallur *et al*. 2021), *Cu. arrhiza*, *Cu. guttata*, *Cu. irregularis*, *Cu. nodosa*, *Cu. regularis*, *Cu. subclavata*, and *Cu. varians* (Zhao *et al.* 2023), were proposed.

Species of *Cunninghamella* are saprobes in soils, fruits, animal excrement and stored grains (Zheng & Chen 2001). However, *Cu*. *bigelovii* and *Cu*. *elegans* have been reported as endophytes (Guo *et al*. 2015b, Sagar *et al*. 2017). Even though it is rare, *Cunninghamella* species may cause mucormycosis in humans with impaired immunity, mostly patients with uncontrolled diabetes, haematological malignancy with neutropenia, immunosuppressive therapy for solid organ or stem cell transplantation (Yu *et al*. 2014, Bellanger *et al*. 2018, Cinteza *et al*. 2022), and mucormycosis reports in immunocompetent patients are even rarer than in immunocompromised ones (Zeilender *et al*. 1990, Jayasuriya *et al*. 2006, Hallur 2021, Portillo *et al*. 2021).

Ecological and economic significance

Species of *Cunninghamella* are of economic significance based on their ability to produce secondary metabolites with biological importance. Their mycelium can adsorb dyes and heavy metals mediated by chitin and chitosan, and both carbohydrates show antimicrobial activity against fungal phytopathogens. Because of the cytochrome P450 monooxygenase systems, many enzymes useful in the biotransformation of drugs and xenobiotic compounds are produced by *Cunninghamella* species.

Bioremediation processes

Fungi play a major role in bioremediation owing to their robust morphology and diverse metabolic capacity, being a cost-effective and environment-friendly method to degrade or remove toxic pollutants (Adenipekun & Lawal 2012, Hussain *et al.* 2017). According to Ambrósio *et al*. (2012), the inactive mycelium of *Cu*. *elegans* can efficiently adsorb reactive orange II, reactive black, reactive red (dyes commonly used in textile industries), and a mixture of them. The adsorption is mediated by the chitin and chitosan (polysaccharides of cellular fungal wall) binding to dyes. Hussain *et al*. (2017) reported that *Cu*. *elegans* biofilm was able to adsorb reactive black-5, acid orange 7, direct red 81 and brilliant blue G dyes concomitantly with Cr(VI). In this work, *Cu. elegans* could degrade triphenylmethane dye malachite green (MG) into leucomalachite green. Extracted chitin and chitosan from the mycelial biomass of *Cu. elegans* were able to adsorb Fe^2, Pb^{2+} and Cu^{2+} in an aqueous solution (Franco *et al.* 2004), and *Cu. bertholletiae* also showed good potential for Cu^{2+} adsorption (Ren *et al.* 2018b). Both chitosan and chitosan nanoparticles had high adsorption capacity to Pb^{2+} and Cu^{2+} in aqueous solution and soil contaminated with both ions (Alsharari *et al.* 2018). In addition, *Cunninghamella* species are able to metabolise a wide variety of xenobiotics using both phase I (oxidative) and phase II (conjugative) biotransformation mechanisms. By having cytochrome P450 monooxygenase systems analogous to those in mammals, species of *Cunninghamella* are models of mammalian drugs and xenobiotic metabolism, including biotransformation of fluorinated biphenyls (Amadio & Murphy 2010), polycyclic aromatic hydrocarbon (PAH) pollutants (Tortella *et al*. 2005), pesticides (Palmer-Brown 2019, Zhao *et al*. 2020), and anilinopyrimidine fungicide mepaniprim (Zhu *et al*. 2010).

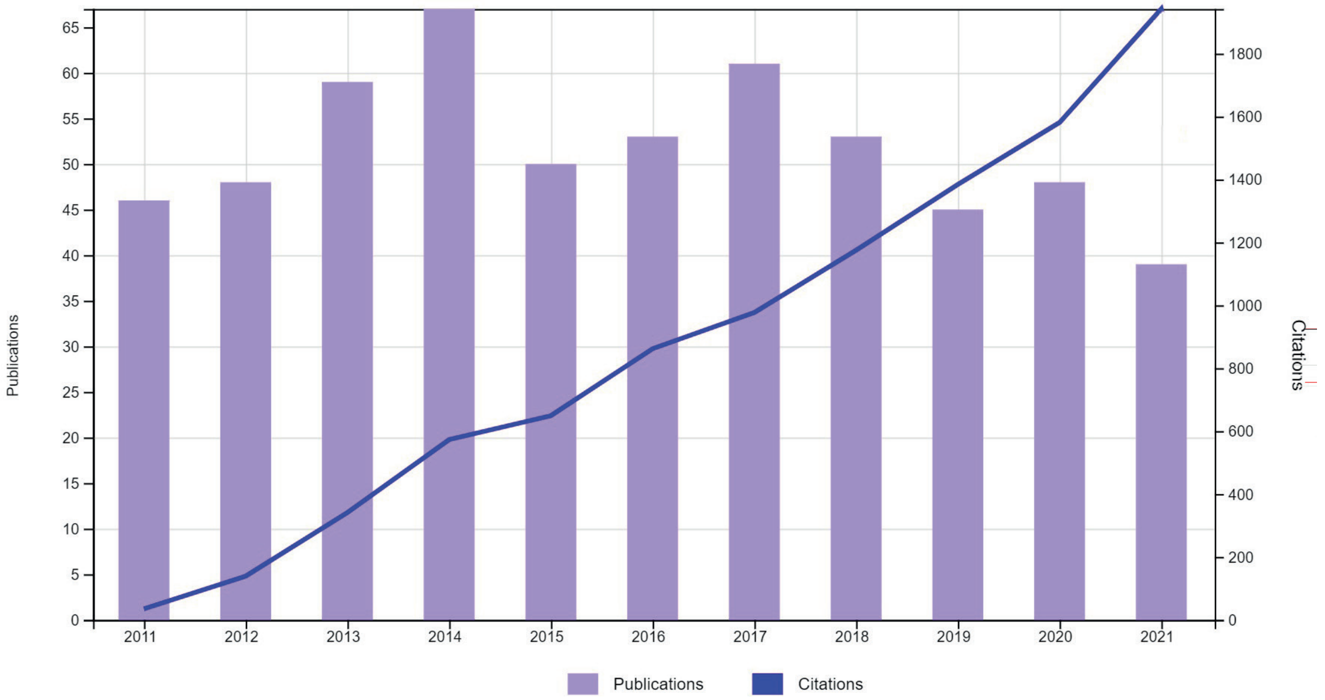

Fig. 96. Trends in research of *Cunninghamella* in the period 2011–2021.

Antimicrobial activities

Many studies have reported the antimicrobial activities of *Cunninghamella* (mostly *Cu. blaskesleeana*). *Cunninghamella blakesleeana* alcohol extract of 10 fatty acids contents showed *in vitro* antimicrobial activities against *Staphylococcus aureus* and *Streptococcus pyogenes*, with the lowest activity for *Candida albicans* and *Pseudomonas aeruginosa* (Alasmary *et al*. 2020). According to another study, *Cu. elegans* total extract, ethyl acetate and ether successive extracts showed high activity against *S. aureus.* Ten compounds were formed by *Cu. elegans* from which adenosine was the most active against *S. aureus* (Awaad *et al*. 2014). Chegaing *et al*. (2020) reported the transformation of norandrostenedione, an anabolic-androgenic steroids related to testosterone with *Cu. blakesleeana.* Four compounds were formed with varied anti-bacterial activity against *Pseudomonas aeruginosa*, *Escherichia coli*, *Salmonella typhi*, *Klebsiella pneumoniae*, *S. aureus*, and *S. faecalis.* Additionally, *Cu. blakesleeana* is able to biotransform a contraceptive drug, desogestrel, yielding four compounds, of which two show potent activity against *S. aureus*, and one shows significant activity against vancomycin-resistant *S. aureus* (Wahab *et al*. 2018).

Biological control

Chitosan obtained from *Cu. elegans* has the potential to control post-harvest pathogenic *Botrytis cinerea* and *Penicillium expansum* when applied as a coating in grapes (*Vitis labrusca*), by inhibiting

Table 73. Top 10 cited articles related to *Cunninghamella* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Epidemiology and clinical manifestations of mucormycosis	604	Petrikkos *et al*. (2012)
2	A global analysis of mucormycosis in France: The RetroZygo study (2005–2007)	271	Lanternier *et al.* (2012)
3	Mucormycosis caused by unusual mucormycetes, non-*Rhizopus*, -*Mucor*, and -*Lichtheimia* species	224	Gomes *et al.* (2011)
4	The epidemiology and clinical manifestations of mucormycosis: a systematic review and meta-analysis of case reports	213	Jeong *et al*. (2019)
5	Biotechnological conversions of biodiesel derived waste glycerol by yeast and fungal species	203	Chatzifragkou *et al.* (2011)
6	Invasive non-*Aspergillus* mold infections in transplant recipients, United States, 2001-2006	188	Park *et al.* (2011)
7	DNA barcoding in *Mucorales*: an inventory of biodiversity	176	Walther *et al*. (2013)
8	Early clinical and laboratory diagnosis of invasive pulmonary, extrapulmonary, and disseminated mucormycosis (Zygomycosis)	162	Walsh *et al*. (2012)
9	Healthcare-associated mucormycosis	153	Rammaert *et al.* (2012)
10	Antifungal susceptibility and phylogeny of opportunistic members of the order *Mucorales*	93	Vitale *et al*. (2012)

mycelial growth, spore germination and causing morphological changes in the spores of fungal strains (Oliveira *et al*. 2014). Chitosan from *Cu*. *elegans* shows antimicrobial activity against *Fusarium oxysporum f. sp. tracheiphilum* and induces defense mechanisms in cowpea plants by activation of the antioxidant enzymes catalase and peroxidase (Berger *et al*. 2016). Berger *et al*. (2018) reported that chitosan from *Cu*. *elegans*, growing in a mixture of corn steep liquor and papaya juice, inhibits the growth of *Colletotrichum asianum*, *Col*. *fructicola*, *Col*. *tropicale* and *Col*. *siamense* strains characterised as anthracnose-causing agents in fruit.

Research interests

There are 569 publications and 8 997 citations from 2011–2021 in the Web of Science (Fig. 96), with the top 10 most cited articles listed in Table 73. Most of the publications focused on biotechnology applied microbiology, biochemistry, molecular biology, microbiology and pharmacology.

Biotransformation of drugs and xenobiotic compounds

The biocide tributyltin can be degraded by *Cu*. *echinulata*, forming less hazardous compounds dibutyltin and monobutyltin (Soboń *et al*. 2016). *Cunninghamella elegans* and *Cu*. *blakesleeana* are capable of biotransforming the anti-inflammatory flurbiprofen (Amadio *et al*. 2010) into four metabolites, whereas *Cu*. *blakesleeana* can transform the proton-pump inhibitor pantoprazole into six metabolites (Xie *et al*. 2005). Naproxen, a potent inhibitor of prostaglandin synthesis and prescribed for the treatment of rheumatoid arthritis, can be transformed into two metabolites, desmethylnaproxen and desmethylnaproxen-6-O-sulfate by *Cu*. *elegans*, *Cu*. *echinulata* and *Cu*. *blakesleeana*, but the capability of *Cu. echinulata* to transform naproxen is weaker than that of the other two strains (Da-Fang *et al*. 2003). An extensive list with examples of mammalian *vs Cunninghamella* species metabolism of drugs was provided by Asha & Vidyavathi (2009).

Production of biosurfactants

Surfactants are amphipathic molecules composed of a polar hydrophilic and non-polar hydrophobic moiety, exhibiting high surface and emulsifying activities (Lins *et al*. 2017, Da Silva *et al*. 2021). These molecules are applied in the environmental, food, cosmetic and pharmaceutical industries (De Souza *et al*. 2018, Singh *et al*. 2018). Biosurfactants from microbes have received great attention for being environmentally friendly with low toxicity and high biodegradability (Montero-Rodrigues *et al*. 2015). *Cunninghamella echinulata* has the potential of producing a low surface tension biosurfactant using corn-steep liquor and soybean oil after frying with the ability to remove diesel and kerosene from marine sand (De Souza *et al*. 2018). Lins *et al*. (2017) reported the production of biosurfactants by *Cu phaeospora* converting soybean oil and corn liqueur with potential application in the bioremediation of sites polluted by hydrophobic compounds. According to De Medeiros *et al*. (2022), *Cu*. *elegans* produces biosurfactant growing on media composed of 2 % instant noodle waste, 2 % corn steep liquor and 0.5 % post-frying soybean oil, with a carbon/nitrogen ratio of 30:1.

Production of chitin and chitosan

Chitosan is a cationic biopolymer formed by the deacetylation of chitin, a polysaccharide found in the exoskeleton of shellfish, shrimps, crabs and lobster (Ghormade *et al*. 2017). Both chitosan and chitin occur in *Cunninghamella* cell walls (Amorim *et al*. 2006) and can be applied in agriculture (De Oliveira *et al*. 2014, Berger *et al*. 2016), food (Manigandaman *et al*. 2018) and pharmaceutical (Cheung *et al.* 2015) industries. Results based on fermentation strategies suggest that mucoralean fungi can provide an alternative source of chitin and chitosan (Stamford *et al.* 2007), and researchers have been studying eco-friendly and low-cost alternatives for the production of this polymer by *Cunninghamella* and other mucoralean fungi. Of note is the high potential for the application of chitosan from *Cu. elegans* in biological control strategies (De Oliveira *et al.* 2014).

Oleaginous Cunninghamella species

Microorganisms called "oleaginous species", which can accumulate more than 20 % of their dry biomass as oil (Fakas *et al*. 2009), offer excellent alternatives for the production of nutritionally important fatty acids (Laoteng *et al*. 2011). However, oil extraction from the microbial mass is still an expensive process, which has led researchers to consider low-cost substrates for the production of lipids by fungi (Gema *et al*. 2020). *Cunninghamella echinulata* growing on nitrogen-limited media having xylose as carbon and energy source can accumulate γ-linolenic acid (GLA), indicating that xylose is an efficient substrate for lipid accumulation by this species (Fakas *et al*. 2009). GLA can also be produced by *Cu*. *echinulata* growing on various nitrogen media containing corn steep, whey concentrate, yeast extract, and tomato waste hydrolysate (Fakas *et al*. 2008). Good production of this acid can also be observed from *Cu. echinulata* in culture media with soluble starch and lactose as carbon sources, and with urea as a nitrogen source (Chen & Chang 1996).

Mucormycosis

Among documented cases of mucormycosis caused by *Cunninghamella*, *Cu. bertholletiae* is the species mostly reported (Jeong *et al*. 2019), with unusual reports of infections caused by *Cu*. *echinulata* (LeBlanc *et al*. 2013), *Cu*. *elegans* (Shirane *et al*. 2021) and *Cu*. *blakesleeana* (García-Rodríguez *et al*. 2012). Unfortunately, mortality associated with *Cunninghamella* infections is significantly higher than those caused by other species of *Mucorales* (Hiramoto *et al*. 2020, Jeong *et al*. 2021). According to Yamamoto *et al.* (2021), this high mortality is due to the minimum inhibitory concentration of amphotericin B, which is relatively higher than those for other pathogens. *Cunninghamella* infection is most common after inhalation of airborne spores, especially in pulmonary and rhinocerebral infections, but a few cutaneous (Quinino *et al*. 2004, Belliere *et al*. 2019, Portillo *et al*. 2021) and endocarditis (Zhang *et al*. 2022) cases have been reported.

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68. ***Diaporthe*** Nitschke, Pyrenomyc. Germ. 2: 240. 1870.

Type species: *Diaporthe alnea* Fuckel

Classification: *Ascomycota*, *Pezizomycotina*, *Sordariomycetes*, *Diaporthales*, *Diaporthaceae.*

Background

Diaporthe species are plant pathogens and endophytes in healthy plants, or saprobes on decaying tissues of a wide range of hosts worldwide (Udayanga *et al*. 2011). Species of *Diaporthe* are well-known as causal agents of major plant diseases, including root and fruit rots, dieback, stem cankers, leaf spots, leaf and pod blights, and seed decay (Santos *et al.* 2011, Udayanga *et al.* 2011). A list of hosts and *Diaporthe* species was provided by Hongsanan *et al.* (2023). The paraphyletic nature of *Diaporthe* was demonstrated (Gao *et al*. 2017) with *Ophiodiaporthe* (Fu *et al.* 2013), *Pustulomyces* (Dai *et al.* 2014), *Phaeocytostroma*, and *Stenocarpella* (Lamprecht *et al.* 2011) recognised within *Diaporthe s. lat*. To address this issue, Senanayake *et al.* (2017) subsequently named several additional diaporthe-like clades within *Diaporthales*. Morphological characters such as immersed ascomata and erumpent pseudostroma with elongated perithecial necks in the sexual morph (Udayanga *et al*. 2011), and black conidiomata with dimorphic conidia in the asexual morph (Rehner & Uecker 1994), were the basis for identification of *Diaporthe* species before the molecular era (Van der Aa *et al*. 1990). Recent studies demonstrated that morphology is not always reliable for species level identification due to variability under changing environmental conditions (Gomes *et al*. 2013). The current trend in *Diaporthe* taxonomy is directed toward the use of a large number of strains from different locations to better understand species delimitation (Gao *et al.* 2016b). Intraspecific variability within different complexes was demonstrated rather than resolving different taxa. For example, Hilário *et al.* (2021) synonymised eight species under the name *D. amygdali* providing evidence that it is a single species. Thus, an overestimated description of species within this genus is assumed and should be investigated in future studies.

Ecological and economic significance

Diaporthe species are widely distributed, and commonly found as saprobes (Marin-Felix *et al.* 2019b, Hyde *et al.* 2020a, Phukhamsakda *et al.* 2020, Chethana *et al.* 2021c, 2023, Norphanphoun *et al.* 2022, Hongsanan *et al.* 2023). Their role as decomposers is important in carbon cycles. Their behaviour as endophytes or pathogens gives an opportunity for *Diaporthe* species to become early colonisers of decaying host materials (Promputtha *et al*. 2007, 2010, Hyde *et al*. 2007, Luo *et al.* 2022). As with many other coelomycetes, *Diaporthe* species have a significant impact on agriculture and biochemistry by causing disease on economically important crops or as biocontrol agents and production of secondary metabolites (Udayanga *et al*. 2011).

Studies have revealed the importance of *Diaporthe* species as biocontrol agents (Charudattan 2000, Trujillo 2005). The ability of *Diaporthe* species to become obligate pathogens, to produce extensive sporulation and to be highly persistent in the environment makes them a good candidate to develop as mycoherbicides on weeds (Rosskopf *et al*. 2000). *Diaporthe amaranthophila* on *Amaranthus* sp. (Ortiz-Ribbing & Williams 2006), and *Diaporthe* sp. on *Carthamus lanatus* (Ash *et al*. 2010) are two examples for putative mycoherbicides. From already identified *Diaporthe* taxa, the majority have been reported as plant endophytes. It has been proposed that these endophytes can act as a second barrier of plants against pathogens. These fungi could also be the key to identifying novel antimicrobial compounds and medicines (Dong *et al.* 2021). *Diaporthe* species cause numerous economically important plant diseases and four of them are detailed below.

Citrus melanose

Globally 22 species of *Diaporthe* were determined to be associated with *Citrus* based on a polyphasic approach. Huang *et al*. (2013b) reported *D. citri* as the predominant species in China and described *D. citriasiana* and *D. citrichinensis* as two new taxa. Huang *et al.* (2015a) identified various *Diaporthe* species as *Citrus* endophytes, such as *D. endophytica*, *D. eres*, *D. hongkongensis*, *D. sojae*, and different taxa clustering in the *D. arecae* species complex. They also described *D. biconispora*, *D. biguttulata*, *D. discoidispora*, *D. multigutullata*, *D. ovalispora*, *D. subclavata*, and *D. unshiuensis* as new species associated with *Citrus*. Guarnaccia & Crous (2017) revealed a high diversity of *Diaporthe* species recovered from *Citrus* in European countries such as Greece, Italy, Malta, Portugal and Spain. Two newly described species *D. limonicola* and *D. melitensis* were associated with severe cankers. *Diaporthe citri* is known as a major pathogen of *Citrus*, causing stem-end rot and melanose of fruits, young leaf and shoot gummosis, and blight of perennial branches and trunks (Kucharek *et al*. 1983, Timmer & Kucharek 2001, Udayanga *et al*. 2014a). This species occurs in many *Citrus* growing regions of the world (Timmer *et al*. 2000). Several *Diaporthe* (or *Phomopsis*) species were previously considered as synonyms of *D. citri*, such as *D. citrincola* and *Pho. californica*, *Pho. caribaea* and *Pho. cytosporella*, described from the Philippines, California, Cuba and Italy, respectively (Fawcett 1922). Udayanga *et al*. (2014a) re-assessed strains of *D. citri* from China, Korea, New Zealand, and the USA based on molecular phylogenetic analysis of conserved ex-type and additional strains, collected exclusively from symptomatic *Citrus* tissues and demonstrated that *D. citri* is not present in Europe. This was initially confirmed after a broad survey conducted by Guarnaccia & Crous (2017). However, Guarnaccia & Crous (2018) isolated *D. citri* associated with symptomatic plants of *C. reticulata* in the Azores Island, Portugal, reporting the presence of the pathogen in Europe for the first time.

Diaporthe stem blight of blueberry (*Vaccinium corymbosum*)

Diaporthe includes species affecting blueberry growing areas worldwide (Lombard *et al.* 2014). Sixteen *Diaporthe* species have been reported on blueberry plants: *D. ambigua*, *D. asheicola*, *D. australafricana*, *D. baccae*, *D. crousii*, *D. eres*, *D. foeniculina*, *D. nobilis*, *D. rudis*, *D. passiflorae*, *D. oxe*, *D. phillipsii*, *D. rossmaniae*, *D. sterillis*, *D. vaccini*, and *D. vacuae* (Gomes *et al.* 2013, Hilário *et al.* 2020, Lombard *et al.* 2014, Guarnaccia *et al.* 2020). Twig blight, stem canker, and dieback are the symptoms caused by *Diaporthe* species on blueberries. Apical necrosis of the shoots, brown to red necrotic lesions on stems, discoloration of the vascular tissues, leaf spots, and fruit rot are occasionally present (Cardinaals *et al.* 2018). Although *D. vaccinii* is a quarantine pathogen in Europe, as a causal agent of blueberry diseases, its pathogenicity, virulence and host specificity are not clear (Lombard *et al.* 2014).

Diaporthe stem diseases of soybean (*Glycine max*)

Several *Diaporthe* species cause major diseases in soybean and affect its production worldwide (Santos *et al.* 2011). Five *Diaporthe*-associated diseases are known: pod and stem blight caused by *D. sojae* and *D. longicolla* (Mathew *et al.* 2015, Udayanga *et al.* 2015); northern stem canker caused by *D. caulivora* (Santos *et al.* 2011); southern stem canker caused by *D. aspalathi* and *D. phaseolorum* (Van Rensburg *et al.* 2006); stem disease caused by *D. gulyae* (Mathew *et al.* 2018); Phomopsis seed decay caused by *D. longicolla* (Udayanga *et al.* 2015). Soybean stem canker is one of the most common diseases in the main soybean growing areas.

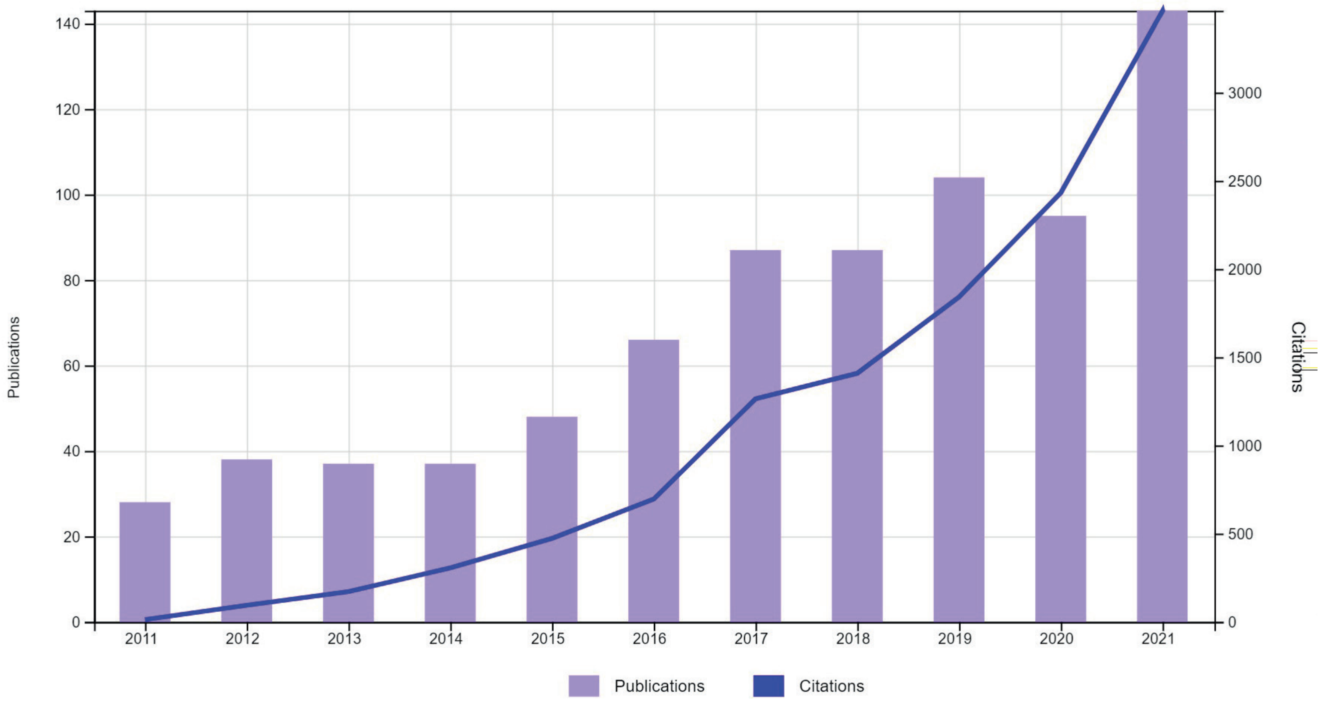

Fig. 97. Trends in research of *Diaporthe* in the period 2011–2021.

Differences in virulence were observed among all the *Diaporthe* species involved and within populations of one species isolated on susceptible soybean plants (Mena *et al.* 2020).

Phomopsis dieback of grapevine

Phomopsis dieback of grapevine (*Vitis vinifera*) caused by *D. ampelina* (*Phomopsis viticola*) triggers serious losses worldwide, due to shoots breaking off at the base, stunting, dieback, loss of vigour, reduced bunch set and fruit rot (Pearson & Goheen 1994, Van Niekerk *et al.* 2005, Úrbez-Torres *et al.* 2013a, Lawrence *et al.* 2015, Guarnaccia *et al.* 2018). In eastern North America, Phomopsis cane and leaf spot caused by *D. ampelina* is a foliar disease of grape but, in the Mediterranean climate of western North America, *D. ampelina* is primarily associated with wood cankers along with other *Diaporthe* species (Baumgartner *et al.* 2013). In much drier regions, *D. ampelina* is better known as a wood-canker pathogen (Van Niekerk *et al.* 2005, Úrbez-Torres *et al.* 2006). Besides Phomopsis cane and leaf spot, *Diaporthe* species are known to cause Phomopsis dieback on grapevines. Thirty species of *Diaporthe* are known to be associated with grapevine Phomopsis dieback worldwide. These are *D. ambigua*, *D. ampelina*, *D. amygdali*, *D. australafricana*, *D. baccae*, *D. bohemiae*, *D. celeris*, *D. chamaeropis*, *D. cynaroidis*, *D. cytosporella*, *D. eres*, *D. foeniculina*, *D. guangxiensis*, *D. gulyae*, *D. helianthi*, *D. hispaniae*, *D. hongkongensis*, *D. hubeiensis*, *D. hungariae*, *D. kyushuensis*, *D. nebulae*, *D. novem*, *D. perjuncta*, *D. pescicola*, *D. phaseolorum,* *D. rudis*, *D. serafiniae*, *D. sojae*, *D. unshiuensis* and *D. viniferae* (Mostert *et al.* 2001, Van Niekerk *et al.* 2005, Baumgartner *et al.* 2013, Úrbez-Torres *et al.* 2013b, Udayanga *et al.* 2014a, b,

Table 74. Top 10 cited articles related to *Diaporthe* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	*Diaporthe*: a genus of endophytic, saprobic and plant pathogenic fungi	352	Gomes *et al.* (2013)
2	The genus *Phomopsis*: biology, applications, species concepts and names of common phytopathogens	265	Udayanga *et al.* (2011)
3	One stop shop: backbones trees for important phytopathogenic genera: I (2014)	235	Hyde *et al.* (2014)
4	Insights into the genus *Diaporthe*: phylogenetic species delimitation in the *D. eres* species complex	175	Udayanga *et al.* (2014)
5	A multi-locus phylogenetic evaluation of *Diaporthe* (*Phomopsis*)	170	Udayanga *et al.* (2012)
6	Species limits in *Diaporthe*: molecular re-assessment of *D. citri*, *D. cytosporella*, *D. foeniculina* and *D. rudis*	135	Udayanga *et al.* (2014)
7	Identification of diverse mycoviruses through metatranscriptomics characterization of the viromes of five major fungal plant pathogens	128	Marzano *et al.* (2016)
8	Resolving the *Diaporthe* species occurring on soybean in Croatia	108	Santos *et al.* (2011)
9	Stem cankers on sunflower (*Helianthus annuus*) in Australia reveal a complex of pathogenic *Diaporthe* (*Phomopsis*) species	108	Thompson *et al.* (2011)
10	The *Diaporthe sojae* species complex: Phylogenetic re-assessment of pathogens associated with soybean, cucurbits and other field crops	106	Udayanga *et al.* (2015)

Dissanayake *et al.* 2015, Guarnaccia *et al.* 2018, Lesuthu *et al.* 2019, Manawasinghe *et al*. 2019).

Research interests

There are 770 publications and 8 987 citations from 2011–2021 in the Web of Science (Fig. 97), with the top 10 most cited articles listed in Table 74. Most publications focused on disease management (fungicide resistance, disease resistance), and research on pathogenic *Diaporthe* species (opportunistic behaviour, production of secondary metabolites, taxonomy and phylogeny).

Opportunistic behaviour

Diaporthe species are ubiquitous (Udayanga *et al*. 2011, Gomes *et al.* 2013). They vary in nutritional mode as well as ecological niches. However, the pathogenic nature of these species is currently a hotspot study area. As discussed in the previous sections, species of this genus are causal organisms of economically important hosts (Udayanga *et al*. 2011). Some species can infect different hosts within the same locality and also more than one species can cause disease on a single host (Yang *et al*. 2018b, Manawasinghe *et al*. 2019, Guarnaccia *et al.* 2022, Dardani *et al.* 2023, Martino *et al.* 2023). One of the well-established examples is "Phomopsis dieback of grapevine" as discussed above. Twelve *Diaporthe* species are associated with grapevines in China while 30 species are associated with grapevines worldwide (Mostert *et al.* 2001, Van Niekerk *et al.* 2005, Baumgartner *et al.* 2013, Úrbez-Torres *et al.* 2013c, Udayanga *et al.* 2014a, b, Dissanayake *et al.* 2015, Guarnaccia *et al.* 2018, Lesuthu *et al.* 2019, Manawasinghe *et al.* 2019). Within one host, certain *Diaporthe* species can occur as endophytes, pathogens or saprobes (Udayanga *et al*. 2011, Gomes *et al.* 2013, Huang *et al*. 2015a). As given in the data analysis, one of the most cited publications on this genus addresses these life modes (Gomes *et al.* 2013). However, it is unclear what triggers these species to change their life mode from endophytic to pathogenic, saprobic to pathogenic, or *vice versa*. When it comes to the disease associated with crops and woody plants, the changing environment and human interferences might be creating a challenging environment for these opportunistic pathogens (Manawasinghe *et al*. 2019). However, this needs further in-depth study.

Introducing new species and records of novel disease emergence reflects the high and rapid evolution potential of *Diaporthe* species. This would result in developing into species with higher virulence and possible host shifts. With these facts what is more challenging is developing control measures on *Diaporthe* species associated with above mentioned as well as other diseases not discussed in the present study. The application of fungicides on common fungal pathogens may unintentionally trigger the pathogenicity of non-target fungal species, especially *Diaporthe* and other opportunistic species (Manawasinghe *et al*. 2018). To overcome this, further studies are necessary to understand interactions among host microbiomes with *Diaporthe* species.

Production of secondary metabolites

Many novel bioactive compounds are produced by species of *Diaporthe* (Chepkirui & Stadler 2017). Promising antibiotics were identified in several endophytic fungi which provide a potential source of anti-bacterial with the benefits of low toxicity and environmental impact (Kalyanasundaram *et al.* 2015). Many metabolites recently reported from *Diaporthe* were isolated from endophytic strains of medicinal plants. Endophytic *Diaporthe* species produce specific enzymes and secondary metabolites (Huang *et al.* 2011) with wide potential applications for pharmaceutical and agronomic purposes (Kumaran & Hur 2009). Chepkirui & Stadler (2017) concluded that the genus *Diaporthe* is a good source of bioactive substances, and future studies should certainly explore novel secondary metabolites. Nonetheless, future research should be directed toward the possible role and concrete applications of all these metabolites in the ecological relationships of the host plants (Tanapichatsakul *et al.* 2018).

Taxonomy and phylogeny

Five loci (ITS, *tef1*, *tub*, *his*, and *cal*) are commonly used in recent phylogenetic studies of *Diaporthe* species (Gomes *et al.* 2013, Udayanga *et al.* 2014a, b). With a detailed evaluation of multi-locus phylogenies for species boundaries determination in the genus, Santos *et al.* (2017) revealed that species delimitation is enhanced once five loci (ITS, *tef1*, *tub*, *his* and *cal*) are simultaneously involved to build the phylogenies. Recently, the genus has become overwhelming with more than 200 species (Dissanayake *et al*. 2017), due to the introduction of numerous novel species based on molecular phylogenetic approaches and morphological characterisation. Hence, a modern revision based on analysing all available type species is required.

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69. ***Bipolaris*** Shoemaker, Canad. J. Bot. 37: 882. 1959.

Type species: *Bipolaris maydis* (Y. Nisik. & C. Miyake) Shoemaker

Classification: *Ascomycota*, *Pezizomycotina*, *Dothideomycetes*, *Pleosporales*, *Pleosporaceae.*

Background

Bipolaris includes several significant plant pathogens (Manamgoda *et al*. 2014). There are 140 species epithets listed in Index Fungorum (2022) under *Bipolaris*, but several epithets have been transferred to *Curvularia* and only 46 species are accepted (Bhunjun *et al.* 2020, Lane *et al.* 2020). Species have also been recorded as saprobes and endophytes of a wide range of hosts (Hyde *et al.* 2020a). The sexual morph was known as *Cochliobolus*, which is synonymised under *Bipolaris* (Manamgoda *et al.* 2012). Even though *Cochliobolus* was the oldest name, the generic name of *Bipolaris* was conserved as it is more commonly used by plant pathologists and in taxonomic literature (Rossman *et al.* 2013).

Bipolaris was introduced by Shoemaker (1959) and it was previously classified in *Helmisporium*, which was later renamed *Helminthosporium* (Persoon 1822). Following several revisions, *Helminthosporium* was separated into *Bipolaris*, *Curvularia*, *Drechslera* and *Exserohilum* (Sivanesan 1987). *Drechslera* was synonymised with its sexual morph *Pyrenophora* (Marin-Felix *et al.* 2019b). All these genera are characterised by distoseptate conidia which can lead to wrong identifications (Manamgoda *et al.* 2012, 2014, Hernández-Restrepo *et al.* 2018, Marin-Felix *et al.* 2019b, 2020). *Bipolaris* is distinguished from *Curvularia* based on the curvature of the conidia, being throughout the length in *Bipolaris*, while in *Curvularia* it is based on its inordinately enlarged intermediate cells (Ellis 1971, Sivanesan 1987, Manamgoda *et al.* 2012). The conidia in *Bipolaris* are usually longer than those of *Curvularia* (Marin-Felix *et al.* 2017b). Molecular analyses are therefore needed to accurately delineate between these morphologically similar genera (Berbee *et al.* 1999, Manamgoda *et al.* 2012, Marin-Felix *et al.* 2017a, 2019, Hyde *et al.* 2020a, Jayawardena *et al.* 2022). The lack of ex-type or authenticated sequences is problematic for accurate identification in *Bipolaris* (Cai *et al.* 2011, Manamgoda *et al.* 2012) and there are only 28 species that have an ex-type (Bhunjun *et al.* 2020, Lane *et al.* 2020). The *gapdh* gene is the best marker to delineate species in this genus (Berbee *et al.* 1999, Manamgoda *et al.* 2014, Bhunjun *et al.* 2020). It is recommended to apply a polyphasic approach when introducing new taxa in *Bipolaris* based on phylogenetic analyses and molecular-based approaches such as Automatic Barcode Gap Discovery and Objective Clustering methods (Bhunjun *et al.* 2020).

Bipolaris species have been used in biotechnological applications, genetic manipulation and they are also responsible for several devastating diseases. Accurate identification and an understanding of virulent genes are important to accessing accumulated knowledge for disease control (Jayawardena *et al.* 2020). Whole-genome data and genetic manipulation have resulted in the development of maize varieties resistant to several pathogenic *Bipolaris* species (Mehta & Angra 2000, Badu-Apraku *et al.* 2009).

Ecological and economic significance

Bipolaris species cause several economically important plant diseases, mainly in high value field crops in *Poaceae* which includes rice, maize, wheat and sorghum (Manamgoda *et al.* 2014). These species can also occur on non-grass hosts, but the ecology and host association of several species remain poorly understood. *Bipolaris* can be found worldwide in both temperate and tropical environments. Several species including *B. maydis*, *B. sacchari*, *B. sorokiniana*, *B. victoriae* and *B. zeicola* can occur on a wide range of hosts while some species including *B. clavata*, *B. gossypina* and *B. heveae* have been associated with only one host (Manamgoda *et al.* 2012, 2014). As pathogens and saprobes, *Bipolaris* species can occur on over 60 plant genera in *Anacardiaceae*, *Araceae*, *Euphorbiaceae*, *Fabaceae*, *Malvaceae*, *Poaceae*, *Rutaceae* and *Zingiberaceae* (Sivanesan 1987, Manamgoda *et al.* 2011). These species are linked with several disease symptoms including leaf spots, leaf blights, melting outs, root rots and foot rots. These diseases can also be seed-borne.

Environmental conditions and abiotic stresses can influence the ability of pathogens to cause devastating diseases (Fajolu *et al.* 2013). Warm and humid environments provide ideal conditions for pathogens on seasonal grass and crops (Eisa *et al.* 2013). *Bipolaris* species have been associated with devastating diseases on staple crops. *Bipolaris oryzae* was responsible for causing extensive damage to rice cultivation in India, thus causing famine during 1943–1944 (Scheffer 1997). *Bipolaris maydis* was responsible for catastrophic losses in maize crops in the USA and UK, by causing southern corn leaf blights that generated losses of approximately 1 billion US dollars (Manamgoda *et al.* 2011, Lev *et al.* 1999). *Bipolaris sorokiniana*, which is responsible for common root rot and leaf spot of wheat and barley, was one of the most economically important foliar pathogens of wheat in warm regions (Ahmadpour *et al.* 2012). Leaf spot diseases are usually associated with small brown-red water-soaked spots on leaves, which subsequently turn brown or black, elliptical or fusiform lesions (Ahmadpour *et al.* 2012). Root rot diseases are usually associated with brown to black lesions on the roots and yellowing of the plants (Arabi & Jawhar 2013).

Research interests

There are 967 publications and 8 933 citations from 2011–2021 in the Web of Science (Fig. 98), with the top 10 most cited articles listed in Table 75. Most publications focused on its taxonomy, disease management (host resistance) and its active secondary metabolites with potential use as a source of microbial drugs.

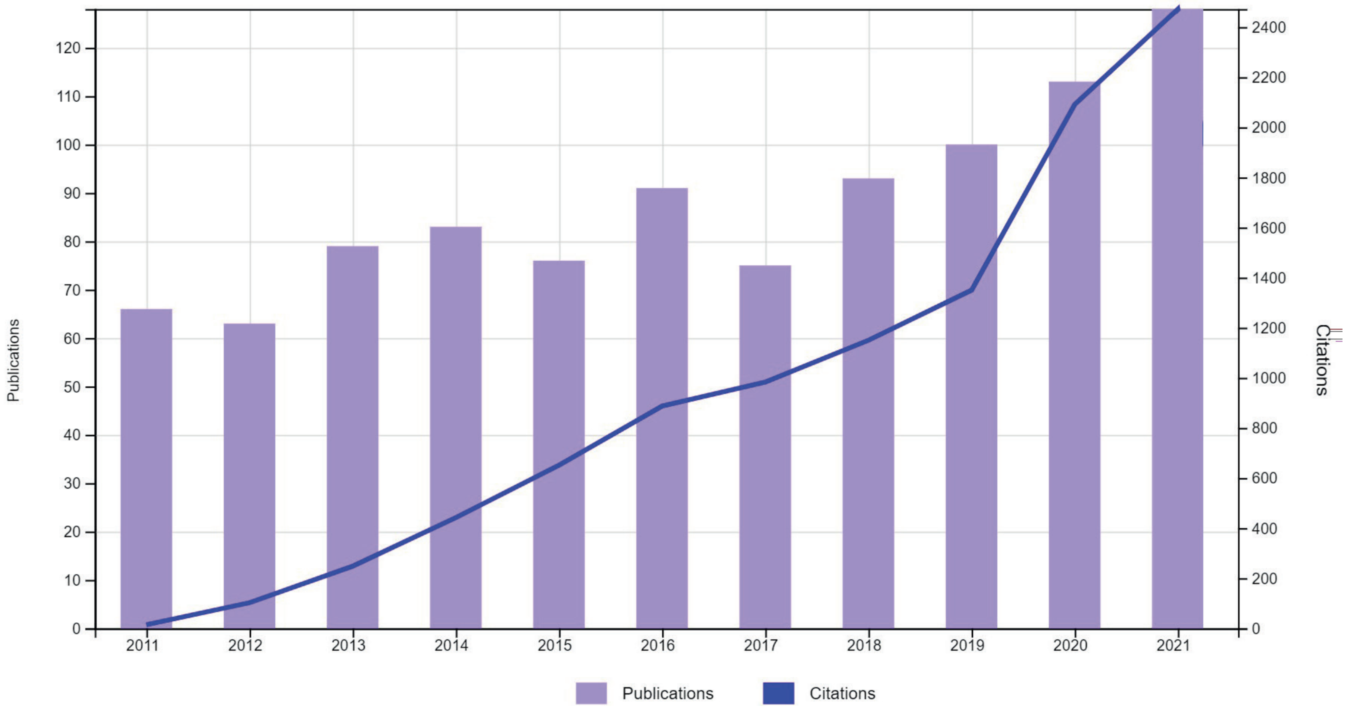

Fig. 98. Trends in research of *Bipolaris* in the period 2011–2021.

Table 75. Top 10 cited articles related to *Bipolaris* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	One stop shop: backbones trees for important phytopathogenic genera: I (2014)	235	Hyde *et al.* (2014)
2	Genera of phytopathogenic fungi: GOPHY 1	185	Marin-Felix *et al.* (2017a)
3	The genus *Bipolaris*	143	Manamgoda *et al.* (2014)
4	A phylogenetic and taxonomic re-evaluation of the *Bipolaris-Cochliobolus-Curvularia* complex	139	Manamgoda *et al.* (2012)
5	Fungal Planet description sheets: 154–213	126	Crous *et al.* (2013b)
6	Allergic bronchopulmonary mycosis due to fungi other than *Aspergillus*: a global overview	119	Chowdhary *et al.* (2014a)
7	*Cochliobolus*: an overview and current status of species	117	Manamgoda *et al.* (2011)
8	Ophiobolin A induces paraptosis-like cell death in human glioblastoma cells by decreasing BKCa channel activity	107	Bury *et al.* (2013)
9	The ectopic expression of a pectin methyl esterase inhibitor increases pectin methyl esterification and limits fungal diseases in wheat	101	Volpi *et al.* (2011)
10	An R2R3 MYB transcription factor in wheat, Ta PIMP 1, mediates host resistance to *Bipolaris sorokiniana* and drought stresses through regulation of defense-and stress-related genes	91	Zhang *et al.* (2012)

Taxonomy and phylogeny

The majority of the most cited publications focused on the taxonomic revision of *Bipolaris*. These publications provided detailed information about the morphology, disease symptoms and host association of *Bipolaris* species (Manamgoda *et al.* 2014). Some of these publications also introduced new species such as *B. drechsleri, B. saccharicola* and *B. variabilis* (Crous *et al*. 2013, Marin-Felix *et al.* 2017a). Multi-locus analyses allowed the correct placement of some species previously identified as *Bipolaris* in other helminthosporioid genera such as *Curvularia crustacea*, *C. dactyloctenii* and *C. micropus* (Tan *et al.* 2014, Hernández-Restrepo *et al.* 2018). Molecular data has resulted in the taxonomic revision of several species, including the transfer of *B. gigantea* from *Drechslera* to *Bipolaris* (Lane *et al.* 2020). A high number of helminthosporioid species remain molecularly unstudied. Therefore, it is of utmost importance to provide sequence data of these species to properly determine their taxonomic placement.

Disease management

Spot blotch disease is responsible for major yield loss to wheat crops. Previous studies have shown the importance of pectin methyl esterification in resistance against pathogens in monocot and dicot plants (Wydra & Beri 2006). Volpi *et al.* (2011) demonstrated that the expression of pectin methyl esterase inhibitors from *Actinidia chinensis* improves the resistance of durum wheat against *B. sorokiniana*. This resulted in a significant reduction of spot blotch disease symptoms caused by the pathogen. The increased resistance was due to the impaired ability of *B. sorokiniana* to grow on methyl-esterified pectin (Volpi *et al.* 2011).

Drought and root rot have a profound effect on the growth and productivity of *Triticum aestivum.* Previous studies have highlighted the importance of MYB proteins in several developmental and physiological processes including defence responses to biotic and abiotic stresses (Dubos *et al.* 2010). Zhang *et al.* (2012) demonstrated that overexpression of the MYB gene *TaPIMP1* provides resistance against *B. sorokiniana* and it can also significantly enhance the host resistance against drought.

Bioactive compounds

Secondary metabolites with different bioactivities and therefore potential use as microbial drugs, have been recently isolated from *Bipolaris* species such as the antibiotic compounds bipolatoxin D and ophiobolin A (Shen *et al.* 2020a). Antifungal compounds have also been obtained from this genus, such as bipolamides A and B (Siriwach *et al.* 2014). Campos *et al.* (2008) and do Nascimento *et al.* (2015) isolated cochlioquinone A, isocochlioquinone A and anhydrocochlioquinone A from different strains of *Bipolaris*, which showed antileishmanial activity.

Other secondary metabolites found in *Bipolaris* include cytotoxic compounds which may hold great potential for cancer treatment. Bury *et al.* (2013) investigated the activity of ophiobolin A against human glioblastoma multiforme, which is the most lethal and malignant form of brain tumour. Ophiobolin A is a phytotoxin produced by *Bipolaris* species that infect crops in *Poaceae.* Bury *et al*. (2013) demonstrated that Ophiobolin A can induce apoptosis in mouse leukaemia cells, which could potentially inhibit human cancer cell growth. Berestetskiy *et al.* (2020) also isolated cochlioqionones and fusaroproliferin compounds with cytotoxic activity from *Bipolaris sorokiniana*.

Authors: C.S. Bhunjun and Y. Marin-Felix

70. ***Lentinula*** Earle, Bull. New York Bot. Gard. 5: 416. 1909.

Type species: *Lentinula cubensis* (Berk. & M.A. Curtis) Earle ex Pegler

Classification: *Basidiomycota*, *Agaricomycotina*, *Agaricomycetes*, *Agaricales*, *Omphalotaceae.*

Background

Berkeley (1877) described shiitake mushrooms and classified them as *Armillaria.* Subsequently, it was classified into nine genera (*Tricholoma*, *Agaricus*, *Cortinellus*, *Lepiota*, *etc*.), and given more than 12 species names (Pegler 1983a, Hibbett 1992). *Lentinula* was initially established by Earle (1909) based on the synonym

Lentinus cubensis (now renamed *Lentinula boryana*) of the genus *Lentinus*. Singer (1877) classified shiitake mushrooms into *Lentinus* and named *Le. edodes* (Singer 1941). Pegler (1975a) found that *Lentinus* has two mycelial types (reproductive mycelium, and skeleton-liaison mycelium), while *Lentinula* has only one mycelial type (reproductive mycelium) based on morphological characters, and it was assigned to the Shiitake genus by Pegler and renamed *Lentinula edodes*. Hibbett identified *Lentinula* as a separate genus using a combination of morphological characters and molecular identification, based on 133 nucleotide sequences in the 5' coding region of the large subunit rRNA, for phylogenetic evolutionary relationships (Hibbett & Vilgalys 1993).

The genus *Lentinula* is a lignicolous fungus which causes white rot in broad-leaved trees, especially in *Fagaceae* and *Nothofagaceae* (Pegler 1983a, Mata & Petersen 2001). *Lentinula* is mainly distributed in the temperate to subtropical zones of the Northern Hemisphere (Pegler 1983b). *Lentinula* has been resolved as a monophyletic group within the *Omphalotaceae* (*Agaricales*), which also contains *Gymnopus*, *Rhodocollybia*, and other collybioid mushrooms (Wilson & Desjardin 2005, He *et al*. 2019b, Oliveira *et al*. 2019). A search of *Lentinula* in the MycoBank database has now reported eight species based on geographical distribution, morphological characterisation and phylogenetic analysis: *Le. edodes* (eastern Asia), *Le. boryana* (Gulf Coast of North America to South America), *Le. aciculospora* (Costa Rica), *Le. guarapiensis* (Paraguay), *Le. raphanica* (Florida, Louisiana, Puerto Rico, Costa Rica, Venezuela, and Brazil), *Le. lateritia* (southeast Asia and Australasia), *Le. novae-zelandiae* (New Zealand) and *Le.*

Fig. 99. Cultivated *Lentinula edodes* on a farm in China.

madagasikarensis (Madagascar) (Spegazzini 1883, Pegler 1983b, Looney *et al*. 2020).

Shimomura *et al.* performed a hybridisation test between the shiitake mushroom (*Le. edodes*) from East Asia, the brick red shiitake mushroom (*Le. lateritia*) from Southeast Asia and the New Zealand shiitake mushroom (*Le. novae-zelandiae*). The results indicated that there was no reproductive isolation within the three species and that they should be considered different morphospecies of the same species. This was also confirmed using molecular methods (Shimomura 1992, Fukuda *et al*. 1994, Nicholson & Royse 1997). Therefore, it has been suggested that these three morphospecies be named Shiitake or Asian-Australasian *Lentinula* population (Hibbett *et al*. 1995, Nicholson *et al*. 2009). All three morphospecies belong to *Le. edodes* as originally named by Berkeley, and for ease of differentiation, the *Le. edodes* species of the three morphospecies were designated *Le. edodes s. str.* (Xu *et al*. 2006), and the total name of the three morphospecies was renamed *Le. edodes s. lat.* (Hibbett *et al*. 1995). Researchers conducted a cluster analysis of *Le. edodes s. lat.* using ITS sequences and found that in addition to the three existing morphospecies, a hidden morphospecies also exists, mainly in the southwestern and northwestern regions of China, the “alpine kingdom”-Nepal and the high-altitude regions of India (Hibbett *et al*. 1995, 1998, Xu *et al*. 2006). Xu *et al.* (2006) found that *Le. edodes s. str.* has a tendency to diverge into two branches. One branch is mainly distributed in northern East Asia (northeast and northwest China, Russia, Japan, and Korea), and the other branch is mainly distributed in southern East Asia (central and southern China, Thailand) (Xu *et al*. 2006). In terms of the distribution of shiitake mushrooms in the world, China should be the centre of the distribution of important natural populations of shiitake mushrooms (Xu *et al*. 2006).

Ecological and economic significance

Lentinula edodes, commonly known as “Shiitake” in Japan and “Xianggu” in China, is the most studied species within *Lentinula*. *Lentinula edodes* are more and more popular because of their high nutritional and medicinal value; it is rich in protein and amino acids, vitamins, minerals, trace elements and volatile flavour substances (Chang 1980, Li *et al*. 2019c). In addition to seven essential amino acids, it also contains 18 amino acids, such as aspartic acid, glutamic acid, and alanine (Li *et al*. 2020d). It has been proven that lentinan in *Le. edodes* could inhibit tumour growth (Mallard *et al*. 2019). Additionally, it contains many pharmaceutical compounds with antiviral, anti-tumour, antioxidant, and immune-enhancing properties (Cao *et al*. 2013c, Kang *et al*. 2013, Rincão *et al*. 2013, Xu *et al*. 2013a, Dai *et al*. 2015).

Lentinula edodes is a traditional food in East Asia and it has reportedly been artificially cultivated in China during the Song dynasty (Chang & Miles 1987). Currently, it is one of the most economically important cultivated mushrooms (Fig. 99), and China has the highest *Le. edodes* production and export in the world (Chang & Miles 1989) accounting for over 90 % of the total global production (Royse *et al*. 2017). According to the statistics of the China Edible Fungi Association (http://www.cefa.org.cn), the total output of edible mushrooms in China was 40.61 million tons in 2020, of which *Le. edodes* accounted for 11.88 million tons, or 29.23 % of the total Chinese edible mushroom production, which represents a year-on-year increase of 6 % and a value of 13.42 billion US dollars. There was a 30-fold production increase in the past several decades (Royse *et al*. 2017). According to the statistics of China’s ministry of commerce, China exported 606 600 tons of *Le. edodes* in 2020, With Asia, Africa, North and South America, and Oceania being the main export regions.

Research interests

There are 821 publications and 8 733 citations from 2011–2021 in the Web of Science (Fig. 100). The top 10 most cited articles are listed in Table 76. Most publications focused on food science, chemical composition and pharmacological activity, as well as molecular research.

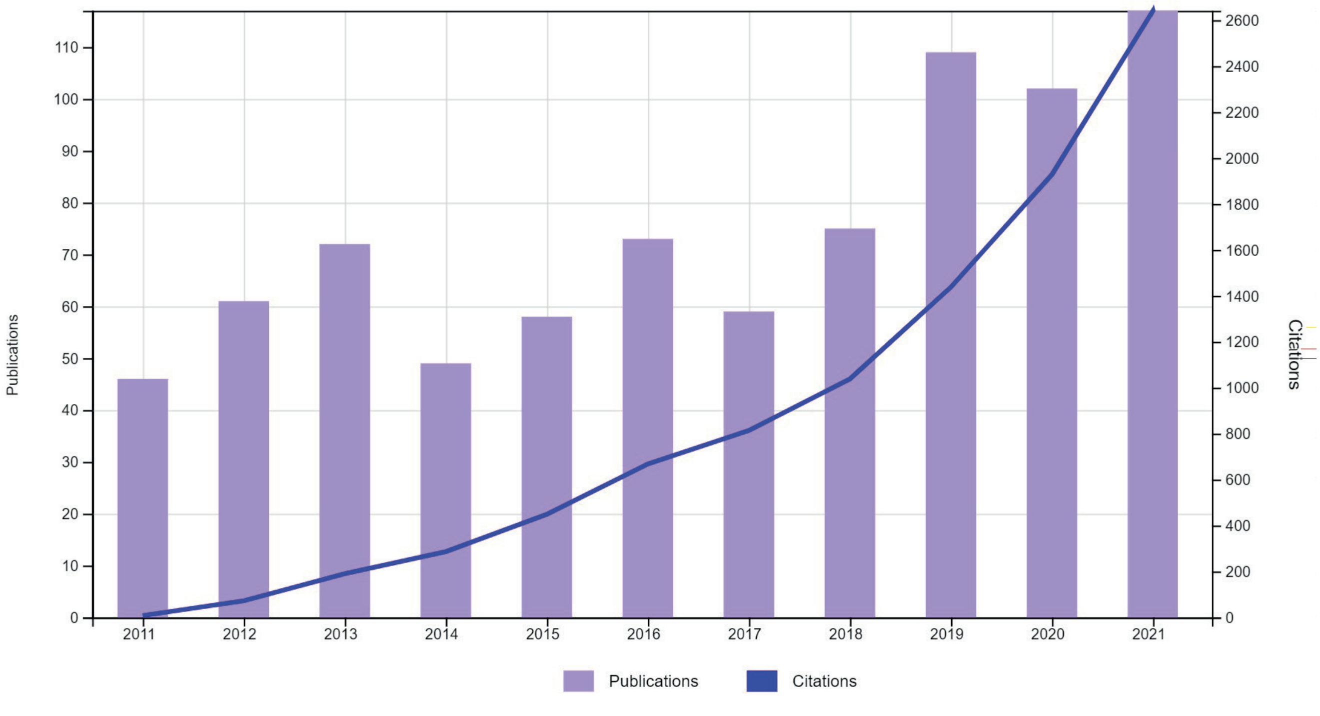

Fig. 100. Trends in research of *Lentinula* in the period 2011–2021.

Table 76. Top 10 cited articles related to *Lentinula* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Chemical composition and nutritional value of the most widely appreciated cultivated mushrooms: An inter-species comparative study	267	Reis *et al.* (2012a)
2	Macro and trace mineral constituents and radionuclides in mushrooms: health benefits and risks	238	Falandysz & Borovička (2013)
3	Laccase immobilization on chitosan/poly(vinyl alcohol) composite nanofibrous membranes for 2,4-dichlorophenol removal	144	Xu *et al.* (2013b)
4	Correlation evaluation of antioxidant properties on the monosaccharide components and glycosyl linkages of polysaccharide with different measuring methods	129	Lo *et al.* (2011)
5	Antimicrobial and antitumor activities of chitosan from shiitake stipes, compared to commercial chitosan from crab shells	127	Chien *et al.* (2016)
6	Genome sequence of the edible cultivated mushroom *Lentinula edodes* (Shiitake) reveals insights into lignocellulose degradation	126	Chen *et al.* (2016a)
7	Laccase immobilization and insolubilization: from fundamentals to applications for the elimination of emerging contaminants in wastewater treatment	103	Ba *et al.* (2013)
8	The effect of ultrasound-assisted immersion freezing on selected physicochemical properties of mushrooms	93	Islam *et al.* (2014)
9	Can fungi compete with marine sources for chitosan production?	89	Ghormade *et al.* (2017)
10	Biodiversity of *Trichoderma* (*Hypocreaceae*) in Southern Europe and Macaronesia	87	Jaklitsch & Voglmayr (2015)

Nutrition composition and pharmacological activity

Lentinula edodes is rich in nutrients such as protein, fat, carbohydrates, crude fibre, trace elements and vitamins. In recent years, many scholars have found that lentinan from *Le. edodes* has various biological activities such as anti-tumour, antioxidation and immune regulation. Sun *et al*. (2015) combined lentinan and other drugs to treat bladder cancer, significantly reducing the number of cancer cells. Suga *et al.* (2017) found that lentinan combined with Tegafur oral agent for cancer treatment in BALB/c mouse colon cancer model can reduce the number of apoptotic bodies in ileal recess and significantly reduce the toxic and side effects of Tegafur oral agent ($P < 0.05$ or $P < 0.01$). Li *et al.* (2018b) proved that lentinan can stimulate autophagy by detecting autophagosome and autophagy flow. Tian *et al*. (2012) found that lentinan can effectively remove hydroxyl free radicals and achieve the purpose of antioxidants. Lentinan can selectively treat the inflammatory symptoms of melanoma, reduce adriamycin mediated bone marrow suppression (Liu *et al*. 2016c), and trigger humoral immunity and other related immune responses in mice by activating mouse peritoneal macrophages and producing bioactive serum factors (Zákány *et al*. 1980).

Molecular research

Molecular research on *Le. edodes* has focused on genetic diversity, genomic features, gene functions, *etc*. Moon *et al.* (2021) constructed a CRISPR/Cas9-mediated genome editing system in *Le. edodes*, laying the foundation for subsequent gene function studies. The genomic features of different *Le. edodes* strains have been reported and it has been revealed that *Le. edodes* has a rapid sporocarp autolysis system, and there have been insights into lignocellulose degradation, genetic architecture, breeding history and genes related to cadmium accumulation (Chen *et al*. 2016a, Sakamoto *et al.* 2017, Yu *et al*. 2022b). Genes involved in lignocellulose degradation cadmium resistance were always studied in *Le. edodes* (Ohga & Royse 2001, Zhao *et al*. 2015c, Chen *et al*. 2016a, Yan *et al*. 2019b, Yu *et al*. 2021, 2022). It could be beneficial to reveal the degradation mechanism of lignocellulose, search for replacing agricultural straws, and elucidate heavy metal resistance in basidiomycete fungi. Genetic maps of *Le. edodes* have been constructed using many molecular markers (SSR, SRAP, TRAP, InDel, *etc*.); based on these genetic maps, many important agronomic traits were mapped by QTL (Gong *et al*. 2014, 2018, Li *et al*. 2017a).

Food science

As the second most eaten mushroom in the world (Tian *et al*. 2016), it is necessary to improve product quality and flavour, as well as extend its storage period. Shi *et al.* (2020) found that low-dose γ-irradiation could decrease water loss, retain the freshness, and extend the shelf-life of fresh *Le. edodes* mushrooms. It is useful as a potential preservative method. *Lentinula edodes* flavour is crucial to its quality; 25 volatile compounds have been considered key flavour components in *Le. edodes*, and microwave vacuum drying is an effective method to maintain larger amounts of taste-active amino acids (Tian *et al*. 2016, Li *et al*. 2019d).

Authors: R. Xu and C. Phukhamsakda

71. ***Erysiphe*** DC., in Lamarck & de Candolle, Fl. franç., Edn 3 (Paris) 2: 272. 1805, *nom. sanct.* (Fr., Syst. Mycol. 3(1): 234. 1829).

Type species: *Erysiphe polygoni* DC.

Classification: *Ascomycota*, *Pezizomycotina*, *Leotiomycetes*, *Helotiales*, *Erysiphaceae.*

Background

Erysiphe is the largest genus of the powdery mildews (*Erysiphaceae*, *Helotiales*, *sensu* Johnston *et al.* 2019), with approximately 450 species (Braun & Cook 2012), comprising many common, widespread taxa (Takamatsu *et al.* 2015a, b). Some are taxonomically unresolved species complexes that are difficult to distinguish either morphologically or based on common species DNA barcode sequences (*e.g.*, Bereczky *et al.* 2015, Braun *et al.* 2017, Bradshaw *et al*. 2021). All powdery mildews are obligate biotrophic plant pathogens, taking up nutrients exclusively from living host plant tissues through specialised organs known as haustoria (Hückelhoven & Panstruga 2011); they cannot grow and develop spores without being functionally connected to infected host plant tissues. *Erysiphe* species produce haustoria in the living epidermal cells of their host plants (Gil & Gay 1977, Heintz & Blaich 1990). Their mycelia, consisting of hyphae, conidiophores, conidia, and in sexually reproducing species also their sexual sporocarps, known as chasmothecia, are ectophytic, being produced on the aerial host plant surfaces, mostly on leaves, green stems, young fruit, and other photosynthesizing organs (Glawe 2008). The superficial mycelia of *Erysiphe* appear as easily recognisable whitish and powdery spots on aerial plant surfaces, which sometimes cover large areas or the entire surface of the infected organs, eventually causing their distortion, yellowing and premature leaf fall or even death. At the seedling stage, infections caused by *Erysiphe* spp. can kill entire plants in the field (Marçais & Desprez-Loustau 2014, Demeter *et al.* 2021) while in adult plants, including shrubs and trees, infections may cause measurable biotic stress under natural conditions (Desprez-Loustau *et al.* 2014, Bert *et al.* 2016), serious yield losses in cropping systems (Calonnec *et al.* 2004, Fondevilla & Rubiales 2012, Fuller *et al.* 2014, Dunn & Gaynor 2020, Heick *et al.* 2020a, Kelly *et al.* 2021), and reduction of aesthetic value of ornamentals (Vajna *et al.* 2004, Seko *et al.* 2008).

Some *Erysiphe* species infect a single host plant species while others infect many, only distantly related plants (Braun & Cook 2012). The same host plant species can be infected by several *Erysiphe* spp., and also by other powdery mildew species that belong to other genera (Braun & Cook 2012, Marçais & Desprez-Loustau 2014, Takamatsu *et al.* 2016, Desprez-Loustau *et al.* 2018). *Erysiphe* conidia are airborne, short-lived, and their long-distance dispersal is debated (Glawe 2008). Many species regularly produce sexual morphs with ascospores, which survive unfavourable conditions in the field, such as winter, and initiate the polycyclic life cycle of the pathogen when fresh green host plant tissues become available again in the environment (Rossi *et al*. 2010, Gadoury *et al*. 2012, Vági *et al.* 2016). Overwintering as dormant mycelia in buds (Rügner *et al.* 2002, Csikós *et al.* 2020) or on evergreen leaves (Szentiványi & Kiss 2002) also occurs in some *Erysiphe* species. Many powdery mildew taxa, especially those that attack crops and cause damage in forestry, have a global distribution and are considered invasive species (Kiss 2005, Jones & Baker 2007, Desprez-Loustau *et al.* 2018). Interestingly, a recent analysis indicated that powdery mildews were completely absent from Australia until 1788, the beginning of European colonisation of the continent (Kiss *et al.* 2020).

Erysiphe was introduced by De Candolle (1805) and was applied in a very broad sense, covering almost all powdery mildews until a comprehensive generic revision of the *Erysiphaceae* (Léveillé 1851). Léveillé (1851) confined *Erysiphe* to species characterised by having sporocarps with mycelium-like appendages and numerous asci, irrespective of the characteristics of the asexual morphs. Salmon (1900) published the first powdery mildew monograph in which he followed Léveillé's generic concept of *Erysiphe*. Salmon (1900) cited and treated *Erysiphe polygoni* as the first species under *Erysiphe*, which probably influenced Clements & Shear (1931) who designated *E. polygoni* as lectotype species. The generally wide species concept, with some modifications, prevailed in almost all subsequent taxonomic treatments of powdery mildew (*e.g.*, Homma 1937, Blumer 1933, 1967, Braun 1987), except for the exclusion of *Erysiphe graminis*, the powdery mildew of cereals and grasses, which was placed in a genus of its own, *Blumeria* (Speer 1973). The further splitting of *Erysiphe s. lat.* commenced when Braun (1978, 1981) divided *Erysiphe* into sections – *Erysiphe*, *Golovinomyces* and *Galeopsidis*. Heluta (1988) raised sect. *Golovinomyces* to genus rank. Braun (1999) introduced the new genus *Neoerysiphe* for *Erysiphe* sect. *Galeopsidis*. Braun & Takamatsu (2000) reduced *Microsphaera* and *Uncinula*, including various smaller segregated genera, to synonymy with *Erysiphe*, based on the first broad-based phylogenetic examinations of the *Erysiphaceae* (Saenz & Taylor 1999, Mori *et al*. 2000), which laid the foundation for the current taxonomy of *Erysiphe*. Further refinements of the circumscription and subdivision of *Erysiphe* were made in Braun & Cook (2012), based on results of previous and additional sequence analyses of particular groups of phylogenetically allied powdery mildew, such as the introductions of *Erysiphe* sect. *Californiomyces* (bas. *Californiomyces*) and *Erysiphe* sect. *Typhulochaeta* (bas. *Typhulochaeta*). A recent genome-scale phylogenetic analysis of the *Erysiphaceae* supported the delimitation of *Erysiphe* and other powdery mildew genera (Vaghefi *et al.* 2022). The most comprehensive phylogenetic studies on *Erysiphe* species were published by Takamatsu *et al.* (2015a, b), recently followed by Bradshaw *et al.* (2023a, b) who published the first two parts of a comprehensive phylogenetic-taxonomic treatment of *Erysiphe* species.

Ecological and economic significance

Being obligate biotrophic plant pathogens, all *Erysiphe* species cause plant diseases. Some are responsible for serious economic damage to important crops and forestry and pose plant health biosecurity risks due to their invasive nature as detailed below.

Powdery mildew of grapevine (*Vitis vinifera*) caused by *Erysiphe necator* is one of the economically most important plant diseases in the global crop protection market in terms of fungicide use (Gadoury *et al.* 2012). If no management strategies are implemented, the disease may result in up to 100 % yield loss and unmarketable juice and wine. Most wine, table and raisin grape varieties grown worldwide are highly susceptible to *E. necator*. Therefore, their production heavily relies on repeated fungicide applications during each season (Gadoury *et al.* 2012). It was estimated that grape powdery mildew control costs could be as high as 48 million US dollars per year in California alone (Fuller *et al.* 2014). Resistance to different groups of fungicides that control *E. necator* (Dufour *et al.* 2011, Frenkel *et al.* 2015) has already complicated disease management strategies worldwide (Vielba-Fernández *et al.* 2020). Most probably, *E. necator* was introduced to Europe and all other grapevine producing regions from North America (Brewer & Milgroom 2010), although a recent study of powdery mildew on domesticated and wild *Vitis* spp. in the Middle East questioned this hypothesis (Gur *et al.* 2021). Another recent study did not support the hypothesis on the temporal isolation of two widespread genotypes of *E. necator*, A and B, with implications for fungicide resistance (Csikós *et al.* 2020).

Powdery mildew of oaks (*Quercus* spp.) can be caused by up to 33 powdery mildew species and two varieties belonging to

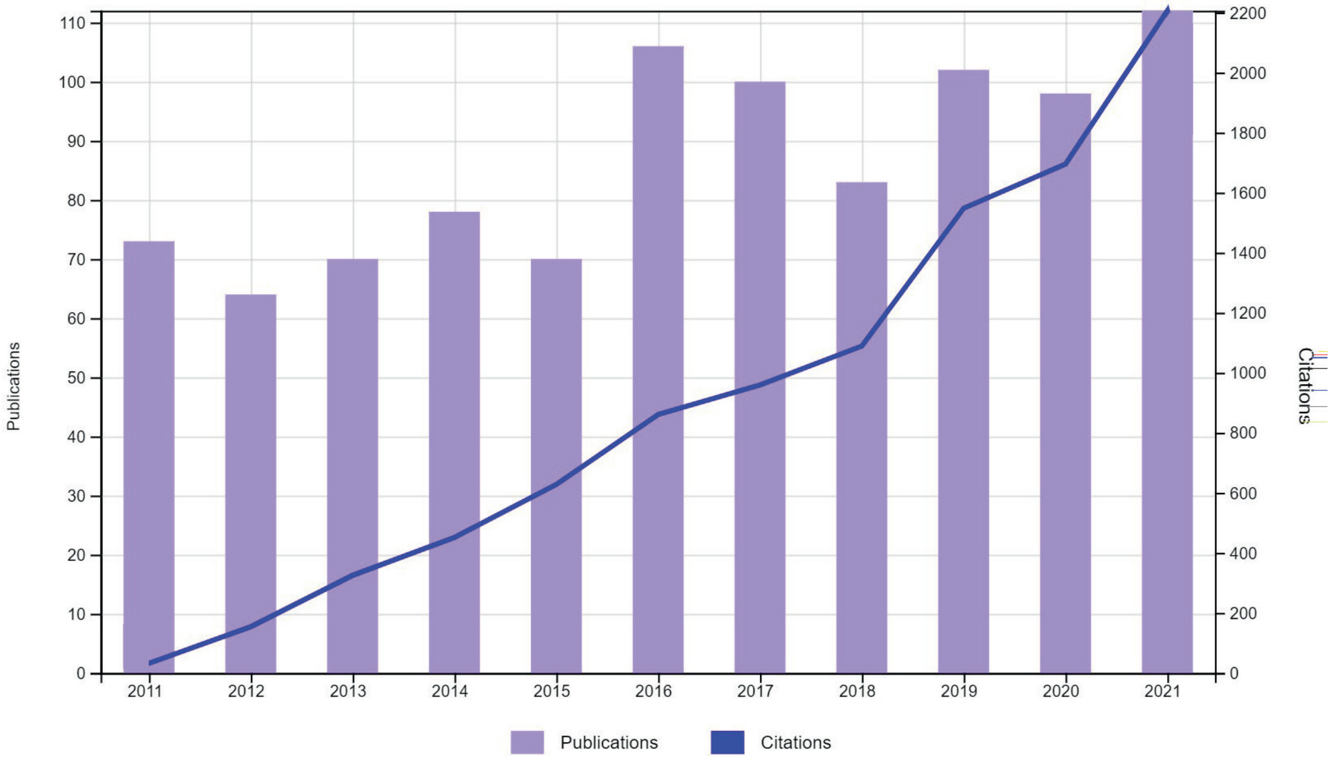

Fig. 101. Trends in research of *Erysiphe* in the period 2011–2021.

four genera in different parts of the world (Braun & Cook 2012, Meeboon *et al*. 2017, Cho *et al*. 2018, Siahaan *et al*. 2018). There is no other plant genus affected by so many powdery mildew species. Among oak powdery mildew, *E. alphitoides* and *E. quercicola* are the most intensively studied species due to their importance in forestry (Marçais & Desprez-Loustau 2014, Desprez-Loustau *et al.* 2018). The intricate, confused nomenclature, phylogeny and taxonomy of the two species has recently been clarified by Bradshaw *et al.* (2022a) and Braun *et al.* (2022). These two species may be responsible for the failure of the natural regeneration of pedunculate oak (*Q. robur*) forests in Europe as they often kill seedlings and young plants in large areas (Demeter *et al.* 2021). Older *Q. robur* and *Q. petraea* trees seem to be much less affected by the disease, but infections caused by *E. alphitoides* decrease tree radial growth over the years, and have a cumulative and delayed impact on tree development (Bert *et al.* 2016). In addition to oaks, *E. quercicola* also infects a wide range of tropical fruit trees, such as cashew, citrus, durian, mango, rambutan, tamarindo, and jujube, and many other plants, as well, including *Acacia* spp., *Bauhinia purpurea*, *Bixa orellana*, *Hevea brasiliensis*, and *Jatropha curcas*, in subtropical and tropical areas (Limkaisang *et al*. 2005, 2006, Siahaan *et al*. 2016, Desprez-Loustau *et al.* 2017, Meeboon & Takamatsu 2020, Young & Kiss 2021). The host range of diverse *E. quercicola* strains, as well as their ecology and epidemiology in the subtropics and the tropics are only poorly known.

Powdery mildew of sugar beet (*Beta vulgaris* subsp. *vulgaris*) is an economically important foliar crop disease that may result in sugar yield losses of up to 25–30 % under conducive environmental conditions and if no management strategies are implemented (Francis 2002, Heick *et al.* 2020a). *Erysiphe betae*, the causal agent of the disease, became widespread in most sugar beet growing regions around the world by the 1960s (Francis 2002, Francis *et al.* 2007). The economic damage caused is mainly due to the reduction of the photosynthetic leaf area, which is mostly prevented by repeated applications of quinone outside inhibitor (QoI) and triazole fungicides every season (Karaoglanidis & Karadimos 2006, Heick *et al.* 2020a). Resistance of *E. betae* populations to QoI fungicides was reported in the USA (Bolton & Neher 2014) and Scandinavia (Heick *et al.* 2019). In addition to *Beta* spp., *E. betae* also occurs on *Spinacia oleracea* and the invasive weed *Dysphania ambrosioides* (bas. *Chenopodium ambrosioides*) (Braun & Cook 2012). Infections of the latter host by *E. betae* have been confirmed by ITS sequences of the pathogen (Park *et al*. 2012c, Anwar *et al*. 2020).

Research interests

There are 956 publications and 8 683 citations from 2011–2021 in the Web of Science (Fig. 101). The top 10 most cited articles are listed in Table 77. Most of the publications focused on the resistance of crops and *Arabidopsis thaliana* to *Erysiphe* infections, identification and phylogeny of different species, including new records in different parts of the world, *Erysiphe* spp. causing disease of diverse crops and oaks, fungicide use, and other management options to control crop powdery mildew infections.

Disease management

Historically, grape powdery mildew was amongst the first crop diseases extensively controlled with fungicide sprays, *i.e.*, lime sulphur, in the 19th century (Gadoury *et al.* 2012). Sulphur is still widely used to suppress powdery mildew infections of grapes and many other crops throughout the world, because of its efficacy, low cost, and lack of resistance development in the target pathogen populations (Fondevilla & Rubiales 2012, Gadoury *et al.* 2012, Nasir *et al.* 2014). Modern fungicides used against *Erysiphe* spp. and other powdery mildews include benzimidazoles, ergosterol biosynthesis

Table 77. Top 10 cited articles related to *Erysiphe* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Hyperspectral imaging for small-scale analysis of symptoms caused by different sugar beet diseases	167	Mahlein *et al.* (2012)
2	Evolution and expression analysis of the grape (*Vitis vinifera* L.) WRKY gene family	162	Guo *et al.* (2014)
3	Genome and transcriptome analysis of the grapevine (*Vitis vinifera* L.) WRKY gene family	159	Wang *et al.* (2014c)
4	Identification of the dehydrin gene family from grapevine species and analysis of their responsiveness to various forms of abiotic and biotic stress	121	Yang *et al.* (2012f)
5	Grapevine powdery mildew (*Erysiphe necator*): a fascinating system for the study of the biology, ecology and epidemiology of an obligate biotroph	118	Gadoury *et al.* (2012)
6	Durable broad-spectrum powdery mildew resistance in pea er1 plants is conferred by natural loss-of-function mutations in PsMLO1	113	Humphry *et al.* (2011)
7	Design, synthesis, biological activities, and 3D-QSAR of new N,N'-diacylhydrazines containing 2-(2,4-dichlorophenoxy) propane moiety	97	Liu *et al.* (2011)
8	Modelling the impact of climate change on the interaction between grapevine and its pests and pathogens: European grapevine moth and powdery mildew	89	Caffarra *et al.* (2012)
9	Using a limited mapping strategy to identify major QTLs for resistance to grapevine powdery mildew (*Erysiphe necator*) and their use in marker-assisted breeding	86	Riaz *et al.* (2011)
10	The Chinese wild grapevine (*Vitis pseudoreticulata*) E3 ubiquitin ligase *Erysiphe necator*-induced RING finger protein 1 (EIRP1) activates plant defense responses by inducing proteolysis of the VpWRKY11 transcription factor	84	Yu *et al.* (2013)

inhibitors (sterol demethylation inhibitors, DMIs, and morpholines), succinate dehydrogenase inhibitors (SDHIs), quinone outside inhibitors (QoIs), and quinolines. Many of these fungicides have single-site modes of action and their extensive use has already led to the development of reduced sensitivity or complete resistance in some target *Erysiphe* spp. populations (Dufour *et al.* 2011, Gadoury *et al.* 2012, Frenkel *et al.* 2015, Vielba-Fernández *et al.* 2020). Integrated pest management (IPM) strategies can prevent, delay, or manage such situations, and extend the effective life of most highly specific, single-site fungicides (Vielba-Fernández *et al.* 2020). Sprays with biofungicides and other alternative products such as soluble silicon, oils, salts, and plant extracts have shown some promise in controlling *E. necator*, other *Erysiphe* spp., and other powdery mildews (Fondevilla & Rubiales 2012, Gadoury *et al.* 2012, Legler *et al.* 2016), but none have become widely used on a commercial scale. Breeding cultivars that are resistant or tolerant to *Erysiphe* spp. was successful in some crops, such as soybean (Dunn & Gaynor 2020), tomato (Seifi *et al.* 2014), pea (Humphry *et al.* 2011, Fondevilla & Rubiales 2012, Sun *et al.* 2016) and mung bean (Kelly *et al.* 2021), but not in *Vitis vinifera*, where a real breakthrough in breeding grape varieties resistant to *E. necator* has not yet happened (Barba *et al.* 2014, Fuller *et al.* 2014, Merdinoglu *et al.* 2018).

Taxonomy and phylogeny

To date, nrDNA ITS sequences have been the most widely used DNA barcodes for species delimitation in *Erysiphe* (Takamatsu *et al.* 2015a, b). Other DNA markers have also been tested for this purpose in *Erysiphe* and other powdery mildew genera (Seko *et al.* 2011, Desprez-Loustau *et al.* 2017, Ellingham *et al.* 2019, Shirouzu *et al.* 2020, Bradshaw *et al.* 2022b), but these studies have not resulted in the development of new DNA barcodes that are useful to distinguish species across the genus. The first comprehensive genome-scale phylogenetic analyses of the *Erysiphaceae* based on 751 single-copy orthologous sequences extracted from 24 selected powdery mildew genomes have largely confirmed previous phylogenies based on nrDNA sequences (Vaghefi *et al.* 2022). These analyses have also revealed serious quality issues with some of the published powdery mildew genomes, including the genomes of some *Erysiphe* spp. (Vaghefi *et al.* 2022, Kusch *et al.* 2023). Another bias of the molecular identification of *Erysiphe* spp. is the lack of DNA sequence information from the type specimens of hundreds of species described decades ago. Epitypification (ICNafp, Art. 9.9) is an established and useful tool to overcome such problems in many fungal groups, including *Erysiphe* (Bradshaw *et al*. 2020a, b). On the other hand, new methods to sequence old herbarium specimens of powdery mildew have recently been developed (Bradshaw & Tobin 2020, Smith *et al*. 2020, 2021, Bradshaw *et al.* 2022a), and have recently been successfully applied to *Erysiphe* spp. (Bradshaw et al. 2023b, c). The new techniques have already allowed successful sequencing of DNA species barcodes of powdery mildew specimens from the 19th century, and provide an additional useful tool to get sequences from old type collections and other herbarium samples, at least when the condition and quantity of the specimens enable the extraction of DNA, and if destructive methods are allowed.

Authors: L. Kiss, U. Braun and S. Takamatsu

72. ***Scedosporium*** Sacc. Ex Castell. & Chalm., Manual of Tropical Medicine (London): 1122. 1919.

Type species: *Scedosporium apiospermum* Sacc. ex Castell. & Chalm.

Classification: *Ascomycota*, *Pezizomycotina*, *Sordariomycetes*, *Microascales*, *Microascaceae.*

Background

Historically, *Scedosporium* species have been reported to produce opportunistic infections in humans. The first report of *Scedosporium apiospermum* was a case of foot subcutaneous infection in a man in Italy (Radaeli 1911). Different sorts of localised infections have been described in humans, such as the production of eumycetoma, muscle-bone-joint infections, and keratitis by traumatic inoculation of fungal-contaminated fomites such as spines or wood chips. In addition, disseminated infections occur in immunocompromised patients (Ramirez-Garcia *et al.* 2018). Especially during the last two decades, *Scedosporium* spp. and phylogenetically related taxa in the order *Microascales* have become important pathogens for cystic fibrosis patients. *Scedosporium* spp. can grow on/in diverse substrata and are the inhabitants of different substrates, mainly soils and dung (Rougeron *et al*. 2018, Mouhajir *et al*. 2020). *Scedosporium* was proposed by Pier Andrea Saccardo (Saccardo 1911) to relocate *Monosporium apiospermum* (which was isolated and described by Francesco Radaeli in 1911, but P.A. Saccardo erected the new taxon), based on morphological differences to *Monosporium acremonioides* (syn. *Harzia acremonioides*) (Costantin 1888). The genus *Scedosporium* was later validated by Aldo Castellani and Albert John Chambers in 1919, who accepted *Sc. apiospermum* over *M. apiospermum*. Pablo Negroni and Ida Fischer (Negroni & Fischer 1943) isolated a fungus which simultaneously produced the asexual and sexual morphs. Despite its morphological similarity to *Allescheria boydii*, they erected the new genus and species *Pseudallescheria shearii*. Subsequently, the holomorph received a different scientific name than the most common asexual morph (*Scedosporium*). In 2014, thanks to the premise “One Fungus = One Name” adopted by “The Amsterdam Declaration” of The International Code of Botanical Nomenclature (Hawksworth *et al*. 2011), *Pseudallescheria* was proposed as a synonym of *Scedosporium* (Lackner *et al*. 2014). *Scedosporium* is a pleomorphic genus, whose species may or may not reproduce sexually (homothallic and heterothallic species, respectively), but also present one or more asexual reproductive morphs (scedosporium-like, graphium-like, polycytella-like and sessile conidia) (Abrantes *et al.* 2021). Morphological discrimination between the species, especially within the *Scedosporium apiospermum* species complex, is difficult (Ramirez-Garcia *et al.* 2018). However, species of *Scedosporium* are easily distinguishable by comparing the nucleotide sequences of a fragment of the *tub* gene (Chen *et al.* 2016b, Ramirez-Garcia *et al.* 2018). Fifteen species are recognised, namely *Scedosporium angustum*, *Sc. apiospermum*, *Sc. aurantiacum*, *Sc. boydii*, *Sc. cereisporum*, *Sc. desertorum*, *Sc. dehoogii*, *Sc. ellipsoideum*, *Sc. fusoideum*, *Sc. haikouense*, *Sc. hainanense*, *Sc. minutisporum*, *Sc. multisporum*, *Sc. rarisporum* and *Sc. sanyaense* (Saccardo 1911, Gilgado *et al*. 2005, 2007, Borman *et al*. 2006, Lackner *et al*. 2014, Crous *et al*. 2016, Han *et al*. 2017, Abrantes *et al*. 2021, Zhang *et al*. 2021f). However, according to the latest phylogenetic tree using ITS region (ITS plus the 5.8S nrRNA gene) and *bt2* (other fragments of the *tub* gene) nucleotide sequences (Zhang *et al.* 2021f), *Sc. haikouense* and *Sc. rarisporum* should be transferred to *Sc. cereisporum*. It is important to note that *Sc. inflatum*, a very important multi-drug resistant fungal opportunistic pathogen, has been transferred to a different genus as *Lomentospora prolificans*, due to results of the phylogenetic reconstruction of the genus *Scedosporium* and by the aforementioned nomenclatural changes (Lackner *et al*. 2014).

Ecological and economic significance

Since the description of *Scedosporium apiospermum*, the type species of the genus, from a case of human eumycetoma (Radaeli 1911), most of the environmental reports (mainly from human clinical specimens) of *Scedosporium* spp. are from organic matter-rich subtracts, such as soil and dung (Rougeron *et al*. 2018). Studies on the ecology and distribution of *Scedosporium* spp. have been carried out in Australia (Harun *et al.* 2010), Austria and the Netherlands (Kaltseis *et al.* 2009), Chile (Alvarez *et al.* 2016), France (Rougeron *et al.* 2015), Mexico (Elizondo-Zertuche *et al*. 2017), Morocco (Abdallaoui *et al.* 2007, Hallouti *et al.* 2017, Mouhajir *et al.* 2020), Nigeria (Nweze & Okafor 2010) and Thailand (Luplertlop *et al*. 2016). *Scedosporium apiospermum* was the most abundant species in Austria, Mexico, The Netherlands and

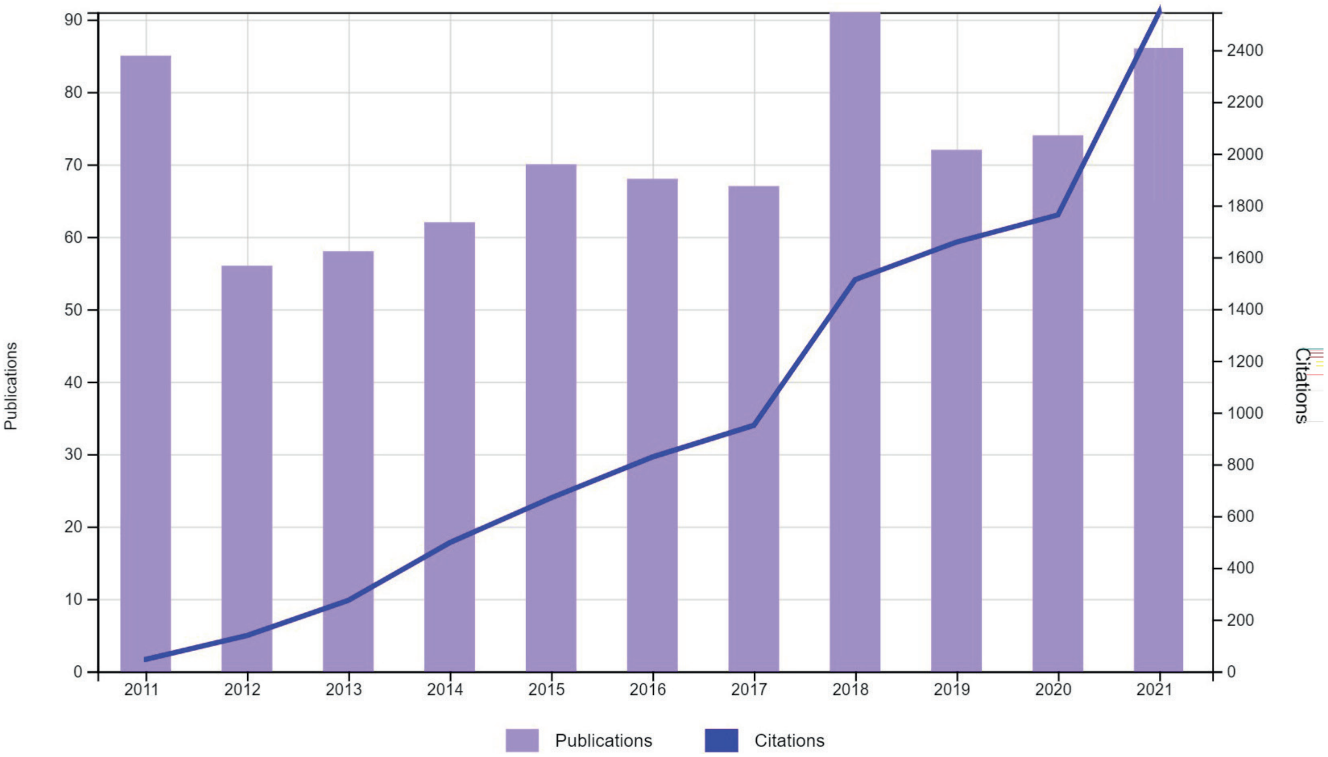

Fig. 102. Trends in research of *Scedosporium* in the period 2011–2021.

Table 78. Top 10 cited articles related to *Scedosporium* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Histopathologic diagnosis of fungal infections in the 21st century	375	Guarner & Brandt (2011)
2	ESCMID and ECMM joint guidelines on diagnosis and management of hyalohyphomycosis: *Fusarium* spp., *Scedosporium* spp. and others	271	Tortorano *et al.* (2014)
3	Mycotic keratitis: epidemiology, diagnosis and management	245	Thomas & Kaliamurthy (2013)
4	Invasive non-*Aspergillus* mold infections in transplant recipients, United States, 2001-2006	188	Park *et al.* (2011)
5	Antifungal resistance: current trends and future strategies to combat	180	Wiederhold (2017)
6	Species-specific antifungal susceptibility patterns of *Scedosporium* and *Pseudallescheria* species	176	Lackner *et al.* (2012)
7	International Society of Human and Animal Mycology (ISHAM)-ITS reference DNA barcoding database-the quality controlled standard tool for routine identification of human and animal pathogenic fungi	175	Irinyi *et al.* (2015)
8	Triazole antifungal agents in invasive fungal infections a comparative review	174	Lass-Flörl (2011)
9	European Society of Clinical Microbiology and Infectious Diseases Fungal Infection Study Group; European Confederation of Medical Mycology. ESCMID and ECMM joint clinical guidelines for the diagnosis and management of systemic phaeohyphomycosis: diseases caused by black fungi	173	Chowdhary *et al.* (2014c)
10	The changing epidemiology of invasive fungal infections	168	Enoch *et al.* (2017)

Thailand, but *Sc. aurantiacum* was most common in Australia and *Sc. dehoogii* in Western France. *Scedosporium* spp. are also present in water and soils highly contaminated with xenobiotics due to human economic activities, probably due to the metabolic ability of the fungus to use them as sources of carbon and energy (Davies *et al.* 1973, Claussen & Schmidt 1988, Janda-Ulfig *et al.* 2008, Skinner *et al.* 2009, Tigini *et al.* 2014).

Species of *Scedosporium* are thermotolerant, can survive at very low levels of oxygen in the atmosphere, and tolerate high salt concentrations and high osmotic pressures (Guarro *et al*. 2006, Cortez *et al.* 2008, Kaltseis *et al.* 2009). One study proved that the abundance of *Scedosporium* spp. in soils rises when the pH range is between 6 and 7.5 and the nitrogen concentration increases (Kaltseis *et al.* 2009).

Different culture media have been developed for the selective isolation of *Scedosporium* spp. from environmental samples: DRBC plus benomyl (Gilgado *et al.* 2005), and Sce-Sel+ or Scedo-Select III (Rainier *et al.* 2008, Pham *et al.* 2015).

Research interests

There are 789 publications and 8 662 citations from 2011–2021 in the Web of Science (Fig. 102) with the top 10 most cited articles listed in Table 78. Most publications are focused on diagnosis, susceptibility and resistance to antifungals, among other topics.

Diagnosis

Species identification in *Scedosporium* and other *Microascales* is mainly based on the sequencing of a fragment of the beta-tubulin gene (*tub* or *bt2*) or by using the comparison among MALDI-TOF generated ribosomal protein mass spectra (Sitterle *et al*. 2014). This implies the necessity of obtaining a pure culture from clinical specimens. Identification of *Lomentospora/Scedosporium* at the species level is very important in terms of clinical presentations or outcomes (Bronnimann *et al*. 2021). Other molecular markers and methodologies are under study. For patients with cystic fibrosis, an ELISA test based on the detection of IgG against whole cell proteins displayed very high sensitivity and specificity to discriminate *Lomentospora/Scedosporium* infections from those produced by *Aspergillus* spp. (Martin-Souto *et al.* 2020). However, certain of the antigens of these whole cell crude extracts are common between *Aspergillus* and *Scedosporium* spp., and this is the reason why immunological tests usually display cross-reactions. Consequently, other antigens able to discriminate between infections caused by *Aspergillus* and *Scedosporium* spp. have been studied. Among them, the *Scedosporium* catalase A1 and cytosolic Cu, Zn-superoxyde dismutase were the most promising to develop a highly sensitive and specific ELISA assay (Mina *et al.* 2017).

Therapy

An important problem with *Lomentospora prolificans*/*Scedosporium* spp. infections are low susceptibility to the available antifungals. So, many researchers are exploring substances that act on new molecular targets. One of these promising molecules is F901318, a potent inhibitor of the dihydroorotate dehydrogenase having potent *in vitro* activity on *L. prolificans* and *Scedosporium* spp. (Wiederhold *et al.* 2017). This antimycotic drug called olorofim displays promising *in vitro* activity against *L. prolificans*/*Scedosporium* spp. (Rivero-Méndez *et al.* 2020), and also in murine models (Seyedmousavi *et al*. 2021).

Author: A.M. Stchigel

73. ***Zymoseptoria*** Quaedvl. & Crous, Persoonia 26: 64. 2011.

Type species: *Zymoseptoria tritici* (Roberge ex Desm.) Quaedvl. & Crous

Classification: *Ascomycota*, *Pezizomycotina*, *Dothideomycetes*, *Mycosphaerellales*, *Mycosphaerellaceae.*

Background

The genus *Zymoseptoria* was established by Quaedvlieg *et al.* (2011) to accommodate *Zy. brevis* and three previously described *Septoria* species, namely *Zy. halophila (syn. S. halophila), Zy. passerinii* *(syn. S. passerinii), Zy. tritici (syn. S. tritici).* Subsequently, several more species were added to the genus, including *Zy. ardabiliae, Zy. pseudotritici* (Stukenbrock *et al.* 2012), *Zy. verkleyi* and *Zy. crescenta* (Crous *et al.* 2012, 2018). Species of *Zymoseptoria* can be morphologically distinguished from *Septoria* by the yeast-like growth in culture, and the mode of conidiogenesis, *e.g.*, phialidic, with periclinal thickening and inconspicuous percurrent proliferation(s), as well as the formation of up to three different conidial types (Type I, pycnidial conidia; Type II, phragmospores on aerial hyphae; Type III, yeast-like growth proliferating via microcyclic conidiation; Quaedvlieg *et al.* 2011, Videira *et al.* 2017). *Zymoseptoria* formed a single clade apart from *Septoria* based on the 28S nrDNA phylogeny (Quaedvlieg *et al.* 2011), and for accurate identification of species, multi-locus sequences of ITS, *act, tub*, *cal*, *rpb2*, and *tef1* are often used (Quaedvlieg *et al.* 2011, Crous *et al.* 2012, 2018, Stukenbrock *et al.* 2012, Videira *et al.* 2017).

Zymoseptoria species have been recorded causing leaf spots or leaf blotch worldwide on graminicolous hosts including *Aegilops triuncialis*, *Dactylis* sp., *Elymus* sp., *Hordeum* spp., *Lolium* sp., *Phalaris* spp., *Poa annua* and *Triticum eastivum* (Quaedvlieg *et al.* 2011, Crous *et al.* 2012, 2018, Stukenbrock *et al.* 2012, Videira *et al.* 2017).

Ecological and economic significance

Zymoseptoria species are important causal agents of diseases in wheat and barley, which lead to severe yield losses, and two are detailed below.

Septoria tritici blotch of wheat (*Triticum aestivum)* caused by *Zymoseptoria tritici* is a serious and persistent threat in the fields of temperate climates throughout the world, and the most devastating foliar disease in Europe (Fones & Gurr 2015). *Zymoseptoria tritici* (formerly *Mycosphaerella graminicola*) was voted one of the top 10 fungal pathogens (Dean *et al.* 2012). The fungus *Zy. tritici* undergoes a prolonged and asymptomatic phase as a biotroph during the initial infection on wheat and then switches to a necrotroph after the host has triggered a strong necrotic response (Sánchez-Vallet *et al.* 2015, Hartmann *et al.* 2018). The sexual ascospores are airborne for long-distance dispersal as a primary source of inoculum (Shaw & Royle 1989, Stukenbrock *et al.* 2007), while the asexual conidia are dispersed via rain splash as a secondary source of inoculum (Banke & McDonald 2005, Fones & Gurr 2015, Tiley *et al.* 2018). The disease causes 5–10 % year-on-year losses in France, Germany and the UK with direct costs ranging between 120 and 700 million euros, and up to 50 % yield losses during severe epidemics, with fungicide control costs exceeding 1 billion euros (70 % of all fungicides) per year in Europe alone (Eyal *et al.* 1973, 1987, Fones & Gurr 2015, Torriani *et al.* 2015). High relative humidity, frequency of wet days and moderate temperatures have important effects on the development of the disease (Berraies *et al.* 2014). Weather fluctuations and farming practices may also affect the severity of the disease (Fones & Gurr 2015). Management of this disease relies mainly on the use of fungicides, but there is reduced sensitivity to certain classes of fungicides (Tiley *et al.* 2018). Although the planting of resistant varieties is one of the most effective practices to alleviate yield losses, there are no wheat varieties fully resistant to *Zy. tritici (*Berraies *et al.* 2014, Fones & Gurr 2015, Tiley *et al.* 2018). Currently, there is no completely durable method for controlling Septoria tritici blotch of wheat (Tiley *et al.* 2022).

Septoria speckled leaf blotch of barley (*Hordeum vulgare* and closely related species) caused by *Zymoseptoria passerinii* is one of the most common foliar diseases in Northern Europe, North America, Northern Africa, Western Asia and Australia (Shearer *et al.* 1997, Mathre 1997, Cunfer & Ueng 1999, Lee & Neate 2007, Ware *et al.* 2007). This disease can cause yield losses of up to 38 % in Minnesota and North Dakota of the United States, and 20 % in Canada. In addition, the disease significantly reduces kernel weight and measured bushel weight of barley (Green & Bendelow 1961, Toubia-Rahme & Steffenson 1999, Ware *et al.* 2007). The application of fungicides is most effective in reducing

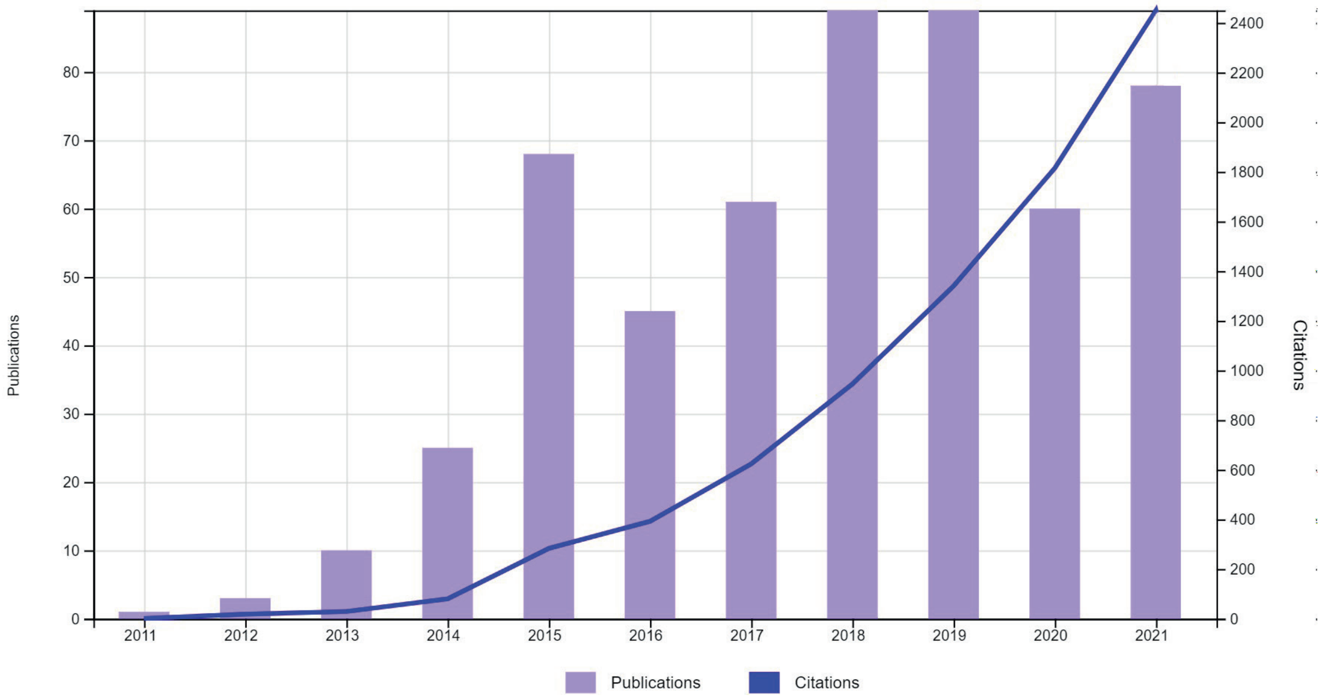

Fig. 103. Trends in research of *Zymoseptoria* in the period 2011–2021.

Table 79. Top 10 cited articles related to *Zymoseptoria* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	The top 10 fungal pathogens in molecular plant pathology	1 769	Dean *et al*. (2012)
2	Finished genome of the fungal wheat pathogen *Mycosphaerella graminicola* reveals dispensome structure, chromosome plasticity, and stealth pathogenesis	360	Goodwin *et al.* (2011)
3	The two-speed genomes of filamentous pathogens: waltz with plants	240	Dong *et al.* (2015)
4	The impact of *Septoria tritici* Blotch disease on wheat: An EU perspective	202	Fones & Gurr (2015)
5	The evolution of fungicide resistance	200	Lucas *et al.* (2015)
6	Analysis of two *in planta* expressed LysM effector homologs from the fungus *Mycosphaerella graminicola* reveals novel functional properties and varying contributions to virulence on wheat	196	Marshall *et al.* (2011)
7	Transcriptome and metabolite profiling of the infection cycle of *Zymoseptoria tritici* on wheat reveals a biphasic interaction with plant immunity involving differential pathogen chromosomal contributions and a variation on the hemibiotrophic lifestyle definition	159	Rudd *et al.* (2015)
8	A review of wheat diseases-a field perspective	153	Figueroa *et al.* (2018)
9	The evolutionary origins of pesticide resistance	153	Hawkins *et al.* (2019)
10	Update on mechanisms of azole resistance in *Mycosphaerella graminicola* and implications for future control	147	Cools & Fraaije (2013)

disease severity, but resistant cultivars are more economical and environment-friendly to control the disease (Yu *et al.* 2010).

Research interests

There are 529 publications and 8 661 citations from 2011–2021 in the Web of Science (Fig. 103) with the top 10 most cited articles listed in Table 79. Most publications focused on the pathogenic species, *Zymoseptoria tritici* (colonisation pattern, host-pathogen interaction, population biology, genome evolution) and management strategies for disease control (fungicide resistance, disease resistance).

Disease management

Research on the control of leaf diseases caused by *Zymoseptoria* on *Poaceae* has been widely conducted. It is suggested that a related dynamically diverse combination of methods should be employed, which integrates cultural, chemical, biological and resistance breeding strategies (Torriani *et al.* 2015, McDonald & Mundt 2016, Arraiano & Brown 2017, Figueroa *et al.* 2018, Tiley *et al.* 2018). Disease control has relied heavily on fungicides, which belong to two classes, 14α-demethylase inhibitors (azole; DMI) and succinate dehydrogenase inhibitors (carboxamide; SDHI) (Jørgensen *et al.* 2018, Heick *et al.* 2020b). However, due to the rapid adaptation of *Zymoseptoria* populations, resistance to fungicides has evolved (Figueroa *et al.* 2018, Heick *et al.* 2020a). The evolution of fungicide resistance is mainly determined at the regional scale, and spatiotemporal patterns of resistance evolutions have been reported primarily in Europe (Wieczorek *et al.* 2015, Heick *et al.* 2017, Garnault *et al.* 2020, Mäe *et al.* 2020). The use of a mixture consisting of different active, cross-resistant chemicals is recommended to avoid resistance to fungicides (Heick *et al.* 2020b). Major specific resistance genes which act on gene-for-gene relationships, and numerous minor-effect resistance quantitative trait loci have been mapped genetically (Yu *et al.* 2010, Brown *et al.* 2015, Saintenac *et al.* 2018, Tiley *et al.* 2018). Great efforts to study the mechanisms of genetic resistance would support the development of a new breeding strategy, which places prior emphasis on accumulating independent sources of quantitative resistance (McDonald & Mundt 2016).

Authors: Q. Chen and L. Cai

74. ***Phellinus*** Quél., Enchir. Fung. (Paris): 172. 1886.

Type species: *Phellinus igniarius* (L.: Fr.) Quél.

Classification: *Basidiomycota*, *Agaricomycotina*, *Agaricomycetes*, *Hymenochaetales*, *Hymenochaetaceae.*

Background

The genus *Phellinus* was established by L. Quelét in 1886, with *Phe. igniarius* as the type species. Several hundred species are acknowledged within *Phellinus s. lat.* and associated genera included in it (Larsen & Cobb-Poulle 1990, Index Fungorum 2022). The generic concept of *Phellinus s. lat.* was traditionally based on characters of the hyphal system (dimitic) and consistency of the sporocarps (perennial), but is nowadays widely accepted as being artificial (Fiasson & Niemelä 1984, Dai 1995, 1999, Hansen & Knudsen 1997, Wagner & Fischer 2001, 2002). Numerous characters derived from morphology, anatomy, sexuality, nuclear behaviour and ecology suggest *Phellinus s. lat.* to be heterogeneous (Murrill 1905, 1907, Fiasson & Niemelä 1984, Fischer 1996, Hansen & Knudsen 1997). In addition, extensive molecular data, based on ITS and LSU sequences and discussed in relation to the characters above, were generated subsequently. As a result, *Phellinus s. lat.* has been split into several smaller, more natural genera (Wagner & Fischer 2001, 2002, Larsson *et al*. 2006, Dai 2010, Wu *et al*. 2022). These include *Phellinus s. str.*, *Fomitiporia*, *Fomitiporella*, *Porodaedalea*, *Ochroporus*, *Fulvifomes*, *Fuscoporia*, *Phylloporia*, *Phellopilus*, *Phellinopsis*, *Tropicoporus*, or *Phellinidium*. Additional DNA regions such as *tef1* and *rpb2* genes may be necessary for further refinement within species groups of *Phellinus s. lat.*, and well-studied examples are *Phellinus s. str.* (*Phe. igniarius* and relatives; Tomšovský *et al*. 2010b), *Fomitiporia* (*Phe. robustus* and relatives; Decock *et al.* 2007, Amalfi *et al.* 2012) or *Porodaedalea* (*Phe. pini* and relatives; Brazee & Lindner 2013).

In the present overview, *Phellinus* is treated in the broad sense, with cross references to the smaller units when necessary. *Phellinus s. lat.* has a worldwide distribution (Gilbertson & Ryvarden 1987, Ryvarden & Gilbertson 1994) and species live as parasites and/or saprobes on a wide variety of angiosperms and/or gymnosperms. For instance, more than 100 species of host plants are recorded for *Phe. igniarius* in the fungal databases (Farr & Rossman 2022), however, entries in part are based on questionable classification of collections as given in the underlying literature. Species of *Phellinus s. lat.* cause a white rot, essentially degrading the wood components, *i.e.*, cellulose, hemicellulose and lignin (Gilbertson & Ryvarden 1987). Some of the taxa play a prominent role in forest ecosystems, orchards as well as street and park trees (Erkillä & Niemelä 1986, Hansen 1979, 1986, Adaskaveg & Ogawa 1990, Hansen & Goheen 2000, Schmidt *et al*. 2011).

Sporocarps are poroid throughout, resupinate, effused-reflexed or pileate. To some degree, the shape of sporocarps is variable, however, in relation to the position on the host, it may range between different shapes within single species or between closely related species.

In general, information is still sparse on the exact geographic distribution and life strategies of single members of *Phellinus s. lat.* Notwithstanding the necessity of molecular-based measures, this is due to the following reasons: (i) occurrence of the particular species is limited to the vegetative stage, *i.e.*, the mycelium living inside the host plant; (ii) sporocarps may be inconspicuous, for instance by forming crust-like layers only; and (iii) sporocarps are in poor condition (without spores) in relation to specific climate conditions, in this way hampering a proper identification.

Usually, the natural dispersal of species of *Phellinus s. lat.* is by airborne basidiospores, produced in considerable quantities by actively growing sporocarps (Jahn 1963, Niemelä 1972, 1975). Spores are the predominant source of infection. They are spread by wind, water, and, to a minor degree, human impact such as logging. For some species, a biotic vector transmission by insects has been discussed (Nuss 1986; see also Moyo *et al.* 2014). The main reasons for infection are the removal or loss of branches from adult trees (Seehann 1979). Frost cracks or pruning wounds also provide easy entry into exposed trees, especially in forests, parks and on roadsides (Erkillä & Niemelä 1986, Adaskaveg & Ogawa 1990). The possibility of infection with *Phellinus* spp. increases with the lifespan of the host plant (Erkillä & Niemelä 1986). For instance, park trees are kept much longer than is usual in forest rotation, in this way increasing the probability of decay. As an exception to the above pattern, *Phellinus weirii* has been demonstrated to spread mostly by ectotrophic mycelia, growing from tree to tree (Wallis & Reynolds 1965, Hansen & Doheen 2000). All species belonging to *Phellinus s. lat.* cause a white rot in the wood of affected hosts. The life strategy may be either parasites and/or saprophytes.

Species of *Phellinus s. lat.* examined to date exhibit a homothallic or a heterothallic, unifactorial pattern of sexuality (Fischer 1987, 1996, Mallett & Myrholm 1995, Wagner & Fischer 2001). The heterokaryotic formation is reached by the fusion of hyphae in the contact zone between compatible single-spore isolates. The resulting heterokaryotic mycelium is typically, but not always, restricted to the contact zone. Hyphal fusions between incompatible isolates result in the formation of a line of demarcation and, apparently, the death of the fusion cells (Fischer 1987).

Ecological and economic significance

Species of *Phellinus s. lat.* cause diseases both in crop plants as well as in forests, orchards and parks.

Esca of grapevine (*Vitis vinifera and Vitis spp.*) *and associated diseases*: In recent decades, Grapevine Trunk Diseases (GTDs) have become apparent in all vine growing countries worldwide. As a result, a serious reduction in the longevity and productivity of vineyards is to be observed. The worldwide estimated annual loss is estimated to be more than 1.5 billion US dollars (Fontaine *et al*. 2016, Gramaje *et al*. 2018). Esca and associated diseases are caused by an array of different fungi belonging to different taxonomic groups such as (mitosporic) ascomycetes and basidiomycetes (Mugnai *et al*. 1999, Bertsch *et al*. 2013). The pathogens are responsible for a wide range of symptoms affecting leaves, berries and the wood of host plants. Once established in the host the disease(s) are able to persist for many years. Several members of *Phellinus s. lat.* have been confirmed as being associated with wood deterioration of *Vitis* spp. worldwide. Involved species within the most prominent genus, *i.e.*, *Fomitiporia* (*Phe. robustus* group), include *Fomitiporia mediterranea* (described from Europe, Northern Africa and parts of Asia; Fischer 2002, 2006), *F. polymorpha* and *F. ignea* (North America; Fischer & Binder 2004, Brown *et al.* 2019), *F. australiensis* (Australia; Fischer *et al*. 2005), and *F. capensis* (South Africa; Cloete *et al*. 2014). Other species are *Fomitiporella* sp. (Fischer 2006), *Phellinus resupinatus* (Cloete *et al*. 2016), or *Tropicoporus texanus* (Brown *et al.* 2019). Additional taxa belonging to the *Hymenochaetales* and, possibly, *Phellinus s. lat.*, have been demonstrated by Cloete *et al.* (2015) and Fischer & González Garcia (2015). Pathogenic significance is not fully resolved for most of the above taxa and it remains an open question to what degree they are acting as sole agents and/or in combination with other fungal pathogens, such as *Phaeomoniella chlamydospora* and *Phaeoacremonium* spp. Further studies both in the field and under defined greenhouse conditions are therefore necessary for more definite statements.

Diseases in forests and parks: *Phellinus weirii* and relatives cause laminated root rot in conifers especially in Northwestern North America (Larsen *et al*. 1994, Hansen & Goheen 2000). Members of the *Phe. pini* group (*Porodaedalea*) are pathogens that cause heartwood rot on a wide range of conifers worldwide, mostly affecting butts and trunks (Jahn 1963, Niemelä & Kotiranta 1982, Gilbertson & Ryvarden 1987, Ryvarden & Gilbertson 1994, Dai 1999, Tomšovský *et al*. 2010a, b, Brazee & Lindner 2013, Wu *et al*. 2019b). Members of the *Phe. igniarius* group (*Phellinus s. str.*; Tomšovský *et al*. 2010b) such as *Phe. igniarius*, *Phe. alni* or *Phe. tremulae* occur as wound parasites/saprobes or as parasites in forests, orchards and park trees, where they cause extensive heart rot along the trunk and branches (Niemelä & Kotiranta 1982, Erkillä & Niemelä 1986, Adaskaveg & Ogawa 1990, Ryvarden & Gilbertson 1994). Control of wood decay caused by *Phellinus* spp. involves proactive measures such as cultural practices that prevent stress and promote adequate tree vigour for rapid wound healing. When possible, pruning measures should be carried out when inoculum (basidiospores) is low or absent. Once the tree has succumbed to heart rot, no cure is possible (Erkillä & Niemelä 1986, Schmidt *et al.* 2012).

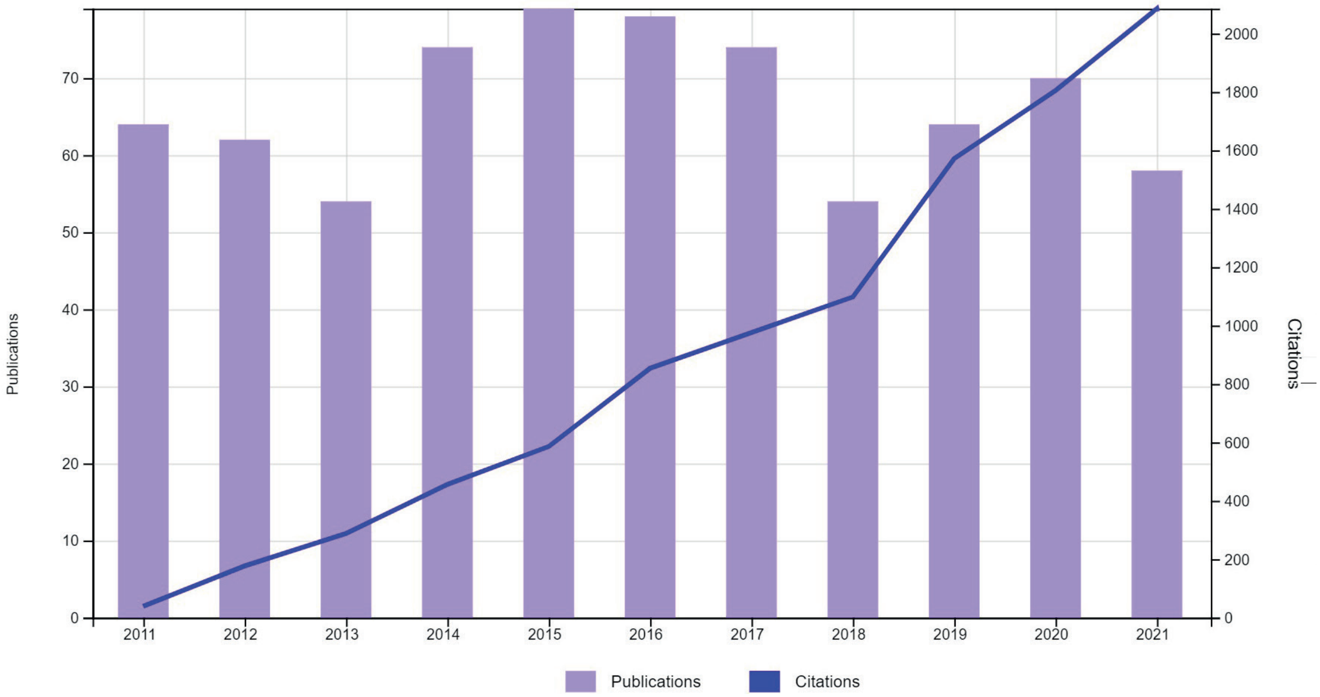

Fig. 104. Trends in research of *Phellinus* in the period 2011–2021.

Research interests

There are 731 publications and 8 392 citations between 2011 and 2021 in the Web of Science core collection (Fig. 104), with the top 10 most cited articles presented in Table 80. Most articles are focused on "Human uses", such as pharmacological applications, and plant diseases such as grapevine trunk diseases ("Esca") and related disease management. Based on different modes of species recognition and concept, numerous studies have been performed aiming at a more accurate classification of the related taxa.

Human uses

Phellinus linteus (with obligate synonyms *Inonotus linteus* and *Fulvifomes linteus*) is a widely used medicinal mushroom in China (there known as "sanghuang"), Japan ("meshimakobu") and Korea ("sangwhang") for more than 2 000 years (Zhu *et al*. 2008, Dai *et al*. 2009, Lee & Yun 2011, Chen *et al*. 2019c, He *et al*. 2021). Numerous studies have been conducted on this taxon and its relatives, with particular emphasis on medicinal properties and species identity. Several bioactive components such as polysaccharides, triterpenoids, polyphenols and furans have been isolated both from sporocarps and mycelium (Kozarski *et al*. 2011, Chen *et al*. 2019c), and are thought to be useful against several diseases including cancer or diabetes. Sporocarps occur on a variety of deciduous trees and have been demonstrated in East Asia, tropical America and Africa (Chen *et al*. 2019c). The correct classification of *Phe. linteus* and related species has been a constant source of discussion and its precise circumscription

Table 80. Top 10 cited articles related to *Phellinus* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Grapevine trunk diseases: complex and still poorly understood	292	Bertsch *et al.* (2013)
2	Managing grapevine trunk diseases with respect to etiology and epidemiology: current strategies and future prospects	187	Gramaje *et al.* (2018)
3	Conservation ecology of boreal polypores: A review	141	Junninen & Komonen (2011)
4	Phytotoxins produced by fungi associated with grapevine trunk diseases	140	Andolfi *et al.* (2011)
5	Medicinal mushrooms in prevention and control of diabetes mellitus	133	De Silva *et al.* (2012)
6	Styrylpyrone-class compounds from medicinal fungi *Phellinus* and *Inonotus* spp., and their medicinal importance	125	Lee *et al.* (2011)
7	Global diversity and taxonomy of the *Inonotus linteus* complex (*Hymenochaetales*, *Basidiomycota*): *Sanghuangporus gen. nov.*, *Tropicoporus excentrodendri* and *T-guanacastensis gen. et spp. nov.*, and 17 new combinations	78	Zhou *et al.* (2015a)
8	Species clarification for the medicinally valuable 'sanghuang' mushroom	63	Wu *et al.* (2012b)
9	Purification, characterization and antitumor activity of polysaccharides extracted from *Phellinus igniarius* mycelia	62	Li *et al.* (2015a)
10	Maxent modeling for predicting the potential distribution of Sanghuang, an important group of medicinal fungi in China	61	Yuan *et al.* (2015)

and exact relationships between collections derived from different geographic areas remain unresolved (Tian *et al*. 2013b, Zhou *et al*. 2015b, Han *et al*. 2016a).

Specimens putatively belonging to the *Phe. igniarius* group have been used by Native Americans for smoking and as a substitute for chewing tobacco (Blanchette 2001). In Alaska, and probably elsewhere in North America, the fungi were collected from paper birch (*Betula papyrifera*) trees; its use was widespread among Indian and Eskimo groups in Alaska (Agar & Agar 1980). The sporocarps were burned and the ashes were added to tobacco and other plant mixtures, such as cottonwood bark, for chewing. There is evidence that the fungus ash/cottonwood bark mixture was used until the 1940s (Blanchette 2001).

Disease management of grapevine trunk diseases

Control measures are variable among wine-growing regions. However, two main categories of control, both based on pruning wound protection in young and mature vines, may be distinguished (overviews in Bertsch *et al*. 2013, Fontaine *et al*. 2016, Gramaje *et al*. 2018). (i) Chemical treatment, for instance with a combination of Boscalid / Pyraclostrobin as part of a polymer suspension; and (ii) organic treatment using applications of *Trichoderma* spp. (Fourie *et al*. 2001, Halleen & Fourie 2016, Gramaje *et al*. 2018, Mondello *et al*. 2018a). For both types of treatment, the application is recommended as being timely with the winter pruning measures in the field. However, winter pruning wounds are susceptible for several weeks under field conditions (Eskalen *et al*. 2007, Elena & Luque 2016). Cultural practices such as minimum pruning or specific pruning techniques are thought to possibly reduce losses to the disease and also to inhibit its spread (Dumot *et al.* 2012, Kraus *et al*. 2019). No species of *Phellinus s. lat.* are involved with regard to plant material, where proactive measures such as hot-water treatment of plant material (usually 50 °C for 30 min) have been tested (Crous *et al*. 2001b, Fourie *et al*. 2001, Rooney & Gubler 2001, Edwards *et al*. 2004, Gramaje & Di Marco 2015). Results however remain inconclusive and may be dependent on the specific cultivar and overall nursery conditions (Whiting *et al.* 2001, Armengol *et al*. 2007). In consequence, control ideas all are directed to delay the (re)colonisation of grapevine tissues by the causative fungal pathogens, including members of *Phellinus s. lat*.

Systematics and taxonomy, including species concepts/recognition

Phellinus s. lat. represents a suitable field to study different modes of species recognition (for basic principles on speciation, species recognition and species concepts, see Petersen & Hughes 1999, Taylor *et al*. 2000, Kozak *et al.* 2011), which have been demonstrated in more detail in *Phellinus s. str.* (Niemelä 1975, Parmasto 1985, Mallett & Myrholm 1995, Fischer & Binder 2004, Sell 2008, Tomšovský *et al*. 2010b), the *Phe. robustus* group (*Fomitiporia*; Fischer & Binder 2004, Decock *et al*. 2007, Amalfi *et al*. 2010, 2012), and in the *Phe. pini* group (*Porodaedalea*; Fischer 1994, Tomšovský *et al.* 2010a, Brazee & Lindner 2013, Wu *et al*. 2019a). Relationships of putatively conspecific collections originating from different locations and/or different hosts should preferably be resolved by using an integrative approach of different operational concepts (Taylor *et al.* 2000), including morphology and microscopy (morphological species recognition), mating pattern and pairing tests of single spore mycelia (biological species recognition) as well as molecular data, preferably derived from different gene regions (phylogenetic species recognition). Separate or incomplete application of recognition modes may lead to differing results concerning the status and the number of species, geographic distribution and host range, evident for instance in the treatment of the taxa next related to *Phellinus igniarius* (Niemelä 1975, Tomšovský *et al.* 2010b), or *Fomitiporia punctata* (Fischer 2002, Decock *et al*. 2007, Dai 2010, Moretti *et al*. 2021, Wu *et al*. 2022).

Authors: M. Fischer and F.H. Behrens

75. ***Sporothrix*** Hektoen & C.F. Perkins, J. Exp. Med. 5: 80. 1900.

Type species: *Sporothrix schenckii* Hektoen & C.F. Perkins

Classification: *Ascomycota*, *Pezizomycotina*, *Sordariomycetes*, *Ophiostomatales*, *Ophiostomataceae.*

Background

Sporothrix is the most important medically relevant genus in the order *Ophiostomatales*, with more than 110 species epithets listed in Index Fungorum (2022), and about 53 recognised species (Rodrigues *et al.* 2020). *Sporothrix schenckii*, a conidial relative of *Ophiostoma*, produces primary single-celled conidia in a sympodial manner. The hyaline conidia are usually ovoid to ellipsoid (2–3 × 3–6 µm) and are displayed in a flower-like arrangement (“daisy-like bouquet”) at the tip of conidiophores. In a few species, a second type of conidia (sessile conidia) emerges from undifferentiated hyphae; they are melanised, of different shapes, such as pyriform and ovoid to spherical (2–4 × 2–6 µm). As is true of some of the onygenalean animal parasites, several *Sporothrix* species are known to develop a yeast-like state at elevated temperatures (35–37 °C), which are cigar-shaped, round, or oval-bearing budding cells (3–5 × 5–10 µm). Remarkably, within a genus exhibiting an essentially environmental core, a few thermodimorphic species have emerged in recent years with the potential to infect warm-blooded hosts. They are especially abundant in tropical and subtropical regions (Chakrabarti *et al.* 2015).

The classical species, *Spo. schenckii*, typifies *Sporothrix* (Hektoen & Perkins 1900). Benjamin R. Schenck published the first clinical case of sporotrichosis in 1898, based on the isolation of the agent from a patient’s finger injuries at John Hopkins Hospital in the United States (Schenck 1898). Schenck meticulously described the morphological characteristics, growth conditions, and outcomes of this microorganism infection. Based on these phenotypic features, Dr Erwin F. Smith (Department of Agriculture in Washington, USA) placed the fungus in *Sporotrichum* (*Basidiomycota*, *Polyporales*).

Hektoen & Perkins introduced the genus *Sporothrix* (*Ascomycota*, *Ophiostomatales*) in 1900, two years after Schenck’s isolation of the fungus. Two human cases were reported in Chicago during this period (Hektoen & Perkins 1900). Afterwards, the fungus was erroneously transferred to the genus *Sporotrichum* and named *Sporotrichum schenckii* for nearly 60 years (Beurmann & Ramond 1903). However, *Sporothrix schenckii* does not in the least resemble *Sporotrichum* (Carmichael 1962). Over the following years, *Sporothrix schenckii* and related species became the most important human and animal pathogens of the order *Ophiostomatales* (Guarro *et al.* 1999).

Lutz & Splendore (1907) identified a disease in rats (*Mus decumanus*) naturally infected in São Paulo’s sewage system. Natural infection (rat to rat) is caused by bites that introduce the causative agent into the host tissues. *Sporothrix* was isolated several times from the oral mucosa, and morphologically similar forms were discovered in the stomach mucosa, confirming this transmission route (Lutz & Splendore 1907). The first case of zoonotic sporotrichosis (cat-human) was identified in 1952 in New York (Singer & Muncie 1952).

A century after discovering *Sporothrix* (Schenck 1898), we know that this genus is recognised for its remarkable genetic and ecological diversity, as reflected in the many different associations between species and their hosts or niches (Rodrigues *et al.* 2018). Historically, *Sporothrix* taxonomy has been inconsistent due to extensive genetic, ecological, and biological diversities. A landmark in the *Sporothrix* classification system is the pioneering work of Marimon *et al.* that demonstrated the species boundaries in *Sporothrix*, leading to the description of *Spo. brasiliensis*, *Spo. globosa*, and *Spo. luriei* in addition to *Spo. schenckii s. str.* (Marimon *et al.* 2006, 2007, 2008). Recent progress eliminates dilemmas of paraphyly inherent in previous classifications by splitting *Sporothrix* and *Ophiostoma* and providing diagnoses of these genera (De Beer *et al.* 2016b). These developments were only possible with the introduction of a taxonomy approach incorporating phenotypic and genotypic features (De Beer *et al.* 2003, Marimon *et al.* 2006).

Ecological and economic significance

Sporothrix schenckii and *Spo. globosa* are cosmopolitan pathogens transmitted after a traumatic inoculation through infected plant debris in the field. This classical route (sapronosis) has been known as “rose gardener’s disease” for over a century, affecting various occupational groups such as farm workers and gardeners. On the other hand, *Spo. brasiliensis*, a highly virulent offshoot, is related to animal infections, and zoonotic transmission occurs through deep scratches and bites from infected cats (alternative route).

A host jump from plant to animal transmission is an emerging feature among the *Ophiostomatales*, suggesting that cat-transmitted sporotrichosis is an occupation-independent disease. Therefore, animal transmission and plant origin are the two primary sources of clinical sporotrichosis in mammals and often escalate to outbreaks or epidemics.

Human sporotrichosis

The ophiostomatalean *Sporothrix schenckii* and related species are well-known human pathogens. As a classical mycosis of implantation, *Sporothrix* propagules are traumatically introduced into the skin. Sporotrichosis is most frequently a chronic infection characterised by nodular lesions of the cutaneous or subcutaneous tissues and adjacent lymphatics that suppurate, ulcerate, and drain (Orofino-Costa *et al.* 2017). *Sporothrix* frequently affects the skin and mucous membranes, but it may also disseminate and affect the joints, bones, central nervous system, and lungs in unusual clinical manifestations (Queiroz-Telles *et al.* 2017). Over three years, a mass infection of nearly 3 000 miners occurred in many South African gold mines (Pijper & Pullinger 1927). Infested mine timbers were found to be the source of infection, which had an environment held at a constant optimal temperature of about 25 ºC and relative humidity of nearly 100 % in the mines. Recent studies revealed that the fungus could proliferate in certain types of wood, but much remains unknown about its ecology. A few other *Ophiostomatales* associated with wood may cause sporadic infection in humans, and they are embedded in the *Sporothrix pallida* complex (*e.g.*, *Spo. chilensis*, *Spo. mexicana*, and *Spo. pallida s. str.*) (Rodrigues *et al.* 2016). Despite limited global data, in 2017, Bongomin *et al.* estimated the annual incidence of sporotrichosis at > 40 000 cases globally (Bongomin *et al.* 2017), with highly endemic areas in Brazil, China, and South Africa (Lopez-Romero *et al.* 2011).

Feline sporotrichosis

Felines develop a wide variety of clinical sporotrichosis, from single lesions to disseminated systemic forms that are lethal. The most common manifestations seen in cats are multiple skin lesions with mucosal involvement, especially mucous membranes of the respiratory tract (Gremião *et al.* 2015). Skin lesions with nodules and ulcers, occur most frequently in the cephalic region, especially on the nose, and lymphangitis and lymphadenitis, may be found in three or more noncontiguous anatomical sites (Gremião *et al.* 2017).

Sporothrix is easily transmitted from symptomatic cat to cat, and cat to human, through deep scratching and biting, which inoculates a high burden of *Sporothrix* yeasts (Macêdo-Sales *et al.* 2018). Phylogenetic evidence supports a recent habitat shift in *Sporothrix* from plant to cat in southeastern Brazil, leading to the emergence of *Spo. brasiliensis*, which relies on its feline host to spread (Rodrigues *et al.* 2013b). Cats are the primary vectors of *Spo. brasiliensis* transmission to humans in Brazil, but the role of other mammals (*e.g.*, rats) should also be evaluated.

The metropolitan area of Rio de Janeiro (Brazil) was the epicentre of a long-lasting epidemic of cat-transmitted sporotrichosis, with more than 5 000 human cases during 1998–2015 and 5 113 feline cases during 1998–2018 diagnosed with an overwhelming frequency of *Spo. brasiliensis* (Gremião *et al.* 2020). Similar epidemics are emerging in the Rio Grande do Sul, São Paulo, and Espírito Santo (Brazil), where *Spo. brasiliensis* infections are prevalent. Epizooties caused by *Spo. brasiliensis* seems to be driven by urban areas with high feline population densities (Montenegro *et al.* 2014, Sanchotene *et al.* 2015, Rocha *et al.* 2020).

Ecology of *Sporothrix* species

Commensalism, mutualism, and parasitism are examples of relationships in *Sporothrix*, and they can be found worldwide (Rodrigues *et al.* 2017). Beetles are undoubtedly an essential mode of dispersal for environmental *Sporothrix* and *Ophiostoma* species (Zipfel *et al.* 2006, Romon *et al.* 2014). However, we cannot extrapolate this route to medically relevant *Sporothrix* (Rodrigues *et al.* 2017). Therefore, little is known about the ecology of medically relevant *Sporothrix*, making it difficult to predict the emergence and promote public health policies in the future to mitigate the spreading of sporotrichosis.

Pathogenic *Sporothrix* have been found in soil with a broad temperature range (6.6–28.8 °C) and a wide relative humidity range (37.5–99 %), but they are also associated with a variety of trees, flowers, rotting wood, and cane leaves, potentially aiding their development and spread in nature (Ramírez-Soto *et al.* 2018). Several studies linked the fungi isolated in nature and the agents isolated from human lesions. However, it is not unusual to find evidence of a lack of pathogenicity in environmental strains, as well as reduced fungal growth at elevated temperatures (35–40 °C) or even poor thermal dimorphism (Howard & Orr 1963, Ghosh *et al.* 2002, Mehta *et al.* 2007, Criseo & Romeo 2010, Madrid *et al.* 2010, Romeo *et al.* 2011). Overall, these examples show that these historical environmental isolates are likely part of the environmental clade (mostly members of the *Spo. pallida* and *Spo. stenoceras* complexes). Therefore, it is essential to use molecular diagnostic tools to correctly speciate *Sporothrix* present in the environment

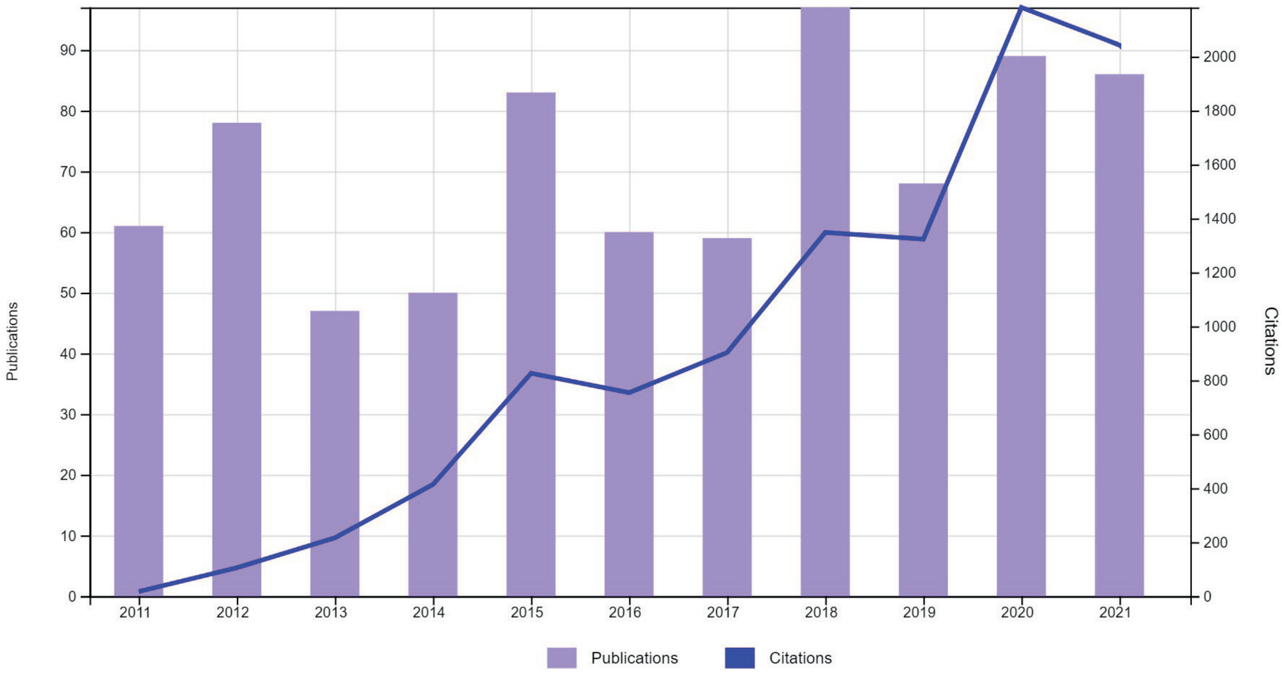

Fig. 105. Trends in research of *Sporothrix* in the period 2011–2021.

(Criseo & Romeo 2010, Rodrigues *et al.* 2015a). Robust ecological surveys are needed to uncover the elements related to *Sporothrix* density, diversity, seasonal fluctuation, and distribution in nature (Rodrigues *et al.* 2014a).

Research interests

There are 778 publications and 8 267 citations from 2011–2021 in the Web of Science (Fig. 105), with the top 10 most cited articles listed in Table 81. Most of the publications focused on *Sporothrix* taxonomy (species boundaries and phylogenetic analysis), case reports (patient and diagnosis), antifungal activity, and research on host-pathogen interaction (cell biology and murine model of infection).

Taxonomy and phylogeny

The developments achieved following the new taxonomic classification in *Sporothrix* are fascinating. Differences among pathogenic *Sporothrix* spp. include morphological (Zhao *et al.* 2015), physiological (Fernandes *et al.* 2009), genetic (Sasaki *et al.* 2014), epidemiological (Rodrigues *et al.* 2013b), serological (Rodrigues *et al.* 2015b), and virulence traits (Fernandes *et al.* 2013), as well as varying susceptibility to antifungals (Rodrigues *et al.* 2014b, Brilhante *et al.* 2016), among other biological aspects. As it is a diverse genus, studies involving the biology of the fungus and genetic diversity should include, whenever possible, representatives of the clinical and environmental clades. This will undoubtedly bring uplifting answers to understand the drivers of the emergence of *Sporothrix*.

Marimon *et al.* (2006) revealed that *Cal* is a strong candidate for species delimitation in *Sporothrix* along with *tub* and *tef1*. The ITS regions in the rDNA (ITS1+5.8S+ITS2) work as a primary barcoding marker, capable of recognising species embedded in the clinical clade (Zhou *et al.* 2014). The use of a consilient taxonomy approach to identify *Sporothrix* species is mandatory (Rodrigues *et al.* 2013a).

Table 81. Top 10 cited articles related to *Sporothrix* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	*Sporothrix schenckii* and sporotrichosis	289	Barros *et al.* (2011)
2	Global epidemiology of sporotrichosis	221	Chakrabarti *et al.* (2015)
3	Phylogenetic analysis reveals a high prevalence of *Sporothrix brasiliensis* in feline sporotrichosis outbreaks.	154	Rodrigues *et al.* (2013b)
4	Zoonotic epidemic of sporotrichosis: Cat to human transmission	122	Gremião *et al.* (2017)
5	*Sporothrix schenckii* complex and sporotrichosis, an emerging health problem	115	Lopez-Romero *et al.* (2011)
6	The divorce of *Sporothrix* and *Ophiostoma*: solution to a problematic relationship	113	De Beer *et al.* (2016a)
7	Neglected endemic mycoses	113	Queiroz-Telles *et al.* (2017)
8	Phylogeography and evolutionary patterns in *Sporothrix* spanning more than 14 000 human and animal case reports	112	Zhang *et al.* (2015)
9	Characterization of virulence profile, protein secretion and immunogenicity of different *Sporothrix schenckii sensu stricto* isolates compared with *S. globosa* and *S. brasiliensis* species	100	Fernandes *et al.* (2013)
10	Emergence of pathogenicity in the *Sporothrix schenckii* complex	95	Rodrigues *et al.* (2013a)

Epidemiology

Epidemiological data are scarce and vary from country to country based on case reports. Therefore, it is difficult to establish the actual magnitude of the disease globally. Until mid-2018, *Spo. brasiliensis* was restricted to the south and southeast of Brazil (Rodrigues *et al.* 2014c), but recently zoonotic sporotrichosis spread towards northeast Brazil (Rodrigues *et al.* 2020). Moreover, zoonotic sporotrichosis due to *Spo. brasiliensis* is spreading to neighbouring countries in Latin America, especially those bordering the southern region of Brazil (*e.g.*, Argentina and Paraguay) (Córdoba *et al.* 2018). The rise of *Spo. brasiliensis* is of international concern due to the harmful potential of *Sporothrix* for humans and animals.

Ongoing outbreaks and epidemics should be tracked using robust genetic markers. The primary markers used in epidemiological and genetic diversity studies include protein coding genes and the ITS region (Zhou *et al.* 2014, Zhang *et al.* 2015). Most epidemiological studies were carried out using a single marker, which may mask cryptic diversity in less diverse species. Markers capable of large-scale screening polymorphisms across the genome are desirable in settings where hundreds of isolates are recovered during outbreaks. Therefore, AFLP markers and microsatellites stand out to reveal hidden diversity in *Sporothrix* (De Carvalho *et al.* 2020). Likewise, the sequencing of complete genomes will allow us to understand the evolution of pathogenicity in *Sporothrix* (Cuomo *et al.* 2014).

Antifungal agents

The spread of the fungus is not followed at the same pace as new drugs are discovered and applied to treat sporotrichosis. The recommended therapeutic agents are itraconazole, amphotericin B and its lipid formulations (invasive/disseminated disease), terbinafine, and fluconazole; a saturated solution of potassium iodide has been an alternative for lymphocutaneous/cutaneous infections (Barros *et al.* 2011, Espinel-Ingroff *et al.* 2017). Intrinsic antifungal resistance in *Sporothrix* has also been found, and studies correlating antifungal susceptibility and genetic diversity among etiological agents are essential to uncover isolates that are potentially refractory to therapy and to overcome the limitations of currently existing antifungal classes (Rodrigues *et al.* 2014b, Borba-Santos *et al.* 2015).

Author: A.M. Rodrigues

76. ***Macrophomina*** Petr., Ann. Mycol. 21(3/4): 314. 1923.

Type species: *Macrophomina phaseolina* (Tassi) Goid.

Classification: *Ascomycota*, *Pezizomycotina*, *Dothideomycetes*, *Botryosphaeriales*, *Botryosphaeriaceae.*

Background

Macrophomina is a cosmopolitan genus but mainly occurs in tropical and subtropical areas around the world (Liu *et al.* 2012b, Phillips *et al.* 2013, Slippers *et al.* 2013). The genus *Macrophomina* has been associated with damping-off, seedling blight, stem and charcoal rot of more than 800 plant species, such as soybean, common bean, corn, sorghum, cowpea, peanut and cotton (Su *et al*. 2001, Ndiaye *et al*. 2010, Sarr *et al*. 2014, Machado *et al*. 2019, Farr & Rossman 2022, Poudel *et al*. 2021).

Macrophomina is an asexual pycnidial fungus, without a known sexual morph. Charcoal rot occurs in hot and dry conditions. The pathogen attacks during moisture stress. Its life cycle consists of four phases, germination, penetration, parasitic, and saprophytic phases (Dhingra & Sinclair 1978). It can infect the roots of the host plant at the seedling stage via multiple germinating hyphae. During the short parasitic phase of its disease cycle, *Macrophomina* penetrates and colonises living root tissues. Necrosis of the host tissues also causes fragility of the root tissues and inadequate nutrient and water uptake by the host, leading to arrested plant growth and yield reduction (Anis *et al*. 2013, Lodha & Mawar 2020). Severe infections cause defoliation, wilting and premature seedling death due to occlusion of xylem vessels by penetrating hyphae which restrict nutrients and water uptake. The saprophytic phase of the fungus in host tissue is in the form of mycelia, pycnidia, and microsclerotia. Microsclerotia are small and black or greyish-black and produced in abundance on heavily infected plants. The microsclerotia germinate and are released into the soil during the decomposition of the host (Basandrai *et al*. 2021). They can overwinter in soil for 2–15 years (Meyer *et al.* 1974, Gupta *et al.* 2012a) and serve as the primary source of inoculum (Zveibil *et al.* 2012). The population of viable microsclerotia present in the soil is directly correlated to disease severity (Gupta *et al*. 2012a). Soil moisture content is an important factor that influences the survival of microsclerotia. High soil moisture and flooding may significantly reduce the viability of microsclerotia to a few weeks (Dhingra & Sinclair 1975, Pratt 2006a, Zveibil *et al*. 2012). *Macrophomina* can also survive as mycelium and microsclerotia in symptomatic seeds (Dhingra & Sinclair 1978, Gupta *et al.* 2012a).

Nine species have been assigned within *Macrophomina*, *viz*. *M. euphorbiicola*, *M. limbalis*, *M. phaseoli*, *M. phaseolina*, *M. philippinensis*, *M. pseudeverniae*, *M. pseudophaseolina*, *M. tecta* and *M. vaccinia*. However, *M. limbalis* was transferred to *Dothiorella* (as *D. limbalis*), *M. pseudeverniae* to *Didymocyrtis* (as *D. pseudeverniae*), while *M. phaseoli* and *M. philippinensis* were treated as the synonym of *M. phaseolina*. Thus, only five species, *M. euphorbiicola*, *M. phaseolina*, *M. pseudophaseolina*, *M. tecta* and *M. vaccinii* are currently accommodated within *Macrophomina* (Sarr *et al*. 2014, Machado *et al*. 2019, Zhao *et al*. 2019a, Poudel *et al*. 2021).

Macrophomina is characterised by brown to hyaline, septate mycelium with abundant production of black microsclerotia, and pycnidial unilocular conidiomata with papillate ostiole. Conidiophores are reduced to phialidic conidiogenous cells with a minute collarette. Conidia are aseptate, cylindrical to fusiform, hyaline with apical mucoid appendages when young, sometimes becoming dark and septate with age. Ascomata have not been reported (Crous *et al*. 2006b, Phillips *et al*. 2013).

Macrophomina phaseolina is the type species of the genus and is also the most common species. It was originally described from *Phaseolus* collected in Italy (Tassi 1901). It is a necrotrophic pathogen with a broad host range of nearly 900 plant species (Farr & Rossman 2022), many of which are economically important crops (Gupta *et al.* 2012a, Sarr *et al.* 2014). *Macrophomina euphorbiicola* has only been reported as the causal agent of charcoal rot on *Ricinus communis*, *Jatropha gossypiifolia* and sweet potato (*Ipomoea batatas*) in Brazil (Machado *et al*. 2019, De Mello *et al*. 2021). *Macrophomina pseudophaseolina* has been reported to cause charcoal rot disease on a few plant species, namely, *Abelmoschus esculentus*, *Arachis hypogaea*, *Hibiscus sabdariffa*, and *Vigna unguiculata* in Senegal (Sarr *et al.* 2014), *Lens culinaris* in Algeria (Kouadri *et al.* 2021), *Sorgum bicolor* in Australia (Poudel *et al.* 2021, 2022), *Arachis hypogaea*, *Gossypium hirsutum*, *Ricinus communis*, and associated with seed decay of *Jatropha curcas* in Brazil (Machado *et al*. 2019). *Macrophomina tecta* was isolated from stems of *Sorghum bicolor* and *Vigna radiata* with charcoal rot symptoms in New South Wales and Queensland (Poudel *et al*. 2021, 2022) and *Macrophomina vaccinii* has been reported to cause blueberry stem blight (Zhao *et al*. 2019a) and stem and root rot of patchouli (*Pogostemon cablin*) in China (Fang *et al*. 2022).

Ecological, economic and health significance

Charcoal rot is the most economically important disease caused by *M. phaseolina* which affects many crop plants in North and South America, Asia, Africa and some parts of Europe (Wrather *et al*. 1997). Plant hosts with the most publications with *Macrophomina* cited in the past 10 years are soybean and sunflower. *Macrophomina phaseolina* has also been reported as an opportunistic human pathogen. The economic importance of charcoal rot on soybean and sunflower as well as its role as an opportunistic human pathogen is detailed below.

Charcoal rot of soybean, caused by *Macrophomina phaseolina*, is one of the most important soil-borne or seed-borne pathogens (Su *et al*. 2001, Babu *et al*. 2007, Sarr *et al*. 2014). It is among the most destructive diseases resulting in significant losses in yield and seed quality (Kaur *et al*. 2012, Marquez *et al*. 2021). Symptoms of charcoal rot are referred to as dry-weather wilt or summer wilt because it often occurs when plants are under heat and drought stresses. These stresses can also occur in irrigated soybeans causing losses from 6 to 33 % in experimental plots (Mengistu *et al*. 2011). The combination of stress and the presence of *M. phaseolina* caused higher yield loss on soybeans than drought alone, with the combined effects contributing an additional 7 % yield loss (Mengistu *et al*. 2011). In South America, charcoal rot has caused severe problems in soybean crops in Paraguay, where the prevalence of the disease was 100 % in 48 localities evaluated from April to August 2008 (Orrego Fuente *et al*. 2009). In Brazil, the disease has reduced yields by up to 50 % where drought occurs in January (Wrather *et al*. 2010). In the USA, charcoal rot has been a problem for soybean farmers for many years. From 1974 to 1994, charcoal rot caused significant yield losses estimated at 8.54 × 10^5 tonnes per year in non-irrigated fields in the 16 southern states (Wrather *et al*. 2006, 2009). The disease was ranked in the top six among economically important diseases in the USA from 2006–2009 (Koenning & Wrather 2010, Wrather *et al*. 2010). Yield reduction due to charcoal rot in the top eight soybean-producing countries during 2006 was estimated at 2.505 million metric tons (Wrather *et al*. 2010). Wrather & Koenning (2010) stated that average yield losses due to charcoal rot in the USA were estimated at 27 million bushels of soybeans per year from 1996 to 2009. From 2010 to 2014, charcoal rot was nearly always in the top five diseases causing the most yield losses. Losses from charcoal rot, a disease favoured by hot and dry conditions, were greater in 2012 than losses caused by that disease in any other year (Allen *et al*. 2017). Information on the influence of charcoal rot on seed composition (protein, oil, and fatty acids) is scarce (Bellaloui *et al*. 2008, 2012, 2021).

Charcoal rot of sunflowers, caused by *M. phaseolina*, is also a significant threat to yield production (Ijaz *et al*. 2013, Iqbal *et al*. 2014). In Pakistan, sunflower charcoal rot results in significant yield losses (Khan 2007). Mirza & Beg (1983) reported yield losses of up to 90 % due to *M. phaseolina* in the central and northern areas of Pakistan. The disease can cause a significant reduction in plant height, stem width and head weight (Ijaz *et al*. 2013) and can negatively influence oil production. Tewari & Arora (2014) observed up to 70 % reduction in oil production in salinised regions.

Opportunistic human infections can be caused by *Macrophomina phaseolina*, especially in immunosuppressed patients, including those receiving prophylactic antifungal therapy (Tan *et al*. 2008, Srinivasan *et al*. 2009, Arora *et al*. 2012). As the organism is soilborne, patients may acquire the infection from environmental exposure. From the early 1970s, in immunosuppressed patients, disseminated infection with various fungal cultures including *M. phaseolina* was among the common problems. The major routes of infection could be soil

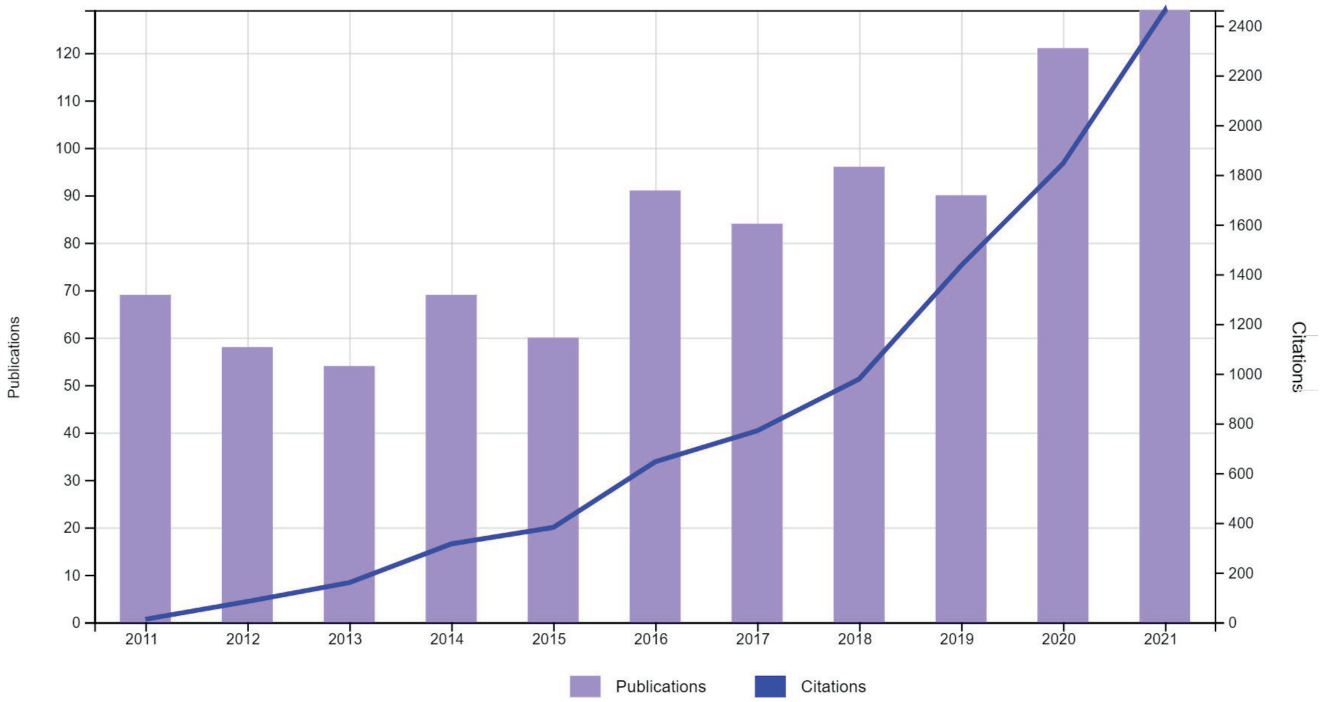

Fig. 106. Trends in research of *Macrophomina* in the period 2011–2021.

Table 82. Top 10 cited articles related to *Macrophomina* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	*Bacillus* strains isolated from rhizosphere showed plant growth promoting and antagonistic activity against phytopathogens	223	Kumar *et al.* (2012)
2	Towards a natural classification of *Botryosphaeriales*	215	Liu *et al*. (2012b)
3	Soybean yield loss estimates due to diseases in the United States and Ontario, Canada, from 2010 to 2014	214	Allen *et al.* (2017)
4	Optimization for rapid synthesis of silver nanoparticles and its effect on phytopathogenic fungi	202	Krishnaraj *et al.* (2012)
5	Synthesis of chitosan based nanoparticles and their *in vitro* evaluation against phytopathogenic fungi	159	Saharan *et al.* (2013)
6	Tools to kill: Genome of one of the most destructive plant pathogenic fungi *Macrophomina phaseolina*	129	Islam *et al.* (2012)
7	Identification of diverse mycoviruses through metatranscriptomics characterization of the viromes of five major fungal plant pathogens	128	Marzano *et al.* (2016)
8	Green synthesis of protein capped silver nanoparticles from phytopathogenic fungus *Macrophomina phaseolina* (Tassi) Goid with antimicrobial properties against multidrug-resistant bacteria	97	Chowdhury *et al*. (2014)
9	Role of allelochemicals in plant growth promoting rhizobacteria for biocontrol of phytopathogens	97	Saraf *et al.* (2014)
10	Emerging phytopathogen *Macrophomina phaseolina*: biology, economic importance and current diagnostic trends	87	Kaur *et al.* (2012)

contamination of hands and feet and inhalation and ingestion of aerosolised conidia. At times, the risk of invasive infections is amplified by skin trauma, sinusitis, burns, and corneals by conquering the local host factors (Arora *et al.* 2012).

Research interests

There are 921 publications and 8 240 citations from 2011–2021 in the Web of Science (Fig. 106), with the top 10 most cited articles listed in Table 82. Most publications focused on the use of nanoparticles and biocontrol agents in disease management strategies, and research on pathogenicity mechanisms and interactions, as well as taxonomy.

Disease management strategies

Several disease management strategies have been evaluated in recent decades, including chemical control, agronomic practices, biological control, plant metabolites, and elicitors of plant defense (Marquez *et al*. 2021); however, none have proved to be commercially reliable for treating charcoal rot. The chemical control of *M. phaseolina* is difficult since there are no systemic fungicides available that can successfully be taken up by the roots. As far as we know, no fungicides have been registered to control this pathogen. However, systemic and non-systemic fungicides (*i.e*., carbendazim, difenoconazole, benomyl, azoxystrobin, dazome) at different concentrations were evaluated *in vitro* and *in vivo* against *M. phaseolina* (Marquez *et al*. 2021). Due to the excessive use of chemical fungicides, and environmental hazards to humans, flora and fauna major concerns have been raised over the years. Uncontrolled use of chemical agents can also cause the development of resistance in phytopathogenic fungi against fungicides (Saharan *et al*. 2013).

In the last few decades, much research has focused on environmentally friendly alternative control methods including biological control agents (BCAs) as well as plant metabolites and elicitors of plant defenses (Marquez *et al*. 2021). *Trichoderma* spp. are effective BCAs for several soil-borne fungal plant pathogens including *M. phaseolina* (Bastakoti *et al*. 2017, Hyder *et al*. 2017). *Bacillus* and *Streptomyces* isolates can inhibit the growth of *Macrophomina* sp. (Gopalakrishnan *et al*. 2011, 2014, Kumar *et al*. 2012b, Verma *et al*. 2015, Torres *et al*. 2016). Endophytic fluorescent *Pseudomonas* bacteria (Tewari & Arora 2014, 2016, Moin *et al*. 2020), antagonistic and growth-promoting yeast *Brettanomyces naardensis* combined with arbuscular mycorrhizal fungi (Nafady *et al*. 2019) also showed promising results for control of charcoal rot on sunflower. Secondary metabolites such as terpenes, phenolics, nitrogen and sulphur-containing compounds, secreted by the BACs act as natural fungicides (Saraf *et al*. 2014, Zaynab *et al*. 2018). Other management strategies including cultural practices, organic amendments, seed treatment and genetic host resistance have been recommended (Gupta *et al*. 2012a, Siddique *et al*. 2021), however, they are limited and do not provide complete control against charcoal rot (Cross *et al*. 2012).

Marzano *et al*. (2016) used the metatranscriptomics approach to characterise fungal viromes of five major fungal pathogens including, *M. phaseolina.* They recovered 14 mycoviruses from *M. phaseolina*, including some putative novel viruses, and postulated that these viruses may have the potential to be used as biocontrol agents against their fungal hosts.

In the last few years, there has been considerable research interest in the use of nanoparticles due to their wide application potential to combat disease in agricultural systems. Synthesis of silver nanoparticles using green chemistry, *i.e*., producing nanoparticles using biological sources such as leaf extracts (Krishnaraj *et al.* 2012, Bahrami-Teimoori *et al.* 2017, Ruiz-Romero *et al.* 2018, Bernardo-Mazariegos *et al.* 2019), chitosan (Saharan *et al.* 2013) and cell-free filtrates of the fungus *Macrophomina phaseolina*, antagonistic and growth-promoting yeast *Brettanomyces naardensis* combined with arbuscular mycorrhizal fungi, were studied. These nanoparticles proved to be effective in vitro to inhibit the growth of fungi such as Macrophomina phaseolina (Krishnaraj *et al*. 2012, Saharan *et al*. 2013, Bahrami-Teimoori et al. 2017, Jogee *et al*. 2017, Ruiz-Romero *et al*. 2018, Bernardo-Mazariegos *et al*. 2019).

Pathogenicity mechanisms and interactions

The wide host range and persistence of *M. phaseolina* in the soil as microsclerotia make disease control challenging. Therefore, understanding the basis of the pathogenicity mechanisms as well as pathogen interactions with host plants is crucial for controlling the pathogen (Marquez *et al*. 2021). To better understand the underlying mechanisms of resistance, several functional genomic strategies, including proteomics and transcriptomics, have been performed to analyse the interactions between several cultivars of various host plants and *M. phaseolina*. Islam *et al*. (2012) reported the *M. phaseolina* genome, which provided a framework for the infection process at the cytological and molecular level and uses a diverse arsenal of enzymatic and toxin tools to destroy the host plants. Further understanding of the *M. phaseolina* genome-based plant-pathogen interactions will be instrumental in designing rational strategies for disease control, essential to ensuring global agricultural crop production and security (Islam *et al*. 2012, Sarr *et al*. 2014).

Taxonomy and phylogeny

The genus *Macrophomina* was assigned to *Botryosphaeriaceae* (*Botryosphaeriales*) with type species *M. phaseolina* (Crous *et al*. 2006b, Liu *et al*. 2012b, Phillips *et al*. 2013). Conidia have apical mucous appendages early in their development, which has in the past led to confusion and the allocation of this species to the genus *Tiarosporella* (Von Arx 1981). Although *M. phaseolina* can have apical mucoid appendages as found in *Tiarosporella* (Sutton & Marasas 1976), it is distinguished by having percurrent proliferating conidiogenous cells (Phillips *et al*. 2013). The concatenation of multiple loci has been widely used for taxonomic studies of phytopathogenic fungi (Groenewald *et al*. 2013, Sarr *et al*. 2014). Sarr *et al*. (2014) conducted a multi-gene DNA analysis looking at five loci in the pathogen genome. Although they found considerable variation within the species, this genetic variation could not be correlated to host or geographic origin. Therefore, there will most probably be more new species to be discovered than the currently known five *Macrophomina* species.

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77. ***Flammulina*** P. Karst., Meddeland Soc. Fauna Fl. Fenn. 18: 62. 1891.

Type species: *Flammulina velutipes* (Curtis) Singer

Classification: *Basidiomycota*, *Agaricomycotina*, *Agaricomycetes*, *Agaricales*, *Physalacriaceae.*

Background

Flammulina belongs to the family *Physalacriaceae* (*Agaricales*), which harbours nearly 20 species mainly distributed in the Northern Hemisphere (Bas 1983, 1995, Redhead & Petersen 1999, Redhead *et al.* 2000, Ge *et al*. 2008, 2015, Wang *et al*. 2018e). Most species occur in temperate regions, although a few species, such as *F. rossica*, *F. yunnanensis*, and *F. mexicana*, have been collected from subtropical regions but often at higher altitudes (Redhead & Petersen 1999, Redhead *et al*. 2000, Ge *et al*. 2008, Ge *et al*. 2015). Many species of *Flammulina* sporulate during late autumn to early spring and hence are often called “Winter Mushroom” (Ingold 1980, Fultz 1988). All species are wood-decayers, growing on dead wood of *Salix*, *Picea*, *Quercus*, and *Lithocarpus*, among others (Bas 1983, Redhead & Petersen 1999, Ge *et al*. 2008, 2015, Wang *et al*. 2018e). Some species show a specific correlation with host plants, such as *F. ononidis* and *F. populicola* with their substrates of *Ononis spinosa* and *Populus* spp., respectively (Arnolds 1977, Redhead & Petersen 1999).

The most popular species is the edible golden needle mushroom (Enokitake) in East Asia, which was previously regarded as “*F. velutipes* (Curtis) Singer”. However, Wang *et al*. (2018h) revealed that “*F. velutipes*” in East Asia differs from the European *F. velutipes* based on morphological and molecular evidence. Similar results were also demonstrated in other studies (Hughes *et al*. 1999, Hughes 2000, Methven *et al*. 2000, Ge *et al*. 2008, 2015, Ripková *et al*. 2010). Therefore, Enokitake in East Asia was described as an independent species, *F. filiformis* (Wang *et al*. 2018e).

Like most species of *Basidiomycota*, *Flammulina* species are heterothallic with a tetrapolar mating system, which is different from species in *Ascomycota* (Kües 2000, Du & Yang 2021, Virágh *et al*. 2021, Xie *et al.* 2021). Recently, genome-based studies revealed the structure of *F. filiformis* mating-type loci HD and PR (Van Peer *et al*. 2011, Wang *et al*. 2016h). Cross experiment indicates the HD-b sub-locus and PR loci are involved in compatible nuclei recognition and migration, while the function of the HD-a sub-locus remains unclear (Wang *et al*. 2016h). The sexual life cycle starts with the haploid spores developing into monokaryotic mycelia (Kües 2000, Virágh *et al*. 2021). Compatible monokaryotic mycelia may fuse and become dikaryotic mycelia (Kües 2000, Virágh *et al*. 2021). Then, environmental factors (nutrient, light, temperature, *etc*.) may trigger the dikaryotic mycelium to aggregate and develop into primordia, which then differentiate into sporocarps (Ingold 1980, Kües 2000). Karyogamy and meiosis will take place in the basidia within the hymenium, and additional mitosis results in basidiospores (Kües 2000). In addition, both monokaryotic and dikaryotic mycelia could produce monokaryotic oidia to complement the asexual life cycle (Ingold 1980).

Ecological and economic significance

As wood-decayers, *Flammulina* species play an essential role in nutrient cycling in the ecosystem. Genome and transcriptome studies revealed that *F. filiformis*, *F. rossica*, *F. elastica* and *F. ononidis* harbour abundant lignin, cellulose, carbohydrate, and alcohol dehydrogenase genes and they are dynamically expressed in the vegetative mycelium (Park *et al*. 2014, 2019, Wang *et al.* 2015d, Park & Kong 2018, Yu *et al*. 2021). This suggests the potential application of *Flammulina* species in the bioconversion of agro-residues, which cause serious environmental problems all over the world, especially in developing countries (Leifa *et al*. 2001, Harith *et al*. 2014, Park *et al*. 2014, Xie *et al*. 2017a, Hyde *et al*. 2019a, Ibitoye *et al*. 2021).

Flammulina filiformis is one of the top five cultivated edible mushrooms in the world and is cultivated on a large scale in East Asia (Royse 2014). China is currently the largest producer of *F. filiformis* with more than 2.5 million tons per year (Liu *et al*. 2016e). However, the cultivation of *F. filiformis* requires a low temperature (≤ 15 °C), which costs large amounts of energy, especially in summer (Fultz 1988, Kong *et al*. 2004a, Kang *et al*. 2013, Kim *et al*. 2015). This is also the main reason that countries in Southeast Asia need to import *F. filiformis* from China, Japan, or South Korea (Royse 2014). Therefore, a heat-resistant strain with perfect commodity traits may have a potentially big market.

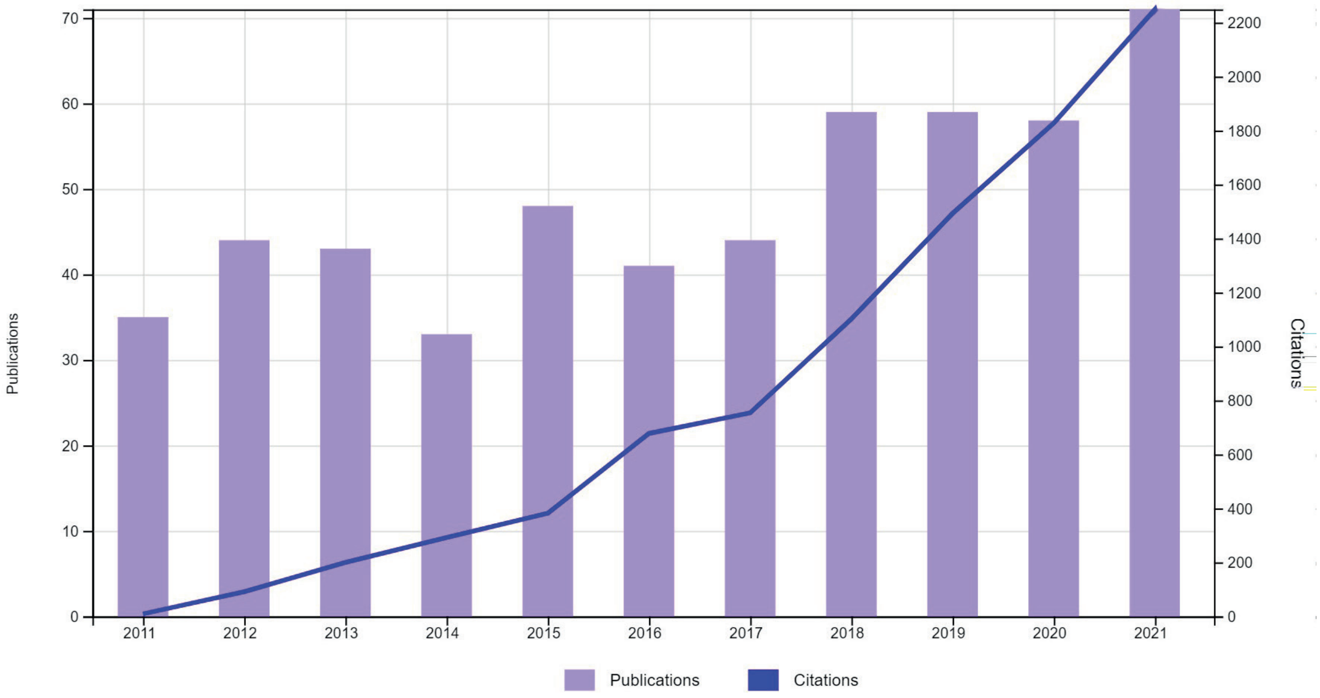

Fig. 107. Trends in research of *Flammulina* in the period 2011–2021.

Over the past 50 years, more than 100 cultivars have been selected for cultivation (Liu *et al*. 2016e, Gao *et al*. 2021). However, strain name confusion is common, which is caused by the different nomenclature systems used by breeders (Liu *et al*. 2016e). The same situation also exists in other edible mushrooms (Ramírez *et al*. 2001, Xiao *et al*. 2010, Li *et al*. 2019a, c). Thus, researchers developed multiple molecular markers aimed to identify genetically different strains (Palapala *et al*. 2002, Zhang *et al*. 2010, Kong *et al*. 2014b, Liu *et al*. 2016e, Wang *et al*. 2018f, Shen *et al*. 2020b, Gao *et al*. 2021a). Moreover, researchers further constructed the core germplasm of *F. filiformis* which includes cultivars and wild-type strains (Liu *et al*. 2018c, Gao *et al*. 2021a). These studies provide a potential way to help precisely identify and choose the proper strains in further breeding work.

Research interests

There are 535 publications and 8 218 citations from 2011–2021 in the Web of Science (Fig. 107), with the top 10 most cited articles listed in Table 83. Most of the publications focused on bioactive compounds, taxonomy and phylogeny, and sporocarp development.

Bioactive compounds

Flammulina filiformis is the most popular species in this genus and has attracted much research on its bioactive compounds. *Flammulina filiformis* (often under the name *F. velutipes*) can produce abundant polysaccharides, sterol, terpenes, glycoproteins, norsesquiterpe alkaloid, thione and lectins. These compounds possess antioxidant, anti-tumour, immunomodulatory, and antimicrobial activity, among others (Ko *et al*. 1995, Yang *et al*. 2001, 2012d, Beluhan & Ranogajec 2011, Xu *et al*. 2011b, Chen *et al*. 2012a, Patel & Goyal 2012, Reis *et al*. 2012a, El Enshasy & Hatti-Kaul 2013, Yi *et al*. 2013, Guo *et al*. 2015a, Kumar *et al*. 2015, Tao *et al*. 2016, Wang *et al*. 2016f, Fukushima-Sakuno 2020). Interestingly, studies revealed cultivars and wild-type strains have different chemical compositions, including sugar, fatty acid, and tocopherols profiles (Reis *et al*. 2012a). A wild-type strain collected from subtropical areas in China was reported to have rich and specific sesquiterpenoids compared with other cultivars (Tao *et al*. 2016, Chen *et al*. 2020b). Recent studies of *F. rossica* revealed it contains diverse enokipodins and exopolysaccharides which have antimicrobial and anti-tumour activity (Tabuchi *et al*. 2020). In addition, Enokitake exhibited a high umami taste and flavour components (Phat *et al.* 2016, Yang *et al.* 2016b). Since *Flammulina* species are widely distributed, and only *F. filiformis* was extensively studied so far, it is worth including other species/strains from different habitats to explore the bioactive compounds and their functions.

Taxonomy and phylogeny

Flammulina is easily characterised by its more or less yellow-brown pileus, yellowish lamellae, and brown to dark brown stipe densely covered with brown velvety hairs (Ge *et al*. 2008, 2015). However, due to morphological plasticity, species in this genus look similar to one another. Before the 1970s, *Flammulina* was thought to consist of a single species with a pan-northern hemisphere distribution (Hughes 2000). Arnolds (1977) described *F. ononidis* on *Ononis spinosa* from Germany. Later, Bas (1983) reported *F. fennae* as a new species based on spore shape and size and summarised the *Flammulina* species in Europe (Bas 1983, 1995). Several new species were recognised in North America, based on morphological data and mating experiments, such as *F. rossica*, *F. populicota* and *F. elastica* (Petersen *et al*. 1999, Redhead & Petersen 1999, Redhead *et al*. 2000). Over the past 10 years, researchers discovered several new species based on molecular phylogeny and morphological data, indicating that East Asia is a biodiversity centre for *Flammulina*. They found the pileipellis structure is important in species delimitation in this genus and declared the golden needle mushroom (Enokitake) an independent species, named *F. filiformis*, which is different from *F. velutipes* (Wang *et al*. 2018e). Future phylogenomic studies may well elucidate the origin and evolution of the genus.

Sporocarp development

Based on morphological study, researchers described cell number variation, cell differentiation, and programmed cell death during

Table 83. Top 10 cited articles related to *Flammulina* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Chemical composition and nutritional value of the most widely appreciated cultivated mushrooms: An inter-species comparative study	267	Reis *et al.* (2012a)
2	Recent developments in mushrooms as anti-cancer therapeutics: a review	216	Patel & Goyal (2012)
3	Recent trends in the use of natural antioxidants for meat and meat products	215	Kumar *et al.* (2015)
4	Mushroom immunomodulators: unique molecules with unlimited applications	165	El Enshasy & Hatti-Kaul (2013)
5	Evaluation of umami taste in mushroom extracts by chemical analysis, sensory evaluation, and an electronic tongue system	154	Phat *et al.* (2016)
6	Bioactive proteins from mushrooms	142	Xu *et al.* (2011c)
7	Chemical composition and non-volatile components of Croatian wild edible mushrooms	136	Beluhan & Ranogajec (2011)
8	Contents of lovastatin, γ-aminobutyric acid and ergothioneine in mushroom fruiting bodies and mycelia	120	Chen *et al.* (2012a)
9	Effect of hot air drying on volatile compounds of *Flammulina velutipes* detected by HS-SPME-GC-MS and electronic nose	110	Yang *et al.* (2016b)
10	Easy conversion of protein-rich enoki mushroom biomass to a nitrogen-doped carbon nanomaterial as a promising metal-free catalyst for oxygen reduction reaction	109	Guo *et al.* (2015a)

sporocarp development, and also investigated light/dark influence on cap expansion and stipe elongation (Aschan & Norkrans 1953, Aschan-Åberg 1960, Bevan & Kemp 1958, Sakamoto *et al*. 2004). Besides the development of molecular biology, researchers identified hydrophobin, chitin deacetylase, expansin, and other sporocarp-specific genes in *F. filiformis* (Ando *et al*. 2001, Yamada *et al*. 2005, 2008, Sakamoto *et al*. 2007, Fang *et al*. 2014). In recent years, RNAseq-based studies uncovered a large number of sporocarp-specific genes related to sexual development, water absorption, stipe elongation, basidium formation, and sporulation, among others (Park *et al*. 2014, Yan *et al*. 2019a, Liu *et al*. 2020a). Interestingly, most of the sporocarp developmental genes showed conserved expression patterns among other mushroom-forming fungi (Liu *et al*. 2020a, Merényi *et al*. 2020). For some important genes, researchers performed RNAi approaches to further elucidate their roles in sporocarp formation (Tao *et al*. 2019, Wu *et al*. 2019d, 2020b, Meng *et al*. 2021). The low-temperature sporulation property drove researchers to investigate its heat/cold response from morphological, chemical, protein, and gene expression levels (Ko *et al*. 2007, Liu *et al*. 2016b, Liu *et al*. 2017c, Liu *et al*. 2020a). The above studies uncovered several important genes involved in sporocarp development. However, the difficulty with gene manipulation in mushroom-forming fungi hindered further understanding of these gene functions. Currently, the CRISPR/Cas9 gene-editing tool is widely used in model organisms. Therefore, building the CRISPR/Cas9 system in *Flammulina* species to further investigate the gene function should be the future perspective.

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78. ***Pseudogymnoascus*** Raillo, Zentralbl. Bakteriol. 2. Abt. 78: 520. 1929.

Type species: *Pseudogymnoascus roseus* Raillo

Classification: *Ascomycota*, *Pezizomycotina*, *Leotiomycetes*, *Thelebolales*, *Pseudeurotiaceae.*

Background

Pseudogymnoascus is a diverse collection of psychrophilic or psychrotolerant ascomycete fungi (Rice & Currah 2006). Species of *Pseudogymnoascus* are commonly isolated from soils, rotting wood, and plant-associated rhizospheres (Rice & Currah 2006). Despite the almost ubiquitous presence of gymnothecia, there is a relatively high diversity of other characteristics and morphological features, such as conidia production, ascospore morphology, and hyphal structure within the genus (Rice & Currah 2006). This diversity has resulted in the movement of several species between *Pseudogymnoascus* and its allied genera, particularly *Geomyces* and *Gymnostellatospora*.

Index Fungorum (2022) lists 16 distinct species within *Pseudogymnoascus*. The genus was erected in 1929 by Raillo for two newly described species, *Ps. roseus* and *Ps. vinaceus* (Raillo 1929). No type species existed for the genus until 1972 when a taxonomic treatment resulted in the retention of three species (*Ps. roseus*, *Ps. bhatti* and *Ps. caucasicus*) and the synonymisation of *Ps. vinaceus* with *Ps. roseus*, and *Ps. roseus* designated as the type species (Samson 1972). Despite receiving relatively little research interest during the 20th century, several additional species were described. *Pseudogymnoascus alpinus* was isolated and described from Swiss alpine soil (Muller 1982) and *Ps. dendroideus* from Algerian cattle dung (Locquin-Linard 1982). Additionally, Rice and Currah isolated and described both *Ps. appendiculatus* and *Ps. verrucosus* from Canadian tundra soil (Rice & Currah 2006).

In 2013, the causative fungal pathogen of emerging white-nose syndrome (WNS) in bats was identified as a species of *Geomyces* (*G. destructans*), sparking a huge surge of research interest in the genus and its allies. Subsequent phylogenetic analyses resulted in the reclassification of *G. destructans* and several other species of *Geomyces* and *Gymnostellatospora* into *Pseudogymnoascus* (Minnis & Lindner 2013). This reclassification resulted in an additional three *Pseudogymnoascus* species, *Ps. destructans*, *Ps. carnis*, and *Ps. pannorum*. Increased survey efforts of bat hibernacula in North America, in response to the emergence

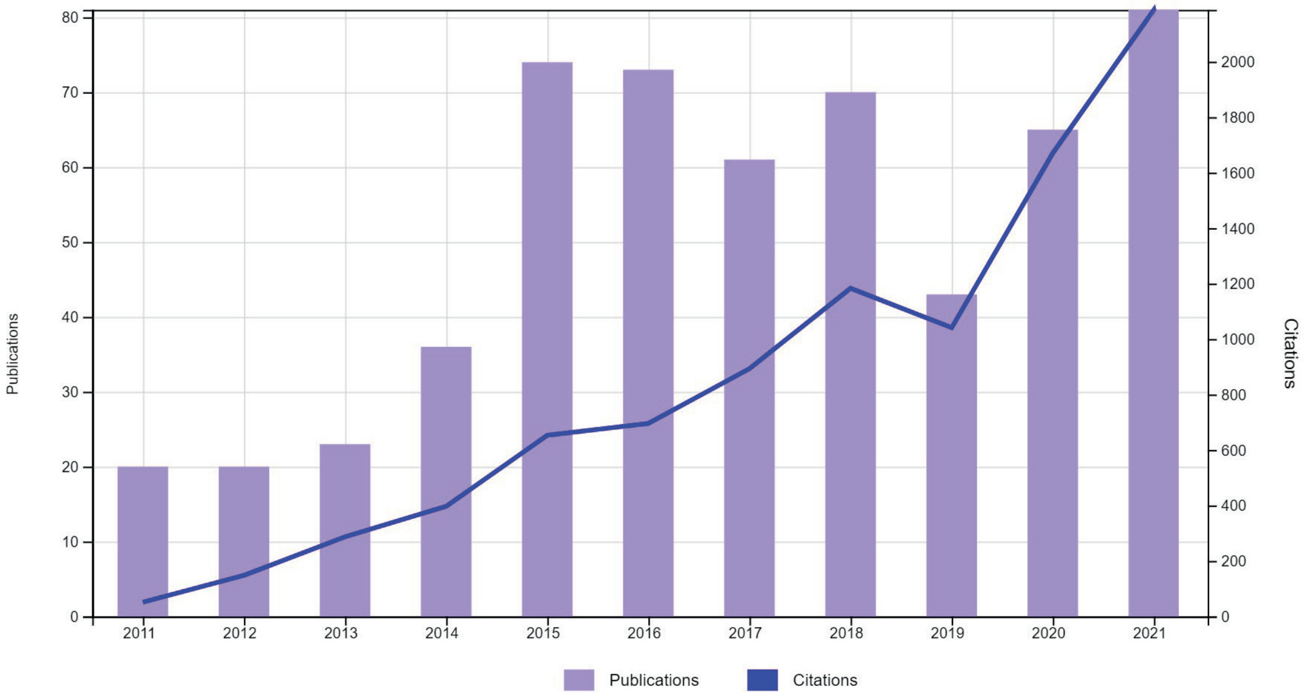

Fig. 108. Trends in research of *Pseudogymnoascus* in the period 2011–2021.

of WNS, have identified numerous undescribed isolates likely belonging to *Pseudogymnoascus* (Lorch *et al.* 2013a). Subsequent efforts have seen three of these uncharacterised isolates, *Ps. turneri*, *Ps. linderni* and *Ps. palmeri*, raised to species status (Crous *et al.* 2020a). Surveys of Chinese soils have also discovered three more species of *Pseudogymnoascus*, *Ps. shaanxiensis*, *Ps. guizhouensis* and *Ps. sinensis* (Zhang *et al.* 2020).

Ecological and economic significance

The ecological and economic significance of the genus *Pseudogymnoascus* is undoubtedly attributable to the emerging fungal pathogen *Ps. destructans*, which is responsible for WNS, one of the deadliest wildlife diseases ever observed (Blehert *et al.* 2009). Initial classification placed *Ps. destructans* into the allied genus *Geomyces* (Gargas *et al.* 2009); however subsequent genetic analyses prompted a reclassification into *Pseudogymnoascus* (Minnis & Lindner 2013).

White-nose syndrome is a fungal skin disease which impacts hibernating bat species in North America (Blehert 2012). Typically, diseased bats exhibit visible fungal growth around the muzzle, lending the disease its name (Lorch *et al.* 2011). However, infection with *Ps. destructans* also affects the wings and fungal growth around the muzzle is not required for severe disease to present (Meteyer *et al.* 2012). White-nose syndrome was first observed in bats in a single cave in New York State in 2006 but has now been

Table 84. Top 10 cited articles related to *Pseudogymnoascus* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Experimental infection of bats with *Geomyces destructans* causes white-nose syndrome	313	Lorch *et al.* (2011)
2	Inoculation of bats with European *Geomyces destructans* supports the novel pathogen hypothesis for the origin of white-nose syndrome	263	Warnecke *et al.* (2012)
3	Sociality, density-dependence and microclimates determine the persistence of populations suffering from a novel fungal disease, white-nose syndrome	235	Langwig *et al.* (2012)
4	Phylogenetic evaluation of *Geomyces* and allies reveals no close relatives of *Pseudogymnoascus destructans*, *comb. nov.*, in bat hibernacula of eastern North America	177	Minnis & Lindner (2013)
5	Frequent arousal from hibernation linked to severity of infection and mortality in bats with white-nose syndrome	174	Reeder *et al.* (2012)
6	Temperature-dependent growth of *Geomyces destructans*, the fungus that causes bat white-nose syndrome	153	Verant *et al.* (2012)
7	Disease alters macroecological patterns of North American bats	151	Frick *et al.* (2015)
8	Pan-European distribution of white-nose syndrome fungus (*Geomyces destructans*) not associated with mass mortality	138	Puechmaille *et al.* (2011)
9	Host and pathogen ecology drive the seasonal dynamics of a fungal disease, white-nose syndrome	129	Langwig *et al.* (2015)
10	Investigating and managing the rapid emergence of white-nose syndrome, a novel, fatal, infectious disease of hibernating bats	103	Foley *et al.* (2011)

documented in 33 US States and five Canadian provinces (Blehert *et al.* 2009, Lorch *et al.* 2016b). The emergence of WNS within a bat hibernaculum has the potential to cause significant population decline or even complete extirpation of both single species and multi-species communities (Langwig *et al.* 2015b, Ingersoll *et al.* 2016, Frick *et al.* 2017). During its spread across continental North America, WNS is believed to have caused the death of millions of hibernating bats from several different species (Hoyt *et al.* 2021). Worryingly, still more species of hibernating bats are likely to be impacted by WNS as the westward spread continues (Lorch *et al.* 2016a).

Research interests

Besides the conservation threat to North American bat populations posed by WNS, the ecosystem services provided by bats, both in terms of agricultural pest control and pollination, are valued at hundreds of millions of US dollars annually (Boyles *et al.* 2011). The potentially profound ecological and economic impacts of WNS have therefore spurred significant research efforts. From 2011–2021, 566 publications which focused on *Pseudogymnoascus*, accounting for 7 988 citations, were catalogued in the Web of Science (Fig. 108). Most of these publications detail research into the ecology, pathology and mitigation of WNS (Table 84).

Ecology

To understand the emergence of WNS and to successfully predict how the outbreak will progress, it is critical that the ecology of the disease is fully understood. As such, studies aimed at understanding various aspects of the ecology of WNS have formed a significant portion of the published work regarding *Ps. destructans* and WNS. The cause of WNS was identified in 2011 (Lorch *et al.* 2011). Early efforts to determine the origin of *Ps. destructans* led bat researchers around the world to discover that this fungus is present in bat hibernacula in both Europe and Asia (Puechmaille *et al.* 2011, Leopardi *et al.* 2015, Zukal *et al.* 2016). However, mortality due to WNS, as observed in North America, is absent in Europe and Asia (Puechmaille *et al.* 2011, Zukal *et al.* 2016). Phylogenetic and cross infection studies point conclusively to *Ps. destructans* being an invasive pathogen in North America (Leopardi *et al.* 2015).

Studies regarding the ecological niche of *Ps. destructans* have proved informative in predicting its distribution and spread; for example, it is known that *Ps. destructans* displays optimal growth at around 12 °C and does not proliferate at all at temperatures above 20 °C (Verant *et al.* 2012). In turn, these findings have informed predictive models of disease spread which suggest that bats are responsible for spreading the fungus between hibernacula, particularly during the hibernation season (Frick *et al.* 2015, Langwig *et al.* 2015a). However, *Ps. destructans* is known to persist in the absence of bat hosts (Lorch *et al.* 2013b, Hoyt *et al.* 2015b), and for long periods at elevated temperatures (Campbell *et al.* 2020), characteristics which have potentially profound impacts on its spread potential (Lorch *et al.* 2013b, Campbell *et al.* 2020). Given the uncertainty regarding how *Ps. destructans* is translocated across the landscape, continued surveillance of bat populations and the application of stringent decontamination protocols are key to tracking and limiting the spread of WNS both by bats and other mechanisms, such as humans and to making informed management decisions (Bernard *et al.* 2020).

Susceptibility to WNS varies on a species-by-species basis (Davy *et al.* 2017). Understanding which factors influence this variation in susceptibility is likely to be key in developing effective mitigation strategies against the disease. For example, the severity of the disease is strongly associated with climactic conditions, both in the region as a whole and within the individual hibernaculum (Langwig *et al.* 2012, Maher *et al.* 2012). Continuing preference for hibernating in suboptimal microclimates has been linked to population declines in some bat species (Hopkins *et al.* 2021).

Pathology

A clear understanding of how WNS impacts individual bats is vital foundational knowledge in pursuit of effective mitigation strategies. Much of the research regarding WNS, and by extension *Ps. destructans*, has investigated the pathology of acute WNS infections. During infections, *Ps. destructans* invades and disrupts the dermal tissues of the bat wing (Cryan *et al.* 2013, Warnecke *et al.* 2013). The wings constitute an enormous proportion of the body surface area of bats and wing skin is therefore a particularly vital organ in the maintenance of homeostasis, particularly during hibernation (Cryan *et al.* 2013, Verant *et al.* 2014). Besides locomotion, wing skin plays a critical role in several physiological functions such as thermoregulation, oxygen exchange, water and electrolyte balance (Cryan *et al.* 2013). Through disruption of the wing membranes, infection with *Ps. destructans* causes a cascade of physiological disturbances that causes bats with WNS to arouse more often from torpor during hibernation (Verant *et al.* 2014). This increased rate of arousal in turn results in dehydration and starvation due to a lack of available food and water, which ultimately leads to death (Cryan *et al.* 2010, Ehlman *et al.* 2013, Verant *et al.* 2014, Hayman *et al.* 2017, McGuire *et al.* 2017). Despite the severity of WNS, effective immunological response appears to be limited in many bat species, and potentially limited to periods of arousal during hibernation, likely explaining the devastating impact that WNS is having on North American bat populations (Moore *et al.* 2013, Johnson *et al.* 2015, Lilley *et al.* 2017, Pikula *et al.* 2017). Histological findings do not vary significantly between North American bats and bats in regions where *Ps. destructans* is non-invasive, however, the outcome of acute infections is significantly worse in North America (Pikula *et al.* 2017). Evidence suggests that this is due to selective pressures placed on European bats by a historical exposure to *Ps. destructans* (Harazim *et al.* 2018).

Mitigation

To best prevent WNS from extirpating huge numbers of hibernating bat populations in North America it is essential that researchers develop effective mitigation strategies against the disease. Research into mitigation strategies has formed the third major component of WNS research to date. The bulk of this research aims to interrupt or prevent the spread of *Ps. destructans* across the landscape or to reduce the impact of WNS on individual hosts or poulations.

To date, most research on the mitigation of disease spread has focussed on limiting the potential for long distance transmission of *Ps. destructans* by humans who recreate in bat hibernacula. Decontamination protocols using both chemicals and heat have been assessed and proven to be effective at inactivating *Ps. destructans* (Shelley *et al.* 2013). A more diverse selection of research has focused on limiting the impacts of WNS in individual bats and whole populations. Much of this work has investigated the potential of microbial communities which inhabit skin to inhibit the growth of *Ps. destructans*. It has been shown that both the presence of the fungus and species level susceptibility to WNS correlate with the structure of wing microbial communities in bats (Lemieux-Labonté *et al.* 2017, Vanderwolf *et al.* 2020). This research has led to the development of probiotic treatment strategies which aim to augment the microbiomes of susceptible host species with microbial taxa that can inhibit the proliferation of *Ps. destructans* (Hoyt *et al.* 2015a, Cheng *et al.* 2017b, Hoyt *et al.* 2019). Research is also ongoing into the development of an orally administered vaccine which will be distributed throughout bat colonies by leveraging the social behaviours of bats such as grooming (Rocke *et al.* 2019).

Author: L.J. Campbell

79. **Podospora** Ces., Hedwigia 1(15): 103. 1856.

Type species: *Podospora fimiseda* (Ces. & De Not.) Niessl

Classification: *Ascomycota*, *Pezizomycotina*, *Sordariomycetes*, *Sordariales*, *Podosporaceae.*

Background

Podospora is a genus of saprotrophic fungi frequently found in soils, dung, decaying woody materials, and also as an endophyte in many different plants. The genus was introduced by Cesati (1856) and now belongs to the order *Sordariales* (accordingly *Podospora* species reproduce through the production of isolated perithecia coloured with greenish to black melanins). The genus has a complex history because the character used to define *Podospora* species (the form of the ascospore with one large darkly pigmented cell and an apoptosed smaller one-celled pedicel) proved to be highly homoplasic, hence rendering the genus polyphyletic with species now scattered among at least four families. Also, the type species of the genus has been debated (see Vogan *et al.* 2021b for a review). Wang *et al.* (2019d) introduced a new family, the *Podosporaceae*, with three genera: *Podospora* with the type species *Podospora fimicola*, *Cladorrhinum* with the type species *Cladorrhinum foecundissimum* and *Triangularia* with the type species *Triangularia bambusae.* This changed the name of several *Podospora* species, including one of the best-known species from *Podospora anserina* to *Triangularia anserina*. Yet, biologists working with this model continue (and likely will continue) to call it *Podospora anserina*. This prompted synonymising *Podospora*, *Cladorrhinum* and *Triangularia* (Ament-Velásquez *et al.* 2020) and hence *Podospora* now encompasses all species of the family *Podosporaceae*. In a second ongoing step, it is proposed to change the type species of the genus from *Po. fimicola* (syn. *Po. fimiseda*) to *Po. anserina* to conserve the name of this species if further taxonomic modifications are made (Vogan *et al.* 2021b).

Presently, there are over 200 species epithets recorded for *Podospora* in Index Fungorum (2022), but many of these do not belong to *Podospora*. Ongoing taxonomic revisions (Wang *et al.* 2019b, Marin-Felix *et al.* 2020b, Huang *et al.* 2021c) segregate the species into other genera such as *Schizothecium*, *Neoschizothecium* and *Pseudoechria* in the *Schizotheciaceae* or *Rhyphophila* in the *Naviculisporaceae*. Similarly, pending the decision on the type species of the genus, many other species may join *Podospora* (including *Triangularia bambusae*). Because of this taxonomic confusion and awaiting decisions regarding the type genus of *Podospora*, we will mostly focus in this entry on the fungus known to the general audience as *Po. anserina* (Silar 2020) and its sibling species of the *Po. anserina* species complex (Boucher *et al.* 2017).

There are seven species in the *Po. anserina* species complex: *Po. anserina*, *Po. comata*, *Po. pauciseta*, *Po. bellae-mahoneyi*, *Po. pseudoanserina*, *Po. pseudopauciseta* and *Po. pseudocomata* (Boucher *et al.* 2017). All thrive on herbivore dung, and these species may also be isolated from soil (P. Silar, unpubl. data), decaying matter (see for example Griffiths 1901) in which the fungus is called *Pleurage anserina*) or as endophyte (Matasyoh *et al.* 2011). Their closest relative appears to be *Cercophora samala*, which is also coprophilous (Udagawa & Muroi 1979). More distant species belonging to the "*Triangularia*" section of the *Podosporaceae*, such as *Podospora setosa* and *Arnium arizonense* (syn. *Podospora arizonensis*), which are also coprophilous, while others such as *Zopfiella tetraspora*, *Z. longicaudata*, *Triangularia bambusae*, *Apiosordaria backusii* or *A. verruculosa* are soil fungi. The species complex has a worldwide distribution and some geographic separation of the different species is likely (Boucher *et al.* 2017; note that prior to the Boucher *et al.* paper all members of the species complex were thought to belong to the same species limiting our knowledge of the actual division of each species). In Western Europe, the predominant species appears to be *Po. anserina. Podospora comata* can be found in the northern part of Europe (it can, for example, be found fairly frequently in the north of the Hauts-de-France, the most northern French region, but has yet to be found in the Southern regions); conversely, *Po. pauciseta* can be found fairly frequently in Camargue, one of the most southern regions of France but has not yet been isolated from other regions of Europe (P. Silar, unpubl. data).

All seven species are easy to cultivate and reproduce *in vitro* and two (*Po. anserina* and to a lesser extent *Po. comata*) have been used as experimental models to study mechanisms of sexual development, prion and prion-like biology, genome evolution, secondary metabolite production and the degradation of substrates, among others. However, *Po. anserina* is foremost known as an experimental model to study ageing. Indeed, *Po. anserina* in contrast to most other fungi is characterised by a limited lifespan (Rizet 1953). A vigorous thallus develops from a germinating ascospore by hyphal tip growth. After a strain-specific period of a few weeks, growth slows down until it completely stops and the peripheral hyphae die. This phenomenon is exhibited by all the strains of the species complex investigated.

Ecological and economic significance

Podospora anserina and its related species (including those of the "*Triangularia*" section of the *Podosporaceae*) are saprotrophic and live usually on dead decaying plant materials, although they can also be found as endophytes. Few are known to cause diseases in humans and animals and to the best of our knowledge, none are known to infect plants. Indeed, there is a single documented case of keratitis caused by these fungi, that of *Po. austroamericana* resulting in the removal of an eye in a patient (Rameshkumar *et al.* 2018). However, species more closely related to *Po. fimiseda* and known either as *Papulaspora* spp. or *Cladorrhinum* spp. can cause keratitis in horses and humans, albeit rarely (Shadomy & Dixon 1989, Reed *et al.* 2013, Selvin *et al.* 2014).

Sordariales fungi, including *Podospora* spp., are very common in the soil since they are among those most frequently identified in metagenomic analyses (Egidi *et al.* 2017). Unfortunately, we do not have a clear idea of the contribution of *Po. anserina* and related species of the *Podosporaceae* to this presence, since metagenomic analyses usually do not go beyond the identification of the species as belonging to *Sordariales* and they have not yet implemented the recently newly defined families. *Sordariales* species appear to be associated with soils in good health (see for example Liu *et al.*

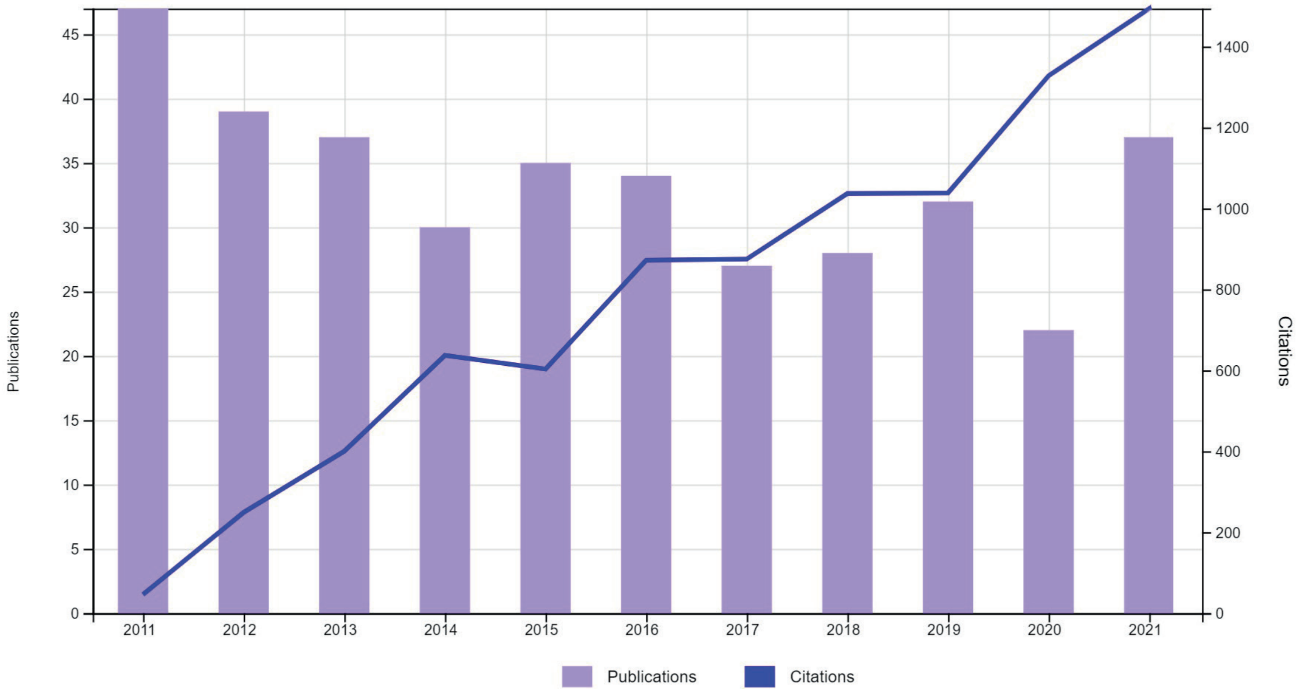

Fig. 109. Trends in research of *Podospora* in the period 2011–2021.

2019b). As stated above, *Po. anserina* and its related species may be isolated from soils. Nevertheless, they are mostly reported from dung from all regions around the world, on which they are very frequent (Mirza & Cain 1969).

Overall, *Po. anserina* and related species' importance and roles in the ecosystems, beyond the fact that they are ubiquitous and that they degrade dead plant materials, are poorly known. Note that they are not reported as being involved in damage to artefacts such as books, paintings and historical monuments. Also, since few have impacts on humans, farm animals and crop health they have limited economic significance apart from providing interesting enzymes and secondary metabolites for industrial purposes (Matasyoh *et al.* 2011). This genus is thus best-known thanks to *Po. anserina*, which is a very effective model system, especially in studies involving genetic studies, which prompted an early determination of its genome sequence and the development of genomic tools for this fungus (Bidard *et al.* 2011, Grognet *et al.* 2014a, Guevara *et al.* 2016, Espagne *et al.* 2018, Benocci *et al.* 2019).

Research interests

There are 368 publications and 7 890 citations from 2011–2021 in the Web of Science (Fig. 109), with the ten most cited articles listed in Table 85. The majority of the publications focused on four main

Table 85. Top 10 cited articles related to *Podospora* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Comparative genomics yields insights into niche adaptation of plant vascular wilt pathogens	314	Klosterman *et al.* (2011)
2	Horizontal transfer of a large and highly toxic secondary metabolic gene cluster between fungi	160	Slot & Rokas (2011)
3	Substrate specificity and regioselectivity of fungal AA9 lytic polysaccharide monooxygenases secreted by *Podospora anserina*	159	Bennati-Granier *et al.* (2015)
4	Age-dependent dissociation of ATP synthase dimers and loss of inner-membrane cristae in mitochondria	149	Daum *et al.* (2013)
5	Soil fungal community structure along a soil health gradient in pea fields examined using deep amplicon sequencing	138	Xu *et al.* (2012a)
6	Cello-oligosaccharide oxidation reveals differences between two lytic polysaccharide monooxygenases (family GH61) from *Podospora anserina*	125	Bey *et al.* (2013)
7	The mechanism of toxicity in HET-S/HET-s prion incompatibility	88	Seuring *et al.* (2012)
8	The [Het-s] prion of *Podospora anserina* and its role in heterokaryon incompatibility	85	Saupe (2011)
9	*Podospora anserina* hemicellulases potentiate the *Trichoderma reesei* secretome for saccharification of lignocellulosic biomass	76	Couturier *et al.* (2011)
10	Structural and biochemical analyses of glycoside hydrolase families 5 and 26 beta-(1,4)-mannanases from *Podospora anserina* reveal differences upon manno-oligosaccharide catalysis	69	Couturier *et al.* (2013)

topics: ageing, development, prion biology, and biodegradation of substrates.

Ageing

The basis of ageing of *Po. anserina* has been extensively investigated over more than 60 years and it has served as a model to unravel mechanisms of ageing and lifespan in biological systems from yeasts to humans. Since the ageing process is very complex and since various molecular pathways and many environmental factors impinge on lifespan, research on *Po. anserina* can be expected to provide significant novel clues in this field of biology in the future.

Ageing and lifespan of *Po. anserina* are controlled by environmental and genetic traits. Early investigations revealed both nuclear as well as extranuclear factors (Marcou 1961, Esser & Keller 1976). Since this time, investigations of the genetic basis of ageing in *Po. anserina* developed into a model organism in ageing research in which mechanisms of ageing on the organismic level are extensively studied. These studies uncovered a key role of mitochondria and a network of pathways controlling the quality of mitochondria which strongly affects the ageing process (Scheckhuber & Osiewacz 2008, Osiewacz & Schürmanns 2021). From these studies, a general knowledge of various molecular pathways was generated (Fischer *et al.* 2012). But more relevant pathways remain to be identified. In addition, interactions between the different pathways remain to be precisely unravelled. In this kind of work, the genetic modulation of *Po. anserina* via deletion or overexpression of selected genes and the analysis of the impact of such interventions was and will be instrumental to generate a holistic view of processes involved in ageing. This view will also in the future be of great value to investigate corresponding processes in other organisms including the human species (Osiewacz *et al.* 2013).

Mitochondrial DNA reorganisation

Investigations aimed at the identification of the genetic traits controlling the ageing process of *Po. anserina* identified mitochondrial DNA (mtDNA) as the genetic information that grossly rearranges during the ageing process. A covalently closed circular molecule, termed plasmid-like DNA (plDNA), was found to accumulate during ageing in mitochondria (Stahl *et al.* 1978, Cummings *et al*. 1979). In juvenile cultures, this DNA corresponds to the first intron of the gene coding for cytochrome c oxidase subunit I and becomes liberated and amplified as a circular plasmid (Kück *et al.* 1981, Osiewacz & Esser 1984). This element acts as a genetic mutator that reintegrates at specific “homing sites” into the mtDNA and generates duplicated sequences between which reorganisation processes occur leading to the deletion of large parts of the mtDNA (Kück *et al.* 1985, Sellem *et al.* 1993). During this process, essential mitochondrial genes are deleted leading to defective mitochondria.

Mitochondrial dynamics and ultrastructure

During the ageing of *Po. anserina* mitochondria change their morphology from branched filamentous to punctate units. Molecular interventions by deletion of the *PaDnm1*, which controls mitochondrial fission, were found to lead to a strong lifespan extension by increasing cellular resistance to the induction of apoptosis (Scheckhuber *et al.* 2007). Another series of experiments uncovered age-related changes in the ultrastructure of mitochondria. During ageing the inner mitochondrial membrane reorganises. Instead of mitochondria with a tubular cristae structure, mitochondria from old cultures have no cristae and contain vesicles inside the mitochondrial matrix (Brust *et al.* 2010, Daum *et al.* 2013, Strobel & Osiewacz 2013). These vesicles are thought to give rise to a disruption of the outer mitochondrial membrane releasing the content of the organelle to the cytoplasm and induction of apoptosis. The process of reorganisation of the inner mitochondrial membrane is linked to the impaired formation of F_1F_o-ATP-synthase dimers (Davies *et al.* 2011, Daum *et al.* 2013, Rampello *et al.* 2018, Warnsmann *et al.* 2021).

Oxidative stress and ROS scavenging

Reactive oxygen species (ROS), which are generated by metabolic processes (*i.e.*, respiration), are essential signalling molecules in organism development. However, if their abundance passes threshold limits, they are dangerous and cause molecular damage and contribute to biological ageing. In *Po. anserina* this aspect has been demonstrated in various studies. For instance, specific mutants which generate reduced mitochondrial superoxide free radical anions live longer than the wild type (Gredilla *et al.* 2006). Also, specific strains overexpressing ROS scavengers like carotinoids or the methyltransferase PaMTH1are protected against oxidative stress (Kunstmann & Osiewacz 2008, 2009, Strobel *et al.* 2009, Chatterjee *et al.* 2015). In contrast, overexpression of the mitochondrial superoxide dismutase gene *PaSod3*, did not lead to a lifespan increase demonstrating that a fine-tuned balancing of cellular ROS levels is of paramount importance for unimpaired development and growth (Zintel *et al*. 2010).

Proteases

During the lifespan of every organism, damage to cellular components accumulates. The degradation of damaged proteins and the resynthesis of functional ones can be beneficial. For the degradation of proteins, there are specific proteases active. In *Po. anserina* overexpression of the gene coding for the mitochondrial matrix protease PaLON was found to increase the health span. In this mutant, damaged aconitase, an essential enzyme of the Krebs cycle, was found to be degraded (Luce & Osiewacz 2009). Deletion of *PaLon* resulted in a short-lived phenotype (Adam *et al.* 2012). Studies investigating the role of two other mitochondrial proteases led to unexpected results. Deletion of the gene coding for the mitochondrial inner membrane protease PaIAP resulted in a lifespan increase. The same is true for the deletion of the two proteins PaCLPP and PaCLPX of the PaCLPXP complex. In the *PaIap* deletion strain, it was found that at laboratory growth temperature the respiratory super complexes were stabilised leading to the observed positive effect (Weil *et al.* 2011). This effect is not observed at increased growth temperature. In the *PaClpXP* deletion strains, the induction of autophagy as the vacuolar degradation of cellular material is induced and compensates for the loss of the ablated protease (Fischer *et al.* 2013). Recently, high confident substrates of the CLPXP were identified in *Po. anserina* (Fischer *et al.* 2015). The demonstration of some substrate overlaps in *Po. anserina*, the plant *Arabidopsis thaliana* and mice suggests some conservation in the function of this specific mitochondrial protease (Huang *et al.* 2020) which, in humans, is linked to cancer and hearing loss (Gispert *et al.* 2013, Cole *et al.* 2015).

Autophagy

More recent studies found that the expression of genes coding for components of autophagy first increases during ageing before decreasing in very old age. In parallel, the expression of genes coding for proteins of the proteasome decreases, suggesting that autophagy acts as a mechanism of compensation impairment in proteasomal functions (Philipp *et al.* 2013). The same compensation function of autophagy was found in cases in which other components (*e.g.*, PaSOD3, PaCLPXP) are affected in function (Knuppertz & Osiewacz 2017, Knuppertz *et al.* 2017). Ablation of PaATG1, a key protein involved in the control of autophagy, leads to a reduced lifespan (Knuppertz *et al.* 2014) demonstrating that autophagy is a longevity assurance mechanism. Moreover, autophagy induced by low-stress conditions was found to be beneficial while excessive stress leads to adverse effects resulting in "autophagy-dependent cell death" (ADCD) or "type-II programmed cell death (PCD)" (Kramer *et al.* 2016, Warnsmann *et al.* 2021). Autophagy, including selective autophagy of mitochondria (mitophagy), can be triggered by the addition of exogenous substances like curcumin and gossypol (Warnsmann & Osiewacz 2016, Warnsmann *et al.* 2018), or by the increase of endogenous oxidative stress resulting from induced impairments in mitochondrial functions (Rampello *et al.* 2018, Warnsmann *et al.* 2021). The mitochondrial peptidyl prolyl-cis,trans-isomerase (cyclophilin D, PaCYPD) was found to be active in the induction of ADCD (Kramer *et al.* 2016).

Apoptosis

In *Po. anserina* an apoptosis-like form of programmed cell death, termed "type-I programmed cell death (PCD)", is also active (Hamann *et al.* 2008). Generally, specific proteins (caspases, metacaspases) control this process (Minina *et al.* 2020). In *Po. anserina*, two copper-dependent metacaspases, different "apoptosis-inducing factors", and cyclophilin D, are components involved in this form of PCD (Hamann *et al.* 2007, Brust *et al.* 2010a, b).

Podospora anserina as a model for studying incompatibility, regulated cell death and amyloid prion propagation and structure

Podospora anserina has been developed as a model species for the study of heterokaryon incompatibility since the late 1940s by Georges Rizet and Jean Bernet in particular (Rizet 1952, Bernet 1965). Incompatibility denotes the occurrence of a cell death reaction following cell fusion between two distinct strains. This allorecognition process is genetically controlled by so-called *het* loci. With *Neurospora crassa* and *Cryphonectria parasitica*, *Podospora anserina* is a species in which the molecular aspects of incompatibility have been most studied (Daskalov *et al.* 2017). Genetically, nine *het* loci have been identified in that species (*het-b*, *c*, *d*, *e*, *q*, *r*, *s*, *v*, *z*) and of those eight have currently been characterised at the molecular level (*het-c*, *d*, *e*, *q*, *r*, *s*, *v*, *z*) (Pinan-Lucarre *et al.* 2007). Genetically, incompatibility can result from allelic interactions (between two antagonistic alleles) or non-allelic interactions (between alleles of distinct unlinked genes). In one case, however, the apparent allelic interaction (*het-z1/het-z2*) was found to be pseudo-allelic and to involve interaction between distinct but tightly linked genes (Heller *et al.* 2018). In line with their biological role in non-self-recognition, incompatibility genes in *Podospora* appear subjected to positive selection (diversifying and/or balancing selection), a situation also described in *Neurospora crassa* and *Cryphonectria parasitica* (Wu et *al.* 1998, Paoletti *et al.* 2007, Bastiaans *et al.* 2014, Zhao *et al.* 2015b, Milgroom *et al.* 2018, Ament-Velásquez *et al.* 2022). Some general trends have emerged from the characterisation of the *het*-genes in *Po. anserina*, which at least in some instances seems to apply also to other species. Several domains and domain architectures identified in *het*-gene encoded proteins are also found in immune signalling cascades from metazoans and plants (Daskalov 2023). Several of the *het* loci encode for proteins with a NLR domain architecture (Espagne *et al.* 2002, Chevanne *et al.* 2009, Saupe *et al.* 2015, Heller *et al.* 2018). Nod-like receptors are intracellular immune receptors controlling host defence and immune cell death both in animals and plants, they display a tripartite domain architecture associating an N-terminal effector domain to a central NOD (nucleotide-binding and oligomerisation domain) and C-terminal superstructure forming repeats (most often of the LRR, leucine-rich repeat type) (Jones *et al.* 2016). Filamentous fungi contain large and diversified repertoires of genes encoding proteins with related architectures (although the superstructure forming repeats are generally of the ANK, TPR or WD-type) and their identification as incompatibility genes has shown that at least some of them also have roles in non-self-recognition and regulated cell death similar to their animal and plant counterparts (Dyrka *et al.* 2014, Daskalov *et al.* 2020). The HET domain which has a role in cell death execution (Paoletti & Clave 2007), was identified in many different *het*-genes in *Podospora* and other species (Smith *et al.* 2000a) and shows a remote homology with the TIR domain which is found in various immune-related proteins in plants and animals (Dyrka *et al.* 2014). Characterisation of the *het-s* gene of *Po. anserina* also led to the identification of a prion system in that fungus and subsequently of related prion-forming domain in the same species and a range of other filamentous fungi (Coustou *et al.* 1997, Saupe 2020). The *het-s* locus displays two incompatible alleles termed *het-s* and *het-S*. The HET-s protein can exist under a soluble state [designated (Het-s*)] and an infectious aggregated prion state (Het-s). Incompatibility is triggered when the prion form of HET-s interacts with the HET-S and converts its prion forming region to the amyloid fold (Seuring *et al.* 2012). This conformational transition in turn induces activation of the N-terminal HeLo domain which targets the cell membrane and induces cell death as a pore-forming toxin. Importantly, the HeLo domain shows homology to membrane-targeting cell-death execution domains acting in plant and animal immune cell death pathways (Daskalov *et al*. 2016, Hofmann 2020). There is another pathway that can lead to the activation of HET-S and involves a NLR protein termed NWD2 encoded by the gene immediately adjacent to *het-s* and relying on an amyloid signalling mechanism found in *Podospora* but also in many other filamentous fungi (Daskalov *et al.* 2015). The *het-s* system also displays an effect during the sexual cycle as the *het-s* gene was found to behave as a meiotic drive element leading to spore-killing (Dalstra *et al.* 2003), the mechanism of spore-killing appears based on the same mechanism as the cell death observed in incompatibility and to differ from the other spore-killing systems described in *Po. anserina* (Grognet *et al.* 2014b, Vogan *et al.* 2019). As the characterisation of *het*-genes progresses, it becomes possible to propose a general scheme for the emergence of these allorecognition systems. What is currently believed is that these systems are derived by exaptation from genes that are part of the general fungal immune system and that in particular control regulated cell death in the context of host defense (Paoletti & Saupe 2009, Daskalov & Saupe 2015, Clavé *et al.* 2022, Daskalov 2023). The C-terminal prion forming domain of HET-s [HET-s(218–289)] has also become a relatively popular model system to study various aspects of the biophysics of amyloids (see for instance Wan & Stubbs 2014, Walti *et al.* 2017, Terruzzi *et al.* 2020). In particular, the structure of the amyloid state of the HET-s prion forming domain solved by solid state NMR has arguably been the first high-resolution structure of a prion to be established (Wasmer *et al.* 2008).

Podospora anserina as a model to study sexual reproduction

Podospora anserina has also been instrumental in understanding sexual reproduction in ascomycetes. Although it was not the first fungus for which the mating type loci were identified, it has been used to analyse the molecular and cellular pathways enabling sexual mating compatibility (Debuchy & Coppin 1992, Debuchy *et al.* 1993, Zickler *et al.* 1995, Martin *et al.* 2010, Ait Benkhali *et al.* 2013). This includes both the role of the mating pheromones (Coppin *et al.* 2005) and the deciphering of the network of HMG transcription factors, including those located at the mating type locus, which controls their expression (Ait Benkhali *et al.* 2013). Knowledge of mating type biology led to the construction of a self-fertile strain in which recessive mutations affecting zygotic development could easily be obtained (Xie *et al.* 2017b). Also, methods based on genetic mosaics and sporulation grafting (Silar 2011, 2014) and powerful cytological methods (see Thompson-Coffe & Zickler 1994, López-Fuentes *et al.* 2021 as examples) enable to delineate finely the tissues and stages at which proteins involved in development are required. Overall, *Po. anserina* has contributed to uncover the roles of organelles (*e.g.*, peroxisomes, mitochondria and endoplasmic reticulum; reviewed in Navarro-Espíndola *et al.* 2020, see also López-Fuentes *et al.* 2021), homeobox transcription factors (Coppin *et al.* 2012), MAP kinase pathways (Lalucque *et al.* 2012) and inositol phosphate signalling (Xie *et al.* 2017b) among others to build and to shape the sporocarps.

Podospora anserina and the study of genome evolution

Podospora anserina was among the first species for which a high-quality nuclear genome sequence was available, at first only for the *S mat*+ homokaryon (Espagne *et al.* 2018) and later on for the *S mat*- one (Grognet *et al.* 2014a). This was in line with the fact that its complete 100-kb mitochondrial genome sequence was determined as early as the 1980s (Cummings *et al.* 1990). The availability of both sequences, in addition to boosting reverse genetic and enabling microarray/RNAseq analyses in the case of the nuclear genome sequence, triggered several studies dealing with genome content and evolution. Among the significant results obtained, one can cite the demonstration that mitochondrial group II introns are transposons (Sellem *et al.* 1993), the finding that the recombination inhibition in the region surrounding the mating type was not associated with an inversion complex (Grognet *et al.* 2014a), is labile and vary between strains of *Po. anserina*, but also of its sibling species (Hartmann *et al.* 2021b) or that spore killer genes shape the genomes (Vogan *et al.* 2019) and especially are likely involved in the propagation of massive transposon-like elements (Vogan *et al.* 2021b). Importantly, these three latter studies (Vogan *et al.* 2019, 2021b, Hartmann *et al.* 2021a) involved the determination of genome sequence for several strains of *Po. anserina* and its sibling species, providing tools to further study genome evolution. A recent study indicated that *Po. anserina* populations are split into two reproductively isolated groups as a result of sexual incompatibility arising as a by-product of heterokaryon incompatibility (Ament-Velásquez *et al*. 2022).

Podospora anserina and biomass degradation

Determination of *Po. anserina* genome sequence showed that it is endowed with a large repertoire of enzymes involved in plant biomass degradation, including several auxiliary enzymes involved in lignin breakdown (Espagne *et al.* 2018). Accordingly, this fungus has recently been shown to break down lignin (Dicko *et al.* 2020, Van Erven *et al.* 2020). Owing to this large repertoire and the ease of its genetic and biochemical manipulation, *Po. anserina* is now a convenient model used to study biomass breakdown (Couturier *et al.* 2016). Research on biomass breakdown with *Po. anserina* has followed three main lines of investigation. Firstly, fine biochemical characterisations were made on several enzymes involved in polysaccharide breakdown (see Couturier *et al.* 2016 for a review). Secondly, studies aimed to develop enzymatic cocktails to breakdown biomass were reported (Mäkelä *et al.* 2017). Finally, reverse genetic studies involving targeted deletion of several genes potentially involved in cellulose and/or lignin break down have for example evidenced the crucial role *in vivo* of catalases and multicopper oxidases for efficient biomass degradation (Bourdais *et al.* 2012, Xie *et al.* 2014, 2015).

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80. ***Amanita*** Pers., Neues Mag. Bot. 1: 145. 1794.

Type species: *Amanita muscaria* (L.) Lam.

Classification: *Basidiomycota*, *Agaricomycotina*, *Agaricomycetes*, *Agaricales*, *Amanitaceae.*

Background

Amanita is a well-known and globally distributed basidiomycete genus encompassing species producing mostly epigeous, ballistosporic, or in rare cases hypogeous statismosporic sporocarps. Approximately 1 600 taxa are registered in Index Fungorum (2022), about 600 of which are thought to be good species (Cui *et al*. 2018, Yang *et al*. 2018c). Although the genus is phenotypically diverse, the majority of species produce stipitate and pallid-spored basidiocarps with a schizohymenial ontogeny, with basidiocarps typically emerging from an ephemeral universal veil, the remnants of which are usually preserved at the base of the stipe in the form of a discrete “volva”. However, the universal veil can be adnate in some species leaving no obvious volva at the base, while a handful of taxa produce sequestrate or non-stipitate cleistocarpic basidiocarps. Microscopically, species are characterised by bilateral lamellar trama, hyaline basidiospores, and clavate or long-clavate (acrophysalidic) cells in the tissue, usually more prominent in the stipe trama (Bas 1969, Yang & Oberwinkler 1999, Tulloss *et al*. 2016, Cui *et al*. 2018, Yang *et al*. 2018c).

Most species of the genus are symbiotic, forming ectomycorrhizal (EcM) associations with a wide range of trees and shrubs, mostly members of the *Betulaceae*, *Fagaceae*, *Myrtaceae*, *Nothofagaceae* and *Pinaceae* (Cripps & Miller 1995, Yang *et al.* 2000, Neville & Poumarat 2004, Tedersoo *et al*. 2010a, Wolfe *et* al. 2012b, Cui *et al.* 2018, Hyde *et al.* 2018b). *Quercus* and certain members of *Pinaceae*, in particular, are important hosts (Tulloss 2005). Some taxa are known from Arctic and Alpine dwarf-shrub (*Rosaceae*, *Salicaceae*) ecosystems (Gulden *et al*. 1985, Watling 1985, 1987, Knudsen & Borgen 1987, Hutchison *et al*. 1988, Cripps & Horak 2010), while others, especially in the Mediterranean region, are broadly or strictly associated with shrubs of the *Cistaceae* family such as *Cistus*, *Halimium* and *Helianthemum* (Comandini *et al*. 2006, Loizides 2016, Vizzini *et al*. 2016, Leonardi *et al*. 2020). In sect. *Lepidella* (subg. *Lepidella*), on the other hand, species like *Am. pruittii*, *Am. thiersii*, or *Am. vittadinii*, are putative saprotrophs and grow without the presence of an obvious host (Wolfe *et al*. 2012a, b, Redhead *et al*. 2016, Tulloss *et al*. 2016, Vizzini *et al*. 2017). While some species like *Am. phalloides* show considerable ecological plasticity with a transcontinental distribution and an invasive potential (Pringle & Vellinga 2006, Wolfe *et al*. 2009), other species-aggregates like *Am. caesaria s. lat.* or *Am. muscaria s. lat.*, encompass several regionally endemic cryptic lineages with highly specific ecological niches (Geml *et al*. 2006, Sánchez-Ramírez *et al*. 2015). Most of these lineages appear to be climatic refugia that formed as a result of fragmentation and geographic isolation of the ancestral populations, formed by the dramatic climate fluctuations in the late Tertiary and Quaternary (Geml *et al*. 2008, Sánchez-Ramírez *et al*. 2015).

With the advent of molecular phylogenetics, a great deal of cryptic and previously overlooked diversity has been recognised, and the number of described taxa in the genus has significantly increased (Wartchow *et al*. 2009, Cho *et al*. 2015, Hosen *et al*. 2015, Wartchow & Cortez 2016, Truong *et al*. 2017, Cui *et al*. 2018, Kiran *et al.* 2019a, b, Mighell *et al*. 2019, Jabeen *et al*. 2019). Especially in the species-rich sect. *Vaginatae* (subg. *Amanita*), large numbers of previously undescribed lineages have been detected, the majority of which appear to be highly regionalised or continentalised (Davison *et al*. 2015a, Malysheva & Kovalenko 2015, Tang *et al*. 2015, Mehmood *et al*. 2016, Cui *et al*. 2018, Lambert *et al*. 2018, Liu *et al*. 2017b, Crous *et al*. 2018, 2020, 2021, Loizides *et al*. 2018, Thongbai *et al*. 2018, Hanss & Moreau 2020, Ševčíková *et al*. 2021).

Ecological and economic significance

The genus is remarkable in that it accommodates some of the most potently toxic fungi exemplified by the highly lethal *Am. phalloides*, but also prime edibles of economic value. Species of *Amanita* are responsible for most human poisonings and fatalities by fungi worldwide. Moreover, due to their psychoactive properties, the fly agaric (*Amanita muscaria*) and related species have long been used by humans as entheogens and occupy a central place in ethnomycology. According to Wasson (1968), the Soma, as described in the Vedic hymns, strongly resembles *Am. muscaria*. The sacralisation of the “inebriating” urine of the consumer, as well as the metaphorical use inspired by the red colour of the fungus, seem to corroborate this hypothesis. The psychoactive properties of *Am. muscaria* are now better understood from a toxicological perspective: inebriating, prostration, hallucinations or coma partly define the neurotoxic effects of this poisoning syndrome. Ibotenic acid and muscimol, the two compounds responsible for the psychoactive properties of *Am. muscaria*, are indeed present in urine (Eugster *et al*. 1965). Ethnographers report that its usage must have been widespread due to recent accounts of its entheogenic use by some Finno-Ugric North European populations (Saar 1991); after consumption of the fungus, the urine of the shaman would be highly esteemed for its effects. Its origins as an entheogen might be traced to the Indo-Iranian peoples of Eurasia, linguistically demonstrated by many borrowings from Uralic languages. Wasson (1968) detected the verbal form “Pon” which connotes the mushroom, the drum of the shaman, the drunkenness, which might be the origin of the Greek word “sphongos” and the Latin word “fungus” (Jacquession 2016). On this somewhat speculative basis, Wasson proposed the entheogenic theory of religions, later popularised and discussed by Lévi-Strauss (1973).

On another note, several species of the genus are edible, either raw or cooked. Because the most prized *Amanita* species are mostly endemic and decay quickly after picking, they are only sold fresh in local markets and do not contribute significantly to the international mushroom trade, representing only 4 % out of an estimated ~1 018 edible species worldwide (Pérez-Moreno & Martínez-Reyes 2014). For instance, the highly sought-after Caesar’s mushroom (*Am. caesarea*) is endemic to western Europe and the Mediterranean basin (Neville & Poumarat 2004) and is sold at local markets for 10–15 US dollars in Turkey (where its harvest was estimated at 33.365 kg in 2019), or 30–100 US dollars in France (Yilmaz & Zenrici 2016, NWFP 2020). Relatives of *Am. caesarea* in Asia and Australia (*Am. caesareoides*, *Am. hemibapha*), as well as North and Central America (*Am. basii*, *Am. hayalyuy*, *Am. laurae*, *Am. yema*), are all locally marketed (Ruan-

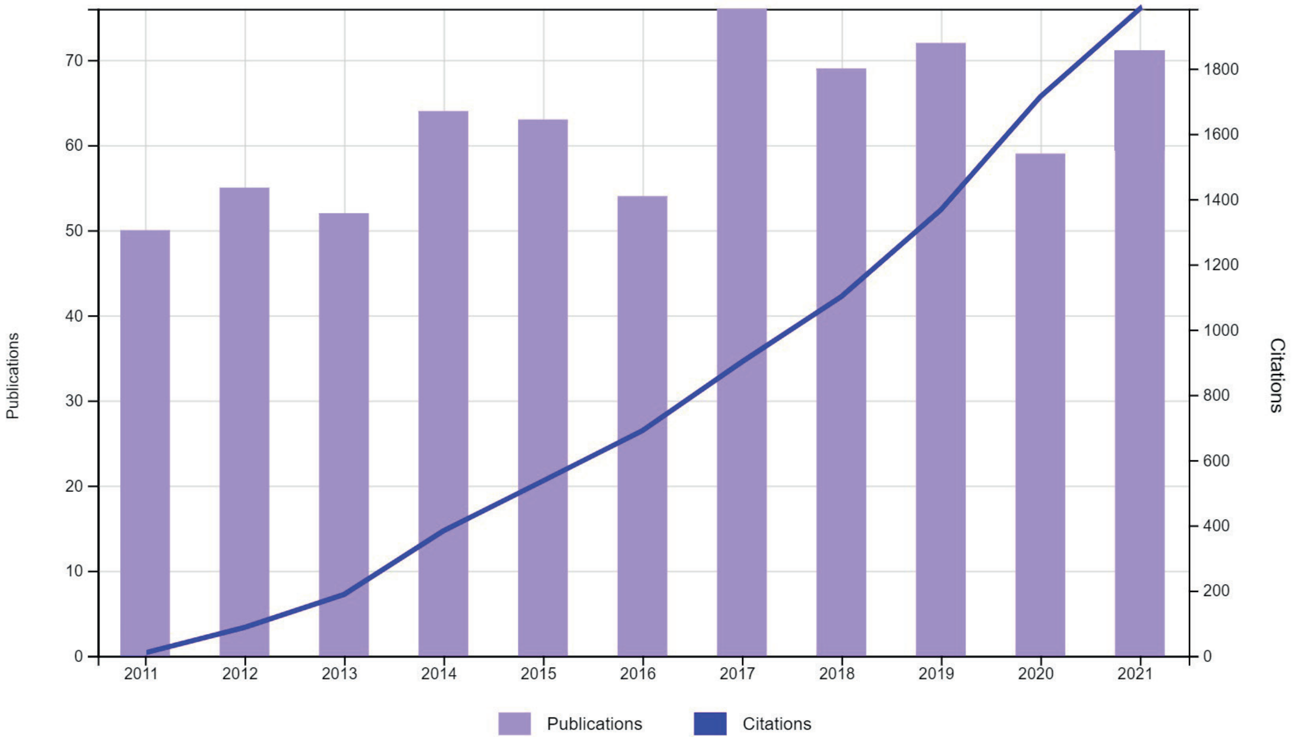

Fig. 110. Trends in research of *Amanita* in the period 2011–2021.

Table 86. Top 10 cited articles related to *Amanita* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Current findings, future trends, and unsolved problems in studies of medicinal mushrooms	267	Wasser (2011)
2	Biosynthesis of betalains: yellow and violet plant pigments	168	Gandia-Herrero & Garcia-Carmona (2013)
3	Evaluation of umami taste in mushroom extracts by chemical analysis, sensory evaluation, and an electronic tongue system	154	Phat *et al.* (2016)
4	Plant betalains: Chemistry and biochemistry	133	Khan & Giridhar (2015)
5	Invasive belowground mutualists of woody plants	113	Nunez & Dickie (2014)
6	Chemical and antioxidant properties of betalains	100	Belhadj Slimen *et al.* (2017)
7	The irreversible loss of a decomposition pathway marks the single origin of an ectomycorrhizal symbiosis	82	Wolfe (2012b)
8	Investigation and analysis of 102 mushroom poisoning cases in Southern China from 1994 to 2012	80	Chen *et al*. (2014e)
9	Community composition of root-associated fungi in a *Quercus*-dominated temperate forest: codominance of mycorrhizal and root-endophytic fungi	80	Toju *et al.* (2013)
10	Multi-locus phylogeny of lethal amanitas: Implications for species diversity and historical biogeography	77	Cai *et al.* (2014)

Soto 2018b, Haro-Luna *et al*. 2019). In southwest Africa, *Am. loosii* is a common species of tropical forests (Miombo woodlands) where it is commonly consumed (Walleyn & Verbeken 1998). However, the most commercially important species of *Amanita* worldwide might be *Am. ponderosa*, a sub-hypogeous spring-fruiting fungus endemic to the southwest Iberian Peninsula (Europe). Locally known as “gurumelo”, *Am. ponderosa* is highly esteemed, fetching the highest commercial yield of a wild mushroom in southern Spain at 631.543 kg/year, or 11 367 776 euros (about 12.5 million US dollars) in the province of Huelva alone (Junta de Andalucia 2019).

Research interests

There are 685 publications and 7 672 citations from 2011–2021 in the Web of Science (Fig. 110), with the 10 most cited articles listed in Table 86. The majority of the publications focused on the properties of chemical compounds identified from *Amanita* sporocarps (Wasser 2011, Phat *et al*. 2016). Betalains, a family of chromo-alkaloid pigments, are cited as an example of biochemical evolutionary convergence between *Amanita muscaria* (in which betalains are responsible for the red colour of the pileus surface), and plants of the *Caryophyllaceae* family.

Toxins and poisoning syndromes

White *et al*. (2018) recently proposed a revised clinical classification of mushroom-poisoning syndromes, in which three distinct syndromes are caused by species of *Amanita*. The species responsible for each syndrome belong to the same phylogenetic clades and corresponding sections, indicating a common evolutionary origin of the toxins implicated in each syndrome.

Cytotoxic poisoning — primary hepatotoxicity: Cyclopeptide containing species in *Amanita* sect. *Phalloideae* such as the transcontinental *Am. phalloides*, the European *Am. verna, Am. vidua* and *Am. virosa*, the North American *Am. bisporigera* and *Am. ocreata*, and the East Asian *Am. exitialis* and *Am. fuliginea*, are responsible for the overwhelming majority of mushroom-poisoning fatalities worldwide (Broussard *et al*. 2001, Karlson-Stiber & Persson 2003, Cui *et al*. 2018, Alvarado *et al.* 2022). Additional species including *Am. amerivirosa*, *Am. arocheae*, *Am. eburnea*, *Am. elliptosperma*, *Am. fuligineoides*, *Am. hygroscopica*, *Am. longitibiale*, *Am. magnivelaris*, *Am. pallidorosea*, *Am. subjunquillea*, *Am. suballiacea*, *Am. tenuifolia* and *Am. virosiformis* have also been found or are suspected to contain cyclopeptides, with the highest concentrations detected in *Am. rimosa*, up to four times higher than in *Am. phalloides* (Ammirati *et al*. 1977, Tulloss 1989, Tulloss *et al*. 1992, 1995, Karlson-Stiber & Persson 2003, Zhou *et al*. 2017d, Tang *et al*. 2016, Tulloss & Yang 2022). Although three groups of toxins are present, namely amatoxins, phallotoxins and virotoxins, the latter two seem to contribute little to poisoning. Amatoxins and especially α-amanitine on the other hand, are thermostable, rapidly absorbed through the gut, and inhibit RNA polymerase II, leading to disintegration of nucleoli and ultimately to massive hepatic central lobular cell necrosis (Fineschi 1996, Vetter 1998, Hallen *et al*. 2007, Garcia *et al*. 2015). Intoxication is biphasic, first presenting with severe gastrointestinal symptoms after a latent period of 8–24 h, followed by acute hepatic failure 36–48 h after ingestion, often accompanied by pronounced hyperbilirubinemia, hyperammonemia, renal failure, metabolic acidosis, hypoglycemia, mucosal haemorrhage, thrombocytopenia, encephalopathy and coma (Benjamin 1995, Santi *et al*. 2012, Garcia *et al*. 2015). The severity of the poisoning is dose-dependent and early onset of symptoms < 8 h is associated with a poor prognosis, for which liver transplantation should be considered (Escudié *et al*. 2007). Despite decades of research, an effective antidote remains elusive. Several symptomatic and supportive treatments have been tried (benzylpenicillin, ceftazidime, cimetidine, N-acetylcysteine, thioctic acid, silybin), all with questionable or suboptimal clinical efficacy and mortality rates remain high at 10–30 % (Enjalbert *et al*. 2002, Tong *et al*. 2007, Poucheret *et al*. 2010).

Cytotoxic poisoning — primary nephrotoxicity: Some species in sect. *Roanokenses*, including the Mediterranean *Am. proxima* and the North American *Am. smithiana*, are nephrotoxic (Tulloss & Lindgren 1992). *Amanita proxima* contains allenic norleucine, an aminohexadienoic acid (AHDA) causing early onset gastrointestinal symptoms, followed by delayed onset renal failure and mild cytolytic hepatitis (Leray *et al*. 1994, Ducros *et al*. 1995, De Haro *et al*. 1998, Courtin *et al*. 2009). Poisoning from *Am. smithiana* is similar, but there is some evidence that the toxin involved might not be identical (Kirchmair *et al*. 2011). Although renal failure is in most cases reversible, it is severe enough to require dialysis and can potentially be fatal (Saviuc & Danel 2006, West *et al*. 2009). *Amanita boudieri*, *Am. gracilior*, *Am. echinocephala*, *Am. neoovoidea* and *Am. oberwinklerana* are probably also nephrotoxic (Kirchmair *et al*. 2011, Fu *et al*. 2017, Lee *et al*. 2018, Wang *et al*. 2020b). Reports implicating *Am. ovoidea* in a number of poisonings (Biagi *et al*. 2014, Li Cavoli *et al*. 2019) are controversial, and its purported toxicity requires more thorough investigations (Riccioni et al. 2019, Loizides *et al*. 2022).

Neurotoxic poisoning — central nervous system neuroexcitatory mushrooms: In sect. *Amanita*, species in the *Am. pantherina s. lat.* and *Am. muscaria s. lat.* aggregates, including a number of undescribed or provisionally named species, as well as *Am. ibotengutake*, *Am. inzengae*, *Am. multisquamosa* and possibly *Am. albocreata*, *Am. gioiosa*, *Am. gemmata*, *Am. parvipantherina*, *Am. pseudopantherina* and *Am. subglobosa*, are neurotoxic (Cornué 1961, Chilton & Ott 1976, Oda *et al*. 2002, Hiroshima *et al*. 2010, Cui *et al*. 2018, Vohra *et al*. 2021, Tulloss & Yang 2022). The psychoactive compounds involved are ibotenic acid and muscimol (isoxazoles), the former acting as a non-selective glutamate receptor agonist and the latter as a selective $GABA_A$ receptor agonist (Michelot & Melendez-Howell 2003). Symptoms appear 30 min to 2 h after ingestion and are unpredictable. They may include drowsiness, nausea, sweating, salivation, vomiting, euphoria, confusion, lethargy, agitation, ataxia, irritability, obtundation, distorted time/space perception and visual/auditory hallucinations, but more serious symptoms like low blood pressure, prolonged psychosis and tonic-clonic seizures followed by coma can also occur (Benjamin 1992, Michelot & Melendez-Howell 2003, Satora *et al*. 2005, Brvar *et al*. 2006). Although fatalities are rare, regular use for recreational purposes might be harmful, and brain lesions in rodents treated with ibotenic acid and muscimol have been reported (Lescaudron *et al*. 1992).

Taxonomy and phylogeny

The systematic classification of *Amanita* has fluctuated over the years and the genus had been either arranged into infrageneric divisions by some authors or split into segregate genera by others (Gray 1821, Roze 1876, Gilbert 1940, Konrad & Maublanc 1948, Bas 1969, Singer 1986). A series of phylogenetic studies in recent years have demonstrated that the genus is monophyletic and subdivided into two highly supported clades, broadly corresponding to subgenera *Amanita* and *Lepidella* (Weiß *et al*. 1998, Drehmel *et al*. 1999, Moncalvo *et al*. 2000, 2002, Zhang *et al*. 2004, Wolfe *et al*. 2012b, Yang *et al*. 2018c). A few sequestrate and hypogeous taxa formerly ascribed to genera *Torrendia* (Bresadola 1902) and *Amarrendia* (Bougher & Lebel 2002) have also been shown to nest within the *Amanita* clade (Justo *et al*. 2010). Redhead *et al*. (2016) introduced the new genus *Saproamanita* for non-EcM species, a split that was contested by others (Tulloss *et al*. 2016, Yang *et al*. 2018c, Riccioni *et al*. 2019) who treated the clade as subgenus *Lepidella*. More recently, Cui *et al*. (2018) proposed a rearrangement of the genus into three subgenera and eleven sections based on five-locus phylogeny: subgen. *Amanita*, encompassing sections *Amanita*, *Amarrendiae*, *Caesareae* and *Vaginatae*; subgen. *Amanitina*, encompassing sections *Amidella*, *Arenariae*, *Phalloideae*, *Roanokenses*, *Strobiliformes* and *Validae*; and subgen. *Lepidella* encompassing section *Lepidella*. Considering phylogenetic relationships within *Amanitaceae* are still largely unresolved, but also that more than two genera and major nomenclatural disruptions would be needed should *Amanita* be split, it seems prudent that the three major clades are tentatively treated as subgenera and the taxonomic arrangement proposed by Cui *et al*. (2018) is for the time being endorsed. A phylotaxonomic revision of west-European *Vaginatae* has recently been published by Hanss & Moreau (2020), but the taxonomy in this challenging group also remains largely unresolved, especially with regard to seminal taxa like *Am. vaginata* and *Am. mairei* which are yet to be genetically characterised and epitypified.

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81. ***Cercospora*** Fresen. *ex* Fuckel, Hedwigia 2(15): 133. 1863.

Type species: *Cercospora apii* Fresen.

Classification: *Ascomycota*, *Pezizomycotina*, *Dothideomycetes*, *Mycosphaerellales*, *Mycosphaerellaceae.*

Background

Cercospora is one of the largest genera of plant pathogenic hyphomycetes (Jayawardena *et al.* 2020) with more than 3 000 species epithets listed in Index Fungorum (2022), with about 700 recognised species (Crous & Braun 2003). Species of *Cercospora* are commonly associated with leaf spots, causing disease on many economically important crops worldwide (Agrios 2005, To-Anun *et al.* 2011, Groenewald *et al.* 2013, Bakhshi *et al.* 2015a, 2018, Braun *et al.* 2020, Senwanna *et al.* 2021, Vaghefi *et al.* 2021). They are especially abundant in humid, tropical and subtropical regions of the world (Crous & Braun 2003, Groenewald *et al.* 2013, Bakhshi *et al.* 2015a, b, Nguanhom *et al.* 2016). Some species of *Cercospora* produce a nonspecific photosensitising perylenequinonoid toxin called cercosporin which enhances the virulence of the pathogen (Kuyama & Tamura 1957, Chen *et al.* 2007, Santos Rezende *et al.* 2020). Cercosporin can absorb light and converts itself to an excited state, which then reacts with oxygen to form both radical and nonradical species of activated oxygen. The activated oxygen then causes damage to the host plant and provides nutrients for fungal growth and propagation (Daub & Hangarter 1983, Daub & Ehrenshaft 2000, Tang *et al*. 2019).

Warm and wet conditions provide an ideal environment for disease development. The important primary source of inoculum is from infected residues in the field. Spores are dispersed by wind, rain splash and irrigation water, or mechanically by humans and equipment. The diseases cause necrotic lesions on leaves, flowers, fruits, seeds, bracts, and pedicels of the host. The symptoms initially formed are small water-soaked or chlorotic lesions, circular to angular, with or without a distinct border, mostly with red-purple to dark brown margins. As the disease progresses, the spots either stay relatively small and separate with an ashy-grey, thin, papery and brittle centre or individual spots enlarge and coalesce, resulting in leaf blights. Concentric rings may be observed. When the disease is severe, the leaves fall and crop yield is reduced (Crous & Braun 2003, Westphal *et al.* 2006, Groenewald *et al.* 2013).

Cercospora was introduced by Fresenius (in Fuckel 1863) with pigmented conidiophores, conspicuous (thickened and darkened) conidiogenous loci and hyaline scolecosporous conidia with thickened and darkened hila (Braun *et al*. 2013, Bakhshi *et al*. 2015a). Comparatively, only a few sexual morphs have been studied (Hyde *et al*. 2013, Vale *et al.* 2021). The first monograph of cercosporoid hyphomycetes was published by Chupp (1954) which followed a very broad generic concept. He reduced many cercosporoid genera to synonymy with *Cercospora*, and also used host specificity to describe and identify new species when they were found on different hosts (Bakhshi *et al.* 2015a). The number of *Cercospora* species increased rapidly to more than 3 000 when Pollack (1987) published her annotated list of *Cercospora* names. The generic concept of *Cercospora s. str.* was continuously revised and divided into smaller generic units by applying a combination of characteristics including mycelia, conidiomatal structures, conidiophores, conidiogenous cells and conidia (Deighton 1967, 1973, 1976, 1990, Ellis 1971, 1976, Braun 1995). Crous & Braun (2003) reviewed the cercosporoid genera and used the structure of conidiogenous loci and hila as well as the absence or presence of pigmentation in conidiophores and conidia as the most important characters in their revision of *Cercospora* and *Passalora*. They recognised 659 species of *Cercospora s. str.*, with a further 281 names referred to synonymy with *Ce. apii* as they were morphologically indistinguishable (Crous & Braun 2003). Modern accounts of *Cercospora* and allied genera based on morphological features and host data were published by Braun *et al*. (2013, 2014, 2015a, b, 2016). With the implementation of molecular analyses, Groenewald *et al.* (2013) conducted a comprehensive molecular examination of *Cercospora s. str.* based on a multi-locus DNA sequence dataset (ITS, *act*, *cal*, histone, and *tef*1 genes). They stated that several species previously referred to *Ce. apii s. lat.* based solely on morphology (Crous & Braun 2003) were separated as different phylogenetic species (Groenewald *et al.* 2013). Bakhshi *et al.* (2015b) elucidated a cercospora-like taxon to represent a new genus, *Neocercospora*, by applying the consolidated species concept (Quaedvlieg *et al.* 2014). These findings led to the conclusion that a polyphasic approach including multi-locus DNA sequences, ecology, morphology and culture characteristics are necessary for delimitation of *Cercospora* species.

Ecological and economic significance

Cercospora species cause numerous economically important plant diseases and three are detailed below.

Cercospora leaf spot of sugarbeet (*Beta vulgaris*) caused by *Cercospora beticola* is one of the most destructive and common foliar diseases worldwide. Infected sugarbeet results in substantial root yield losses and extracted sucrose from the reduction of photosynthetic capacity (Sheane & Teng 1992, Franc 2010). The disease caused 6.29 trillion US dollars in losses from yield and quality reduction, and higher cultural practices and disease management costs in 1998 in ten countries (Wrather *et al*. 2001, Secor *et al.* 2010). Although the disease can be partially managed by growing Cercospora leaf spot tolerant hybrids, crop rotation, and field sanitation (Shrestha *et al*. 2020), applications of fungicide are still required in most sugarbeet cultivation (Secor *et al.* 2010). However, with its high genetic variability, polycyclic nature and prolific sporulation, *Ce. beticola* is considered a high-risk pathogen for fungicide resistance development (Bolton *et al.* 2012, Shrestha *et al*. 2020). Recent molecular studies based on concatenated phylogenetic analyses of eight nuclear loci (ITS, *actA*, *cmdA*, *gapdh*, *his3*, *rpb*2, *tef*1 and *tub*), confirmed the presence of cryptic speciation within *Ce. beticola*, and three species *Ce. americana*, *Ce. gamsiana* and *Ce. tecta* were described within this species complex (Bakhshi *et al.* 2018, Bakhshi & Zare 2020, Vaghefi *et al.* 2021).

Grey leaf spot of maize (*Zea mays*) caused by *Cercospora zeae-maydis* and/or *Ce. zeina* (Crous *et al*. 2006a) is a perennial and economically damaging disease (Wise 2010). The disease may lead

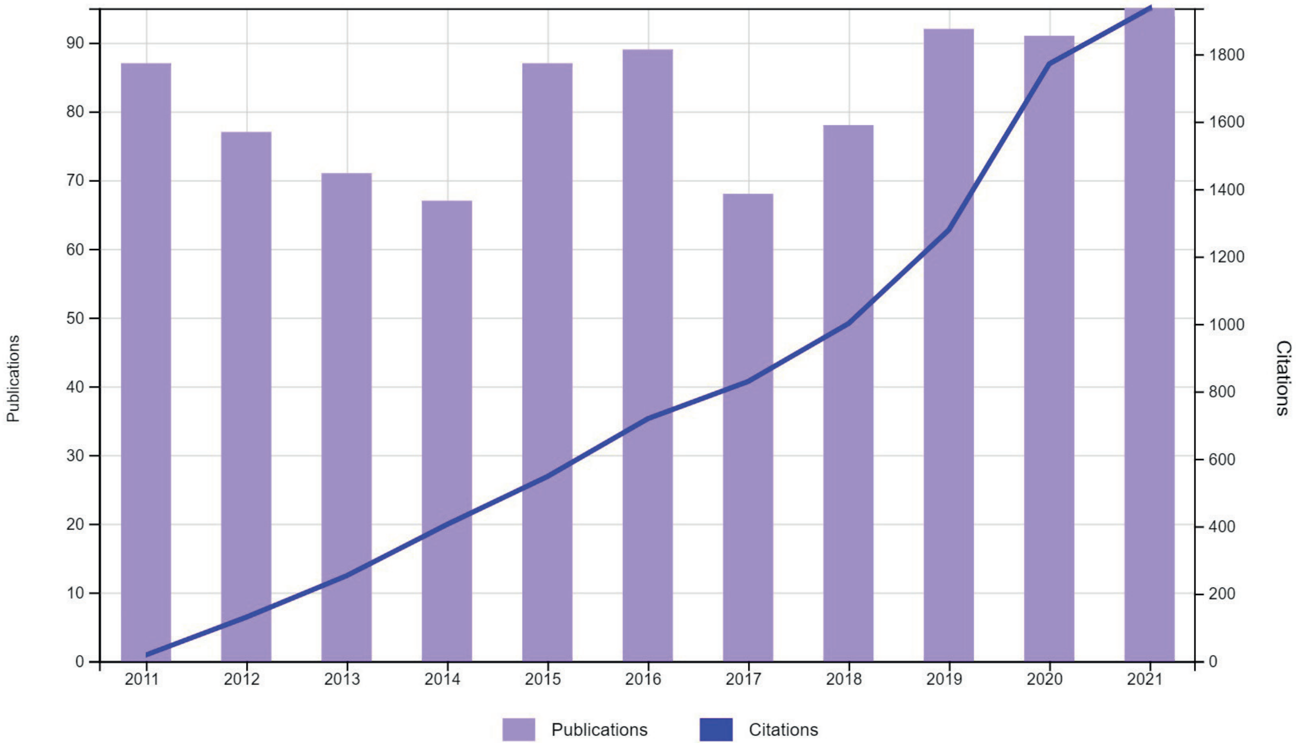

Fig. 111. Trends in research of *Cercospora* in the period 2011–2021.

Table 87. Top 10 cited articles related to *Cercospora* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Tomato immune receptor Ve1 recognizes effector of multiple fungal pathogens uncovered by genome and RNA sequencing	329	De Jonge *et al.* (2012)
2	Xanthones from fungi, lichens, and bacteria: The natural products and their synthesis	271	Masters & Braese (2012)
3	Development of spectral indices for detecting and identifying plant diseases	254	Mahlein *et al.* (2013)
4	Species concepts in *Cercospora*: spotting the weeds among the roses	216	Groenewald *et al.* (2013)
5	A review on the main challenges in automatic plant disease identification based on visible range images	172	Barbedo (2016)
6	Hyperspectral imaging for small-scale analysis of symptoms caused by different sugar beet diseases	165	Mahlein *et al.* (2012)
7	Phylogenetic lineages in *Pseudocercospora*	133	Crous *et al.* (2013a)
8	The evolution of species concepts and species recognition criteria in plant pathogenic fungi	129	Cai *et al.* (2011)
9	*Zymoseptoria gen. nov.*: a new genus to accommodate Septoria-like species occurring on graminicolous hosts	126	Quaedvlieg *et al.* (2011)
10	Xanthone dimers: a compound family which is both common and privileged	117	Wezeman *et al.* (2015)

to severe yield losses of over 50 % in the USA and from 20–60 % in South Africa (Lipps 1998, Nsibo *et al.* 2019). High temperature and humidity, maize monoculture or planting of susceptible hybrids, and the wide use of reduced-tillage (Lipps 1998, Ward *et al.* 1999) are equally important to grey leaf spot disease development. Currently, the use of resistant hybrids is the most efficient, cost-effective, and environmentally friendly method for disease control (Lv *et al*. 2020).

Frogeye leaf spot of soybean (*Glycine max*) caused by *Cercospora sojina* is an important and common disease that infects leaves, stems, and pods under warm and humid conditions. It leads to primary yield loss from lack of photosynthesis and/or premature defoliation. Infected seeds may germinate poorly and the resulting seedlings are weak (Lin & Kelly 2018).

Apart from being pathogens of economically important plants, some *Cercospora* species have also been used as biocontrol agents, such as *Ce. caricis* used to control *Cyperus rotundus* (*Cyperaceae*) (Inglis *et al.* 2001), *Ce. rodmanii* used to control *Eichhornia crassipes* (Praveena & Naseema 2006, Montenegro-Calderón *et al.* 2011) and *Ce. resedae* used to control *Reseda lutea* (*Resedaceae*) (Giles *et al.* 2002).

Research interests

There are 902 publications and 7 493 citations from 2011–2021 in the Web of Science (Fig. 111), with the top 10 most cited articles listed in Table 87. Most of the publications focused on disease management (fungicide resistance, disease resistance), and research on pathogenic *Cercospora* species (*in vitro*, cercosporin toxin biosynthesis, host-species interaction), as well as taxonomy.

Disease management

Disease control strategies for Cercospora leaf spot diseases have been extensively studied, including the laboratory/field trial of fungicides (Ioannidis & Karaoglanidis 2000, Laufer *et al*. 2020), breeding resistant varieties (Mechelke 2000, Wolf & Verreet 2002, Weiland & Koch 2004) and integration of cultural practices. *Cercospora* diseases have been effectively controlled by a combination of protectant (*e.g.*, organo-tins and ditihiocarbamates) and systemic (*e.g.*, quinone outside inhibitors (QoI) and demethylation inhibitors (DMI)) fungicides (Rosenzweig *et al*. 2020). However, the efficacy of fungicides has been continuously marred by the emergence of resistant strains after repeated and widespread use of the same fungicide classes (Giannopolitis 1978, Dixon *et al*. 2020, Rangel *et al.* 2020). Rotating fungicides with a different mode of action have been implemented to suppress the selection of fungicide-resistant strains (Rangel *et al.* 2020). Studies on the inheritance of disease resistance controlled by quantitative trait loci will improve the efficiency of marker-assisted breeding (Menkir & Ayodele 2005, Du *et al.* 2020, Lv *et al.* 2020). Enhanced knowledge of pathogen-host interactions and breeding for effective host resistance cultivars, will continue to be important and provide a good strategy for the integrated management of *Cercospora* diseases.

Toxins

Cercosporin, an important research topic in this genus, is a non-host-specific and light-activated phytotoxin produced by most *Cercospora* species (Daub & Ehrenshaft 2000, Tang *et al*. 2019, Santos Rezende *et al.* 2020). Cercosporin may enhance virulence (Upchurch *et al.* 1991). However, there are phytopathogenic *Cercospora* species that lack the ability to produce cercosporin, and this led to the conclusion that cercosporin is not necessary a pathogenicity factor (Goodwin *et al.* 2001, Weiland *et al.* 2010). Besides, it was reported that not only *Cercospora* spp. but also *Colletotrichum* and *Pyricularia* species have the ability to produce cercosporin (De Jonge *et al*. 2018).

Beticolins (B0 to B19) are another group of non-host-specific and photosensitising phytotoxins produced by *Cercospora beticola* and *Ce. berteroae* (Milat & Blein 1995, Goudet *et al*. 2000). Schlösser (1962) indicated that beticolins have anti-bacterial and phytotoxic properties. Beticolins inhibit tumoural cell growth in mice with an ability to form complexes with Mg^{2+} (Ding *et al.* 1996), interfere with H+-ATPase activity (Gomès 1996), and are able to form ion channels with poor ion selectivity (Goudet *et al.* 2000).

Taxonomy and phylogeny

According to the lack of useful morphological characters and high level of intraspecific variation, traditionally the identification of

Cercospora species has mainly relied on host taxonomy (Chupp 1954, Ellis 1971, Crous & Braun 2003). However, as many *Cercospora* spp. are not restricted to a single host plant, host data should be avoided as the primary criterion for identification purposes (Crous & Braun 2003, Lartey *et al.* 2005, Groenewald *et al.* 2013, Bakhshi *et al.* 2015a, 2018). At the moment, multi-locus phylogenetic investigations combined with ecology, morphology and host data, is the most operational approach for the delimitation of *Cercospora* species (Groenewald *et al.* 2010, 2013, Bakhshi *et al.* 2018).

To date, DNA-based phylogenetic studies of *Cercospora* species have been conducted based on ITS nrDNA (Stewart *et al.* 1999, Crous *et al.* 2000, 2009a, b, Goodwin *et al.* 2001) as well as multi-gene sequence data (Groenewald *et al.* 2005, 2006, 2013, Sharma *et al.* 2013a, Dianese *et al.* 2014, Bakhshi *et al.* 2015a, b, 2018, Shivas *et al.* 2015, Soares *et al.* 2015, Albu *et al.* 2016, Nguanhom *et al.* 2016, Guatimosim *et al.* 2017, Guillin *et al.* 2017, Bakhshi 2019, Vaghefi *et al.* 2021). A backbone phylogeny for *Cercospora* species based on a multi-locus (ITS, *actA*, *cmdA*, *his*3 and *tef*1) phylogenetic investigation of a large sampling of species was provided by Groenewald *et al.* (2013). Three more genomic regions including *gapdh*, *rpb2*, and *tub* were then investigated by Bakhshi *et al.* (2018) to perform eight-gene phylogeny (ITS, *actA*, *cmdA*, *gapdh*, *his*3, *rpb*2, *tef*1 and *tub*) for *Cercospora* spp. Even though none of these genes has discriminatory power to distinguish all *Cercospora* species, Bakhshi *et al.* (2018) indicated that the *gapdh* locus is a promising DNA barcode for improved species recognition in *Cercospora* and provides better insight, especially into species complexes, thus this locus should be used in the concatenated alignment when molecular data from multiple gene loci are considered.

Cercospora taxonomy is complicated and most of the taxa in this genus lack ex-type cultures or sequences from type materials, thus it is problematic to assign existing names to the derived phylogenetic clades (Groenewald *et al.* 2013, Bakhshi *et al.* 2015a, 2018). Therefore, it is necessary to recollect and epitypify the described taxa and amplify all the necessary genes for accurate species delimitation.

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82. *Lactarius* Pers., Tentamen dispositionis methodicae Fungorum: 63. 1797.

Type species: *Lactarius torminosus* (Schaeff.) Pers.

Classification: *Basidiomycota*, *Agaricomycotina*, *Agaricomycetes*, *Russulales*, *Russulaceae.*

Background

Lactarius forms, together with *Lactifluus* and *Russula*, the largest agaricoid genera in *Russulales* (De Crop *et al.* 2021). These genera exhibit a high worldwide diversification. *Lactarius* is a well-known ectomycorrhizal fungus, which produces agaricoid, secotioid to gasteroid basidiomata (Verbeken & Nuytinck 2013), originally characterised by the latex exudation (Persoon 1797). Species of *Lactarius* are popularly known, mainly in the temperate and boreal regions, where conspicuous edible and tasty sporocarps grow.

A recent molecular multi-locus study showed that the milk cap species are spread among three distinct well-supported clades. The smallest one contains russuloid and lactarioid species and was recognised as a monophyletic branch proposed as a new genus called *Multifurca*. The largest, which harbours most of the known milk caps species, was divided into the genera *Lactarius s. str.* and *Lactifluus* (Buyck *et al.* 2008). Despite this partition, no synapomorphies have been satisfactorily found to distinguish *Lactarius* from *Lactifluus*. However, *Lactarius* has a tendency to produce a humid pileus with a zoned surface while *Lactifluus* has a dry and non-zonate one; and *Lactifluus* frequently has thick-walled elements mostly in the pileipellis, and less conspicuous spherocytes in hymenophoral trama (Verbeken & Nuytinck 2013). They also differ in geographic distribution: *Lactarius* is mainly distributed in the Northern Hemisphere, while *Lactifluus* has its main range in the tropics (Verbeken & Nuytinck 2013).

The genus *Lactarius* has approximately 450 accepted species but at least 1 000 species are estimated (He *et al.* 2019b). The genus is formed by three well-supported clades corresponding to the three subgenera that are detailed below.

Lactarius* subg. *Lactarius (the former subg. *Piperites*) with natural distribution in temperate regions, and few representatives in tropical Africa (Verbeken & Walleyn 2010), but also found in the Southern Hemisphere related with an unintentional co-introduction with their ectomycorrhizal host trees *Pinus* (Dickie *et al.* 2010, Sulzbacher *et al.* 2018, Silva-Filho *et al.* 2018, 2020). This subgenus is characterised by slimy to viscid or shiny pileus, with an often zonate surface, sometimes drier or scrobiculated, and with or without a hairy margin; the latex colour may range from white to orange, reddish, wine and greenish, often changing colour; and microscopically it is characterised by an ixocutis pileipellis structure (Verbeken & Nuytinck 2013).

Lactarius* subg. *Russularia is distributed in temperate regions and South-East Asia, from where many new species have been recently described (*e.g.*, Wisitrassameewong *et al.* 2014, 2015). Species of this subgenus are recognised by orange to brick red or brownish basidiomata and a dry to somewhat greasy pileus, the latex is usually white and unchanging, and the pileipellis structure ranges from a trichoderm to trichopalisade with globose elements (Verbeken & Nuytinck 2013, Wisitrassameewong *et al.* 2015).

Lactarius* subg. *Plinthogali is dominant in temperate regions (*e.g.,* Stubbe & Verbeken 2012), but is also well represented in South-East Asia (Le *et al.* 2007, Das & Chakraborty 2014, Lee *et al.* 2015, Das *et al.* 2017) and some taxa in Africa (Verbeken 2000). The subgenus is recognised by dry, velvety and dull-coloured pileus; a grey, brown and cream colour, pinkish or reddish discolouration of the context; white to yellow latex; a palisade, hymeniderm to a trichopalisade pileipellis structure; and highly ornamented zebroid basidiospores (Le *et al.* 2007, Stubbe & Verbeken 2012, Uniyal *et al.* 2018).

Ecological and economic significance

In general, the ectomycorrhizal (ECM) forest community has been composed of numerous fungal species belonging to families *Amanitaceae*, *Russulaceae*, *Thelephoraceae*, *Boletaceae*, *Inocybaceae*, and *Sclerodermatacea*. Among them, *Lactarius* seems to be a dominant genus in this type of ecosystems. Although *Lactarius* is treated as having an almost worldwide distribution, it is more diverse in the temperate-zone ecosystems (Verbeken & Nuytinck 2013). It occurs in forests of arctic tundra and boreal forest (Geml *et al.* 2009), Mediterranean shrubland (Nuytinck *et al.* 2004), as well as tropical and subtropical Africa (Verbeken & Buyck

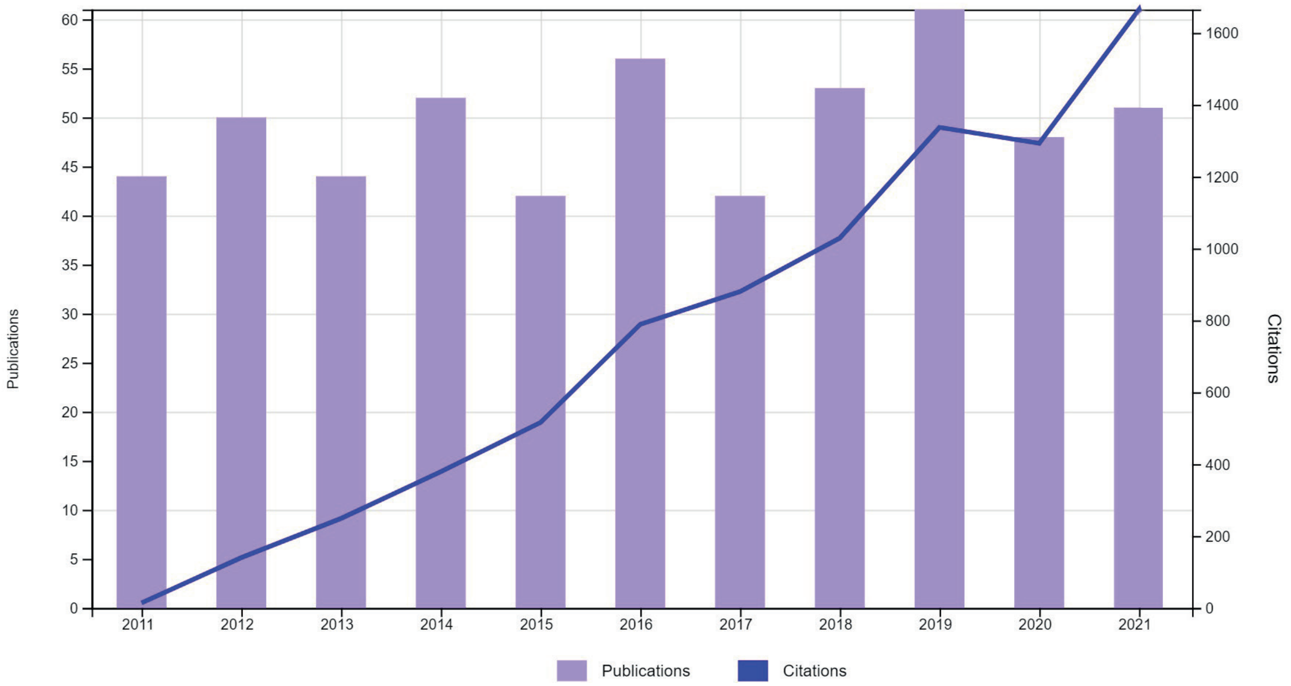

Fig. 112. Trends in research of *Lactarius* in the period 2011–2021.

2002, Riviere *et al.* 2007), tropical Asia (Watling *et al.* 2002, Le *et al.* 2007, Stubbe *et al.* 2007, 2008, Wisitrassameewong *et al.* 2014, 2015), and mesoamerican tropical forests (Lamus *et al.* 2012, Herrera *et al.* 2018). This genus is associated with many different tree species belonging to *Abies*, *Alnus*, *Betula*, *Castanopsis*, *Larix*, *Lithocarpus*, *Pinus*, *Pseudotsuga*, *Quercus*, *Tsuga*, among others (Nuytinck & Verbeken 2005, Nuytinck & Ammirati 2014, Desjardin *et al.* 2015, Wang 2016). Some species have a wide host range while others are very host-specific (Nuythink & Verbeken 2005, Nuytinck *et al.* 2004, Comandini *et al.* 2006).

Wild mushrooms are important components in the human diet (Voces *et al.* 2012), and some *Lactarius* species (mainly *La*. sect. *Deliciosi*) are the most popular edible mushrooms in North America, Europe and Asia, where they are abundant (Boa 2004, Voces *et al.* 2012). Edible *Lactarius* are considered mushrooms of good quality and excellent flavour and a good source of protein, fibre, vitamins and minerals (Barros *et al.* 2007, Kalač 2009). Furthermore, they contain nutritional organoleptic and medicinal characteristics (Kalač 2009, Joshi *et al.* 2013). Species of *Lactarius* have great interest due to containing a large diversity of compounds with a wide range of nutritional and health benefits, such as stimulation of the immune system, providing an anticancer function, control of lipids in humans and antioxidant activity (Kalač 2009, Ferreira *et al.* 2013, Joshi *et al.* 2013). A recent review of the world's edible mushroom species listed 87 edible *Lactarius* species (Li *et al.* 2020a) from approximately 40 countries (Boa 2004).

Table 88. Top 10 cited articles related to *Lactarius* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Antioxidant properties of phenolic compounds occurring in edible mushrooms	250	Palacios *et al.* (2011)
2	Recent developments in mushrooms as anti-cancer therapeutics: a review	216	Patel & Goyal (2012)
3	An arctic community of symbiotic fungi assembled by long-distance dispersers: phylogenetic diversity of ectomycorrhizal basidiomycetes in Svalbard based on soil and sporocarp DNA	121	Geml *et al.* (2012)
4	Ectomycorrhizal fungal diversity and community structure on three co-occurring leguminous canopy tree species in a Neotropical rainforest	114	Smith *et al.* (2011)
5	Anti-inflammatory activity of methanolic extracts from edible mushrooms in LPS activated RAW 264.7 macrophages	113	Moro *et al.* (2012)
6	95% of basidiospores fall within 1 m of the cap: a field- and modeling-based study	102	Galante *et al.* (2011)
7	Environmental drivers of ectomycorrhizal communities in Europe's temperate oak forests	95	Suz *et al.* (2014)
8	Bioactive microconstituents and antioxidant properties of wild edible mushrooms from the island of Lesvos, Greece	87	Kalogeropoulos *et al.* (2013)
9	Community composition of root-associated fungi in a *Quercus*-dominated temperate forest: "codominance" of mycorrhizal and root-endophytic fungi	80	Toju *et al.* (2013)
10	Trace metal contents in wild edible mushrooms growing on serpentine and volcanic soils on the island of Lesvos, Greece	79	Aloupi *et al.* (2012)

Research interests

There are 543 publications and 7 481 citations from 2011–2021 in the Web of Science (Fig. 112), with the top 10 most cited articles listed in Table 88. Most of the publications focused on biotechnological processes (biochemical compounds, chemistry and pharmacology), followed by publications of taxonomy and phylogeny, ecology and ethnomycology.

Biotechnological process

Various bioactive compounds have been isolated from *Lactarius* species, especially from *La. deliciosus*. These include polyols, phenylpropanoid glycoside, steroids, phenolic and acids compounds (Zhou *et al.* 2011, Muszynska *et al.* 2013). Some polysaccharides isolated from this species exhibited significant anti-tumour, and immunostimulant activity, as well as antimicrobial and antibiofilm (Ding *et al.* 2012, Hou *et al.* 2013, Karaca *et al.* 2017). Antioxidant activity was observed from the phenolic contents of *La. salmonicolor* (Athanasakis *et al.* 2013). Anti-bacterial activity has been shown with compounds from *La. sanguifluus* and *La. indigus* (Ochoa-Zarzosa *et al.* 2011, Sagar & Thakur 2013). The polysaccharides extracted from *La. flavidulus* showed anticancer properties (Wu *et al.* 2011). Yellow, orange, and red pigments have been extracted from carotenoids and terpenoids compounds from coloured *Lactarius* species, such as *La. deliciosus*, *La. blennius*, *La. deterrimus* and *La. fuliginosus* (De Bernardi *et al.* 1992, Spiteller & Steglich 2002).

Ecology

Many *Lactarius* species display some level of host-specificity and form ECMs with a single plant species (*e.g.*, *La. porninsis* with *Larix decidua*; Nuythink & Verbeken 2005). Some species form ECM with a single plant genus, for example, *La. quieticolor* with *Pinus sylvestris*, *P. pinaster*, *P. radiata*, and *P. taeda* (Silva-Filho *et al.* 2020). Other taxa are found associated with other plant genera belonging to the same family, *e.g.*, *La. tesquorum* with *Cistus* and *Halimium* (Nuytinck *et al.* 2004, Comandini *et al.* 2006). However, studies with molecular phylogenetic approaches are needed to test the intercontinental conspecificity of *Lactarius* species.

Edibility

As mentioned above, the tradition of eating *Lactarius* species is intense in Europe, Asia and some American countries. Species of sect. *Deliciosi*, for example *La. deliciosus*, *La. quieticolor*, *La. sanguifluus,* and *La. vinosus* are much appreciated in Europe, where they are sold in local markets (Boa 2004). Fresh *La. deliciosus* is among the most popular and highly priced species in many countries as in Spain (Voces *et al.* 2012). Closely related species are also consumed in China and Japan, for example, *La. hatsudake* (Nuytinck *et al.* 2006). *Lactarius resimus* and *La. scrobiculatus* are the highest prized in Russian markets (Singer 1949), *La. indigo* is a very popular edible mushroom in Mexico (*e.g.*, Ruan-Soto 2018a). In South America, the introduced *La. quieticolor* has become better known where it has been commercialised (Silva-Filho *et al.* 2020).

Taxonomy and phylogeny

About 450 species of *Lactarius* have been described, but the real number could reach 1 000 species (He *et al.* 2019b). The diversity in Europe and North America is better known, but most of the novelties in the last years came from Southeast Asia, India, and China, regions that remain under-explored (Wisitrassameewong *et al.* 2014, 2015, Liu *et al.* 2015d). The markers, nuc-ITS, nuc-LSU and *rpb2* gene have been used for taxonomic and systematic studies in *Russulaceae* (*e.g.*, Buyck *et al.* 2008, Stubbe *et al.* 2012), and are effective for *Lactarius*. The ITS, combined with morphological and ecological data, has been shown a good gene marker to delimit species in *Lactarius* (Shi *et al.* 2018, Verma *et al.* 2021). The *rpb2* was also considered a good gene marker for phylogenetic inference in *Lactarius* because it contains most phylogenetic signals at the subgenus and species level (Wisitrassameewong *et al.* 2016).

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83. ***Lasiodiplodia*** Ellis & Everh., Bot. Gaz. 21: 92. 1896.

Type species: *Lasiodiplodia theobromae* (Pat.) Griffon & Maubl.

Classification: *Ascomycota*, *Pezizomycotina*, *Dothideomycetes*, *Botryosphaeriales*, *Botryosphaeriaceae.*

Background

Lasiodiplodia was introduced by Ellis & Everhart (1894) with *L. tubericola* as the type species, but without a description. Clendenin (1896) provided a description, but did not refer to any type or other specimens of the genus or species. A clear concept of *Lasiodiplodia* was provided by Pavlic *et al.* (2004), but the types or any specimens from the original hosts or origins could not be located. Therefore, Phillips *et al.* (2013) designated an ex-neotype culture and a dried specimen as the neotype. As *Botryodiplodia theobromae* was more suitably accommodated in *Lasiodiplodia* (Griffon & Maublanc 1909) and the epithet *theobromae* (1892) is older than *tubericola* (1896), *L. theobromae* was designated as the type species (Phillips *et al.* 2013). *Lasiodiplodia* was previously considered a synonym of *Diplodia* (Denman *et al.* 2000), but are separated in distinct clades in phylogenetic analyses (Slippers *et al.* 2004a, b, Phillips *et al.* 2008). *Lasiodiplodia* is morphologically different from *Diplodia* as it has longitudinal striations on mature conidia (Phillips *et al.* 2008). *Lasiodiplodia* can also be distinguished from closely related genera by the presence of pycnidial paraphyses (Phillips *et al.* 2008). Comprehensive molecular examination of the *L. theobromae* species complex based on ITS and *tef* datasets have led to the identification of cryptic species (Damm *et al.* 2007, Abdollahzadeh *et al.* 2010, Úrbez-Torres *et al.* 2012). There are over 80 epithets listed in Index Fungorum (2021), but only about 35 species have molecular data (Hongsanan *et al.* 2020b, Hyde *et al.* 2020a, Chethana *et al.* 2023).

Ecological and economic significance

Most *Lasiodiplodia* species are plant pathogens and have been associated with several disease symptoms including cankers, dieback, fruit or stem-end or root rot, gummosis and branch blight (Ismail *et al.* 2012, Phillips *et al.* 2013). *Lasiodiplodia* species are mostly distributed in tropical and subtropical regions (Alves *et al.* 2008). They have been reported to cause severe damage to a large number of hosts (Punithalingam 1980a, b, Burgess *et al.* 2006, Abdollahzadeh *et al.* 2010, Phillips *et al.* 2013). *Lasiodiplodia* species also affect crops of economic importance, for example *Mangifera indica* (mango), *Persea americana* (avocado), *Musa* spp. (banana), *Anacardium occidentale* (cashew), *Citrus* spp. (citrus), *Vitis* sp. (grapevine), *Carica papaya* (papaya) and *Citrullus lanatus* (watermelon) (Freire *et al.* 2003, Costa *et al.* 2010, Ismail *et al.* 2012). *Lasiodiplodia* has also been associated with several human infections (Summerbell *et al.* 2004, Kindo *et al.* 2010). The

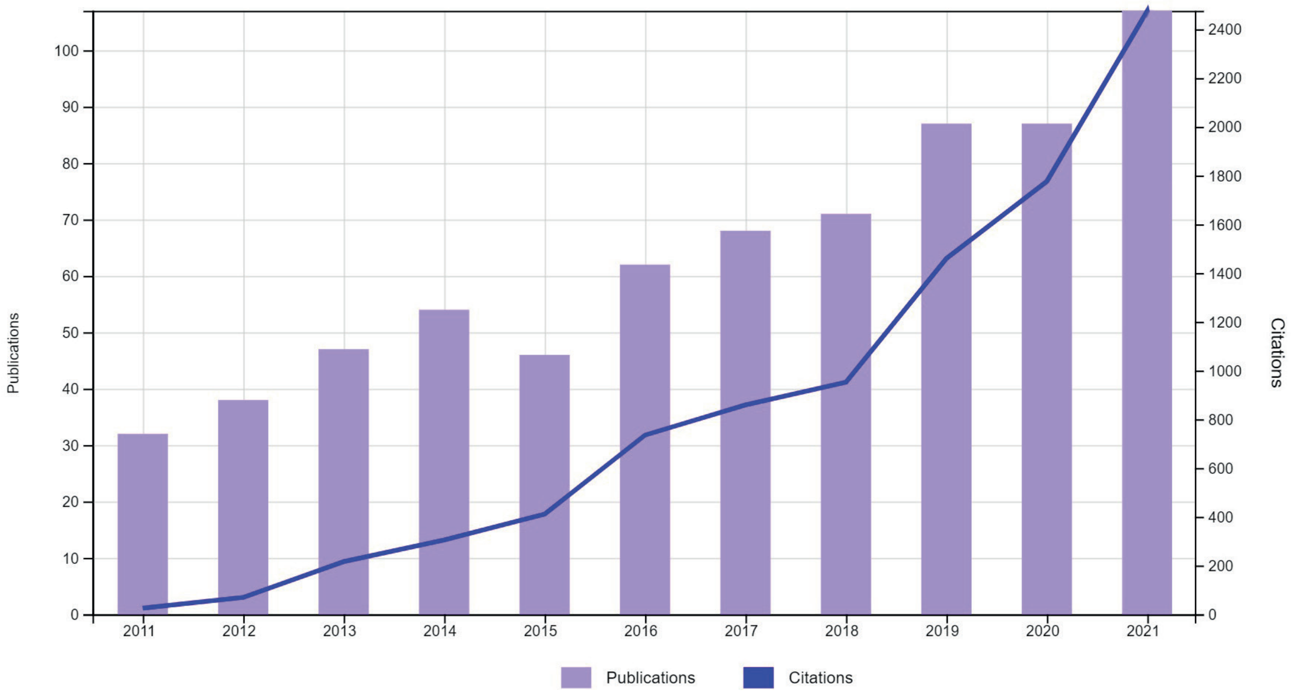

Fig. 113. Trends in research of *Lasiodiplodia* in the period 2011–2021.

most common cases are ocular infections but there are also report of human death (Woo *et al.* 2008).

Research interests

There are 699 publications and 7 394 citations from 2011–2021 related to *Lasiodiplodia* in the Web of Science (Fig. 113) with the top 10 most cited articles listed in Table 89. Most of the publications focused on the pathogenicity of *Lasiodiplodia* species, as well as its taxonomy. Grapevine diseases caused by *Lasiodiplodia* species are among the most cited papers (Urbez-Torres *et al*. 2012, Yan *et al.* 2013). *Lasiodiplodia* species are among the most virulent pathogens causing cankers on grapevines (Urbez-Torres *et al.* 2012).

Authors: C.S. Bhunjun and C. Phukhamsakda

84. ***Exophiala*** J.W. Carmich., Sabouraudia 5: 122. 1966.

Type species: *Exophiala salmonis* J.W. Carmich.

Classification: *Ascomycota*, *Pezizomycotina*, *Eurotiomycetes*, *Chaetothyriales*, *Herpotrichiellaceae.*

Background

Exophiala is an asexual genus regarded as an evolutionary hotspot within the group of black yeasts. The genus contains many genotypically divergent species (De Hoog *et al.* 2003, Sterflinger 2005). Morphologically, the species are similar and defined by annellidic conidiogenesis with the production of slimy heads of conidia (De Hoog *et al.* 2011a). Known sexual morphs belong to *Capronia* (De Hoog *et al.* 2011a). The appearance of black yeasts is caused by dihydroxynaphthalene melanin macromolecules in the

Table 89. Top 10 cited articles related to *Lasiodiplodia* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	The *Botryosphaeriaceae*: genera and species known from culture	515	Phillips *et al.* (2013)
2	The status of *Botryosphaeriaceae* species infecting grapevines	238	Urbez-Torres (2011)
3	One stop shop: backbones trees for important phytopathogenic genera: I (2014)	235	Hyde *et al.* (2014)
4	Towards a natural classification of *Botryosphaeriales*	215	Liu *et al.* (2012b)
5	Families, genera, and species of *Botryosphaeriales*	113	Yang *et al.* (2017a)
6	Diversity and ecology of tropical African fungal spores from a 25,000-year palaeoenvironmental record in southeastern Kenya	108	Van Geel *et al.* (2011)
7	Characterization of fungal pathogens associated with grapevine trunk diseases in Arkansas and Missouri	106	Urbez-Torres *et al.* (2012)
8	*Botryosphaeriaceae*: Current status of genera and species	102	Dissanayake *et al.* (2016)
9	*In vitro* activity of eighteen essential oils and some major components against common postharvest fungal pathogens of fruit	101	Combrinck *et al.* (2011)
10	Species of *Botryosphaeriaceae* involved in grapevine dieback in China	75	Yan *et al.* (2013)

Table 90. Top 10 cited articles related to *Exophiala* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	European Society of Clinical Microbiology and Infectious Diseases Fungal Infection Study Group; European Confederation of Medical Mycology. ESCMID and ECMM joint clinical guidelines for the diagnosis and management of systemic phaeohyphomycosis: diseases caused by black fungi	173	Chowdhary *et al.* (2014c)
2	Unravelling the role of dark septate endophyte (DSE) colonizing maize (*Zea mays*) under cadmium stress: physiological, cytological and genic aspects	165	Wang *et al.* (2016b)
3	Waterborne *Exophiala* species causing disease in cold-blooded animals	150	De Hoog *et al*. (2011c)
4	Dishwashers – A man-made ecological niche accommodating human opportunistic fungal pathogens	141	Zalar *et al.* (2011)
5	Inherited CARD9 deficiency in otherwise healthy children and adults with Candida species-induced meningoencephalitis, colitis, or both	122	Lanternier *et al.* (2015b)
6	Why everlastings don't last	99	Crous & Groenewald (2011)
7	Improved tolerance of maize (*Zea mays* L.) to heavy metals by colonization of a dark septate endophyte (DSE) *Exophiala pisciphila*	92	Li *et al*. (2011d)
8	Inherited CARD9 deficiency in 2 unrelated patients with invasive *Exophiala* infection	86	Lanternier *et al*. (2015a)
9	The diversity and distribution of fungi on residential surfaces	80	Adams *et al.* (2013)
10	Fungi in the cystic fibrosis lung: bystanders or pathogens?	78	Chotirmall & McElvaney (2014)

outer cell. Depending on the environment, most strains can switch between three morphologies, (i) budding yeast-like, (ii) hyphal, or (iii) meristematic growth (De Hoog *et al.* 1994).

The genus was first described in 1966 by Carmichael. To date, 65 *Exophiala* species are listed on MycoBank, of which 19 are associated with human and animal pathogenicity in the Atlas of Clinical Fungi (De Hoog *et al.* 2020). They are also known to be extremely environmentally versatile and polyextremophilic, thriving in harsh environments under acidic, alkaline, toxic and nutrient-deprived conditions as well as with ionising radiation and osmotic stress (Dadachova *et al.* 2007, De Hoog *et al.* 2011b, Zalar *et al.* 2011, Gümral *et al*. 2014). *Exophiala* species are frequently isolated from man-made niches such as sauna facilities or dishwashers (Zalar *et al*. 2011).

Ecological and economic significance

Clinical importance

Within the black yeasts, the genus *Exophiala* compromises the most clinical relevance (Chowdhary *et al.* 2014a) with its entities manifesting in numerous ways. Pathogenic species can cause deep and disseminated human infections in healthy and immunocompromised patients (Revankar *et al.* 2002, Song *et al.* 2017).

The clinical picture caused by *Exophiala* species is phaehyphomycosis, literally meaning "condition of fungi with dark hyphae", which was first introduced in 1974 (Ajello *et al.* 1974, Revankar *et al.* 2002). In contrast to most life-threatening fungal infections, primary phaeohyphomycosis mostly affects immunocompetent patients and adults in their second or third decade of life (Jung & Kim 2014) with a mortality rate of 73 % (Revankar *et al.* 2004). In chromoblastomycosis, black fungi produce characteristic sclerotic bodies in the tissue, especially in tropical areas. Chromoblastomycosis was added to the World Health Organization's list of neglected tropical diseases in 2016. Although associated with black yeasts, chromoblastomycosis is rarely caused by *Exophiala* species (Chowdhary *et al.* 2014a). Additionally, *Exophiala* species can cause mycetomas by myotic granules (McGinnis 1983). *Exophiala* species are frequently reported as coloniser of the respiratory tract from cystic fibrosis patients with a prevalence of 4.8–15.7 % in Germany and Belgium (Pihet *et al*. 2009, Lebecque *et al.* 2010). Known risk factors are mutations in the *CARD9* gene, which is involved in the immune system (Lanternier *et al.* 2014, Wand *et al.* 2014). In the clinical context, the most prevalent *Exophiala* species are *Ex.* (formerly *Wangiella*) *dermatitidis* and *Ex. spinifera,* with a mortality rate of up to 80 % in systemic cases (Song *et al.* 2017). While *Exophiala* dermatitis is isolated worldwide from environmental niches as well as from the respiratory tract of cystic fibrosis patients, its neurotropic manifestation is mainly reported in Asia (Chowdhary *et al.* 2014a).

Exophiala spiniferna causes cases of phaeohyphomycosis and chromoblastomycosis worldwide (Hoerre & De Hoog 1999, Kantarcioglu & De Hoog 2004, Harris *et al.* 2009, Badali *et al*. 2010). In 2014, the European Fungal Infection Study Group and the European Confederation of Medical Mycology published a joint clinical guideline on how to diagnose and treat systemic phaeohyphomycosis (Chowdhary *et al.* 2014c), which to date has been cited over 170 times (Table 90). The infection route hypothesised is related to the colonisation of man-made environments (Zalar *et al.* 2011, Babič *et al.* 2018). Infections happen either through small skin trauma (Sudhadham *et al.* 2011) or through inhalation. The awareness of opportunistic pathogens in man-made environments such as dishwashers, tap water or washing machines changed the importance of the genus for non-scientific audiences.

For human infection, thermotolerance of the pathogenic *Exophiala* species is crucial. Other *Exophiala* species that lack thermotolerance can infect cold-blooded animals such as fish, amphibians, or invertebrates (De Hoog *et al.* 2011c). Especially in farmed fish, infections by *Exophiala psychrophila* or *Ex. salmonis* are frequently reported with up to 50 % mortality (Pedersen & Langvad 1989).

Research interests

There are 551 publications and 7 344 citations in the Web of Science from 2011–2021 (Fig. 114). The ten most cited publications (Table 90) focused on understanding virulence factors, routes of infection, survival in extreme environments and their relation to pathogenicity.

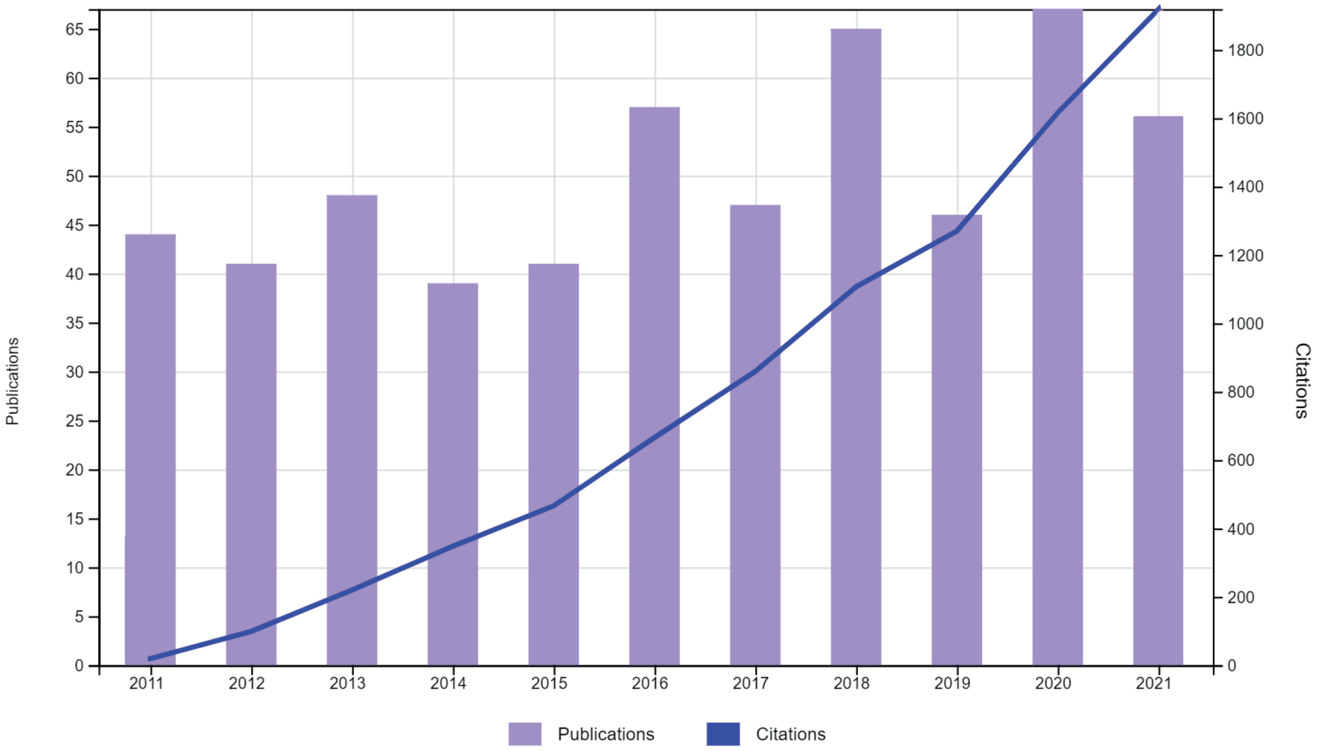

Fig. 114. Trends in research of *Exophiala* in the period 2011–2021.

This increased understanding of the underlying diseases generates suitable therapeutics, and use of non-pathogenic strains as well as their attributes for applications. Although studied for decades, a lot of questions remain.

Melanin

Melanin is a putative virulence factor and an agent to help survive hostile environments. The role of melanin in infections was studied using mice, *Galleria mellonella* larvae or *ex-vivo* skin models in combination with melanin-deficient mutants (Geis *et al.* 1984, Dixon *et al.* 1987, Feng *et al.* 2001, Calvo *et al.* 2010, Poyntner *et al.* 2016, 2018, Song *et al.* 2017, Olsowski *et al.* 2018). Frequently, *Exophiala dermatitidis* was used as a model organism for the group of black yeasts due to its pathogenic and extremophilic traits.

Colonisation of hostile environments

Next to melanin, other adaption factors and strategies to survive high radiation, low and high temperature, pH stress, low nutrient or toxicity were studied (Wang & Szaniszlo 2009, Blasi *et al.* 2015, Tesei *et al.* 2015, Zhao *et al.* 2015a, Schultzhaus *et al.* 2020, Mackenzie 2021). New technologies of the -omics era facilitated various studies on genome, transcriptome, and proteome levels. This enabled insight into the natural evolution of the genus, genomic patterns or genomic adaption to hostile environments (Moreno *et al.* 2018). The presence of circular RNAs (Blasi *et al.* 2015), gene duplication processes (Teixeira *et al.* 2017), fine-tuning of the protein expression (Tesei *et al.* 2015) and expressed genes during alkaline conditions (Chen *et al.* 2014d) were discovered. Species such as *Exophiala macquariensis* (Zhao *et al.* 2010, Isola *et al.* 2013, Zhang *et al.* 2019a) can assimilate toxic monoaromatic hydrocarbons. It was hypothesised that this ability might be related to their pathogenicity due to the similar chemical structure to human neurotransmitters (Prenafeta-Boldú *et al.* 2006).

Overall, the results lead to the conclusion that pathogenic species of *Exophiala* did not originally evolve as pathogens but traits from their saprobic lifestyle allowed them to thrive in their hosts (Song *et al.* 2017, Moreno *et al.* 2018).

Authors: C. Poyntner and K. Sterflinger

85. ***Monilinia*** Honey, Mycologia 20: 153. 1928.

Type species: *Monilinia fructicola* (G. Winter) Honey

Classification: *Ascomycota*, *Pezizomycotina*, *Leotiomycetes*, *Helotiales*, *Sclerotiniaceae.*

Background

Monilinia is a genus of fungi with a pathogenic necrotrophic lifestyle, belonging to phylum *Ascomycota*, class *Leotiomycetes*, order *Helotiales*, family *Sclerotiniaceae* (Jayawardena *et al.* 2020), with about 50 species listed in Index Fungorum (2022). *Monilinia* species occur worldwide, affecting members of the *Rosaceae*, *Ericaceae* and *Empetraceae* families. Diseases caused by *Monilinia* species are often referred to as blossom blight, brown rot and mummy berry agents. The genus *Monilinia* was described by Honey (1928). It is characterised by elongate, stipitate, glabrate cup-like apothecia, originating from pseudosclerotia in mummified fruits or host plant fragments. The apothecia carry cylindrical asci containing eight oblong-ellipsoid spores. *Monilinia* can also produce microconidia (spermatia), globose no-germinative cells (Honey 1928), sometimes involved in the fertilisation process (Martini & Mari 2014). The hyphae are septate, hyaline or variously pigmented (grey, tan, olive green or black). *Monilinia* species are difficult to distinguish as they have similar life cycles, symptoms and host ranges (Batra 1991). The taxonomic classification has been problematic because this genus shares features with *Sclerotinia* (Gjaerum 1969, Penrose *et al.* 1976) and *Ciboria* (Honey 1936, Batra 1991). *Monilinia* has been divided into sections *Disjunctoriae* or *Junctoriae* based on asexual morphology, fungal biology, and host specialisation. Species of section *Disjunctoriae* possess chains of conidia intercalated by disjunctors, and both sexual (teleomorphic) and asexual (anamorphic) stages are frequently present and show high host specificity. Species of section *Disjunctoriae* can induce in host leaves the production of aromatic substances and sugars attractive to pollinator insects. These insects can thus act as vectors of the pathogen. Conidia in section *Disjunctoriae* are produced during a short period on young fruits that are mummified from the ovary wall outward (Holst Jensen *et al*. 1997). Their sporocarps are small and difficult to find in the field. Species in the section *Junctoriae* produce chains of conidia without disjunctors. These species show mainly asexual reproduction and low specificity for the hosts. They are pathogens of several species of domesticated and wild *Rosaceae* and can show also saprophytic behaviour. The conidia of species in section *Junctoriae* are long-lived, produced over a long period, and are dispersed by wind, rain, and insects that visit decayed fruits. The ripe fruits are infected and mummified from the outside inward. Among the *Monilinia* species included in section *Disjunctoriae* are *Mon. vaccinii-corymbosi* and *Mon. oxycocci*, which are causal agents of Monilinia blight and mummy berry disease of blueberries (*Vaccinium corymbosum*) and cranberries (*Oxycoccus* species), respectively, and can result in severe crop losses, especially in North America (Batra 1991, Burchhardt & Cubeta 2015). Other species with minor impact on crops are *Mon. urnula* and *Mon. baccarum*, affecting *Vaccinium* hosts, especially in North America, and North Europe (Rehm 1885, Woronin 1888, Dennis 1968, Palmer 1988, Batra 1991). *Monilinia linhartiana* was reported on quince in Spain (Moral *et al*. 2011). The most destructive *Monilinia* species in agriculture belong to the section *Junctoriae*, and to date, six closely related species of brown rot agents have been reported on stone and pome fruit. Among these, *Mon. fructicola*, *Mon. laxa*, *Mon. fructigena*, and *Mon. polystroma* are among the most important pathogens of cultivated stone and pome fruit, causing significant losses in the field and postharvest (Petróczy *et al*. 2012). Other species involved in brown rot but with limited geographical spread are *Mon. mumeicola* and *Mon. yunnanensis*. *Monilinia fructicola*, *Mon. laxa* and *M. fructigena* have a global distribution (EFSA Panel on Plant Health 2011). *Monilinia laxa* is the most common agent of brown rot in stone fruit in Europe and it is widely distributed around the world, although it is a quarantine pathogen in China and some parts of North America (Martini & Mari 2014). *Monilinia fructicola* was originally identified in North and South America, Australia and Japan (Smith *et al*. 1997). In 2001, it was introduced in France (Lichou *et al*. 2002), and in the following decade, it was found in Spain and Italy (De Cal *et al*. 2009, Pellegrino *et al*. 2009, Landi *et al*. 2016, Abate *et al*. 2018). *Monilinia fructigena* occurs in Europe, Asia, North Africa and some parts of South America, and it is a quarantine pathogen in Canada, USA, Australia and New Zealand (http://www.cabi.org/isc/datasheet/34747). This pathogen is the main cause of brown rot in pome fruit, but it has a relatively low incidence in stone fruit (Martini & Mari 2014). *Monilinia polystroma*, a species closely related to *Mon. fructigena*, was first described in Japan (Van Leeuwen *et al*. 2002). The pathogen spread was restricted to Asiatic and European regions (Petróczy *et al*. 2012, Villarino *et al*. 2013, Rungjindamai *et al*. 2014, Abate *et al.* 2018) and it was reported as less aggressive and prevalent on stone and pome fruits. *Monilinia mumeicola* is another minor species reported on *Prunus mume* in Japan (Harada *et al.* 2004), and on peaches in China (Hu *et al*. 2011b, Yin *et al*. 2014, 2015), while *Mon. yunnanensis* was reported on peaches in China (Hu *et al*. 2011b, Yin *et al*. 2014, 2015). Fungal isolation and micromorphological analysis can be useful for species identification (De Cal & Melgarejo 1999), but morphological features may vary depending on the incubation media and conditions, making an accurate species-specific identification difficult (Byrde & Willetts 1977, Lane 2002). Different assays based on polymerase chain reaction (PCR) amplification of the ITS region (Ioos & Frey 2000), random amplified polymorphic DNA (Boehm *et al*. 2001, Côté *et al*. 2004), PCR with sequence-characterised amplified region (SCAR) primers (Hughes *et al*. 2000), microsatellites using a nested PCR (Boehm *et al*. 2001, Ma *et al*. 2003), quantitative PCR (qPCR) (Van Brouwershaven *et al*. 2009, Guinet *et al*. 2016, Wang *et al*. 2018c), loop-mediated amplification (LAMP) assays (Ortega *et al*. 2019) or droplet digital PCR (ddPCR) (Raguseo *et al*. 2021) have been developed to differentiate the main species of *Monilinia*. Recently, draft *de novo* genome assemblies were generated for *Mon. fructigena* (Landi *et al*. 2018, Rivera *et al*. 2018), *Mon. laxa* (Naranjo-Ortíz *et al*. 2018, Rivera *et al*. 2018, Landi *et al*. 2020), *Mon. fructicola* (Rivera *et al*. 2018, De Miccolis Angelini *et al*. 2019, Vilanova *et al*. 2021), *Mon. polystroma* (Rivera *et al*. 2018), *Mon. vaccinii-corymbosi* (Yow *et al*. 2021), and *Mon. aucupariae* (GenBank Accession Number GCA_002162555.1). These genomes provide new opportunities for studies on evolution and pathogenetic factors in *Monilinia*.

Ecological and economic significance

Monilinia species cause economically important plant diseases, and the most important are detailed below.

Brown rot of pome and stone fruits

Monilinia species are associated with brown rot, one of the most devastating diseases of stone fruits, such as peach, nectarine, apricot, cherry and plum worldwide. This disease affects blossom, twig, and ripe as well as unripe fruits during the pre- and postharvest stages. Despite infection occurring in the field, the main economic losses of brown rot appear during postharvest handling, storage, transportation, and shelf life. In the United States, where the stone fruit market has an annual value of approximately 4.4 billion US dollars (Cox *et al*. 2018), this disease has been associated with up to 80 % fruit loss during postharvest (Egüen *et al*. 2015). The universal annual losses from disease outbreaks have been estimated at 1.7 billion euros (Martini & Mari 2014). *Monilinia laxa* can colonise blossoms, twigs, and fruits, but is generally considered more of a problem on blossoms and twigs. *Monilinia fructigena* is primarily a problem on apples, pears and other pome fruits. *Monilinia polystroma* is reported to cause blossom blight and brown fruit on both pome and stone fruits. Currently, effective brown rot control in the orchard depends on integrated strategies that are largely based on fungicide sprays and cultural practices (Feliziani *et al*. 2013, Martini & Mari, 2014, De Curtis *et al*. 2019, Schnabel & Hopkins 2022). However, innovative strategies based on safer alternatives to synthetic fungicides are available and include biocontrol agents (Larena *et al*. 2005, Oro *et al*. 2014, 2018, Casals *et al.* 2021, 2022), physical methods (Usall *et al*. 2016), natural compounds and resistance inducers (Li & Yu 2000, Feliziani *et al*. 2013, Romanazzi *et al*. 2016).

Monilinia blight or "Mummy berry" is a disease of high economic concern in areas of blueberry production from the southern United States to Canada causing in some years yield reduction of 80 % (Obsie & Drummond 2020, Qu & Sun 2022). In Europe, it was first found in Austria (Gosch 2003). The disease results in the replacement of blueberry fruit with a fungal pseudosclerotium,

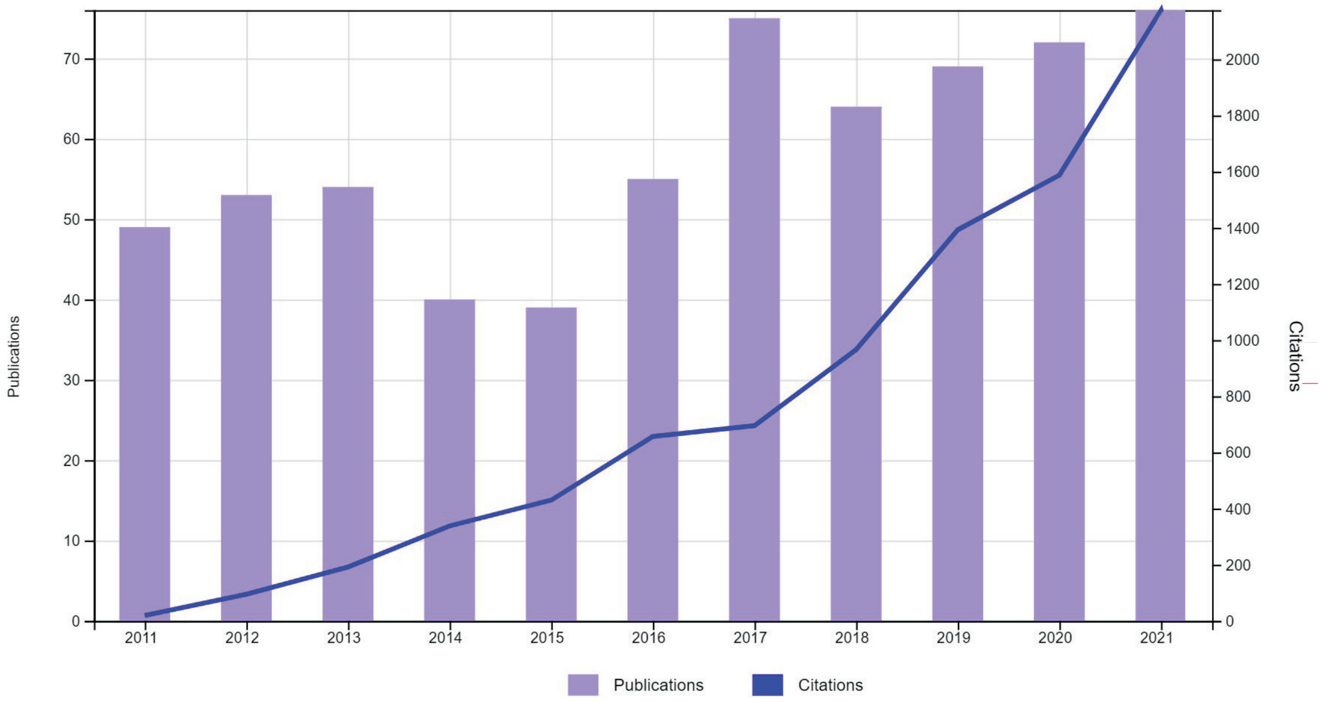

Fig. 115. Trends in research of *Monilinia* in the period 2011–2021.

causing substantial crop loss. Symptoms are manifested in the blighting of emerging leaves and shoots during spring and the mummification of maturing fruit in summer (Batra 1983). Based on field observations, Monilinia blight management is extremely challenging, and fungicides have become the sole economically viable option (Percival *et al.* 2012).

Other diseases caused by *Monilinia* spp.

Other *Monilinia* species have been linked to mummy berry disease. *Monilinia urnula* causes a disease of *Vaccinium vitis-idaea* and was reported in Europe, mainly from Scandinavia, Austria and the United Kingdom (Woronin 1888, Dennis 1968, Gjaerum 1969), and in Japan (Kobayashi 2007). As with *Mon. vaccinii-corymbosi*, it has a complex life cycle. From harvesting time, the mummies, compact masses of fungal tissue formed in infected berries, are found on the soil (Goheen 1953). *Monilinia baccarum* is restricted to *Vaccinium myrtillus*, causing blight of newly emerging shoots, that turn brown and fall. *Monilinia baccarum* is known from Scandinavia, Austria, Belgium, Germany and the UK (Rehm 1885, Woronin 1888, Dennis 1968, Gjaerum 1969, Palmer 1988, Batra 1991). The infected berries turn pale and dry, shrivel, mummify, and fall to the ground. They are called white berries due to the fine whitish layer of host cells (including the epidermis) that cover the berry (Batra 1991).

Table 91. Top 10 cited articles related to *Monilinia* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Genera of phytopathogenic fungi: GOPHY 1	185	Marin-Felix *et al.* (2017a)
2	Antimicrobial activity of bacteriocin-producing lactic acid bacteria isolated from cheeses and yogurts	126	Yang *et al.* (2012a)
3	Identification of endophytic *Bacillus velezensis* ZSY-1 strain and antifungal activity of its volatile compounds against *Alternaria solani* and *Botrytis cinerea*	114	Gao *et al.* (2017)
4	Chitosan and oligochitosan enhance the resistance of peach fruit to brown rot	104	Ma *et al.* (2013c)
5	Synthesis of silver nanoparticles using cow milk and their antifungal activity against phytopathogens	102	Lee *et al.* (2013)
6	Pre- and postharvest treatment with alternatives to synthetic fungicides to control postharvest decay of sweet cherry	81	Feliziani *et al.* (2013)
7	Biological control of peach brown rot (*Monilinia* spp.) by *Bacillus subtilis* CPA-8 is based on production of fengycin-like lipopeptides	81	Yánez-Mendizábal *et al.* (2012)
8	Recommendations on generic names competing for use in *Leotiomycetes* (*Ascomycota*)	79	Johnston *et al.* (2014)
9	Effect of heat treatment on inhibition of *Monilinia fructicola* and induction of disease resistance in peach fruit	78	Liu *et al.* (2012a)
10	*In vivo* antifungal activity of two essential oils from Mediterranean plants against postharvest brown rot disease of peach fruit	73	Elshafie *et al.* (2015)

Research interests

There are 646 publications and 7 268 citations from 2011–2021 in the Web of Science (Fig. 115), with the top 10 most cited articles listed in Table 91. Most publications focused on preharvest and postharvest brown rot management (fungicide activity and fungicide resistant isolates, alternatives to synthetic fungicides, biocontrol agents), and research on physiological and molecular properties of *Monilinia* species (molecular characterisation, host-pathogen interactions, pathogenic factors).

Disease management

Disease management strategies for brown rot have been extensively studied for both preharvest and postharvest on pome and stone fruit. Several studies cover the need for fungicide applications in the field to limit brown rot damage in humid seasons (Dowling *et al*. 2016, Lichtemberg *et al*. 2016). Nevertheless, resistance to site-specific fungicides has been reported for different *Monilinia* species worldwide (Schnabel *et al*. 2004, Chen *et al*. 2013a, Spiegel & Stammler 2006). Strategies based on alternatives to synthetic fungicides cover the effectiveness of biocontrol agents, such as *Bacillus* spp. and *Aureobasidium pullulans* (Mari *et al*. 2012, Yánez-Mendizábal *et al*. 2012, Calvo *et al*. 2017, Gotor-Vila *et al. 2017*, Grzegorczyk *et al*. 2017), or their volatile organic compounds (VOCs) (Gotor-Vila *et al*. 2017, Gao *et al*. 2018, Di Francesco *et al*. 2020) against *Mon. fructicola* and *Mon. laxa*, both *in vitro* and on peach and plum fruits. Studies on natural compounds and basic substances revealed the effectiveness of chitosan-based compounds in pre- and postharvest stages against *Monilinia* spp. in peach and sweet cherries (Romanazzi *et al*. 2003, Feliziani *et al.* 2013, Ma *et al*. 2013c, Kowalczyk *et al*. 2015). Encouraging results were also obtained with applications of essential oils from *Origanum vulgare* and *Thymus vulgaris* (Mancini *et al*. 2014, Elshafie *et al*. 2015, Santoro *et al*. 2018, Gruľova *et al*. 2020).

Investigation of pathogenetic factors

Several studies focused primarily on the *Monilinia* species involved in brown rot have been carried out on virulence/pathogenicity factors. The necrotrophic lifestyle of these pathogens involves secretion of cell-wall-degrading enzymes, such as endo-polygalacturonase (Chou *et al.* 2015), cutinases, α-glucosidases, pectin lyases, proteases (Garcia-Benitez *et al*. 2019, Baró-Montel *et al.* 2019, Rodríguez-Pires *et al*. 2020), and toxic metabolites (Villarino *et al*. 2022) to destroy tissues and degrade plant cell-wall components during the infection process. Some investigations indicated that changes in cellular redox status play a role in the regulation of virulence factors (Chiu *et al.* 2013, Yu *et al.* 2017). Analysis of the *Mon. fructicola* genome (Vilanova *et al.* 2021) and comparative genomics and transcriptomics including other *Monilinia* species (De Miccolis Angelini *et al.* 2018, 2022, Marcet-Houben *et al.* 2021) revealed species-specific and conserved genes encoding pathogenicity factors, such as candidate effectors, carbohydrate-active enzymes, and secondary metabolites biosynthetic gene clusters. They include toxins, cell-death elicitors, and cell-wall-degrading enzymes, as well as other putative virulence factors that might play key determinant roles in pathogenicity. Only a few *Mon. fructicola* genes known as virulence determinants have been characterised by functional analysis (Lee *et al.* 2010, Zang *et al.* 2020). Transcriptional responses during nectarine and *Mon. laxa* interaction provided the top upregulated genes of this pathogen that could be possible target genes for brown rot control (Balsells-Llauradó *et al*. 2019). New technologies might accelerate the translation of these knowledge advancements into tangible benefits for disease management.

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86. ***Coccidioides*** C.W. Stiles, Johns Hopkins Hosp. Rep. 1: 243. 1896.

Type species: *Coccidioides immitis* G.W. Stiles

Classification: *Ascomycota*, *Pezizomycotina*, *Eurotiomycetes*, *Onygenales*, *Onygenaceae.*

Background

The genus *Coccidioides* is an important member of the *Onygenaceae* (Teixeira *et al*. 2021). An important biological aspect of this fungus is thermodimorphism, an evolutionary characteristic that enables this genus to adapt to a parasitic phase into a vertebrate host (mammals). *Coccidioides* is the causative agent of coccidioidomycosis, an important systemic mycosis (Eulalio *et al*. 2001, Graupmann-Kuzma *et al*. 2008, Cordeiro *et al*. 2021). Coccidioidomycosis in humans may cause a disseminated disease from a lung initial infection, with elevated rates of mortality (Crum 2022). Phylogenetic analyses of the genus have revealed a close relationship with other ascomycetes, *Blastomyces dermatitidis*, *Histoplasma capsulatum*, and *Paracoccidioides* spp. The *Coccidioides* clade emerged about 40–50 million years ago (Whiston & Taylor 2015, Crum 2022) and is now known to encompass two species, *Coccidioides immitis* and *Co. posadasii*, both associated with infection in humans and other animals (armadillos, dogs, equines and camelids). The *Coccidioides* species are reproductively (genetically) isolated, having different geographic ranges (Cordeiro *et al*. 2012, 2021, Fernandez *et al*. 2018, Koistinen *et al*. 2018, Davidson *et al*. 2019).

Coccidioides genus and species

The taxonomic status of *Coccidioides* genus is *Ascomycota* (phylum), *Pezizomycotina* (subphylum), *Eurotiomycetes* (class), *Eurotiomycetidae* (subclass), *Onygenales* (order), *Onygenaceae* (family). Initially, only one species, *Co. immitis*, was known to belong to this genus (Stiles 1896), but after molecular phylogeographical studies, with isolates from different locations/countries, the species *Co. posadasii* was added (Fisher *et al*. 2002). The divergence time between these two species is about 5 million years ago. Both species cause coccidioidomycosis in humans. *Coccidioides immitis* infections occur in North and Central America, and *Co. posadasii* infections occur in South America, in the semiarid Northeast of Brazil and Argentina (Fisher *et al*. 2002, Nguyen *et al*. 2013, Crum 2022).

First description

Coccidioides immitis was described in 1896, but the first case of *Coccidioides* infection was reported by Alejandro Posadas, in Buenos Aires, Argentina, four years earlier (Posadas 1892). Posadas reported a soldier with skin ulcerative lesions on the face. The first biopsy demonstrated a *Coccidia*-like (protozoan) organism, as well as in a second case reported in California, USA, in the late 1890s. In both cases, the mycelial growth was discarded as a contaminant. After these cases, Casper Gilcrest and Emmet Rixford, 1896, named the organism as *Coccidioides* ("like *Coccidia*") *immitis*. Ophuls (1905) determined that the *Coccidioides* sp. was not a protozoan but a dimorphic fungus (Hirschmann 2007, Rixford & Gilchrist 1896, Ophuls 1905). The second species, *Co. posadasii*, was not described until 106 years later (Fisher *et al.* 2002), with comparative molecular genotyping of *Co. immitis* recognising it as a distinct species.

Morphological aspects

Coccidioides species have a peculiar cellular form, with important morphology changes in the parasitic phase. They are classified as thermodimorphic fungi that exist as a mycelial form at environmental temperatures and in the saprophytic phase, or as a spherule form, their parasitic phase, at 35–37 °C or in susceptible hosts (Kirkland & Fierer 2018). In nature, the mycelia grow in poor soils, with a shortage of nutrients and little humidity, which is a nutritional poor condition for most fungal species (Taylor & Baker 2019, Teixeira *et al*. 2019). *Coccidioides* maintenance occurs by asexual growth, but according to multi-locus analyses sexual reproduction is possible, although it has never been obtained and observed in the laboratory. On soil or laboratory culture media, the mycelial phase (hyphae) grows by apical extension and forms arthroconidia, 5 µm in diameter (Crum 2022). During the rainy season, the mycelia grow rapidly in soil and remain viable for many years (Chow *et al*. 2016, Crum 2022). The airborne dispersion of the arthroconidia from the soil is caused by mechanical disturbance, by human or other animals (like armadillo) activities, or by the wind. After the aerosolization of *Coccidioides* spores, susceptible hosts may be infected by inhalation of fungal cells, with initial pulmonary manifestations. On the pulmonary site, arthroconidia transform into spherical cells called spherules, a resistant form of *Coccidioides* spp. in the parasitic phase, though the lungs and sinuses sites may also have hyphal growth (Kirkland & Fierer 2018, Crum 2022). Inside the spherules, endospores (4 µm diam) are formed, and after the rupture of the cell wall, about 300 endospores are released and disseminated by hematogenous route (Crum *et al*. 2022). The endospore germination process results in the formation of new spherules after 4 d, completing the *Coccidioides* parasitic life cycle.

Ecological and economic significance

Endemic areas

Coccidioides immitis occurs in North America, from the central region of California (USA) to Southern Mexico (Galgiani *et al*. 2016, Kirkland & Fierer 2018). *Coccidioides posadasii* occurs in semiarid areas of the Northeast region of Brazil (with the highest occurrence in Ceará and Piauí states), and in the Sierras Pampeanas in Argentina (Wanke *et al*. 1999, Canteros *et al*. 2010, Cordeiro *et al*. 2021). *Coccidioides* spp. have been detected in soil samples from these regions by molecular techniques, such as PCR and NESTED-PCR using rRNA genes as targets (De Macêdo *et al*. 2011, Bowers *et al*. 2019). Strategies for environmental detection of *Coccidioides* enable the adoption of measures to prevent and control coccidioidomycosis, which has high mortality rates for infected individuals. Some studies reported the presence of *Coccidioides* in armadillos, making these animals sentinels of the presence of *Coccidioides* in certain geographical locations. Hunting armadillos is considered an infection risk activity, as reported for *Paracoccidioides* spp., the causative agents of other systemic mycoses, that also infect these mammals (Eulalio *et al*. 2001, Bagagli *et al*. 2003). *Coccidioides* spores can disperse for 75 miles or more in strong winds (Johnson *et al*. 2021). Another possible dispersion mechanism is the migration of infected animals to new areas. After the death of these animals, *Coccidioides* spp. may return to the saprophytic phase. These aspects make it possible for *Coccidioides* to grow in a new site, as long as the fungus finds ideal conditions for its saprophytic maintenance (Taylor & Baker 2019).

Coccidioidomycosis and public health

Epidemiological data reveal that the USA has the highest incidence rate of coccidioidomycosis, with California and Arizona states having the largest number of cases. The Center for Disease Control and Prevention (CDC) estimated that the incidence of coccidioidomycosis increased from 5.3 per 100 000 inhabitants in 1998 to 42.6 in 2011 (Smith & Beard 1946, CDC 2013, McCotter *et al*. 2019, Hirschmann & Smith 2020). Mexico is the second most affected country, mainly in states located close to the USA border, which present the highest number of cases and also the highest number of positive tests for cutaneous reactivity to *Coccidioides* antigens (Nguyen *et al*. 2013, Davila *et al*. 2018). Other countries in Latin America have reported coccidioidomycosis cases, including Guatemala, Honduras, Colombia, Venezuela, Brazil, Paraguay, Bolivia, and Argentina (Laniado-Laborin *et al*. 2019). However, in some of these countries, like Brazil, coccidioidomycosis is a non-notifiable disease, which covers up the real incidence of this mycosis and makes it difficult to map the cases. Some host aspects and environmental factors are responsible for the increase in the number of coccidioidomycosis cases, such as ageing, immunosuppression conditions, the incursion into endemic areas (where *Coccidioides* sp. has already been detected in the environment), climate change and natural events (Cordeiro *et al*. 2021, Crum 2022).

Infection/transmission routes and pathogenesis

The infection process occurs by inhalation of airborne fungal arthroconidia, or rarely by trauma implantation with a skin infection and initial lesion on the inoculation site (Wilson *et al*. 1953, Johnson *et al*. 2021). Another possible transmission route is by organ transplantation, mainly in infected lungs, liver, and kidneys (Wright *et al*. 2003, Martin-Davila *et al*. 2008, Nelson *et al*. 2016), or neonatal transmission, mainly by aspiration of infectious vaginal secretions during birth (Charlton *et al*. 1999). In the lungs, arthroconidia germinate to spherules in the bronchiole, usually three weeks after arthroconidia inhalation. Small fungal loads, such as a single arthroconidium, can cause mycosis. The endospores multiply exponentially and cause disseminated disease. The initial cellular immune response to *Coccidioides* occurs by macrophages, neutrophils, and dendritic cells, that try to prevent the germination of arthroconidia (Crum 2022). Immune T-cell response provides asymptomatic or minimally symptomatic respiratory illness. The inflammatory response makes a sequelae lesion on the lungs or cavity process by fibrosis. The immune response may resolve the infection (T-helper cells – Th17) (Donovan *et al*. 2019) and the disease does not progress to severe manifestations. In coccidioidomycosis, the presence of antibodies is not protective but individuals with complement fixation antibodies, T-cell response (Th1 and Th17), and interferon-gamma production present a low risk of dissemination (Johnson *et al*. 2021, Crum 2022).

Clinical manifestation

Coccidioidomycosis (CM) presents variable clinical forms. Serological skin tests estimate that in 60 % of cases, the infection is asymptomatic (Stockamp *et al.* 2016). As observed for other systemic mycoses, in CM the symptoms are clinically very similar to other infectious diseases, such as other fungal parasites (*e.g.*, *Leishmania* sp.), or bacterial infections such as tuberculosis, presenting commonly cough, dyspnea, thoracic pain, fever, arthralgia, myalgia, and fatigue (Thompson 2011, Malo *et al*. 2014, Stockamp *et al*. 2016). In endemic regions, coccidioidal pneumonia may represent up to 29 % of community-acquired pneumonia (Valdivia *et al.* 2006, Twarog & Thompson 2015). Coccidioidomycosis presents four known forms, symptomatic or pulmonary infection, chronic, disseminated, and primary cutaneous. The pulmonary form shows on radiographic images, a lobar, segmental or multifocal tissue consolidation, and nodules. In these cases, spontaneous regression has been reported even without antifungal therapy (Jude *et al*. 2014, Galgiani *et al*. 2016). Chronic disease is defined as when clinical symptoms last more than six weeks. Disseminated disease or extrapulmonary form occurs in 5 % of immunocompetent patients and may involve different sites, like skin, bone marrow, and meninges. The skin is the most reported dissemination focus. The most severe form of extrapulmonary form of CM consists of fungal dissemination to the central nervous system (Parish & Blair 2008, Ampel 2015), presenting meningitis as the most common clinical manifestation, with high mortality rates. Some studies reported dissemination to sites such as the musculoskeletal system, lymph nodes, and pericardium (Arsura *et al*. 2005, Brilhante *et al*. 2008). Studies, mainly in North America, report a major risk of a disseminated form of coccidioidomycosis in African-Americans, that have a twofold chance to evolve to extrapulmonary disease from initial pulmonary infection. Coccidioidomycosis, if not correctly diagnosed and treated, mainly in disseminated forms, shows high mortality rates (Galgiani *et al*. 2016, Odio *et al*. 2017). Clinical diagnosis is controversial, but laboratory approaches make the correct identification of fungal agents possible by demonstration of the fungus in biological samples (by direct visualisation or histopathological examination), culture (gold standard), serological detection (circulating antigens or skin tests) or molecular biology (PCR with use of generic primers or specific gene markers) (Saubolle 2007, Cordeiro *et al*. 2021, Johnson *et al*. 2021, Crum 2022). Manipulation of *Coccidioides* sp. cultures in the laboratory is allowed only in levels 2 or 3 of the biosafety laboratory, due to the high pathogenic capacity of the mycelial phase of these fungi (production of a large number of conidia) (Sutton 2007).

Research interests

There are 580 publications and 6 936 citations from 2011–2021 on the Web of Science (Fig. 116), with the top 10 most cited articles listed in Table 92. Most of the publications focused on disease management (antifungal treatment and resistance, clinical aspects of the disease, and diagnosis) and research on phylogenetic aspects for knowledge of the speciation process of *Coccidioides* species.

Taxonomy, phylogeny and biological aspects

Since the speciation studies that described the divergence between isolates of *Coccidioides* from central California (*Co. immitis*) and isolates from Central America and South America (*Co. posadasii*), a series of studies have reported the genetic variability among these pathogens, which is reflected in some biological aspects, like growth speed; it is faster in *Co. posadasii* than *Co. immitis*, at 37 °C *in vitro* (Mead *et al.* 2020). However, these are considered morphologically cryptic species, so it is necessary to use molecular techniques to differentiate both. Since there are few studies on CM by *Co. posadasii* in endemic areas, it is not clear yet whether the genetic divergence between *Co. immitis* and *Co. posadasii* is reflected in different clinical manifestations, for example, host symptoms, fungal virulence, and treatment resistance. Studies have compared the genome of *Co. immitis* and *Co. posadasii* and reported differences between mycelia and spherule gene expression (Viriyakosol *et al*. 2013, Teixeira *et al*. 2021). The genetic variability in the genus *Coccidioides* indicates the need to use more precise diagnostic techniques, avoiding situations of false

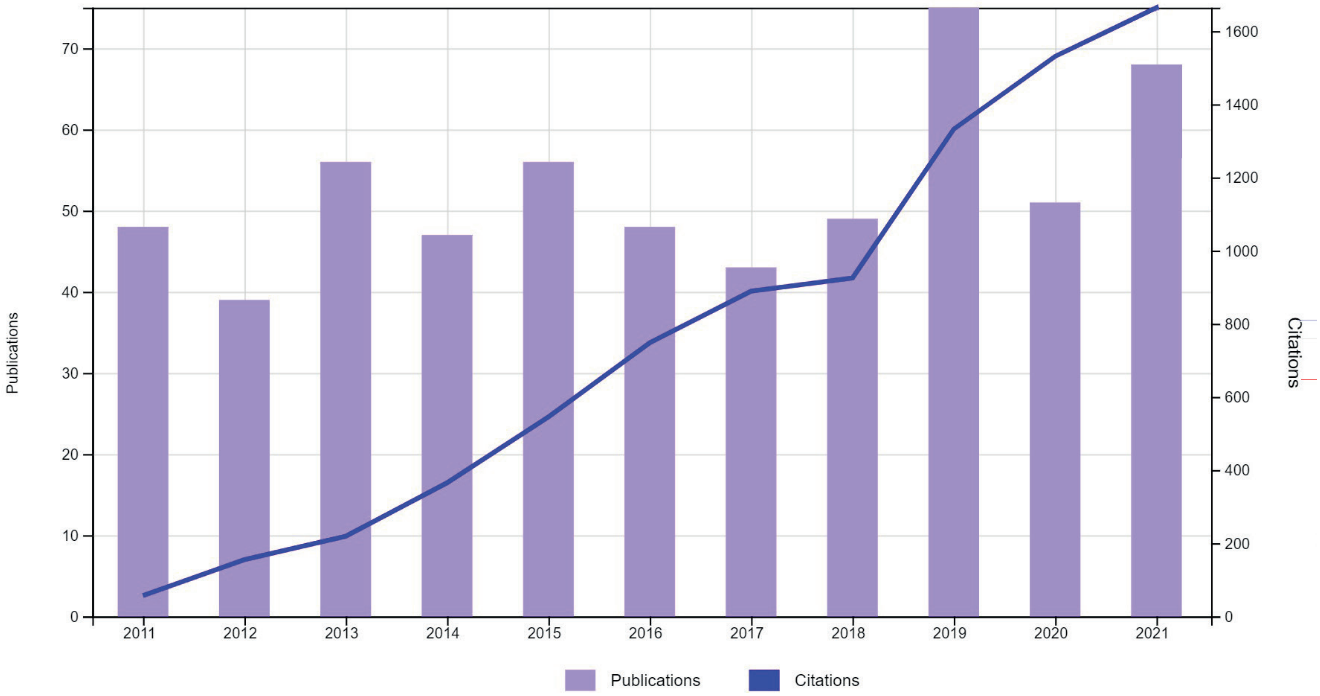

Fig. 116. Trends in research of *Coccidioides* in the period 2011–2021.

Table 92. Top 10 cited articles related to *Coccidioides* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Independent expansion of zincin metalloproteinases in *Onygenales* fungi may be associated with their pathogenicity	378	Li & Zhang (2014)
2	Epidemiology of endemic systemic fungal infections in Latin America	213	Colombo *et al.* (2011b)
3	Vaccine-induced protection against 3 systemic mycoses endemic to North America requires Th17 cells in mice	169	Wuthrich *et al.* (2011)
4	Coccidioidomycosis: epidemiology	163	Brown *et al.* (2013)
5	Human pathogens utilize host extracellular matrix proteins laminin and collagen for adhesion and invasion of the host	160	Singh *et al.* (2012)
6	Recent advances in our understanding of the environmental, epidemiological, immunological, and clinical dimensions of coccidioidomycosis	152	Nguyen *et al.* (2013)
7	Signal transducer and activator of transcription 1 (STAT1) gain-of-function mutations and disseminated coccidioidomycosis and histoplasmosis	142	Sampaio *et al.* (2013)
8	Increase in reported coccidioidomycosis - United States, 1998-2011	140	Tsang *et al.* (2013)
9	Comparative and functional genomics provide insights into the pathogenicity of dermatophytic fungi	137	Burmester *et al.* (2011)
10	Valley Fever: finding new places for an old disease: *Coccidioides immitis* found in Washington state soil associated with recent human infection	105	Litvintseva *et al.* (2015)

negatives and positives. These techniques need to address genetic and phenotypic variations, such as antigenic variation between isolates from different geographic regions. The importance of this genetic variability for the development of diagnostic tools has already been evidenced for other pathogenic fungi, for which cryptic speciation was detected, such as in the genus *Paracoccidioides*, with important differences in the expression of immunodominant antigens in different species, demanding more accurate serological tests (Machado *et al*. 2013, Queiroz Junior *et al*. 2014).

Disease management and vaccine development

Coccidioidomycosis presents a diversity of clinical forms, which may be associated with several aspects, such as exposure factors, climatic changes, host immunity and fungal genetic divergence. The few available clinical studies have reported equal or very close clinical forms in CM caused by *Co. immitis* and *Co. posadasii*. For this reason, more studies should be conducted to evidence possible clinical differences, mainly in the drug response to coccidioidomycosis (Morais *et al*. 2020, Cordeiro *et al*. 2021, Crum 2022).

The treatment of CM is based on the use of drugs from the class of polyenes and azole derivatives, such as amphotericin B and ketoconazole. Drug administration depends on the form and severity of the disease, drug interactions in associated pathologies, responsiveness to treatment, and mainly monitored adverse effects. Some studies report the use of five currently available off-label treatment azoles: fluconazole, itraconazole, posaconazole, voriconazole, and isavuconazole, with variable efficacy (Galgiani *et al*. 2016, Thompson *et al*. 2019, Crum 2022).

Vaccine strategies provided a reduction of disseminated form, mainly in association with severe forms of CM in mice models. Besides the reduction of the severity of coccidioidomycosis, a live-attenuated vaccine is in development and has shown high protection in a mice model, to prevent CM (Narra *et al*. 2016, Shubitz *et al*. 2018, Kollath *et al*. 2019).

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87. ***Melampsora*** Castagne, Observ. Uréd. 2: 18. 1843.

Type species: *Melampsora euphorbiae* (Ficinus & C. Schub.) Castagne

Classification: *Basidiomycota*, *Pucciniomycotina*, *Pucciniomycetes*, *Pucciniales*, *Melampsoraceae.*

Background

Rust fungi are obligate parasites of vascular plants (ferns, gymnosperms, angiosperms) with several unique features and with almost 8 000 accepted species (Kirk *et al*. 2008). As specialised plant parasites, rust fungi cannot be grown or are difficult to grow in axenic culture, although Moricca *et al*. (2000) successfully cultivated *Me. laricis-tremulae* on specific agar cultures (for further literature see the review by Maclean 1982). Rust fungi have the largest genome in the kingdom of *Fungi* (Tavares *et al*. 2014). Species may be restricted to one host or one group of related hosts (autoecious species) or may be host-alternating (heteroecious) infecting two taxonomically non-related plant hosts (the aecial and the telial host) in different stages of their life cycle. They may produce up to five successive spore-producing structures called spermogonia, aecia, uredinia, telia, and basidia. Spores are morphologically characteristic and named with reference to these spore-producing structures, namely spermatia, aeciospores, urediniospores, teliospores, and basidiospores.

Melampsoraceae and the genus *Melampsora* have been monographed only by Sydow & Sydow (1915). We define the family *Melampsoraceae* in a traditional sense consisting of only one genus, *Melampsora* following, *e.g.*, Cummins & Hiratsuka (2003) and Kirk *et al.* (2008), although most recently Aime & McTaggart (2021) suggested to include a species of another genus, *Ceropsora weirii*. The genus *Melampsora* was introduced by Castagne (1843) with the type species *Me. euphorbiae* (≡ *Xyloma euphorbiae*), an autoecious species on the herbaceous plant *Euphorbia exigua* (see Fig. 117 for *Me. euphorbiae* on *Euphorbia carniolica*). The nomenclatural databanks MycoBank and Index Fungorum (2022) list 320 and 283 species epithets, respectively. Kirk *et al.* (2008) accepted 90 species worldwide.

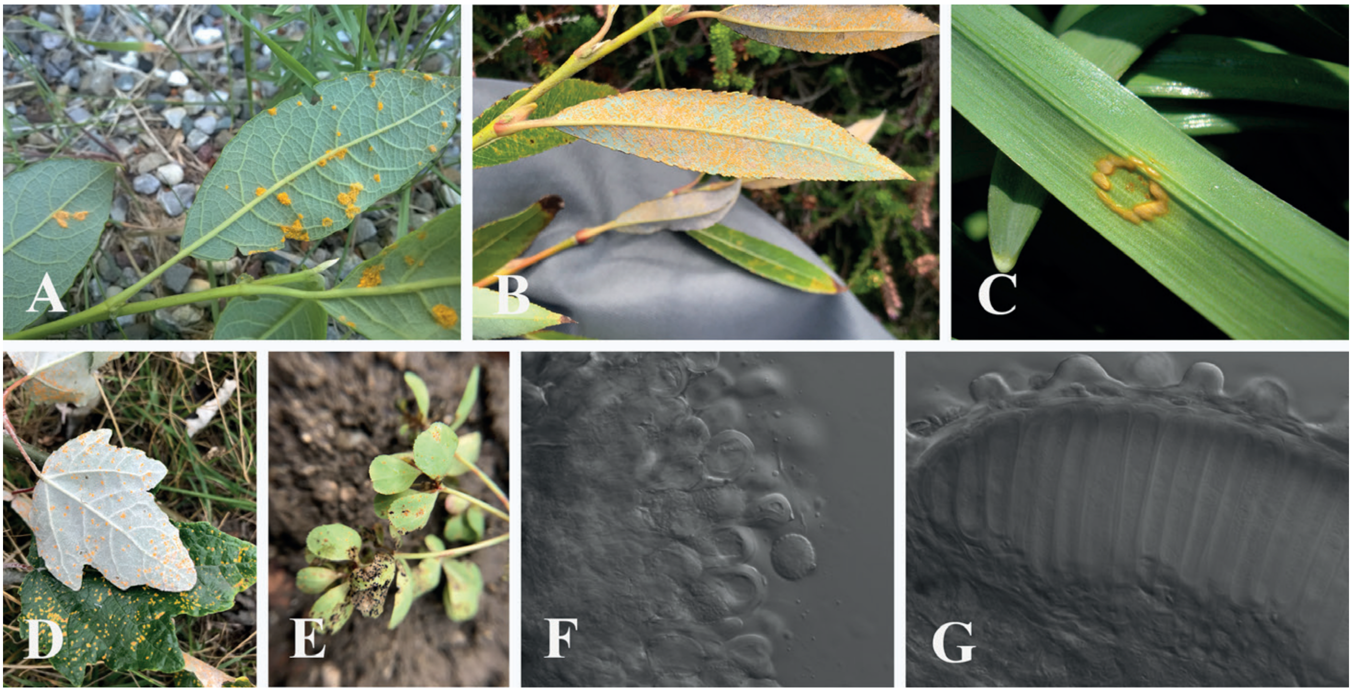

Fig. 117. A. *Melampsora abietis-caprearum*: orange uredinia on leaves of *Salix caprea.* **B.** *Melampsora amydalinae*: orange uredinia on leaves of *Salix triandra.* **C.** *Melampsora galanthi-fragilis* with central spermogonia surrounded by aecia on leaves of *Galanthus nivalis.* **D.** *Melampsora magnusiana*: hypophyllous orange uredinia causing characteristic yellow epiphyllous leaf spots on *Populus alba.* **E.** *Melampsora euphorbiae*: orange uredinia and black crusty telia on *Euphorbia carniolica.* **F.** *Melampsora gelmii*: uredinia with urediniospores and thick-walled paraphyses on leaves of *Euphorbia dendroides.* **G.** *Melampsora gelmii*: telium crust with fused teliospores on *Euphorbia dendroides* [pictures contributed by M. Scholler (Fig. 117A, B, D–G) and J. Kruse (Fig. C)].

After 2008, however, several additional new species were described, *e.g.*, by Damadi *et al.* (2010), Tome & Aime (2014), Ali *et al.* (2016), Wang *et al.* (2020c), and Zhao *et al.* (2014c, 2015f, 2016a, 2017a, 2021b). Consequently, the number of known species is here estimated to be more than 100. But species numbers also depend on the species concept. Delimitation of species in *Melampsora* is problematic because of narrow biological (Klebahn 1894, 1896, 1897, 1899, 1900, 1902, 1903, 1904, 1905, 1907, 1914, Gäumann 1959) as well as morphological concepts leading to a wide species concept (Hylander *et al.* 1953, Wilson & Henderson 1966, Boerema & Verhoeven 1972, Bagyanarayana 2005, Pei 2005, Klenke & Scholler 2015) have been applied in this genus. This particularly concerns species of the *Me. epitea* (*Me. laricis-epitea*) complex (with *Salix* telial hosts) and the *Me. populnea* complex (with *Populus* telial hosts). Today several rust taxonomists prefer a combination of classical (host range, morphology) and molecular genetic (nuclear and mitochondrial loci) features (Feau *et al.* 2009, Vialle *et al.* 2013, Zhao *et al.* 2015e, 2017a, Ji *et al.* 2020). Intense phylogenetic studies were carried out by Bennet *et al.* (2011) in North America and by Milne *et al.* (2012) in subarctic UK (Scotland and northern England) finding numerous “cryptic” taxa. Here, the question arises whether the species are morphologically indistinguishable (“cryptic”) and, if a careful future study confirms this, whether mere phylogenetic species concepts should be sufficient to describe new species. The species concepts for *Melampsora* on *Populus* were reviewed by Vialle *et al.* (2011).

In *Melampsora*, all morphological basic types of spores and sori are formed that we also know from other rust fungi. After Cummins & Hiratsuka (2003), spermogonia are subcuticular or subepidermal, aecia are “caeomoid”, *viz.*, they have verrucose aeciospores formed in chains without peridia, subepidermal uredinia are characterised by having colourless, capitate paraphyses, and urediniospores formed singly on pedicels, with colourless echinulate walls with obscure germ pores (Fig. 117). Telia exhibit the most striking features of the genus. They are formed subepidermal or subcuticular with laterally adherent spores forming a crust. Teliospores are one-celled and sessile, wall brown or brownish, with one terminal germ pore (Fig. 117). Basidia consist of externally formed phragmospores forming four colourless basidiospores on sterigmata. Hyphae are septate and hyaline. No clamp connections are known for the dikaryotic mycelium. Hyphae grow between host cells (intercellular), obtaining nutrients from the host cells by means of haustoria.

Melampsora species are distributed worldwide but with emphasis prominence in the northern hemisphere. This is because most *Melampsora* species infect *Populus* (poplars) and *Salix* (willows), both genera of the *Salicaceae* (tribe *Salicae*, see Chase *et al.* 2002) with roughly 22–45 (*Populus*) and 330–500 (*Salix*) taxa worldwide (Dickmann & Kuzovkina 2014). The emphasis of distribution of both host genera is the temperate northern hemisphere (Dickmann & Kuzovkina 2014). The centre of abundance of *Salix* is in China, with 189 endemic species (Fang *et al.* 1999), followed by Russia and adjacent countries of the former Soviet Union with about 120 species (Skvortsov 1999).

Most *Melampsora* species are host-alternating (heteroecious) and most of them form uredinia, telia, and basidia with *Salicaceae* telial hosts, only a few others prefer other host taxa, *e.g.*, *Saxifraga* (*Saxifragaceae*) and *Ribes* (*Grossulariaceae*). Aecial hosts are various herbaceous or woody dicot angiosperm genera, *e.g.*, *Allium*, *Arum*, *Euonymus*, *Galanthus* (Fig. 117C), *Ribes* and *Saxifraga* or gymnosperms (*Pinaceae*), *e.g.*, *Abies*, *Larix* and *Pinus*. Non-host-alternating (autoecious) species may form all spore states (*e.g.*, *Me. amygdalinae* on *Salix* spp. and *Me. euphorbiae* on *Euphorbia* spp., Fig. 117E), only spermogonia, aecia, telia and basidia (*Me. vernalis* on *Saxifraga*), only uredinia, telia and basidia (*e.g.*, *Me. hypericorum* on *Hypericum*, *Melampsora* × *medusae-populina*, *Me. microspora* both on *Populus*), or they are microcyclic, *e.g.*, *Me. farlowii*, forming only telia and spermogonia on *Tsuga canadensis*.

As mentioned above, most *Melampsora* species are hosts alternating with *Populus* and *Salix* (Fig. 117A, B, D) telial hosts. The life cycle of *Melampsora* rusts on *Populus* telial hosts is nicely illustrated by Vialle *et al.* (2011). In the following, we describe the life cycle of *Me. laricis-epitea* described by Pei (2005). The species host alternates from *Larix* (larch) to *Salix*. Spermogonia are formed in spring on *Larix* needles. They produce light-brown honeydew which attracts insects which transport monokaryotic spermatia and facilitate fertilisation between spermogonia. Two to three days later, the formation of aecia and aeciospores starts. The dikaryotic aeciospores infect *Salix* leaves to produce dikaryotic urediniospores. These are mitotic repeating spores and will infect other susceptible willows. In the late season, telia with teliospores are formed. In the teliospores nuclei fuse (karyogamy) and the fungus usually overwinters as a teliospore. In spring, meiosis takes place in the teliospores. They germinate with a basidium which produces four monokaryotic basidiospores which finally infect the aecial host (*Larix*), producing spermogonia.

The overwintering of species is variable in host-alternating rust fungi. Scholler *et al.* (2019) assume that there are other additional strategies to overwinter, *e.g.*, overwintering as aecio- or urediniospores or as mycelium in perennial plant tissue. Pei (2005) confirmed this for *Melampsora* on *Salix.* He listed eight host-alternating species which overwinter on *Salix* in the uredinial state indicating that their existence “may not depend on the availability of the aecial hosts”. The autoecious species *Me. amygdalinae* (Fig. 117B) can also overwinter in buds and stem cancers of *Salix triandra* (Ogilvie 1932, Raabe 1939, Pei 2005).

Economic and ecological importance

The economic importance of *Melampsora* rusts is mostly related to their occurrence as pathogens on woody plants such as *Populus* spp. and *Salix spp.* An exception is the annual crop plant flax, although in practical cultivation the detrimental effects of the rust disease on flax are limited. Only the most important species are listed below.

Poplar rusts (on *Populus* spp.)

Melampsora laricis-populina and *Me. allii-populina* are Eurasian species that can be found on poplars of the section *Aigeiros*, namely *Populus nigra*, but also on hosts in the section *Aigeiros* originating from North America like *P. deltoides* and *P. trichocarpa* (Pei & Shang 2005). Larch species (*Larix* spp.) are aecial hosts for the first and *Allium* species for the latter *Melampsora* species (*e.g.*, Gäumann 1959). According to Frey *et al.* (2005), *Me. laricis-populina* is the more important pathogen in poplar cultivations. The economic importance of *Me. laricis-populina* is based on the fact that most clones used in commercial poplar cultivation for timber and pulp production in Europe originate from crossings of *Populus deltoides* and *P. nigra* (*P.* × *euramericana*) and *P. deltoides* and *P. trichocarpa* (*P.* × *interamericana*).

Melampsora medusae is a North American species separated into two host-specific formae speciales: *Melampsora* medusae *f. sp.* deltoidis with telial hosts in the section Aigeiros and Me. medusae *f. sp.* tremuloidae with telial hosts in the section *Populus* (Boutigny *et al.* 2013). Aecial hosts are members of the *Pinaceae*, namely *Larix* spp., *Pinus* spp. (especially young plants), and *Pseudotsuga menziesii*. The fungus may cause substantial damage to plantations of *Populus deltoides* and related hybrids in North America (Widin & Schipper 1981). The rust has also been introduced to Australia (Walker *et al.* 1974) and New Zealand (Spiers 1998) infecting introduced *P. deltoides* and related hybrids. In Europe, *Me. medusae f. sp. deltoidis* occurs occasionally on *P. deltoides* and hybrids without causing significant damage (Jeger *et al.* 2018). It is neither considered a quarantine pest nor a regulated non-quarantine pest but should be under further observation (Jeger *et al.* 2018). *Melampsora* medusae *f. sp. tremuloidae* is absent from Europe and is listed as a quarantine pest in annex IIA of implementing regulation (EU) 2019/2072 (European Commission 2019).

Melampsora populnea s. lat. is a complex of Eurasian species, including *Me. magnusiana* (Fig. 117), *Me. rostrupii, Me. laricis-tremulae* and *Me. pinitorqua*. Telial hosts are members of *Populus* sect. *Populus*, namely aspen (*Populus tremula*), white poplar (*Populus alba*) and their hybrids. The economic impact on the telial hosts is relatively low since *P. tremula* and *P. alba* (Fig. 117) are not widely used in plantations (Frey *et al.* 2005). The economic impact on the aecial host depends on the aecial host species. *Melampsora magnusiana* and *Me. rostrupii* infect only economically unimportant herbaceous plants, *Chelidonium majus* and *Mercurialis perennis* (Gäumann 1959). A harmful impact on the natural host population is not known. Economic impacts on larch trees (*Larix* spp.), the aecial host of *Me. laricis-tremulae*, are not known either. *Pinus sylvestris*, *P. pinaster* and other pine species infected by *Me. pinitorqua* (Desprez-Loustau & Wagner 1997), however, are strongly attacked. Spermogonia and aecia develop directly on young shoots of seedlings and induce bending of the infected shoot. This can reduce the height and quality of trees (Mattila 2005).

Willow rust (*Salix* spp.)

Melampsora laricis-epitea is a Eurasian species complex separated into several *formae speciales* (*e.g.*, Pei 2005). On the aecial hosts (*Larix* spp.) no significant economic impacts are known. The telial hosts are willows. The economically most important *forma specialis* is *Me. laricis-epitea f. sp. laricis-epitea* on *Salix*, section *Vetrix*, namely *S. aurita* and *S. cinerea* and section *Vimen*, namely *S. viminalis* (Pei 2005). *Salix viminalis* is grown for basketry (Stott 1992) and as a bioenergy crop in short rotation coppices (McCracken & Dawson 1996). Because of the use of vegetatively propagated willow clones, short rotation coppices can be seriously affected by rust. Infections with the rust of the *Me. laricis-epitea* complex led to problems in the use of short rotation coppices in Great Britain in the early 1990s (McCracken & Dawson 1992).

Lin rust (on *Linum usitatissimum*)

Melampsora lini (syn. *Me. liniperda) causes rust disease on Linum species (linum) including Linum usitatissimum* (common flax) which is cultivated for oil or fibre production. The species is autoecious, *i.e., all spore stages are formed on a single host species*. Apart from the crop plant *L. usitatissimum*, *Me. lini* occurs on several other *Linum* species in Europe, North America, Australia and New Zealand (Lawrence *et al.* 2007). Nowadays, linum rust is not the major pathogen in linseed/flax cultivations in Western Europe, China, Russia and Canada. In reports on flax cultivation (Heller *et al.* 2015, Wang *et al.* 2018i, Stafecka *et al.* 2019) rust disease is

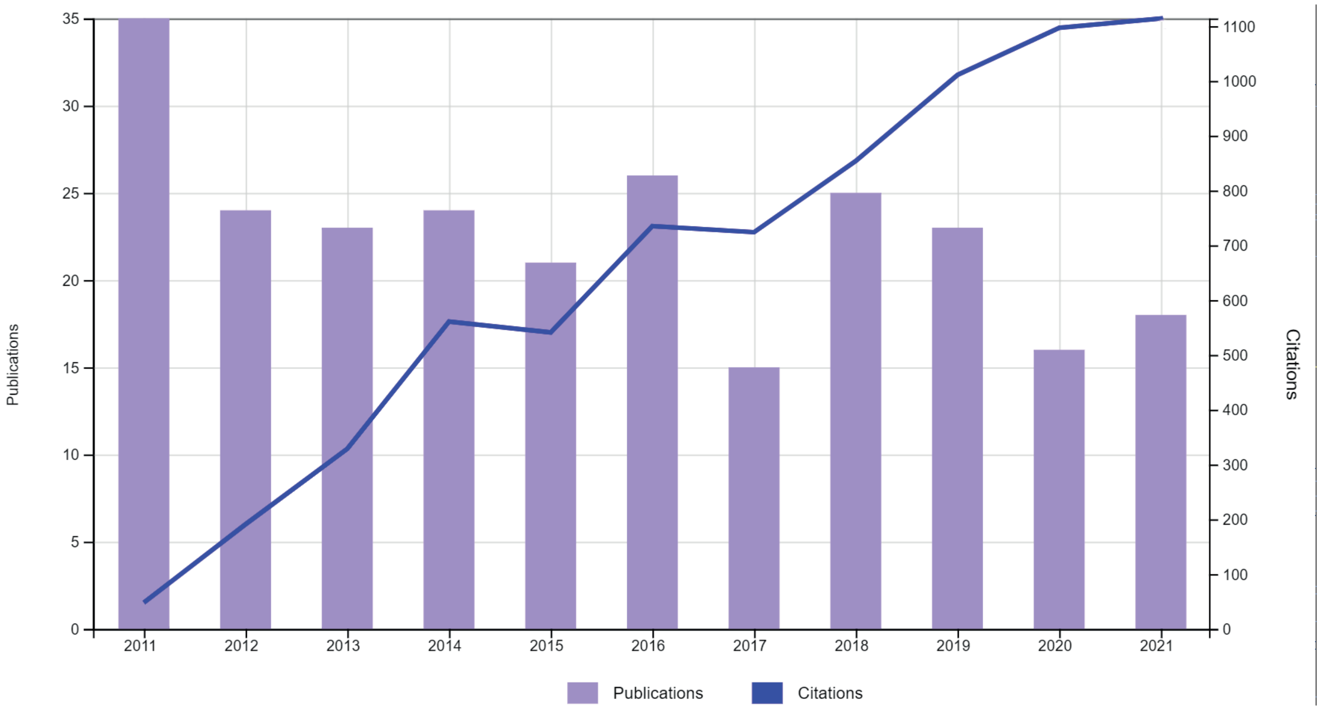

Fig. 118. Trends in research of *Melampsora* in the period 2011–2021.

only listed after wilt (*Fusarium oxysporium f. sp. lini*), anthracnose (*Colletotrichum linicola*) and powdery mildew (*Podosphaera lini*, including *Oidium lini*, Braun *et al.* 2019). One reason for the low prevalence of rust disease in flax cultivation is the relative ease of selecting for rust resistance in classical breeding by crossing (Rashid & Kenaschuk 1994), resulting in at least temporarily resistant lineages. The importance of *Me. lini* is rather not expressed in terms of harm to crop plants but can be seen in its use as a model organism for plant pathology (see below). However, in New Zealand recent attempts to cultivate the seriously threatened Chatham Islands endemic *Linum monogynum* var. *chathamicum* has resulted in heavy rust infections and the death of plants in the nursery (De Lange 2019); the rust was first observed in the Chatham Islands on cultivated plants and was not observed in the wild until 2008.

Research interests

Importance as a model organism

There are 250 publications and 6 915 citations from 2011–2021 in the Web of Science (Fig. 118). Research on *Melampsora* rusts has high importance in plant pathology, mainly because of crossing experiments on flax and its rust *Me. lini* that led to the articulation of the gene-for-gene hypothesis by Harold Henry Flor (Flor 1955, 1971). The experimental system made use of the presence of homozygous cultivars of the host and the possibility of Mendelian crossing analysis with the dikaryotic stages of the rust. The experiments were further facilitated by the autoecious life cycle of *Me. lini*. The hypothesis states that there is a gene-for-gene relationship between the ability of the pathogen to infect the host and the ability of the host to resist the pathogen. It was the starting point for resistance breeding in other crop species (Dean

Table 93. Top 10 cited articles related to *Melampsora* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	The top 10 fungal pathogens in molecular plant pathology	1769	Dean *et al.* (2012)
2	Obligate biotrophy features unravelled by the genomic analysis of rust fungi	415	Duplessis *et al.* (2011)
3	Structural and functional analysis of a plant resistance protein TIR domain reveals interfaces for self-association, signaling, and autoregulation	224	Bernoux *et al.* (2011)
4	Plant-parasite coevolution: bridging the gap between genetics and ecology	163	Brown & Tellier (2011)
5	Using hierarchical clustering of secreted protein families to classify and rank candidate effectors of rust fungi	162	Saunders *et al.* (2012)
6	Genetic improvement of willow for bioenergy and biofuels	141	Karp *et al.* (2011)
7	The role of effectors of biotrophic and hemibiotrophic fungi in infection	132	Koeck *et al.* (2011)
8	Rapid genetic change underpins antagonistic coevolution in a natural host-pathogen metapopulation	130	Thrall *et al.* (2012)
9	Spatial variation in disease resistance: from molecules to metapopulations	122	Laine *et al.* (2011)
10	A comprehensive analysis of genes encoding small secreted proteins identifies candidate effectors in *Melampsora larici-populina* (poplar leaf rust)	99	Hacquard *et al.* (2012)

et al. 2012). Today *Me. lini* is still an important model system as can be seen from Table 93. Among the top 10 *Melampsora* papers, four treat the rust/flax system (Bernoux *et al.* 2011, Laine *et al.* 2011, Dean *et al.* 2012, Thrall *et al.* 2012). The current research takes benefits from the availability of *Agrobacterium*-mediated transformation protocols (Lawrence *et al.* 2010) and the genome sequence of *Me. lini* (Nemri *et al.* 2014).

Resistance/disease management (control)

Interest in *Melampsora* rusts from 1990 to 2010 derived from the planting of short rotation coppices for the production of renewable energy. Short rotation means that trees are cut after three to twenty years, in opposition to the long rotation of 80 to 120 years in classical forestry. Two very suitable genera are *Populus* and *Salix*. They not only have the advantage of fast growth but can also regenerate from root stocks for several rotations (Faasch & Patenaude 2012). Because of the usage of clonally propagated plants (propagation by cuttings), damage can occur when rust susceptible clones are planted (Pei *et al*. 1999). Fungicides are not regularly applied in short rotation coppices; their use has only been restricted to experimental plantations (McCracken & Dawson 1997). One strategy of risk reduction is the use of a mixture of clones. In a comparison of monoclonal and polyclonal willow stands it could be shown that the reduction of the disease impact was comparable between fungicide treatment and the use of a clonal mixture (McCracken & Dawson 1997).

In disease management, it is very important to consider the host range of *Melampsora* species. Sequencing of ITS barcodes is a relatively quick method and even *formae speciales* can be differentiated using this marker, although the difference can be as low as one SNP (Single Nucleotide Polymorphism) between *Me. laricis-epitea f. sp. laricis-daphnoides* and *Me. laricis-epitea f. sp. laricis-epitea* (Bubner *et al*. 2014). Molecular distinction of the two *formae speciales Me. medusae f.* sp. *deltoidis* and *Me. medusae f.* sp. *tremuloidae* can help to confirm that the latter is still absent from Europe *(Boutigny et al*. 2013).

The distinction of *Melampsora* species is also a necessary tool for breeding programs to provide rust-resistant plants (Karp *et al.* 2011). In classical breeding programs, crosses of poplar or willow clones are not only selected for biomass yield but also their rust resistance by scoring susceptibility to natural infection pressure (Bubner *et al.* 2018, Fey *et al.* 2018) or by artificial inoculations (Pei *et al.* 2008). Classical programs are supported by molecular methods such as mapping of quantitative trait loci for rust resistance (Samils *et al.* 2011, Jorge *et al.* 2005). Molecular markers will support rust resistance selection without the need for natural selection pressure or artificial inoculation (Wei *et al.* 2020).

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88. ***Antrodia*** P. Karst., Meddeland. Soc. Fauna Fl. Fenn. 5: 40. 1879.

Type species: *Antrodia serpens* (Fr.) P. Karst.

Classification: *Basidiomycota*, *Agaricomycotina*, *Agaricomycetes*, *Polyporales*, *Fomitopsidaceae.*

Background

Antrodia, one of the largest genera of polypores, was described by Peter Adolf Karsten (1879) with *Antrodia serpens* (syn. *Polyporus serpens*) as the type. The genus has more than 130 records listed in Index Fungorum, with about 50 well-recognised species. Members of the genus are mostly circumscribed by an annual to perennial growth habit; resupinate to effused-reflexed stature of the basidiocarps; the presence of dimitic hyphae; dextrinoid basidiospores shaped oblong-ellipsoid to cylindrical; and causing brown rot diseases of woods (Gilbertson & Ryvarden 1986, Bernicchia & Ryvarden 2001, Núñez & Ryvarden 2001, Dai & Niemelä 2002, Ryvarden & Melo 2014, Han *et al*. 2020). Members of the genus are cosmopolitan in distribution (Han *et al*. 2020). About 70 % of the brown rot fungi belong to the "*Antrodia* clade", which is the clade with the largest number of brown rot fungal species (Garcia-Sandoval *et al*. 2011, Ortiz-Santana *et al*. 2013).

Antrodia within the "*Antrodia* clade" belong to the core genus comprising poroid species (Runnel *et al*. 2019). It is a polyphyletic genus, phylogenetically related to other fungal genera like *Daedalea*, *Fomitopsis*, *Oligoporus*, and *Rhodofomes*, all of which are known for causing brown rot disease of wood (Han *et al*. 2020). *Antrodia* in a broad sense was divided into *Antrodia s. str.*, *Amyloporia*, and *Fibroporia* (Han *et al.* 2020). Based on the study of Spirin *et al.* (2013), it was found *Antrodia s. str.* consists of the *Antrodia heteromorpha* complex (*An. favescens*, *An. serpens*, *An. heteromorpha s. str.*, and *An. tanakae*), together with other taxa like *An. mappa*, and *An. macara* based on the ITS rDNA, and *tef1* sequence data. However, Ortiz-Santana *et al*. (2013) supported the segregation of the genus *Antrodia s. lat.* into *Fibroporia* and *Antrodia* due to a lack of evidence for the monophyly of *Amyloporia*. Spirin *et al.* (2015) delimitated four clades by investigating the phylogeny within the *Antrodia crassa* group, *viz*. the *An. crassa*, *An. pinea*, *An. pini-cubensis* and *An. sitchensis* clades based on morphological, geographical, ecological and three-marker gene region sequence data (ITS and LSU rDNA, and *tef1*). Spirin *et al.* (2016) revised the phylogeny and taxonomy of the *An. malicola* group based on the ITS rDNA, and *tef*1 datasets. Runnel *et al.* (2019) accepted the genus *Antrodia* in a stricter sense based on morphological and phylogenetic results and included *An. griseoflavescens*, *An. multiformis*, and *An. tenerifensis* under the genus. Han *et al.* (2020) used morphological features and molecular data and confirmed the polyphyly of *Antrodia s. lat.* together with other brown rot fungal genera, such as *Daedalea*, *Fomitopsis* and *Rhodofomitopsis*. Han et al. (2020) also stressed better research of this group based on a phylogenetic study with more samples and some better conserved gene markers.

Ecological and economic significance

Antrodia, the brown rot fungi, decompose cellulose and hemicellulose through enzymatic degradation (Baldrian & Valášková 2008, Floudas *et al*. 2012, Ortiz-Santana *et al.* 2013) and support the growth of seedlings, other fungi, and insects (Lonsdale *et al*. 2008, Rajala *et al*. 2012). They also play an important role in the sequestration of carbon (Fukami *et al.* 2010). Some species of the *Antrodia* clade are also known for their economic importance as agents of indoor wood decay and source of biotechnological and pharmaceutical products (Bagley & Richter 2001, Vaidya & Singh 2012). Economic losses due to the species of *Antrodia* have been reported in structural woods of buildings and timber production in North America and Europe (Schmidt & Moreth 2003, Schmidt 2007). *Antrodia camphorata* is a parasite of the plant *Cinnamomum kanehirae*, which is endemic to Taiwan (Soković *et al.* 2018).

Members of the genus are well regarded for their importance in traditional medicine since ancient times (Tzeng & Geethangili

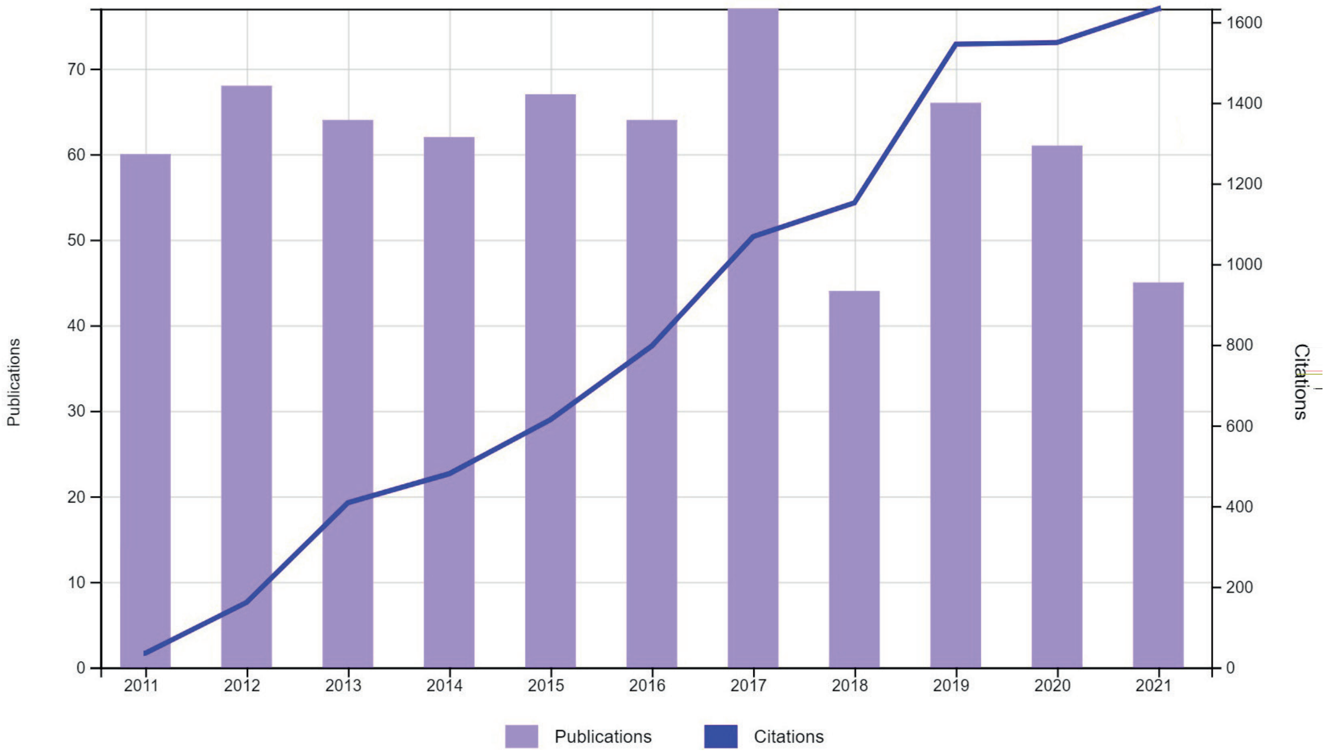

Fig. 119. Trends in research of *Antrodia* in the period 2011–2021.

2011). *Antrodia camphorata*, is used in Taiwan to cure various health-related problems like colds, headaches, influenza, fever, muscle damage, *etc*. (Tzeng & Geethangili 2011). The sporocarps and mycelium extracts prepared from *An. camphorata* have been proven to possess antiproliferative effects on several cancer cell lines. Many studies on its extracts have shown that it can help in generating immune responses in leukaemia BALB/c mice by exhibiting anti-leukemic activity in a hepatoma cell model of humans by activating the immunomodulation of macrophages (Popović *et al.* 2013). A mycelium extract from *An. camphorata* works well against hepatitis B virus without showing any cytotoxic effects on normal cells. The extract also possesses good antioxidant activities and thereby prevents various damages to the liver. Tzeng & Geethangili (2011) used rats as a model and showed that the methanolic extracts of *An. camphorata* reduced hypertension. Wang *et al.* (2017c) reported *An. camphorata* sporocarps have anti-skin cancer, anti-melanogenic, and antioxidant properties. About 78 compounds have been isolated from *An. camphorata* most of which are triterpenoid, having an ergostan, and lanostane skeleton (Popović *et al.* 2013, Soković *et al.* 2018). Some other compounds such as benzoquinones, benzoids, fatty acids, lignans, and polysaccharides have also been found in *An. camphorata* (Soković *et al.* 2018). Ethanol extract from artificially cultured *An. cinnamomea* confirmed its anti-tumour properties without showing any side effects in an *in vivo* animal model. There are reports suggesting that breast cancer cells (T47D) treatment with ethanol

Table 94. Top 10 cited articles related to *Antrodia* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Recent developments in mushrooms as anti-cancer therapeutics: a review	216	Patel & Goyal (2011)
2	Review of pharmacological effects of *Antrodia camphorata* and its bioactive compounds	216	Tzeng & Geethangili (2011)
3	Phylogenetic and phylogenomic overview of the *Polyporales*	196	Binder *et al.* (2013)
4	Contents of lovastatin, γ-aminobutyric acid and ergothioneine in mushroom fruiting bodies and mycelia	120	Chen *et al.* (2012a)
5	Recent research and development of *Antrodia cinnamomea*	111	Lu *et al.* (2013)
6	Lanostanoids from fungi: a group of potential anticancer compounds	102	Ríos *et al.* (2012)
7	Lignin-degrading peroxidases in *Polyporales*: an evolutionary survey based on 10 sequenced genomes	91	Ruiz-Dueñas *et al.* (2013)
8	Revisiting the taxonomy of *Phanerochaete* (*Polyporales*, *Basidiomycota*) using a four gene dataset and extensive ITS sampling	76	Floudas & Hibbett (2015)
9	Nutrient compositions of culinary-medicinal mushroom fruiting bodies and mycelia	76	Ulziijargal & Mau (2011)
10	Antroquinonol from ethanolic extract of mycelium of *Antrodia cinnamomea* protects hepatic cells from ethanol-induced oxidative stress through Nrf-2 activation	71	Kumar *et al.* (2011)

extracts of *An. cinnamomea* induce endoplasmic reticulum stress by expressing inositol-required enzyme 1α and CHOP anticancer protein (Chen *et al.* 2019d). Yue *et al.* (2013) made a detailed review and included various hepatoprotective activities of *An. cinnamonea* including anti-hepatocarcinoma, anti-hepatitis and anti-alcoholism. Wang *et al.* (2019a) summarized the pharmacological effects of *An. camphorata* in various cancer cell lines (such as liver, breast, bladder, cervical, prostate, ovarian, colorectal, lung and pancreatic).

Research interests

There are 678 publications and 6 910 citations from 2011–2021 in the Web of Science (Fig. 119), with the top 10 most cited articles included in Table 94. Most publications focused on pharmacology and therapeutics, and phylogeny and taxonomy.

Pharmacology and therapeutics

Antrodia cinnamomea, an endemic species from Taiwan, is known for its therapeutic and anticancer properties. This Taiwanese mushroom has been prized by tribals as folk medicine, and various classes of compounds have been isolated from the fungus for the treatment of hypertension, inflammatory disorders, hepatitis and cancer (Lu *et al.* 2013). Anticancer compounds such as lanostanoids (tetracyclic terpenoids derived from lansterol), isolated from *An. camphorata*, show cytotoxic effects through the induction of apoptosis (Rios *et al.* 2012). Kumar *et al.* (2011) studied the effect of antroquinonol, another potent compound isolated from the medicinal fungus *An. cinnamomea*, which has shown promising effects for the treatment of liver diseases. Methanol extracts of the mycelia of *An. cinnamomea* showed anti-inflammatory activity both *in vivo* and *in vitro*, also methanolic extracts of sporocarps of *An. camphorata* showed potent anti-inflammatory properties indicating it is a good candidate for hydrocolloid dressings (Wen *et al.* 2011, Tsai *et al.* 2015). The mycelia of *An. salmonea* contains high amounts of lovastatin, known for the reduction of the risk of heart disease (Chen *et al.* 2012a).

Phylogeny and taxonomy

The phylogenetic relationships within the mushrooms of the "*Antrodia* clade" were studied using LSU and ITS rDNA sequence data by Ortiz-Santana *et al.* (2013). Cui (2013) described a new species, *An. tropica* from Hainan, China, on the basis of both molecular (rDNA ITS sequences) and morphological data.

Authors: N. Roy and A.K. Dutta

89. ***Brettanomyces*** Kuff. & Van Laer *ex* Custers, Bull. Soc. Chim. Belgique 30: 276. 1921. .
Synonym: Dekkera Van der Walt, Antonie van Leeuwenhoek 30: 274. 1964

Type species: *Brettanomyces bruxellensis* Kuff. & Van Laer (syn. *Dekkera bruxellensis* Van der Walt)

Classification: *Ascomycota*, *Saccharomycotina*, *Pichiomycetes*, *Pichiales*, *Pichiaceae.*

Background

The genus *Brettanomyces* was described to accommodate yeasts isolated from Belgium lambic beers (Kufferath & Van Laer 1921, Smith 2011), with *Br. bruxellensis* as the only species at that time. In the 5th edition of "The Yeasts, a Taxonomic Study" (TYTS), the genus contained five species (Smith 2011), namely *Br. anomalus* (Custers 1940), *Br. bruxellensis*, *Br. custersianus* (Van der Walt 1964), *Br. naardenensis* (Kolfschoten & Yarrow 1970) and *Br. nanus* (Smith *et al.* 1981, Boekhout *et al.* 1994). Recently, *Br. acidodurans* was described for two strains obtained from olive oil and spoiled olive oil, respectively, using sequence analysis of the D1/D2 domains of large subunit ribosomal DNA (LSU), SSU, and *tef1* that demonstrated that this species is an early diverging lineage of the genus (Péter *et al.* 2017a). Using sequence analysis of SSU it was found that *Brettanomyces*/*Dekkera* formed a well-supported monophyletic clade with a sister relationship to *Pichia membranifaciens* and *P. kudriavzevii* (cited as *Candida krusei*) (Cai *et al.* 1996). Sequence relatedness varied from 94.8–95.4 % between a more basal lineage, *Br. custersianus*, and the other *Brettanomyces* species, but *Dekkera naardenensis* occurred as the most basal lineage. Smith and collaborators described *Eeniella*, a genus with one species, *Eeniella nana* (Smith *et al.* 1981) to accommodate isolates from a number of Swedish breweries that differed morphologically by the small size of the yeast cells that have an enteroblastic, bipolar mode of budding (Smith *et al.* 1981). Using sequence analysis of the D1/D2 domains of the LSU it was found that *Eeniella* clustered within species of the genus *Brettanomyces*, with *Br. custersianus* as basal species (Boekhout *et al.* 1994). Yamada *et al.* (1995) studied sequence divergence between *Eeniella* and *Brettanomyces*/*Dekkera* species using both SSU and partial LSU sequences and concluded that *Eeniella* should be reinstated as a genus. In the 5th edition of TYTS, *E. nana* is, however, included as *Br. nanus* (Smith 2011). Three isolates obtained from sugar cane juice and sugar cane waste isolated in Thailand were considered to represent a new species in a new genus and were described as *Allodekkera sacchari* (Jutakanoke *et al.* 2017). Of note, in contrast to all other species of *Dekkera*/*Brettanomyces*, this species is not able to ferment glucose and does not form acetic acid.

Van der Walt observed the formation of ascospores among strains of *Brettanomyces bruxellensis* and *Br. intermedius*, a current synonym of *Dekkera bruxellensis* (Van der Walt & Van Kerken 1959), and proposed the genus *Dekkera* (Van der Walt 1964) to accommodate these sexually reproducing species. Presently, two species are recognised in the genus *Dekkera*, namely *D. anomala* (Smith & Van Grinsven 1984) and *D. bruxellensis* (Van der Walt 1964). Thus, the generic names *Brettanomyces* and *Dekkera* were introduced to accommodate asexually and sexually reproducing yeasts, respectively, an essential nomenclatural requirement in the past era of dual fungal nomenclature. However, since the introduction of the "One Fungus = One Name" principle, only one name is allowed for a fungal species, and, hence, a choice has to be made between *Brettanomyces* and *Dekkera*. In our opinion, the name *Brettanomyces* may be preferred over *Dekkera* as it is the oldest name and, even more importantly, is most widely used in the brewing world where the term "Brett" refers to characteristics caused by these yeasts.

Ecological and economic significance

Among the most striking features of *Brettanomyces*/*Dekkera* yeasts is their ability to ferment glucose under aerobic conditions, the so-called Crabtree phenomenon, which is linked to the low activity of enzymes involved in the respiratory chain and tricarboxylic cycle (Middelhoven & Kurtzman 2003) and redox imbalances (Blomqvist & Passoth 2015). They also show the Custers effect (also referred to as the negative Pasteur effect), which is the inhibition of alcoholic fermentation under strictly anaerobic conditions and its stimulation in the presence of oxygen (Wikén *et al.* 1961, Scheffers 1966, Carrascosa *et al.* 1981, Rozpedowska *et al.* 2011, Schifferdecker *et al.* 2014). In addition, these yeasts tolerate high ethanol concentrations (14–15 % v/v), produce acetic acid, and tolerate cycloheximide (Scheffers & Misset 1974, Steensel & Verstrepen 2014, Steensels *et al.* 2015). Mechanistically, the Custers effect has been explained by a shortage of NAD^+ due to the activity of redox systems when glucose is added under anaerobic conditions (Scheffers 1966, Scheffers & Misset 1974, Carrascosa *et al.* 1981). These conditions have resulted in the so-called "make, accumulate, consume" life strategy for ethanol and acetic acid (Rozpedowska *et al.* 2011). It has been proposed that this strategy developed due to the evolution of sugar-containing fruit-producing plants ca. 125 MYA (Friis *et al.* 2006, Sun *et al.* 2011, Schifferdecker *et al.* 2014) that provided a new niche for these and other yeasts. This ecosystem engineering life strategy is thought to inhibit competing microorganisms when glucose is in excess and then respire the ethanol after its exhaustion (De Deken 1966, Dashko *et al.* 2014, Zhou 2015, Zhou *et al.* 2017). A comparative study between *Saccharomyces* and *Brettanomyces* yeasts that separated > 200 MYA found that promoter regions of both underwent massive loss of cis-regulatory elements of genes involved in respiration (Rozpedowska *et al.* 2011, Cheng *et al.* 2017a) and suggested that parallel changes between *Dekkera*/*Brettanomyces* and *Saccharomyces* yeasts are caused by changes in the nucleosome occupancy in the promoter regions of genes located in the mitochondria that result in suppression of mitochondrial function in the presence of glucose. Thus, this can be seen as a case of parallel evolution. The features listed above make *Brettanomyces*/*Dekkera* yeasts useful for bioethanol production (Passoth *et al.* 2007, Galafassi *et al.* 2011, De Barros Pita *et al.* 2019). The biofuel production in a Swedish alcohol production plant was found to be a complex process in which *Br. bruxellensis* together with *Lactobacillus vini* and other *Lactobacillus* spp. interact to produce high ethanol yields (Passoth *et al.* 2007; see also below for brewing). The *Brettanomyces* yeasts may outcompete *Saccharomyces* in bioethanol plants due to their tolerance to low pH and high concentrations of ethanol as well as osmolytes. Several strains and species ferment cellobiose, L-arabinose, and D-xylose and can utilise nitrate, all compounds present in lignocellulosic biomass that may further boost their use in industrial bioethanol production (Borneman *et al.* 2014, Steensels *et al.* 2014, Blomqvist & Passoth, 2015).

Brettanomyces/*Dekkera* yeasts are most well known for their presence in sour Belgian beers, such as Lambic and Gueuze beers, but they also pose a major risk during wine production due to the formation of off flavours that are referred to as "clove, spicy, mousy, barnyard, phenolic, plastic, or medicinal", just to give a few names. In the common literature, this is also named "Brett" (Steensels *et al.* 2014). As these yeasts also utilise short oligosaccharides, such as maltose, maltotriose and dextrins, they produce attenuated beers with high ethanol content and low residual sugars (Colomer *et al.* 2019). Brewing of Lambic sour beers and similar beers, such as American Coolship ales, is a multi-kingdom interaction process in which not only *Brettanomyces*/*Dekkera* yeasts participate, but also *Saccharomyces cerevisiae*, and various bacteria, such as acetic acid bacteria (AAB), lactic acid bacteria (LAB) and *Enterobacteriaceae* in a complex process with four stages (Spitaels *et al.* 2014, Spitaels *et al.* 2015): (i) phase 1 with *Enterobacteriaceae* and wild yeasts with limited involvement of AAB; (ii) a main fermentation phase with *S. cerevisiae*/*S. pastorianus*, *Enterobacteriaceae* and AAB; (iii) an acidification phase with AAB; and (iv) a maturation phase with *Brettanomyces*/*Dekkera* yeasts and LAB, with the number of AAB going down (De Roos *et al.* 2019). It has been observed that co-culture with bacteria causes alterations in the genome of the yeasts (Zhou 2017), but whether this also happens during brewing or bioethanol production remains elusive. Dunham and colleagues recently described genomic rearrangements and chromosomal copy number variations occurring as a result of serial repitching in multiple breweries (Large *et al.* 2020). Although the use of these yeasts in brewing is considered safe due to the long use without causing any harm, it has been suggested that the production of biogenic amines might be a potential concern (Steensels *et al.* 2014).

Brettanomyces/*Dekkera* yeasts are considered the main spoilage organism in the production of wines due to the production of off flavours (see above) (Renouf *et al.* 2006, Jolly *et al.* 2014, Di Toro *et al.* 2015, Capozzi *et al.* 2016, Pigao *et al.* 2021). Several volatiles, *e.g.*, ethyl phenols that are produced by *Br. bruxellensis* attract insects, such as *Drosophila melanogaster* that may act as vectors and introduce the yeasts into breweries and wineries (Belda *et al.* 2017b, Becher *et al.* 2018). Moreover, the release of insect attracting volatiles is widespread across the yeast domain, and insect-yeast volatile communication likely predated the origin of dicot angiosperms (*ca.* 300–400 MYA *vs* 125 MYA). It has been suggested that this mechanism may also play a role in the pollination of plants by insects that are attracted by volatiles produced by yeasts present in flowers (Becher *et al.* 2018).

The above studies and applied aspects have sparked the analysis and understanding of *Brettanomyces*/*Dekkera* genomes. Several studies revealed that their genomes are highly dynamic ranging from haploid, diploid to triploid, with several showing hybrid signatures (Hellborg & Piškur 2009, Curtin *et al.* 2012, Borneman *et al.* 2014, Avramova *et al.* 2018, Varela *et al.* 2018, Colomer *et al.* 2020, Roach & Borneman 2020).

A phylogenomics analysis based on a concatenated sequence of 3 482 single-copy orthologous genes, showed that *Brettanomyces*/*Dekkera* species are much more diverged than *e.g.*, *Saccharomyces* spp. (Roach & Borneman 2020). In the genus, two clades are apparent, *bruxellensis*/*anomalus*/*custersianus* and *naardenensis*/*nanus*. The genomes of the species showed poor synteny and many translocations and expansion of some gene families. For instance, *Br. bruxellensis* and *Br. nanus* showed expansion of genes encoding β-glucosidases and β-galactosidases; *Br. bruxellensis* and *Br. custersianus* shared expansions of genes involved in amino acid metabolism; *Br. bruxellensis* and *Br. anomalus* had an expansion of formate dehydrogenases; and *Br. anomalus* contained multiple copies of the gene encoding formate dehydrogenases. Sucrose metabolism by *Br. bruxellensis* and *Br. anomalus* may have resulted from horizontal gene transfer of a bacterial gene (Roach & Borneman 2020). It has been postulated that *Br. bruxellensis* arose via hybridisation of two closely related species of which one was a diploid and the other haploid. Of interest is that several genes encode proteins involved in the utilisation of chitin, N-acetylglucosamine, galactose, mannose, and lactose (Curtin *et al.* 2012).

In a study of 84 strains from various sources, including wine, craft beers, tequila, wood and wild strains, signals of domestication were seen leading to a set of strains with high attenuation and high ester production (Colomer *et al.* 2020). Interestingly, a phenolic off-flavour (POF, Young *et al.* 2014) negative strain was found that lacked the associated genes, and that may be useful for the production of POF-free wine and beers (Colomer *et al.* 2020). In line with the above, DNA fingerprinting also showed a correlation between the population structure and isolation source (Crauwels *et al.* 2014). For instance,

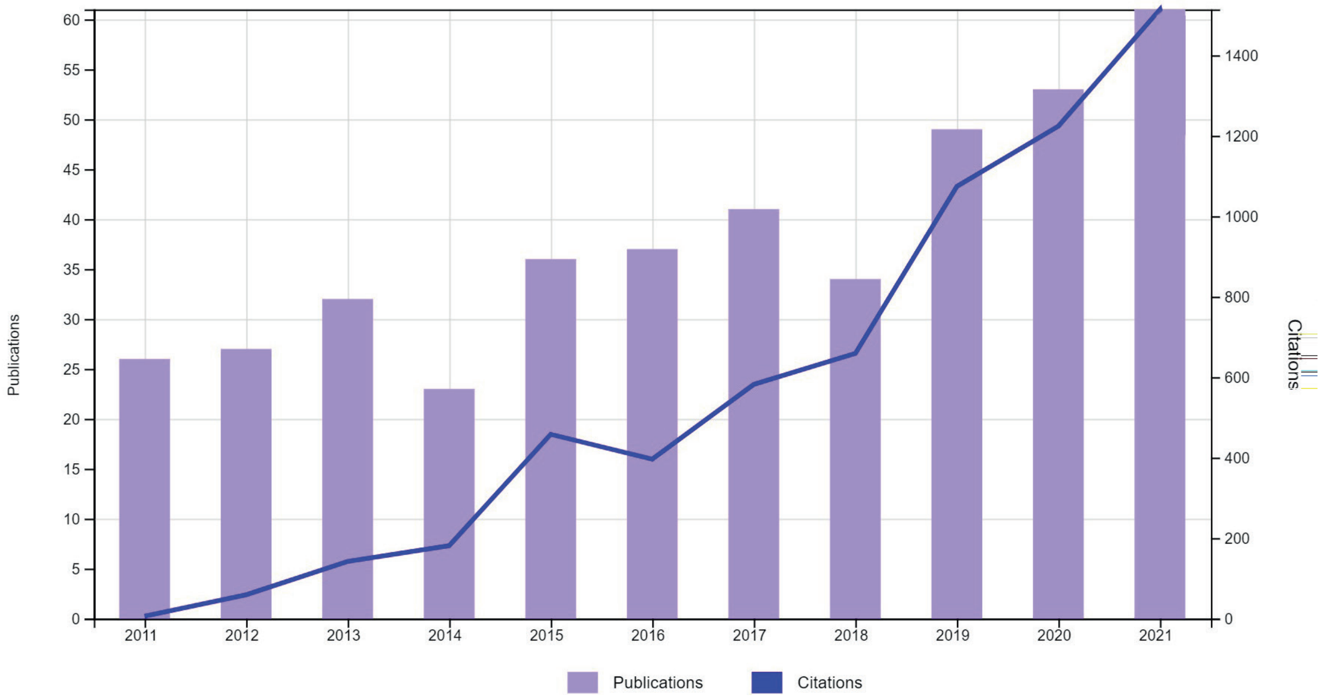

Fig. 120. Trends in research of *Brettanomyces* in the period 2011–2021.

yeasts from beers, biofuel, and soft drinks clustered separately. Due to the importance of early detection of *Brettanomyces*/*Dekkera* yeasts in winemaking, several techniques have been explored, such as DNA fingerprinting, PCR, and Raman spectroscopy (Rodriguez *et al.* 2013, Crauwels *et al.* 2014, Hulin *et al.* 2014).

Early work on mitochondrial genomes (McArthur & Clark-Walker, 1983, Hoeben *et al.* 1993) supported the phylogenomics-based phylogeny presented in Roach & Borneman (2020). Procházka *et al.* (2010) found that genes of the mitochondrial genomes showed only 77–93 % amino acid sequence identity, underlining the huge diversity between species of the genus *Brettanomyces*/*Dekkera* as it is presently recognised.

Research interests

There are 419 publications and 6 693 citations from 2011–2021 in the Web of Science (Fig. 120). The 10 papers containing information on *Brettanomyces*/*Dekkera* that were highly cited (Table 95) all relate to the use of the yeasts in brewing and winemaking, either as a beneficial or spoilage organism, as well as their potential role in the production of biofuels. Aspects included genome make-up, domestication, improving quality and keeping standards, and the underlying "make-accumulate-consume" strategy that is a result of their remarkable physiology (see above). Functional and comparative genomics of these yeasts likely will result in further improvement of these processes. For instance, the identification of a POF-negative strain has the potential to be used in brewing

Table 95. Top 10 cited articles related to *Brettanomyces* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Not your ordinary yeast: non-*Saccharomyces* yeasts in wine production uncovered	465	Jolly *et al.* (2014)
2	The microbial diversity of traditional spontaneously fermented lambic beer	137	Spitaels *et al.* (2014)
3	Taming wild yeast: potential of conventional and nonconventional yeasts in industrial fermentations	134	Steensels *et al.* (2014)
4	*Brettanomyces* yeasts - from spoilage organisms to valuable contributors to industrial fermentations	129	Steensels *et al.* (2015)
5	Microbial contribution to wine aroma and its intended use for wine quality improvement	125	Belda *et al.* (2017b)
6	Microbial terroir and food innovation: the case of yeast biodiversity in wine	112	Capozzi *et al.* (2016)
7	Parallel evolution of the make-accumulate-consume strategy in *Saccharomyces* and *Dekkera* yeasts	112	Rozpedowska *et al.* (2011)
8	Brewhouse-resident microbiota are responsible for multi-stage fermentation of American coolship ale	110	Bokulich *et al.* (2012)
9	Bacteria and yeast microbiota in milk kefir grains from different Italian regions	103	Garofalo *et al.* (2015)
10	*De-novo* assembly and analysis of the heterozygous triploid genome of the wine spoilage yeast *Dekkera bruxellensis* AWRI1499	97	Curtin *et al.* (2012)

and winemaking without the risk of off-flavour production. Also, a better understanding of the ecology of these yeasts may contribute to further improvement of their uses and prevent their introduction, *e.g.*, by insect vectors, in wineries. The unexpected dominance of *Brettanomyces*/*Dekkera* yeasts in a Swedish industrial biofuel plant already yielded many surprises. Further genetic or evolutionary engineering of isolates may improve yields, be it ethanol or acetic acid, sour beers or even some wines. Modern techniques, such as CRISPR-Cas9, may boost these developments given the high number of genomes available.

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90. ***Ascochyta*** Lib., Pl. Crypt. Arduenna, Fasc. (Liège) 1(Praef.): 8. 1830.

Type species: *Ascochyta pisi* Lib.

Classification: *Ascomycota*, *Pezizomycotina*, *Dothideomycetes*, *Pleosporales*, *Didymellaceae.*

Background

The genus *Ascochyta* is one of three main genera in the family *Didymellaceae* and encompasses several phytopathogenic species, along with *Didymella*, *Phoma*, and other allied phoma-like genera also included in the *Didymellaceae* (De Gruyter *et al*. 2013, Chen *et al*. 2017c, Wijayawardene *et al*. 2017a, 2018, Hyde *et al.* 2020a). *Ascochyta* was introduced by Libert (1830) with *Ascochyta pisi* as the type species. The genus has more than 1 300 taxon names listed in MycoBank, with about 400 recognised species (Wijayawardene *et al*. 2017a). Chen *et al*. (2022) mentioned 20 recognised species supported by ex-type cultures or by DNA sequences. Many species were described, allocated or synonymised to *Ascochyta* based on advances in molecular techniques, such as analysis of multi-locus phylogeny using sequences of LSU, ITS, *rpb2* and *tub*, associated with morphological characteristics (Chen *et al*. 2015c, 2017c).

The asexual genus *Ascochyta* was erected to include phytopathogenic species that are characterised by the production of uniseptate hyaline conidia and phialidic conidiogenous cells and recognised as a coelomycetous genus (Hyde *et al*. 2013, Wijayawardene *et al*. 2017a, Chen *et al*. 2022). *Ascochyta* species are important pathogens mainly in plants within *Fabaceae* and *Poaceae*, causing “Ascochyta blight” (AB), a particularly devasting disease on pea (*Pisum sativum*) and chickpea (*Cicer arietinum*) crops worldwide (Chilvers *et al*. 2009, Keirnan *et al*. 2021, Singh *et al*. 2021, Chen *et al*. 2017c, 2022). Some species are saprotrophic on dead plant debris (Hyde *et al.* 2020a). Most species of *Ascochyta* are known as asexual morphs; nonetheless, some taxa present both asexual and sexual morphs or, less commonly, only sexual morphs (Chen *et al.* 2022). Recently, new methods have been applied to the identification of pathogens such as DNA barcodes, multiplex PCR and qPCR assays, which greatly improved our knowledge of this genus (Tripathi *et al*. 2021, Valetti *et al*. 2021). This is relevant taking into account that *Ascochyta* is closely related to *Phoma*, even in its molecular sequences. Recent revisions on *Dydimellaceae*, *Ascochyta*, *Phoma*, and other phoma-like morphs have improved our understanding of the taxonomic status of both *Ascochyta* and its closely related taxa (De Gruyter *et al*. 2013, Chen *et al*. 2017c, Phukhamsakda *et al*. 2018a, Pem *et al*. 2021, Ahmadpour *et al*. 2022). In the Global Biodiversity Information Facility (GBIF) database (https://www.gbif.org/pt/species/8334803/metrics), there are 5 722 occurrences of 799 species registered, most of these records are from Germany (585), United Kingdom (509) and Australia (504), with an increase in occurrences between 2011 and 2017 of 536 (BASE 2022, GBIF 2022). The most recent taxonomic revisions indicate about 400 species in *Ascochyta* (Wijayawardene *et al*. 2017a). Thus, *Ascochyta* and its allies need more taxonomic and phylogenetic studies/revisions, and care must be taken before naming other fungi causing symptoms similar to Ascochyta blight. *Ascochyta* taxa cannot be delimited just by morphological evaluation, but require phylogenetic study to avoid misidentification and dubious records of a genus with quarantine importance.

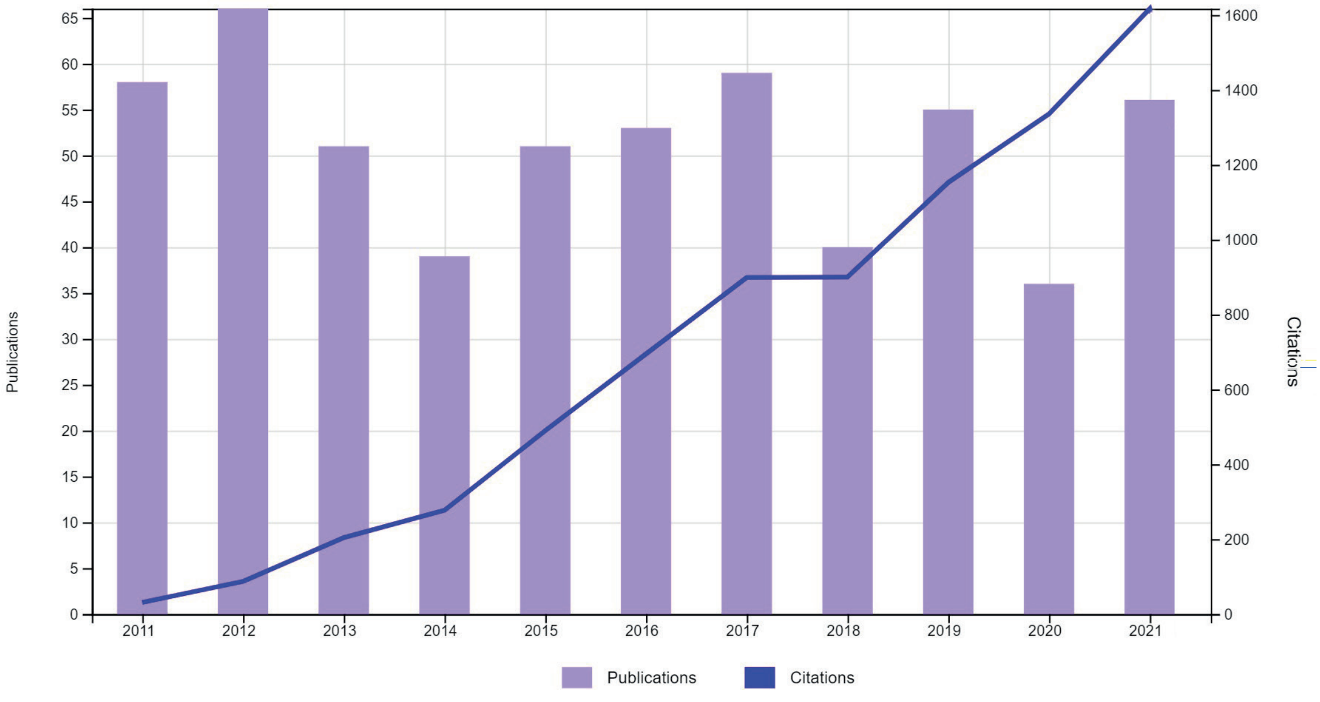

Fig. 121. Trends in research of *Ascochyta* in the period 2011–2021.

Table 96. Top 10 cited articles related to *Ascochyta* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Redisposition of phoma-like anamorphs in *Pleosporales*	221	De Gruyter *et al.* (2013)
2	Resolving the *Phoma* enigma	199	Chen *et al.* (2015c)
3	Achievements and prospects of genomics-assisted breeding in three legume crops of the semi-arid tropics	163	Varshney *et al.* (2013)
4	Synergisms between microbial pathogens in plant disease complexes: a growing trend	138	Lamichhane & Venturi (2015)
5	Soil fungal community structure along a soil health gradient in pea fields examined using deep amplicon sequencing	138	Xu *et al.* (2012a)
6	Marker-assisted backcrossing to introgress resistance to *Fusarium* wilt race 1 and *Ascochyta* blight in C 214, an elite cultivar of chickpea	126	Varshney *et al.* (2014)
7	*Didymellaceae* revisited	116	Chen *et al.* (2017c)
8	Innovations in agronomy for food legumes. A review	109	Siddique *et al.* (2012)
9	Fungal phytotoxins with potential herbicidal activity: chemical and biological characterization	99	Cimmino *et al.* (2015)
10	A new approach to species delimitation in *Septoria*	81	Verkley *et al.* (2013)

Ecological and economic significance

Ascochyta species cause economically important plant diseases, of which, the most relevant in terms of severity and crop production losses is the "Ascochyta blight", also referred to as AB disease. We detail AB disease below.

Ascochyta blight of chickpea (*Cicer arietinum*) caused by *Ascochyta rabiei*, and by some *Ascochyta* species in other pulse crops, is a necrotic disease affecting plant tissues and causing the death of leaves and other plant parts. This pathogenicity is very aggressive to chickpea, the second most important legume crop in the world, due to it being a rich protein food and its atmospheric nitrogen fixation (Nene 1982, Merga & Haji 2019, Singh *et al*. 2021, Chen *et al*. 2022). India is the leading country in chickpea global production (65 % of worldwide production; 9.075 million tons/year), followed by Australia (Merga & Haji 2019). Ascochyta blight symptoms start with elliptical to circular spots, firstly chlorotic, becoming brown to dark brown due to necrosis of tissue. Due to pycnidia formation, lesions with concentric rings appear in leaves, stems and pods affecting the plants' fitness in seed formation, and causing losses that range between 10 to 100 % of the crop (Nene 1982, Atik *et al*. 2011, Pande *et al*. 2011, Singh *et al*. 2021). Other *Ascochyta* species, with host specificity, cause Ascochyta blight affecting other pulse crops, such as faba beans, lentils and field peas, causing major economic losses on a global scale (Merga & Haji 2019, Chen *et al*. 2022).

Research interests

There are 564 publications and 6 690 citations from 2011–2021 in the Web of Science (Fig. 121), with the top 10 most cited articles included in Table 96. Most publications focused on taxonomy, phylogeny and disease management (fungicide resistance, disease resistance, and pathogen detection).

Disease management

The absence of efficient pulses crop management, including crop rotation, removal of infected plants, use of resistant chickpea lineages, fungicide application or biocontrol techniques is the main reason for the extreme severity of AB and its economic losses (Nene 1982, Owati *et al*. 2017, Gayacharan *et al*. 2020, Maya & Maphosa 2020, Ahmad *et al*. 2021). High humidity can favour the disease severity, as demonstrated by Nalçaci *et al*. (2021). Advanced techniques have been applied to control AB in crops. Among these, we highlight the development of a spatiotemporal model, named *ascotraceR*, as a package to R language/environment that simulates the life story of *As. rabiei* and the spread of AB in the field (Khaliq *et al*. 2022), facilitating its control and action at specific points, mitigating the most aggressive effects of the disease, at an advanced stage, before it spreads. In biomolecular aspects, molecular pathotyping tools (Bar *et al*. 2021), pathogen monitoring in an early phase via PCR-based method (Valetti *et al*. 2020), screening for new resistant chickpea cultivars (Newman *et al*. 2021), and fast and reliable methods of fungal detection during quarantine or crop development via DNA barcode, multiplex PCR and qPCR assay (Tripathi *et al*. 2021) are examples of recent tools for management and disease control.

Taxonomy and phylogeny

Since the introduction of the asexual genus *Ascochyta* (Libert 1830), and over subsequent years, species in this genus were mainly characterised based on morphology and host specificity. As mentioned by Pem *et al*. (2021), the difficulty in using morphological characters for *Ascochyta* delimitation is the lack of morphological structures to allow species definition. Many names were synonymised or transferred to other taxa in *Dothideomycetes* and just morphological delimitation is not recommended for *Ascochyta* and its allied or phylogenetically closely related taxa, such as *Phoma* and phoma-like species. Thus, it is necessary to use molecular approaches for species identification using ITS, *tub*, *tef*1 and LSU sequences for best species delimitation (Phukhamsakda *et al*. 2016b, 2017, Pem *et al*. 2021, Ahmadpour *et al*. 2022).

Environment and biotechnology

Apart from being the pathogen of important pulse crops, some species of *Ascochyta*, such as *As. lentis*, the agent causing AB in lentil plants, has been screened for fungal metabolites for biotechnological applications. Lentiquinones A, B, and C and lentisone, pachybasin, ω-hydroxypachybasin, and phomarin were isolated from *As. lentis*, and present antimicrobial activities (Masi *et al*. 2018, Barilli *et al*. 2021). Anthraquinones isolated from *As. lentis* by Barilli *et al*. (2021) seem favourable against fungal pathogens causing rust and powdery mildew of both pea (*Pisum sativum*) and oat (*Avena sativa*).

Authors: F.J.S. Calaça and J.C. Araújo

91. ***Epichloe*** (Fr.) Tul. & C. Tul., Select. Fung. Carpol. (Paris) 3: 24. 1865.

Type species: *Epichloe typhina* (Pers.) Brockm.

Classification: *Ascomycota*, *Pezizomycotina*, *Sordariomycetes*, *Hypocreales*, *Clavicipitaceae.*

Background

Epichloe typhina, the type of the genus, was originally described as *Sphaeria typhina* and later transferred to *Epichloe*, a genus that was described by Tulasne & Tulasne (1865). Presently, 37 species are accepted in the genus with 15 species, three subspecies and five varieties being haploid, and 22 species and one variety representing hybrids (Leuchtmann *et al*. 2014). The common writing as *Epichloë* is considered an orthographic variant in MycoBank. Several taxa are only known in their asexual (anamorphic) forms and until recently these were classified in the genus *Neotyphodium.* However, due to the "One fungus = One Name" principle, all these anamorphic species were nomenclatural recombined in *Epichloe* (Leuchtmann *et al*. 2014). Sexually reproducing *Epichloe* species form yellow-orange stromata on leaf sheaths that surround the immature inflorescences of grasses. Many species occurring as endophytes in grasses are vertically transmissible via the host seeds and are of interest because of toxin production and plant protection aspects (Bacon *et al.* 1977, Omacini *et al.* 2001, Clay & Schardl 2002, see below). The endophytic symbioses between *Epichloe* species and grasses (*Poaceae* subfamily *Pooideae*) are dominated by codivergence and might have emerged during the early evolution of these grasses, and range from mutualism to antagonism (Schardl *et al. 2008).* Flies of the genus *Botanophila* play a role in the dispersal of *Epichloe* species. Using a multigene-based phylogeny concordance between the phylogenetic and biological species concept was seen in one clade, whereas this was not the case in the *Epichloe typhina* species complex that contains mainly antagonistic and horizontally transmitted endophytic species (Craven *et al.* 2001). These authors suggested that the balance of vertical and horizontal transmission promotes host specialisation and speciation due to genetic isolation, whereas only horizontal transmission results in a broader host range with fewer genetically isolated species, with lineage sorting resulting in conflicts between phylogenetic and biological species (Craven *et al*. 2001).

Ecological and economic importance

Epichloe species may cause grass choke disease, which can cause up to 30 % losses in seed yield of *Dactylis glomerata*, in Oregon, USA (Merlet *et al.* 2022). Endophytic *Epichloe* species protect their hosts from herbivores, nematodes, and other stress (Clay & Schardl 2002). A novel model of intercalary growth and hyphal extension, and not apical growth, was proposed for these endophytes (Christensen *et al.* 2008). Hybridisation is a common feature of *Epichloe* species (Tsai *et al.* 1994, Moon *et al.* 2004) and may be linked to increased production of alkaloids (Schardl *et al.* 2012). Four classes of biologically active alkaloids are produced by *Epichloe*: lolines, indole-diterpenes, ergot alkaloids, and peramine (Bush *et al.* 1997, Schardl *et al.* 2012, Chen *et al.* 2019b) and may protect the hosts from herbivores (Clay 1988), nematodes (Timper *et al.* 2005, Bacetty *et al.* 2009), drought stress (Malinowski & Belesky 2000), or may increase growth (Schardl *et al.* 2004). However, some are toxic to livestock (Bacon *et al.* 1977, Fletcher & Harvey 1981).

Research interests

There are 598 publications and 6 496 citations from 2011–2021 in the Web of Science (Fig. 122), with the top 10 most cited articles included in Table 97. The top cited papers on *Epichloe* cover

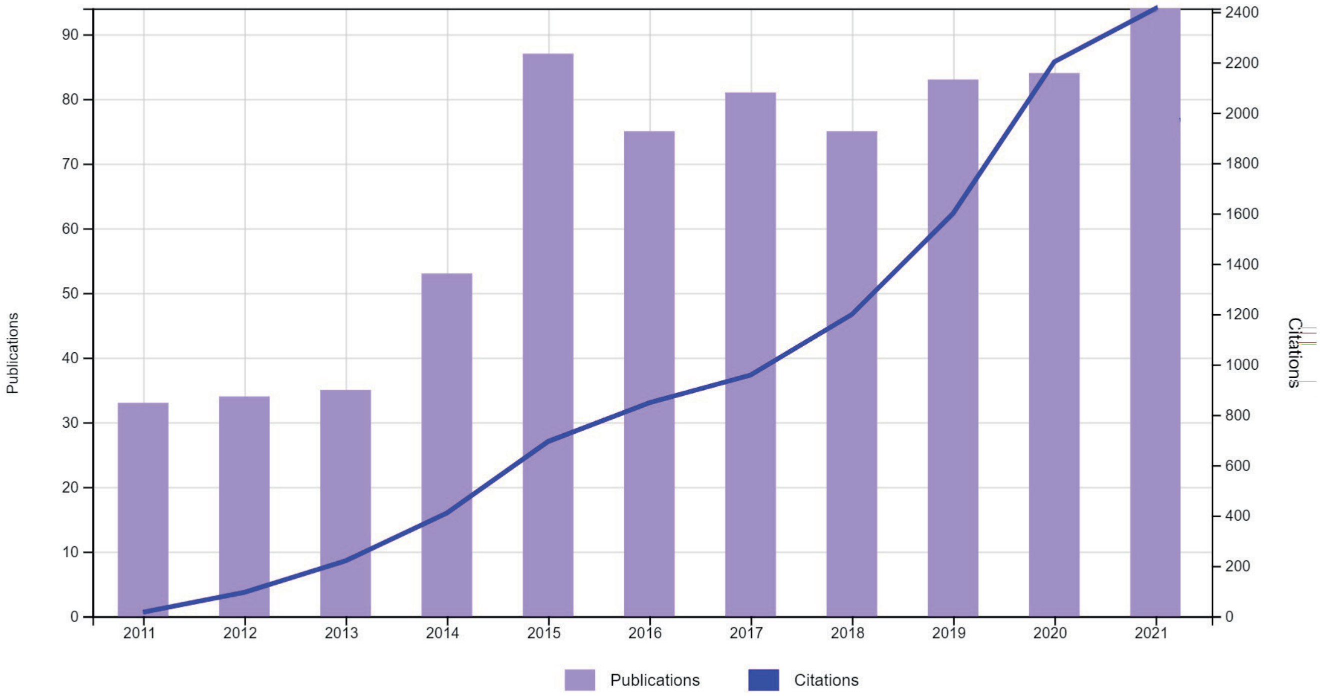

Fig. 122. Trends in research of *Epichloe* between 2011–2021.

Table 97. Top 10 cited articles related to *Epichloe* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Nomenclatural realignment of *Neotyphodium* species with genus *Epichloë*	287	Leuchtmann *et al.* (2014)
2	Plant-symbiotic fungi as chemical engineers: multi-genome analysis of the *Clavicipitaceae* reveals dynamics of alkaloid loci	267	Schardl *et al.* (2013)
3	Mutualist-mediated effects on species' range limits across large geographic scales	127	Afkhami *et al.* (2014)
4	Horizontal gene transfer of *Fhb7* from fungus underlies *Fusarium* head blight resistance in wheat	123	Wang *et al.* (2020a)
5	Fungal endophytes for sustainable crop production	121	Lugtenberg *et al.* (2016)
6	Fungal endophyte infection of ryegrass reprograms host metabolism and alters development	110	Dupont *et al.* (2015)
7	Chemotypic diversity of epichloae, fungal symbionts of grasses	110	Schardl *et al.* (2012)
8	Bioactive alkaloids in vertically transmitted fungal endophytes	109	Panaccione *et al.* (2013)
9	What triggers grass endophytes to switch from mutualism to pathogenism?	105	Eaton *et al.* (2011)
10	Polarity proteins Bem1 and Cdc24 are components of the filamentous fungal NADPH oxidase complex	97	Takemoto *et al.* (2011)

all the above-mentioned aspects of *Epichloe*-related biological and agricultural research, including phylogeny and taxonomy (Leuchtmann *et al.* 2014), hybridisation and reproduction strategies (Charlton *et al.* 2014, Oberhofer *et al.* 2014), aspects of the endophyte lifestyle, including the role of reactive oxygen species (Hamilton *et al.* 2012), sustainable agriculture and horticulture production (Kauppinen *et al.* 2016, Lugtenberg *et al.* 2016), regulation and biosynthesis of bioactive compounds, and their role in biology and agriculture (Panaccione *et al.* 2013, Schardl *et al.* 2013), switches between mutualistic and pathogenic stages (Eaton *et al.* 2011), biosafety aspects for husbandry (Young *et al.* 2013a, Klotz 2015), and morphogenesis (Takemoto *et al.* 2011). Mutualistic fungal endophytes reduced the impact of drought on *Bromus laevipes* and significantly broadened its geographic occurrence into drier habitats. Thus, suggesting that such mutualistic relationships are highly important to withstand the impact of climate change (Afkhami *et al.* 2014). Perennial ryegrass infected with *Epichloe festucae* caused major changes in the expression of host genes, resulting in reprogramming of the metabolism of the host favouring secondary metabolism, and changes in host development, such as trichome formation and cell wall biogenesis. This work also suggested that fungal endophyte relationships may increase tolerance to drought and infection by fungal pathogens (Dupont *et al.* 2015). Comparative genomics yielded some interesting results. Alkaloid profiles were compared with genome data of 10 *Epichloe* spp., three ergot fungi (*Claviceps* spp.), a morning-glory symbiont (*Periglandula ipomoeae*), and a bamboo pathogen (*Aciculosporium take*), and indicated that alkaloid loci have conserved cores that determine the skeleton structures and peripheral genes resulting in the various chemical variants. These peripheral genes occurred close to transposon-derived, AT-rich repeat blocks that may be involved in gene losses, duplications, and neofunctionalisation. The alkaloid loci were found to be unusual structures as they contained large, complex, and dynamic repeat blocks. The genome organisation and dynamics of the alkaloid loci and the abundance of repeat blocks suggest these fungi are under selection for alkaloid diversification, which may relate to their variable life histories, their protective roles as symbionts, and associations with the highly species-rich cool-season grasses (Schardl *et al.* 2013).

Another study identified a glutathione S-transferase encoded by the *Fhb7* gene from the grass *Thinopyrum elongatum* that can detoxify trichothecene toxins. Homologs of Fhb7 homologs are absent in the plant kingdom, but, interestingly, approximately 97 % identity with Fhb7 was found in the genome of an *Epichloe* species suggesting horizontal gene transfer from the fungus to the genome of the wheatgrass. Eventually, the use of the *Fhb7* gene might reduce the toxicity of *Fusarium*-infested crops and increase yields (Wang *et al.* 2020g).

Author: T. Boekhout

92. *Pyrenophora* Fr., Summa Veg. Scand., Sectio Post. (Stockholm): 397. 1849.

Type species: *Pyrenophora phaeocomes* (Rebent.) Fr.

Classification: *Ascomycota*, *Pezizomycotina*, *Dothideomycetes*, *Pleosporales*, *Pleosporaceae.*

Background

Pyrenophora comprises economically important plant pathogenic fungi that cause diseases on graminaceous hosts (Zhang & Berbee 2001). The type species was originally described as *Sphaeria phaeocomes (syn. Pyre. phaeocomes) (*Rebentisch 1804) in *Xylariaceae*. Fries (1849) transferred this genus into *Pleosporales*. Wehmeyer (1961) assigned the genus within *Pleosporaceae.* This classification has been accepted by subsequent studies (Barr 1987b, Berbee 1996, Zhang *et al*. 2012c, Hyde *et al*. 2013, Ariyawansa *et al*. 2014). Species are characterised by immersed to semi-immersed ascomata, lack of pseudoparaphyses, clavate to saccate asci, with a large apical ring, muriform terete ascospores and brown to reddish brown setae present in the neck (Ariyawansa *et al*. 2014). The genus differs from the extant genera of *Pleosporales* in the lack of pseudoparaphyses and the large apical ring in the asci (Ariyawansa *et al*. 2014, Phukhamsakda *et al*. 2015, 2016a, Goonasekara *et al*. 2020, Bhunjun *et al*. 2021c, Su *et al*. 2022, Xu *et al*. 2022a, 2024, Madagammana *et al*. 2023). The asexual morph possesses morphological characteristics of brown and transversely septate conidia (Marin-Felix *et al*. 2019a).

Pyrenophora comprises 95 species (Wijayawardene *et al.* 2020), although 213 species epithets have been linked to this genus (Index Fungorum 2022). *Pyrenophora was* linked to the asexual genus *Drechslera* based on morphological studies and later confirmed by molecular data (Zhang & Berbee 2001, Ariyawansa *et al*. 2014). *Pyrenophora* species have a worldwide distribution but are mainly recorded from Australia, Europe, New Zealand and North America and occur as endophytes, saprobes and pathogens (Zhang & Berbee 2001). The pathogenic species mainly cause diseases on *Poaceae* hosts (Marin-Felix *et al*. 2019a). The delineation of *Pyrenophora* is challenging due to a lack of molecular data for the type species. Traditional classification has been based on morphological characteristics and was not precise due to shared morphological characteristics with *Bipolaris* and *Curvularia*. However, based on phylogenetic analysis based on ITS and *gapdh* gene markers, this genus is monophyletic within *Pleosporaceae*, whereas the asexual *Drechslera* clustered closely with *Pyrenophora (*Zhang & Berbee 2001). Thus, combined multi-gene analysis including ITS, *gapdh* and *rpb2* is recommended for better resolution (Marin-Felix *et al*. 2019a).

This genus needs critical revision due to a lack of molecular data, particularly relating to serious plant pathogens (Goonasekara *et al*. 2020). Pathogenic species cause diseases such as leaf spots, leaf blight, leaf blotch, net blotch, light-brown lesions, melting out, head rot, foot rot, seed-borne diseases, and tan spots on economically important crops like barley, wheat and oats (Hyde *et al*. 2014, Marin-Felix *et al*. 2019a). The saprobic species are important in nutrient cycling, and several species are used as biocontrol agents and for the extraction of phytotoxic components (Aboukhaddour *et al*. 2013, Ariyawansa *et al*. 2014, Hyde *et al*. 2014). Some species such as *Pyre*. *graminea*, *Pyre*. *japonica* and *Pyre*. *teres* cause post- and preharvest disease on barley (Sivanesan 1987) on various plant parts such as leaves, leaf sheaths and kernels (Hyde *et al*. 2014); symptoms depend on the host genotype, pathogen virulence and environmental conditions (Liu *et al*. 2011). The taxonomy and systematics of *Pyrenophora* have changed after the application of phylogenetics (Zhang & Berbee 2001, Zhang *et al.* 2012c, Ariyawansa *et al.* 2014).

Ecological and economic significance

Pyrenophora species cause numerous economically important plant diseases, four of which are detailed below.

Net blotch disease on *Hordeum vulgare* (barley) is caused by *Pyrenophora teres* (Liu *et al*. 2011). *Pyrenophora teres* exist in two forms, *Pyrenophora teres f. teres* and *Pyre. teres f. maculata*, responsible for net form net blotch (NFNB) and spot form net blotch (SFNB) diseases, respectively (Liu *et al*. 2011). Net blotch causes 10–40 % yield losses by reduction of kernel size, plumpness and bulk density and negatively affects the malting and feed quality of barley, eventually resulting in the necrotic and chlorotic death of plant leaves (Smedegård-Petersen 1971, Afanasenko *et al*. 2009, Gupta *et al*. 2012b). The disease can lead to a 44 % grain yield loss when reaching a severe epidemic stage (Jayasena *et al*. 2002, 2007). Net blotch disease is classified as a stubble-borne disease due to the ascocarps produced on the stubble (Liu *et al*. 2011). The life cycle differences between the two forms of *Pyre. teres* are unclear and are thus described collectively (Liu *et al*. 2011). NFNB forms narrow, dark brown, longitudinal and transverse striations on infected leaves as net-like symptoms, while dark brown, circular to elliptical lesions surrounded by a chlorotic or necrotic halo of varying width are identified as SFNB symptoms (Liu *et al*. 2011). Spot form net blotch is a significant foliar disease in Australia and several barley-growing regions in the world (Gupta *et al*. 2012b). The disease has been increasing due to susceptible cultivars, environmental conditions and agricultural practices (Gupta *et al*. 2012b).

Tan spot on *Triticum aestivum* (wheat) caused by *Pyrenophora tritici-repentis* is one of the more serious diseases on wheat found worldwide (Lamari & Bernier 1989, Aboukhaddour *et al*. 2009, 2013). This disease was recorded as a severe pathogen on wheat in North Dakota, USA in 1968 and 1969 (Friesen *et al*. 2005). At the severe epidemic stage, 50 % of yield losses have been reported via a reduction in kernel weight and a high degree of kernel shrivelling (Cheong *et al*. 2004, Gamba *et al*. 2012). The disease was reported as the fastest-spreading disease in the Southern Cone region of South America (Kohli *et al*. 1992) and also had a severe impact on crops in Argentina, Brazil, and Paraguay (Ciuffetti & Tuori 1999). This fungus is also recorded as a saprophyte, and the lifecycle of this pathogen includes both sexual and asexual morphs (Lamari & Bernier 1989). *Pyrenophora tritici-repentis* was initially described in 1823 and isolated in the 1930s (Aboukhaddour *et al*. 2009). The diseased host shows light-brown necrotic blotches that are surrounded by yellow halos or extensive chlorosis on leaf tissue, and these symptoms are mostly influenced by taxon sensitivity genes present in the putative host and the toxicity of the pathogenic isolate (Aboukhaddour *et al*. 2013). Cultivation of susceptible wheat cultivars and changes in agricultural practices such as reduced tillage practices, shorter crop rotation and continuous wheat cultivation led to the emergence of this disease (Aboukhaddour *et al*. 2013). However, pathogenicity depends on the production of its host-selective toxins, and so far, three toxins have been identified, including necrosis-inducing toxin Ptr ToxA and the chlorosis-inducing toxins Ptr ToxB and Ptr ToxC on hosts (Lamari & Strelkov 2010).

Drechslera leaf spot on *Lolium multiflorum* (Italian ryegrass) also referred to as brown leaf spot, is caused by several *Pyrenophora* species such as *Pyre. biseptata*, *Pyre. dematioidea*, *Pyre. dictyoides*, *Pyre. nobleae*, *Pyre. lolii*, and *Pyre. teres*, recorded from China, Florida, Germany, Mississippi, New Zealand and Virginia (Alfieri *et al*. 1984, Pennycook 1989, Roane 2004, 2009, Pratt 2006b, Crous *et al*. 2011). Among these pathogens, *Pyre. dictyoides* was the most commonly recorded pathogen (Xue *et al*. 2020). Drechslera leaf spot caused by *Pyre. dictyoides* was considered one of the most important foliar diseases on ryegrass in New Zealand (Latch 1966).

Leaf stripe in barley on *Hordeum vulgare* (barley) is caused by *Pyrenophora graminea.* This disease is caused when the pathogenic fungus is transmitted through seed and no infections are reported by direct leaf infection (Taylor *et al*. 2001). The susceptibility of cultivated varieties, the kinds of long-term effective control measures and soil temperature lower than 12 °C can all influence the pathogenicity (Porta-Puglia *et al*. 1985). Seed health certification is an effective method to control this disease (Taylor *et al*. 2001).

Pyrenophora species have been also recorded as pathogens on *Triticum*, *Agropyron*, and brome grass (Hosford Jr 1971). Light brown lesions are also an important disease on wheat, caused by *Pyrenophora trichostoma*, and brown leaf spots of smooth bromegrass caused by *Pyre. bromi* are also important symptoms of its pathogenicity (Hosford Jr 1971, Andrie *et al*. 2008). Species of *Pyrenophora* such *Pyre. semeniperda* have been recorded as biocontrol agents for use against *Bromus tectorum*, as this fungus produces useful chemical compounds such as phytotoxic sesquiterpenoid penta-2,4-dienoic acid (pyrenophoric acid) (Meyer *et al*. 2007). *Pyrenophora semeniperda* produces several cytochalasins, such as cytochalasins Z1, Z2 and Z3, which are used as biocontrol

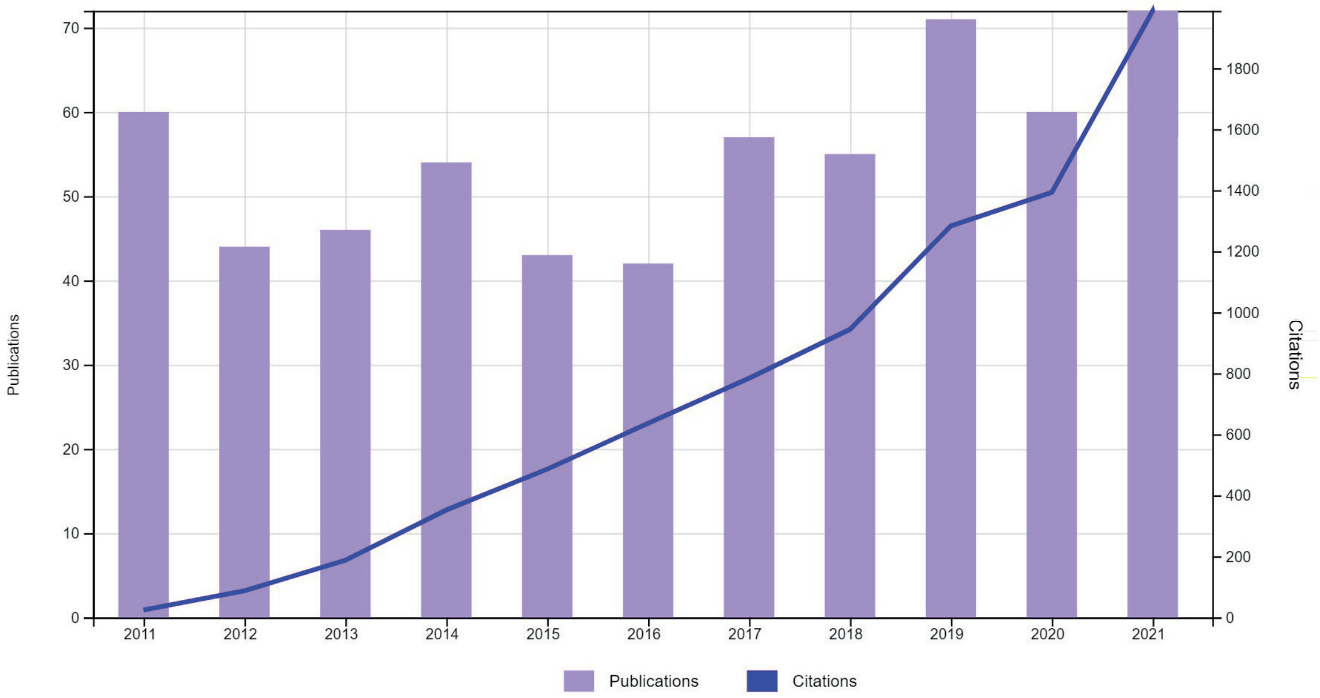

Fig. 123. Trends in research of *Pyrenophora* in the period 2011–2021.

agents against grass weeds (Evidente *et al.* 2012).

Research interests

There are 604 publications and 6 439 citations from 2011–2021 in the Web of Science (Fig. 123), with the top 10 most cited articles included in Table 98. Most publications focused on pathogens (*Pyrenophora teres*, *Pyre. tritici-repentis*, resistance, identification, virulence, gene susceptibility).

Disease management

Application of fungicides, cultural practices such as rotation and innate host resistance can all be used to manage net blotch diseases in barley. Net blotch diseases caused by *Pyrenophora teres f. teres* and *Pyre. teres f. maculata* can genetically be isolated and need to be treated separately (Rau *et al.* 2007). The pathotype of *Pyrenophora tritici-repentis* is identified via qualitative assessment of symptoms, whereas pathogenic isolates are classified into races based on pathogenicity on the host (Lamari & Strelkov 2010). The random amplified polymorphic DNA technique has been used in the genetic determinants for virulence in *Pyre. teres f. teres* (Weiland *et al.* 1999). Purification of toxins, cloning of their respective genes and identification and characterisation of the site and mode of action of the toxins are also important in disease management (Ciuffetti & Tuori 1999). Genome assembly can characterise and isolate genes associated with virulence and avirulence via map-based cloning (Ellwood *et al.* 2010).

Table 98. Top 10 cited articles related to *Pyrenophora* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	One stop shop: backbones trees for important phytopathogenic genera: I (2014)	235	Hyde *et al.* (2014)
2	Effectors as tools in disease resistance breeding against biotrophic, hemibiotrophic, and necrotrophic plant pathogens	217	Vleeshouwers *et al.* (2014)
3	*Pyrenophora teres*: profile of an increasingly damaging barley pathogen	112	Liu *et al.* (2011)
4	Phytotoxic secondary metabolites and peptides produced by plant pathogenic Dothideomycete fungi	110	Stergiopoulos *et al.* (2013)
5	Horizontal gene and chromosome transfer in plant pathogenic fungi affecting host range	106	Mehrabi *et al.* (2011)
6	Comparative genomics of a plant-pathogenic fungus, *Pyrenophora tritici-repentis*, reveals transduplication and the impact of repeat elements on pathogenicity and population divergence	104	Manning *et al.* (2013)
7	Towards a natural classification and backbone tree for *Pleosporaceae*	95	Ariyawansa *et al.* (2015c)
8	Recommended names for pleomorphic genera in *Dothideomycetes*	81	Rossman *et al.* (2015)
9	Genetics of tan spot resistance in wheat	80	Faris *et al.* (2013)
10	The role of effectors and host immunity in plant-necrotrophic fungal interactions	72	Wang *et al.* (2014e)

Resistance

Conidial morphology is important in the identification of *Pyrenophora*. However, identification is changing due to difficulties in producing conidia in axenic cultures, such as in *Pyre. graminea*, *Pyre. dictyoides* and *Pyre. tritici-repentis* (Lepoint *et al*. 2010). Thus, an effective method is needed to produce conidia *in vitro* to study the biological control agents (Xue *et al*. 2020). Tissue culture techniques in wheat may make the toxin of *Pyre. tritici-repentis* useful in the early selection of resistant cells (Lamari & Bernier 1989).

Toxins

Pyrenophora tritici-repentis (Ptr) produces both proteinaceous and non-proteinaceous host-specific toxins (Ciuffetti & Tuori 1999). The necrosis-inducing toxin PtrToxA and the chlorosis-inducing toxin ToxBand are proteins, while the low molecular weight non-protein HST, PtrToxC and uncharacterised toxin PtrToxD have also been identified (Ciuffetti & Tuori 1999, Horbach *et al*. 2011). *Pyrenophora bromi* also produces multiple copies of ToxB (Stergiopoulos *et al*. 2013). *Pyrenophora teres* produces toxins A, B and C grown in a liquid medium. Toxin A was N-(2-amino-2-carboxyethyl) aspartic acid, toxin B was identical to anhydroaspergillomarasmine A (and probably an artefact) while toxin C is identical to aspergillomarasmine A (Bach *et al*. 1978, Lamari & Bernier 1979). The sensitivity of the host to these toxins is conferred by a single gene for each toxin (Manning & Ciuffetti 2005).

Taxonomy and phylogeny

Different molecular markers are used in the identification of *Pyrenophora* species. The LSU gene markers are used at the generic level, while ITS, *gapdh* and *rpb*2 offer high-resolution species delineation of *Pyrenophora* (Hyde *et al*. 2014, Marin-Felix *et al.* 2019a, Hyde *et al.* 2020a).

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93. ***Hymenoscyphus*** Gray, Nat. Arr. Brit. Pl. (London) 1: 673. 1821.

Type species: *Hymenoscyphus fructigenus* (Bull.) Gray

Classification: *Ascomycota*, *Pezizomycotina*, *Leotiomycetes*, *Helotiales*, *Helotiaceae.*

Background

Hymenoscyphus is one of the largest genera of inoperculate discomycetes. More than 550 names have been connected to this genus, and 269 species are currently accepted (Index Fungorum 2022). *Hymenoscyphus* species occur worldwide, mainly in temperate regions, but also in the tropics (Dennis 1964, Lizoň 1992, Gross & Han 2015, Zheng & Zhuang 2013, 2015a). Most of them are saprotrophs colonising leaf residues, small twigs, wood, herbaceous stems, fruits and seeds (Dennis 1964, Lizoň 1992, Baral 2015, Zheng & Zhuang 2015b, Kowalski & Bilański 2021). Those that produce extracellular enzymes may contribute to the degradation of plant cell wall components (Abdel-Raheem & Shearer 2002, Citron *et al.* 2014). A few species are aquatic fungi (Abdullah *et al*. 1981, Fisher & Webster 1983). Some species can occur in living symptomless plant organs as endophytes without causing disease symptoms (Baral & Bemmann 2014, Cleary *et al.* 2016, Inoue *et al.* 2019). Within *Hymenoscyphus* there are no species symbiotically associated with plant roots. The prominent fungus, *Hy. ericae* (asexual morph *Scytalidium vaccini*), known from mycorrhizal association with *Ericaceae*, was excluded from *Hymenoscyphus* and placed initially in *Rhizoscyphus* (Zhang & Zhuang 2004), then in *Pezoloma* (Baral & Krieglsteiner 2006), and finally in *Hyaloscypha* (Fehrer *et al.* 2019). *Hymenoscyphus* includes both species that exhibit a high degree of host specificity, as well as those found on a broad spectrum of host plants (Dennis 1964, Lizoň 1992, Zheng & Zhuang 2013, Baral 2015, Kowalski & Bilański 2019). *Hymenoscyphus* species are culturable on agar media *in vitro*, and a few can produce apothecia under such conditions (Gross & Han 2015).

Some *Hymenoscyphus* species produce secondary metabolites. A broad spectrum of different specialised metabolites has been found especially in pathogenic species, *Hy. fraxineus.* They are important in the necrotrophic activity of the fungus in plant tissue and defence against competing fungi (Grad *et al.* 2009, Andersson *et al.* 2012, Citron *et al.* 2014, Junker *et al.* 2014, Surup *et al.* 2018). Viridiol and volatile lactone are also produced by avirulent sister species, *Hy. albidus* (Citron *et al.* 2014, Junker *et al.* 2014). *Hymenoscyphus epiphyllus* can produce botrydial sesquiterpenoids and other secondary metabolites that exhibit antimicrobial and cytotoxic activities (Thines *et al.* 1997).

Hymenoscyphus was established by Gray in 1821 and initially, nine species were accommodated in the family *Helotiaceae*. Dennis (1964) specified *Hy. fructigenus* as the lectotype for this genus, and transferred to *Hymenoscyphus* more than 70 taxa, with 1–4-celled ascospores, previously placed in *Helotium*. The circumscription of the genus is not well defined (Zhang & Zhuang 2004). Various generic concepts of *Hymenoscyphus* have been proposed (Carpenter 1981, Baral & Krieglsteiner 1985, Eriksson & Hawksworth 1993, Hengstmengel 1996). In a restricted sense, *Hymenoscyphus* comprises many taxa which often exhibit only slight differences in their micromorphological characters (Hengstmengel 1996, Baral *et al*. 2013). Members of the genus are generally characterised by producing white, yellow or orange coloured, stipitate to sessile discoid apothecia. The excipular hyphae are not embedded in a gelatinous matrix. An ectal excipulum is composed of *textura prismatica* to *textura angularis*, a medullary excipulum of *textura intricata* to *textura porrecta*. Asci are cylindrical or clavate, arising from simple hyphae or crozier, and contain eight spores. The genus in a narrower concept can be defined by a special type of apical ring (Baral & Krieglsteiner 1985, Verkley 1993). Ascospores are scutuloid, fusoid or ellipsoid, and may be provided at their ends with one or more hyaline setulae (Hengstmengel 1996, Baral 2015). Ascospores are generally hyaline, but in some species undergo pigmentation before germination (Kowalski & Holdenrieder 2009, Gross *et al*. 2014, Gross & Han 2015, Kowalski & Bilański 2019), or may become pale brown in overmature spores (Baral 2015). The presence of vacuolar guttules in the living paraphyses and ascospores has a significant taxonomic reference value (Baral 2015). Most species of *Hymenoscyphus* produce apothecia directly on the colonised substrate, however, some develop a black pseudosclerotial plate and apothecia emerge only from this structure (Gross & Han 2015, Gross *et al.* 2015, Kowalski & Holdenrieder 2009, Baral & Bemmann 2014, Kowalski & Bilański 2019).

Asexual morphs have been found in about 20 species of *Hymenoscyphus.* They are characterised by a large morphological diversity. Most often, the asexual morph is represented by the genus *Chalara* (Baral & Bemmann 2014, Gross & Han 2015, Gross *et al.* 2015). The most well-known species is *Chalara fraxinea,* the asexual morph of *Hy. fraxineus* (Kowalski 2006, Kowalski & Holdenrieder 2009, Gross *et al.* 2014). Others belong to the genera *Anguillospora, Articulospora, Dimorphospora, Geniculospora,* *Helicodendron, Idriella, sporotrichum-like* and *Tricladium* (Kimbrough & Atkinson 1972, Abdullah *et al.* 1981, Fisher & Webster 1983, Descals *et al.* 1984, Van Vooren & Hairaud 2009, Gross *et al*. 2015).

In recent years, the identification of *Hymenoscyphus* species has been supported by molecular methods. Molecular analysis also supports the separation of different groups within *Hymenoscyphus s. lat.* (Baral *et al. 2013).* The gene regions used for species delimitation mainly concern the ITS, LSU, *cal, tub, act and tef1* (Zhang & Zhuang 2004, 2015a, Baral *et al.* 2006*,* Queloz *et al.* 2011, Gross & Han 2015, Gross *et al.* 2015, Kowalski & Bilański 2019). The whole genome has been sequenced for 11 species of *Hymenoscyphus.* Currently, ITS data is available from GenBank for only 60 *Hymenoscyphus* species. Analysis shows that the genus is not monophyletic (Bilański unpubl. data). Morphological studies supported by phylogenetic analyses lead to the exclusion of some species from *Hymenoscyphus* (Zhang & Zhuang 2004, Baral *et al.* 2013).

Ecological and economic importance

Only two species of *Hymenoscyphus* are known to cause plant diseases. In China, *Hy. repandus* causes stem blight of mint and affects mint yield (Wang *et al.* 2004b, Zheng & Zhuang 2015b). In Europe, *Hy. fraxineus* causes an epidemic disease of ash trees of great ecological and economic importance known as “Ash dieback” (Kowalski 2006, McKinney *et al.* 2014, Enderle *et al.* 2019). *Hymenoscyphus subcarneus* can grow parasitically on liverworts and mosses causing necrotic lesions, however, this species currently belongs to *Roseodiscus* (Baral & Krieglsteiner 2006).

Ash dieback

Dieback symptoms, first observed in the early 1990s in Poland (Kowalski 2001, Przybył 2002) have spread over the native range of *F. excelsior* and reached an epidemic level in most European countries, including Great Britain (Pautasso *et al.* 2013, Gross *et al.* 2014, Enderle *et al.* 2019, Hill *et al.* 2019). The disease affects trees of all ages, especially in dense stands on moist sites, although disease progression is slower in older trees (McKinney *et al.* 2011, Kowalski 2012, Skovsgaard *et al.* 2017). Ultimately, the disease leads to the death of single trees and eventually whole stands. Mortality in ash plantations across Europe reaches up to 85 % (Coker *et al. 2019).* The decline of ash populations has far-reaching implications for silviculture, local economies, and ecosystems in Europe (Pautasso *et al.* 2013, Enderle *et al.* 2019). In the UK, the cost of ash dieback has been estimated at 15 billion British pounds (Hill *et al.* 2019).

Pathogen

Ash dieback is caused by *Hymenoscyphus fraxineus* (Kowalski 2001, 2006, Kowalski & Holdenrieder 2009, Queloz *et al.* 2011, Baral *et al.* 2014). *Hymenoscyphus fraxineus* is native to Asia (Korea, northeastern China, far eastern Russia and Japan), where it occurs as an endophyte or a leaf pathogen of *Fraxinus mandshurica* and *F. chinensis* ssp. *rhynchophylla* (Zhao *et al.* 2012b, Zheng & Zhuang 2014, Gross & Han 2015, Cleary *et al.* 2016, Inoue *et al.* 2019). The ash dieback invasion of Europe was founded by two genetically divergent individuals (McMullan *et al.* 2018). Each year, mainly in summer, *Hy. fraxineus* forms a large number of apothecia, predominantly on the previous year’s leaf petioles in the litter (Kirisits & Woodward 2015, Gross & Holdenrieder 2013, Hietala *et al.* 2018). Wind-disseminated ascospores infect primarily ash leaves and petioles. The fungus spreads to woody tissues and causes dieback of branches and successive crown decline culminating in dieback of the entire tree (Gross *et al.* 2014, Hietala *et al.* 2018, Enderle *et al.* 2019). *Hymenoscyphus fraxineus* can also cause root collar necrosis (Marçais *et al.* 2016). Most isolates have optimum growth at 20 °C, less often at 15 °C or 25 °C (Kowalski 2012). High pathogenicity of *Hy. fraxineus* towards *F. excelsior* and *F. angustifolia* has been confirmed by wound inoculation (Kirisits *et al.* 2010, Husson *et al*. 2011, Kowalski *et al.* 2015, 2017). Fungal isolates originating from Asia show greater virulence than the ones from Europe (Gross & Sieber 2016). Many endophytic and saprotrophic fungi show a strong antagonistic effect *in vitro* toward *Hy. fraxineus* (Schulz *et al.* 2015, Schlegel *et al.* 2018, Halecker *et al.* 2020, Kowalski & Bilański 2021, Bilański & Kowalski 2022).

Disease management

Silvicultural strategies aiming to reduce the economic impact of the disease have been proposed, depending on the severity of the damage, age, local climate, and stand type (Havrdová *et al.* 2017, Skovsgaard *et al.* 2017). Resistance breeding of European ash and the introduction of non-native resistant ash species have also been considered (McKinney *et al.* 2014, Kowalski *et al.* 2015, Skovsgaard *et al.* 2017, Marzano *et al.* 2019). Some fungicides can be used as a preventative treatment in forest nurseries or for injections directly into *F. excelsior* trunk (Dal Maso *et al.* 2014, Hauptman *et al.* 2015, Hrabětová *et al.* 2017). For monitoring and phytosanitary control purposes, modern tools should be used that allow fast and efficient detection of *Hy. fraxineus in planta* (Ioos *et al.* 2009). Elimination of the pathogen in seeds and seedlings can be achieved via thermotherapy (Hauptman *et al.* 2013). Removal of leaf litter and appropriate composting allows for a reduction in the amount of infectious material (Noble *et al.* 2019). However, none of these strategies enables large scale prevention of new infections or the mitigation of serious damage caused by *Hy. fraxineus* in diseased stands (Havrdová *et al.* 2017).

Research interests

There are 346 publications and 6 420 citations from 2011–2021 in the Web of Science (Fig. 124) with the top 10 most cited articles listed in Table 99. Most of the publications after the outbreak of ash dieback epidemics focused on: (i) causal agent, its origin, life cycle, and virulence, (ii) susceptibility of host plants, and (iii) various aspects of epidemiology and disease management.

In addition to research into more effective methods of protecting *Fraxinus* spp. against *Hy. fraxineus*, it can be expected that further intensive work will be carried out on the occurrence of *Hymenoscyphus* species in various regions of the world, on improving the genus concept using modern molecular methods, as well as a comprehensive and updated monograph.

Authors: T. Kowalski and P. Bilański

94. ***Diplodia*** Fr., Ann. Sci. Nat., Bot. 1: 302. 1834.

Type species: *Diplodia mutila* (Fr.) Mont.

Classification: *Ascomycota*, *Pezizomycotina*, *Dothideomycetes*, *Botryosphaeriales*, *Botryosphaeriaceae.*

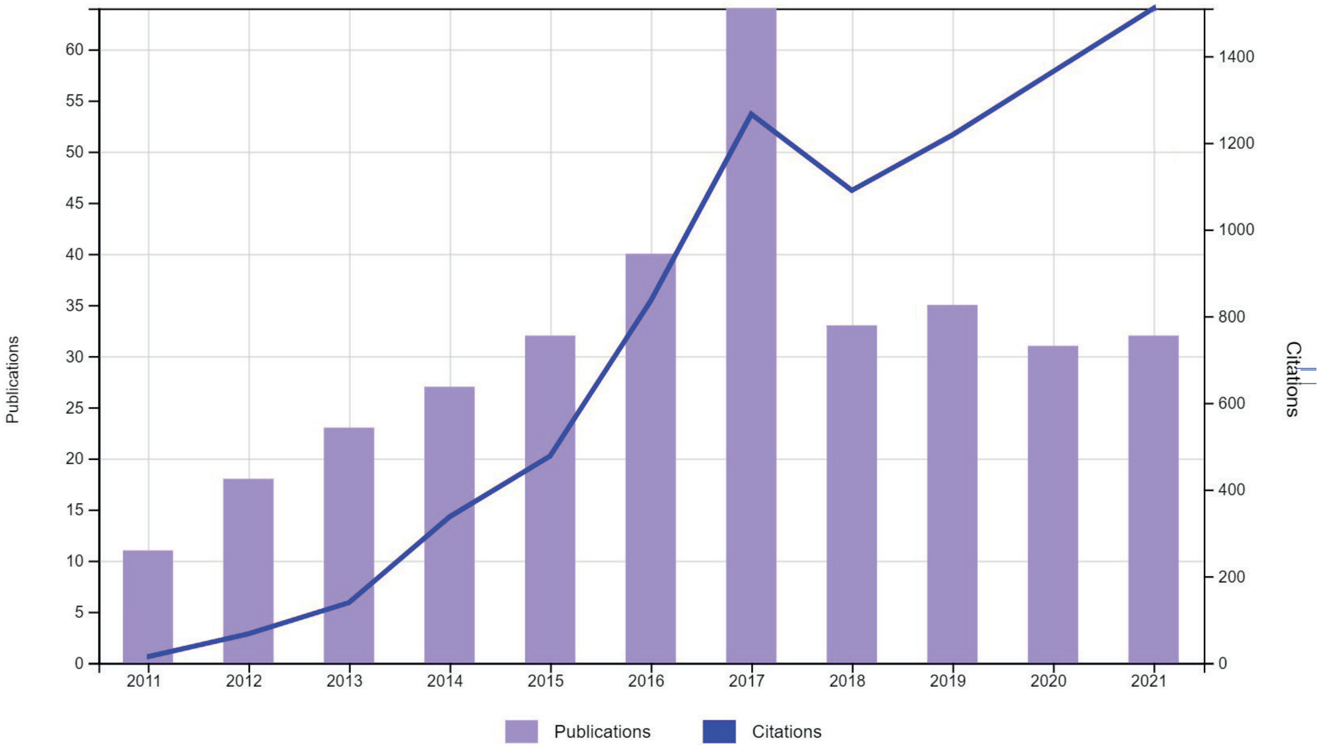

Fig. 124. Trends in research of *Hymenoscyphus* in the period 2011–2021.

Table 99. Top 10 cited articles related to *Hymenoscyphus* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Towards a unified paradigm for sequence-based identification of fungi	1 965	Kõljalg *et al*. (2013)
2	European ash (*Fraxinus excelsior*) dieback - A conservation biology challenge	234	Pautasso *et al*. (2013)
3	*Hymenoscyphus pseudoalbidus*, the causal agent of European ash dieback	224	Gross *et al*. (2014)
4	Cryptic speciation in *Hymenoscyphus albidus*	185	Queloz *et al*. (2011)
5	The ash dieback crisis: genetic variation in resistance can prove a long-term solution	134	McKinney *et al*. (2014)
6	*Hymenoscyphus fraxineus*, the correct scientific name for the fungus causing ash dieback in Europe	120	Baral *et al*. (2014)
7	Presence of natural genetic resistance in *Fraxinus excelsior* (*Oleaceae*) to *Chalara fraxinea* (*Ascomycota*): an emerging infectious disease	113	McKinney *et al*. (2011)
8	*Hymenoscyphus pseudoalbidus*, the correct name for *Lambertella albida* reported from Japan	113	Zhao *et al*. (2012b)
9	Evaluating the potential of WorldView-2 data to classify tree species and different levels of ash mortality	102	Waser *et al*. (2014)
10	Genome sequence and genetic diversity of European ash trees	95	Sollars *et al*. (2017)

Background

In recent years, *Botryosphaeriaceae* (*Botryosphaeriales*) has been subjected to comprehensive taxonomic revisions (Phillips *et al.* 2013, 2019, Dissanayake *et al.* 2016, Yang *et al.* 2017a, Zhang *et al.* 2021e). Among these taxa, *Diplodia* is a genus with economic importance and with many species worldwide (Hyde *et al.* 2020a, Zhang *et al.* 2021e). *Diplodia* was established in Montagne (1834), ascribed to Fries, and based on *Sphaeria mutila*. *Diplodia mutila* was subsequently introduced by Fries (1849). Even though many *Diplodia* species are recorded across many climatic zones in both tropical and temperate regions (Zhang *et al.* 2021e), the majority are confined to temperate climates (Burgess *et al.* 2019). Similar to many botryosphaeriaceous taxa, *Diplodia* species exhibit diverse lifestyles, including pathogenic, endophytic and saprobic on a wide range of hosts. The genus includes economically important pathogens. For example, *Di. sapinea* causes crown wilt, dieback, cankers, shoot and tip blight, and root disease on pines (Jankovský & Palovčíková 2003, Müller *et al*. 2018), *Di. mutila* and *Di. malorum* cause black rot and canker of apples, *Di. seriata* causes frog-eye leaf spots, black rot and canker of apples (Úrbez-Torres *et al.* 2016, Crespo *et al.* 2018), *Di. corticola* causes canker and dieback of oaks (Alves *et al*. 2004, Aćimović *et al*. 2016) and grapevines (Epstein *et al.* 2008, Savocchia *et al.* 2007), *Di. fraxini* and *Di. subglobosa* cause dieback on ash trees (Linaldeddu *et al.* 2020). Furthermore, *Di. sapinea* has also been reported as an endophyte in pines (Bihon *et al.* 2011) and several angiosperms (Damm *et al.* 2007, Lazzizera *et al.* 2008, Inderbitzin *et al.* 2010). In addition, *Diplodia* species produce a variety of secondary metabolites with diverse properties useful for applications in agriculture and medicine (Masi & Evidente 2021, Salvatore *et al.* 2022). The large number of species in this genus can be attributed to its wide host range and different lifestyles.

The concept of *Diplodia* has changed over the years and currently includes species with two distinct conidial morphologies (Lazzizera *et al.* 2008, Zhang *et al.* 2021e). Hence, *Diplodia* is considered a large genus with more than 1 000 species (Phillips *et al.* 2012). There are 1 260 epithets in Index Fungorum (2022) and 719 epithets listed in Species Fungorum (2022). MycoBank lists 1 012 legitimate names under *Diplodia*, excluding illegal names, invalid names, orthographic variants, varieties and entries without author or publication details. Cryptic speciation is another reason for the large number of species introduced in this genus. According to the most recent revision on *Botryosphaeriales*, 25 species are accepted with molecular data (Zhang *et al.* 2021e). Following this study, two novel species, *Di. alanphillipsii* (Boonmee *et al.* 2021) and *Di. fici-septicae* (Tennakoon *et al.* 2021) were introduced, thus increasing the accepted number of species to 27. Due to the simple generic definition composed around a few distinguishing morphological characters, for many years, a large number of *Diplodia* species were described based solely on their host association (Hyde *et al.* 2014). However, Slippers *et al.* (2004a) suggested that host preference should not be considered as a criterion for species differentiation in *Botryosphaeriaceae*. Furthermore, they proposed that many of the existing *Diplodia* species names are most likely to be synonyms. Several *Diplodia* species demonstrate a certain degree of host preference. For example, *Di. sapinea* (Bihon *et al.* 2012, Smith *et al.* 2015) and *Di. scrobiculata* (Burgess *et al.* 2004, Alves *et al.* 2013) occur mostly on conifers, although there are some reports from angiosperms (Damm *et al*. 2007, Lazzizera *et al.* 2008, Inderbitzin *et al.* 2010). Similarly, *Di. rosulata* has been found mainly on *Prunus* spp. (Perez *et al*. 2010, Linaldeddu *et al*. 2016), with very few reports on *Pinus* sp. (Gure *et al.* 2005); *Di. cupressi* prefers *Cupressus* and *Juniperus* hosts (Alves *et al.* 2006) while *Di. corticola* is found mainly on *Quercus* spp. (Alves *et al.* 2004, Urbez-Torres *et al.* 2016).

Lazzizera *et al.* (2008) pointed out the two well-supported phylogenetic clades in *Diplodia* that corresponded with two distinct conidial morphologies. This was confirmed in subsequent comprehensive studies on *Botryosphaeriales* (Phillips *et al.* 2013, 2019, Zhang *et al.* 2021e). Thus, the genus is characterised by two distinct conidial morphologies. In one group, the conidia are hyaline and aseptate, becoming 1-septate and pale to dark brown at maturity. In the other group, the conidia are dark brown at an early stage of development, often before they are released from the conidiogenous cells and remain aseptate, although they occasionally become 1-septate with age. Within these two morphological groups, the species exhibit only small differences in their morphology, sometimes only in the mean value for conidial dimensions. Therefore, molecular characterisation is essential for species differentiation (Phillips *et al.* 2013).

In contrast to single marker phylogenetic analyses, a multi-gene phylogeny provides better resolution for distinguishing *Diplodia* species and revealing species limits (Damm *et al.* 2007, Phillips *et al.* 2013, Alves *et al.* 2014, Taylor *et al.* 2020, Boonmee *et al.* 2021, Tennakoon *et al.* 2021, Senanayake *et al.* 2023). Furthermore, genealogical concordance phylogenetic species recognition has been applied to these multiple gene genealogies to determine species limits in various fungal taxa (Taylor *et al.* 2000, Norphanphoun *et al.* 2020). For example, the ITS phylogeny resolved only five groups within the *Diplodia* clade (Alves *et al.* 2004). Phillips *et al.* (2013) demonstrated that the above-mentioned two morphological groups are supported by two distinct phylogenetic lineages based on combined ITS and *tef1* genes and accepted 17 species in *Diplodia*. However, some species, such as *Di. pinea* and *Di. intermedia*, showed low phylogenetic support while others could not be separated clearly, such as *Di. alatafructa* and *Di. pseudoseriata*. Later Yang *et al.* (2017a) tried to resolve the genus using a *tef1*, ITS and *tub* combined phylogeny and accepted 20 species, with three taxonomic novelties (*Di. pyri*, *Di. citricarpa* and *Di. gallae*) and four other isolates most likely representing new species. Dissanayake *et al.* (2016) applied the same combination of loci as Phillips *et al.* (2013) and accepted 26 species. Jayawardena *et al.* (2019) updated the genus with 30 accepted *Diplodia* species based on combined ITS and *tef1* phylogenetic analysis. In the most recent revision of *Botryosphaeriales* (Zhang *et al.* 2021e), with phylogenies based on ITS, *tef1* and *tub* loci and increased taxon sampling revealing intra-species variation, 25 species were accepted with one taxonomic novelty, *Di. afrocarpi*, and several previously accepted species were synonymised under existing names. Thus, *Di. pyri* and *Di. magnoliigena* were synonymised with *Di. mutila*; *Di. alatafructa*, *Di. pseudoplatani* and *Di. insularis* with *Di. pseudoseriata*; *Di. intermedia*, *Di. rosacearum* and *Di. italica* with *Di. sapinea*; *Di. guayanensis* with *Di. scrobiculata*; and *Di. huaxii* with *Di. seriata*. The status of all the other names listed in Index Fungorum, Species Fungorum and MycoBank remain undetermined and will remain so until they are re-collected and epitypified. However, the possibility that this will ever be done is highly unlikely. Considering that most of the older species were introduced based on host association, a character that is now known to have little or no taxonomic value, and given the minor differences in morphology that separate individual species, it would be safe to assume that most of the older names are synonyms. Therefore, the number of 1 260 species names in *Diplodia* must be regarded as highly exaggerated, and the true number of species in this genus is likely to be in the order of magnitude of the number of species recognised by phylogenetic analyses. Although more new phylogenetic species will no doubt be recognised in the future, it is impossible to predict how many species remain to be identified. However, it would seem reasonable to assume that the actual number of species that exist would be somewhere between the current figure of 27 phylogenetic species and an absolute maximum of double this number.

Ecological and economic significance

Diplodia species cause numerous diseases on economically and ecologically important plants, such as apples, grapevines, oak, pines and ash trees. Among them, the major diseases are discussed below.

Dieback and canker diseases caused by *Diplodia* pathogens

Many *Botryosphaeriaceae* taxa have been reported to cause cankers and dieback disease in tropical and subtropical trees and economic crops (Damm *et al.* 2017, Linaldeddu *et al.* 2020, Diaz *et al.* 2022). *Diplodia* species were reported as one of the main pathogens of diebacks and cankers of woody trees. *Diplodia fraxini* and *Di. subglobosa* have been isolated as the main pathogens of ash trees in many European countries. Furthermore, *Di. mutila* was also identified from ash trees (Linaldeddu *et al.* 2020). *Diplodia mutila* and *Di. seriata* were reported to cause canker and dieback in apple trees worldwide (Úrbez-Torres *et al.* 2016, Diaz *et al.* 2022), *Prunus* sp. (Damm *et al.* 2017), olive trees in the European region and the USA (Úrbez-Torres *et al.* 2013a). In addition, *Di. olivarum* has been identified as a pathogen of dieback disease in several hosts (Lazzizera *et al.* 2008, Alves *et al.* 2014, Linaldeddu *et al.* 2016). *Diplodia seriata* has been identified as one of the most aggressive pathogens from dieback and canker symptomatic tissues in grapevine worldwide (Úrbez-Torres *et al.* 2018, Zhao *et al.* 2021a). In addition, *Di. africana*, *Di. corticola*, *Di. pseudoseriata*, *Di. quercivora* and *Di. scrobiculata* have been identified as pathogens from many economically and ecologically important plants and crops, such as *Fraxinus* sp., oak, cypress, *Prunus* sp., *Pinus* sp. and many other woody hosts (Alves *et al.* 2004, 2014, Aćimović *et al.* 2016, Hlaiem *et al.* 2023). These *Diplodia* pathogens cause economic losses and environmental damages due to the decline of these trees and crops (Sosnowski *et al.* 2021).

Diplodia tip and shoot blights in conifers

Diplodia sapinea and *Di. scrobiculata* were identified as pathogens of tip and shoot blight on pines in Australia, China, Europe, northeast Asia and the USA (Hartman *et al.* 2009, Paez & Smith 2018, Brodde *et al.* 2019, Cheng *et al.* 2021b, Caballol *et al.* 2022). These pathogens can cause serious economic losses by killing new tips and shoots, disrupting the crown, and affecting the quality of stems. Management of these diseases is challenging as many synthetic foliar fungicides and other alternative fungicidal treatments proved ineffective (Hartman *et al.* 2009). Therefore, management strategies should focus on reducing the pathogen inoculum.

Research interests

There are 496 publications with 6 337 citations from 2011–2021 in the Web of Science (Fig. 125), with the top 10 most cited articles listed in Table 100. Most of the publications focused on taxonomy and phylogeny, identification and characterisation of *Diplodia* diseases (pathogen identification, pathogenicity factors), however, recently, much attention has been focused on secondary metabolite production and host-species interactions.

Taxonomy and phylogeny

The concept of *Diplodia* has changed over the years and has been subjected to several revisions based on morphological and multi-locus phylogenetic approaches (Alves *et al.* 2014, Phillips *et al.* 2013, 2019, Zhang *et al.* 2021e). Initially, ITS and *tef1* were applied to resolve the species in this genus (Phillips *et al.* 2013, Dissanayake *et al.* 2016, Jayawardena *et al.* 2019) and later, more protein-coding genes were added to provide better resolutions (Yang *et al.* 2017a). In the most recent revision, 25 *Diplodia* species were accepted based on combined ITS, *tef1* and *tub* phylogeny (Zhang *et al.* 2021e).

Identification and characterisation of Diplodia diseases

Most pathogenesis-related studies identify and characterise the *Diplodia* pathogens on economically and ecologically important hosts. Among these, many studies focused their attention on the dieback and canker disease caused by several *Diplodia* species (Jankovský *et al.* 2003, Epstein *et al.* 2008, Krueger *et al.* 2013, Aćimović *et al.* 2016, Linaldeddu *et al.* 2020, Ferreira *et al.* 2021, Sosnowski *et al.* 2021, Díaz *et al.* 2022, Hlaiem *et al.* 2023). In addition, several other diseases caused by *Diplodia* pathogens, such as tip and shoot blight, black rot and leaf spots, have been subjected to comprehensive studies (Hartman *et al*. 2009, Crespo *et al.* 2018, Brodde *et al.* 2019, Caballol *et al.* 2020, Cheng *et al.* 2021b). These studies discuss disease emergence, distribution, etiology and pathogenesis factors, specifically ecological parameters. Few studies also investigated the disease management strategies for *Diplodia* diseases (Epstein *et al*. 2008). As foliar fungicide applications have failed to control *Diplodia* diseases, they are managed mainly through cultural practices, such as planting less susceptible hybrids and the use of physical

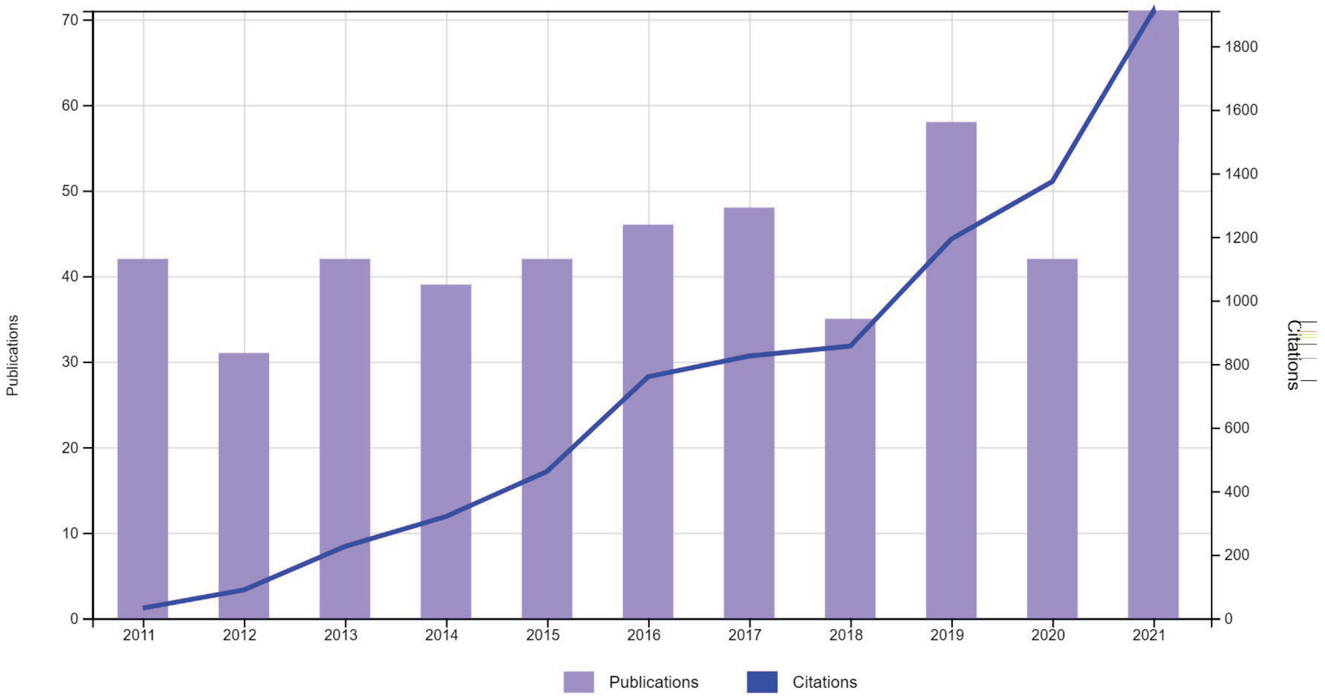

Fig. 125. Trends in research of *Diplodia* in the period 2011–2021.

Table 100. Top 10 cited articles related to *Diplodia* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	The *Botryosphaeriaceae*: genera and species known from culture	515	Phillips *et al.* (2013)
2	One stop shop: backbones trees for important phytopathogenic genera: I (2014)	235	Hyde *et al.* (2014)
3	Towards a natural classification of *Botryosphaeriales*	215	Liu *et al.* (2012a)
4	Grapevine trunk diseases: A review of fifteen years of trials for their control with chemicals and biocontrol agents	124	Mondello *et al.* (2018b)
5	Families, genera, and species of *Botryosphaeriales*	113	Yang *et al.* (2017a)
6	Characterization of fungal pathogens associated with grapevine trunk diseases in Arkansas and Missouri	106	Urbez-Torres *et al.* (2012)
7	Absolute configurations of fungal and plant metabolites by chiroptical methods. ORD, ECD, and VCD studies on phyllostin, scytolide, and oxysporone	104	Mazzeo *et al.* (2013)
8	*Botryosphaeriaceae*: Current status of genera and species	102	Dissanayake *et al.* (2016)
9	Light converts endosymbiotic fungus to pathogen, influencing seedling survival and niche-space filling of a common tropical tree, *Iriartea deltoidea*	100	Alvarez-Loayza *et al.* (2011)
10	Fungal trunk pathogens associated with wood decay of almond trees on Mallorca (Spain)	100	Gramaje *et al.* (2012)

barriers like thiophanate methyl formulations, paints and pastes on wounds (Luna & Wise 2015, del Pilar Martínez-Diz *et al.* 2021b). Furthermore, cultural practices such as crop rotation and tillage have been applied to decrease *Diplodia* infections on corn, mainly Diplodia ear and stalk rot (Steckel 2003). However, very few studies have been conducted to understand the pathogenicity factors and infection biology of *Diplodia* pathogens (Fernandes *et al.* 2014). Further efforts are needed to demonstrate the molecular mechanisms underlying these host and pathogen interactions that can be employed in future studies to alter the balance of these interactions to decrease the virulence of *Diplodia* species.

Secondary metabolites

Pathogenic and endophytic *Diplodia* species are reported as rich sources of bioactive secondary metabolites, including several phytotoxins (Masi *et al.* 2021, Salvatore *et al.* 2022). Several metabolites, including diterpenoids, polyketides, afunanones, pyrones, chetoglobosins, lactones, phenols and organic acids, have been identified with various biological properties, such as phytotoxic, neurotoxic, antimicrobial, insecticidal, herbicidal, and anticancer activities from *Di. sapinea*, *Di. cupressi*, *Di. corticola*, *Di. cupressi* and a few other *Diplodia* species (Liu *et al.* 2019a, Masi *et al.* 2021, Salvatore *et al.* 2022). Among these metabolites, sphaeropsidin A is the most commonly isolated metabolite from *Diplodia* species with multiple biological properties, such as antimicrobial, insecticidal, herbicidal, and anticancer activities that can be applied in agriculture and medicine (Salvatore *et al.* 2022). Studies have revealed that foliar symptoms of dieback disease are usually associated with phytotoxins produced by *Diplodia* species (Reveglia *et al.* 2019). However, more investigations are needed to assess the role of phytotoxins in the symptom expressions of *Diplodia* pathogens. Also, further discoveries of new secondary metabolites from these *Diplodia* species are important for possible future applications in agriculture and medicine.

Authors: K.W.T. Chethana and A.J.L. Phillips

95. ***Inonotus*** P. Karst., Meddeland. Soc. Fauna Fl. Fenn. 5: 39. 1879.

Type species: *Inonotus cuticularis* (Bull.) P. Karst.

Classification: *Basidiomycota*, *Agaricomycotina*, *Agaricomycetes*, *Hymenochaetales*, *Hymenochaetaceae.*

Background

Inonotus was erected by Karsten in 1879 to accommodate pileate polypores with coloured spores and was amended by Donk (1933) to include more species with the features of both coloured spores and a rusty brown fibrous context, with the type species *I. cuticularis* (Ryvarden 1991). There are 282 specific and infraspecific names of *Inonotus* in MycoBank and Index Fungorum (2022), but the actual number of species is currently 141 (Corner 1991, Ryvarden 1999, Cui *et al*. 2011, Gomes-Silva *et al.* 2013, Ryvarden 2020, Xavier de Lima *et al*. 2022).

Inonotus is a cosmopolitan genus characterised by its basidiocarps being annual to rarely perennial, resupinate, effused-reflexed or pileate, sessile to rarely stipitate, solitary to imbricate, corky fleshy to woody hard and brittle on drying. The pileus is small to medium-sized, dimidiate, applanate to conchate; upper surface glabrous, tomentose to hispid, yellowish to dark reddish brown, usually without a crust, hymenophore poroid; pore surface brown, pores 2–10 per mm; context rusty to cinnamon brown, mycelial core absent; hyphal system monomitic, generative hyphae yellowish to brownish, simple septate; setal hyphae present or absent; hymenial or tramal setae present or absent; cystidia none; spores globose to ellipsoid, rarely cylindrical, smooth, hyaline to yellowish or brown; on dead and living hardwoods or coniferous woods, causing a white rot (Dai 2010, Sharma *et al.* 2013b).

Numerous characters from morphology, anatomy, sexuality, nuclear behaviour, pigmentation and ecology suggest that the genus *Inonotus* is heterogeneous (Fiasson 1982, Fiasson & Niemelä 1984, Dai 1995, 1999, Fischer 1996, Zhou *et al.* 2015b, Ryvarden 2020, Xavier de Lima *et al*. 2022). Wagner & Fischer (2002) subdivided *Phellinus s. lat.* and *Inonotus s. lat.* into the genera *Inonotus s. str.*, *Phellinus s. str.*, *Aurificaria*, *Fomitiporella*, *Fomitiporia*, *Fulvifomes*, *Fuscoporia*, *Inocutis*, *Inonotopsis*, *Mensularia*, *Onnia*, *Phylloporia*, *Porodaedalea* and *Pseudoinonotus* based on 28S rDNA-based phylogenetic analyses. However, *Inonotus s. str. sensu* Wagner and

Fischer is still a broadly defined genus. *Inonotus s. lat.* has been well studied, particularly in Asia, Europe and North America (Gilbertson & Ryvarden 1986, Ryvarden & Gilbertson 1993, Dai 2010, Zhou *et al.* 2015b). Gottlieb *et al.* (2002) provided the morphology, cultural characters and molecular analyses of *Inonotus s. lat.* in Argentina, while Ryvarden (2005) published a monograph on *Inonotus s. lat.*, which deals with 101 species including 10 new species and six new combinations. The genus is heterogeneous and polyphyletic based on molecular characters (Niemelä *et al.* 2001, Wagner & Fischer 2001, 2002, Dai 2010, Zhou *et al.* 2015b, Xavier de Lima *et al*. 2022).

In traditional taxonomy based on anatomical and morphological data, *Inonotus s. lat.* was characterised by annual basidiocarps with a fibrous to soft or fragile consistency and a monomitic hyphal system (Pilát 1936, Cunningham 1946, Ryvarden & Johansen 1980, Gilbertson & Ryvarden 1986, Ryvarden & Gilbertson 1993, Núñez & Ryvarden 2000, Dai 2010). A combination of these characters makes it easy to distinguish it from another large genus in the *Hymenochaetaceae*, *Phellinus s. lat.* with woody and perennial basidiocarps as well as a dimitic hyphal system (Pilát 1936, Ryvarden & Johansen 1980, Gilbertson & Ryvarden 1987, Ryvarden & Gilbertson 1994, Núñez & Ryvarden 2000). However, the delimitation between *Inonotus s. lat.* and *Phellinus s. lat.* was questioned, since there are some intermediate species sharing characters of the two genera (Domanski *et al.* 1973, Jahn 1981, Fiasson & Niemelä 1984, Corner 1991, Dai 1995, 1999, Hansen & Knudsen 1997, Zhou *et al.* 2015b).

Inonotus s. lat. and its relatives, *Asterodon*, *Aurificaria*, *Coltricia*, *Coltriciella*, *Hydnochaete* and *Hymenochaete*, have been studied in China by Dai & Niemelä (2006). Previously, 31 species of *Inonotus s. str.* have been recorded in China (Dai 2010, 2012a, b, Cui *et al.* 2011). Investigations into wood-decaying fungi in southern China led to several new polypores being described (Dai *et al.* 2003, 2004, 2011, Cui *et al.* 2009, Zhou & Jia 2010). However, many specimens were not identified at the species level. Based on morphological study and phylogenetic analysis, a new species *Inonotus tenuicontextus* was described by Zhou & Qin (2012), who also provided an identification key to *I. tenuicontextus* and phylogenetically closely related species. Zhou *et al.* (2015b) used morphological and phylogenetic data based on global samples and inferred from nLSU and ITS datasets that *Inonotus* is polyphyletic comprising at least three clades. Ten species were transferred to the new genus *Sanghuangporus* and seven to *Tropicoporus*. *Tropicoporus excentrodendri* and *T. guanacastensis* were described as new species and their distinctive characters were discussed. Keys were also provided for *Inonotus s. str.* and the two new genera (Zhou *et al.* 2015b).

Ecological and economic significance

Inonotus species play a key role as food, and as sources for enzymes and medicine, based on their important and potential applications in biomedical engineering and biodegradation (Dai *et al.* 2009, Levin *et al.* 2016, Bankole *et al.* 2020). As a white rot fungus, *I. obliquus* is valued as an edible and medicinal resource (Song *et al.* 2013).

In biomedical engineering, *Inonotus obliquus* has been widely used as a folk medicine in Russia, Poland and most of the Baltic countries (Mu *et al.* 2012). In Russia, it has been used as a traditional remedy to cure 49 diseases such as cancer, cerebrovascular diseases, diabetes, and 50 gastrointestinal diseases since the sixteenth century (Sun *et al.* 2008, Choi *et al.* 2010, Ma *et al.* 2012). For centuries, *I. obliquus* (Chaga mushroom) has been used in Kiev to cure lip tumours, and it is a traditional medicine in Siberia (Szychowski *et al.* 2021). *Inonotus obliquus* was found to significantly inhibit transplanted tumours in animals *in vivo* (Gorzkowski 1955). Water extract of *I. obliquus* had potential anticancer activity against B16-F10 melanoma cells *in vivo* (Youn *et al.* 2009). *Inonotus obliquus* polysaccharide, made by water extraction and alcohol precipitation, with obvious inhibitory effects on sarcoma S180 in mice was also observed (Zhang *et al.* 2007). The most abundant triterpene compound, inotodiol, was investigated for its tumour-inhibitory effect in a two-stage carcinogenesis test on mouse skin and was found to have potent anti-tumour promoting activity in an *in vivo* carcinogenesis test (Nakata *et al.* 2007). Bao *et al.* (2017) reported on the morphology, habitat and geographical distribution of “Sanghuang” (*Inonotus hispidus*) in both ancient literature on herbal medicine and modern literature on medicinal fungi.

In biodegradation, the components of *Inonotus obliquus* mainly include lanolin alkane triterpenes isolated from, lignin, melanin, *etc.* (Kahlos *et al.* 1984, Kahlos & Hiltunen 1986, He & Feng 2001, Shin *et al.* 2000, 2001a, b, c, 2002, Nakata *et al.* 2007, Sayaka *et al.* 2007, Taji *et al.* 2008, Ham *et al.* 2009). Three new lanostane triterpenoids were isolated from petroleum ether extracts of *Inonotus obliquus* (Zhong *et al.* 2009). In addition, several species previously in *Phellinus s. lat.* were transferred to *Inonotus*, such as *I. baumii* and *I. vaninii* (Wagner & Fischer 2002). Both of these species yield polysaccharides, proteoglycans and polyphenols, and thus have medicinal functions, including antioxidation, anti-tumour, and improving immunity (Dai *et al.* 2010a).

Research interests

There are 535 publications and 6 331 citations from 2011–2021 in the Web of Science (Fig. 126), with the top 10 most cited articles listed in Table 101. Most of the publications focused on chemistry, applications in medical sectors, taxonomy and phylogeny.

Chemistry and applications in medical sectors

In Russia, *Inonotus obliquus* has been used as a traditional remedy to cure various diseases such as cancer, cerebrovascular diseases, diabetes and gastrointestinal diseases since the sixteenth century (Sun *et al.* 2008, Choi *et al.* 2010). Triterpenes, polysaccharides, polyphenols and melanin were found in *I. obliquus*, which were responsible for the anticancer and anti-tumour activities (Song *et al.* 2008, Handa *et al.* 2012), anti-inflammatory ability (Van *et al.* 2009), antioxidant effect (Ma *et al.* 2012), hypoglycemic ability (Lu *et al.* 2010), immunomodulatory activity (Fan *et al.* 2012) and antimutagenic properties (Ham *et al.* 2009).

Submerged culture of medicinal fungi is believed to be a promising alternative for the efficient production of mycelia and metabolites and has received increasing attention worldwide. However, despite several decades of effort, the production of secondary metabolites by submerged culture of medicinal fungi including *I. obliquus* is still encountering many biological, physiological, and engineering limitations (Zheng *et al.* 2010).

Song *et al.* (2013) showed that *I. obliquus* produces a diverse range of secondary metabolites, including phenolic compounds, melanins, and lanostane-type triterpenoids. Among these are active components for antioxidant, anti-tumoural, and antiviral activities and for improving human immunity against infection of pathogenic microbes. Their anticancer activities have become a hot

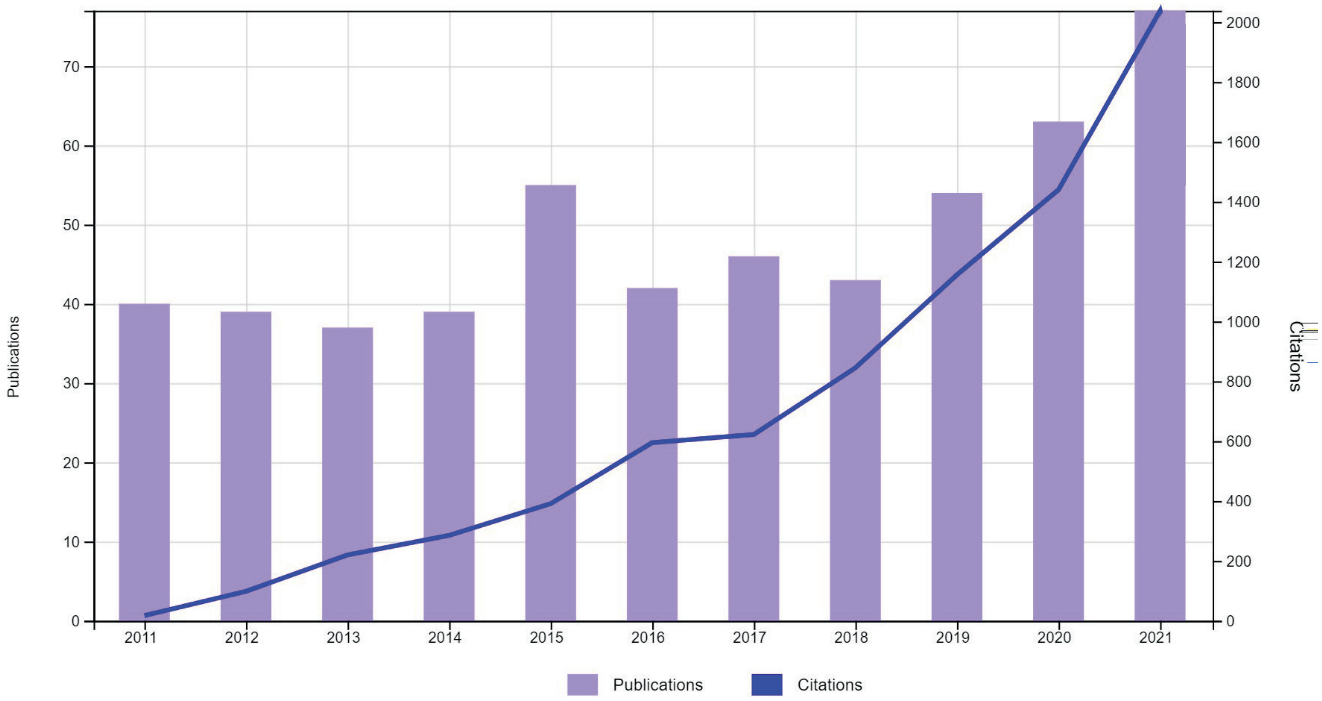

Fig. 126. Trends in research of *Inonotus* in the period 2011–2021.

topic recently but with relatively little knowledge of their modes of action. Polysaccharides from *I. obliquus* can indirectly be involved in anticancer processes mainly via stimulating the immune system. The antioxidative ability of *I. obliquus* extracts can also prevent the generation of cancer cells.

Taxonomy and phylogeny

According to the phylogenetic results of Li *et al.* (2016a), four narrowly defined genera, namely *Inocutis*, *Inonotopsis*, *Mensularia*, and *Onnia*, segregated from *Inonotus s. lat.*, while some species with perennial basidiocarps and a dimitic hyphal system were transferred to *Inonotus* (Wagner & Fischer 2002, Dai 2010, Wu *et al.* 2012b, Vlasák *et al.* 2013). Zhou (2015a) introduced a monotypic genus *Cylindrosporus* for a species previously belonging to *Inonotus*, while Zhou *et al.* (2015b) segregated *Sanghuangporus* and *Tropicoporus* from *Inonotus* and proposed that the remaining species in *Inonotus* still have polyphyletic origins. It is, therefore, necessary to recollect and epitypify the described taxa and amplify all the necessary genes for accurate species delimitation (Zhou *et al.* 2015b).

Authors: C.L. Zhao, K.Y. Luo, D.Q. Wang and J.J. Li

96. ***Ophiostoma*** Syd. & P. Syd., Ann. Mycol. 17: 43. 1919.

Type species: *Ophiostoma piliferum* (Fr.) Syd. & P. Syd.

Classification: *Ascomycota*, *Pezizomycotina*, *Sordariomycetes*, *Ophiostomatales*, *Ophiostomataceae.*

Table 101. Top 10 cited articles related to *Inonotus* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Current findings, future trends, and unsolved problems in studies of medicinal mushrooms	267	Wasser (2011)
2	Recent developments in mushrooms as anti-cancer therapeutics: a review	216	Patel & Goyal (2012)
3	Mushroom immunomodulators: unique molecules with unlimited applications	165	El Enshasy & Hatti-Kaul (2013)
4	Anti-inflammatory and anticancer activities of extracts and compounds from the mushroom *Inonotus obliquus*	149	Ma *et al.* (2013a)
5	Medicinal plants of the Russian pharmacopoeia; their history and applications	141	Shikov *et al.* (2014)
6	Medicinal mushrooms in prevention and control of diabetes mellitus	132	De Silva *et al.* (2012)
7	Effect of different drying methods on physicochemical properties and antioxidant activities of polysaccharides extracted from mushroom *Inonotus obliquus*	123	Ma *et al.* (2013b)
8	Contents of lovastatin, γ-aminobutyric acid and ergothioneine in mushroom fruiting bodies and mycelia	120	Chen *et al.* (2012a)
9	Chemical modification and antioxidant activities of polysaccharide from mushroom *Inonotus obliquus*	116	Ma *et al.* (2012)
10	Antitumor and immunomodulatory activity of water-soluble polysaccharide from *Inonotus obliquus*	103	Fan *et al.* (2012)

Background

The taxonomy of the *Ophiostomatales* has been challenging due to the limited number of morphological characters and the convergent evolution of features such as darkly pigmented ascocarps wherein short-lived asci are produced randomly at the base. These asci deliquesce upon maturation and the ascospores are extruded in a slimy droplet from the ostiole at the tip of the perithecial neck. The genus *Ophiostoma* was first proposed by Sydow & Sydow (1919) with *Ophiostoma piliferum* as the type species, but Baskshi (1951) and Hunt (1956) considered *Ophiostoma* to be a synonym of *Ceratocystis*. As most fungi assigned to *Ophiostoma* and *Ceratocystis* have adapted to be dispersed by insects they have converged and resemble each other morphologically. This has led to rather complex nomenclatural histories for these two genera; both at the ordinal level with proposals of these fungi being assigned to the *Microascales* or *Ophiostomatales* and at the generic level such as transferring members of *Ophiostoma* to the genus *Ceratocystis s. lat.* along with proposals for defining new genera to subdivide *Ophiostoma* and *Ceratocystis* (see Olchowecki & Reid 1974, Updadyay 1981, Zipfel *et al.* 2006, De Beer & Wingfield 2013, De Beer *et al.* 2014, 2016a, Holland *et al.* 2019, Marincowitz *et al.* 2020). De Beer *et al.* (2022) suggested that the order *Ophiostomatales* is comprised of 16 genera (but possibly up to 24 genera).

Ophiostoma (*Ophiostomataceae*) is one of the largest genera that includes tree-or wood-infecting fungi, with about 154 recognised species (De Beer *et al*. 2013a, b, 2022, Table 103). One hundred and thirteen taxa reside in *Ophiostoma s. str.* as defined by De Beer & Wingfield (2013), and most can be arranged in phylogenetically six well-supported species complexes, *O. clavatum*, *O. ips*, *O. minus*, *O. piceae*, *O. pluriannulatum*, and *O. ulmi*, although some do not form part of a well-defined species complex such as the type species, *O. piliferum* (Linnakoski *et al.* 2010, 2016, De Beer & Wingfield 2013, De Beer *et al.* 2022). Other species group in several unresolved smaller phylogenetic lineages or complexes within *Ophiostoma s. lat.* (De Beer & Wingfield 2013). Recently, De Beer et al. (2022) defined three new genera *Jamesreidia*, *Masuyamyces* and *Heinzbutinia* based on lineages previously included within *Ophiostoma*. Due to a lack of type material or DNA sequences, some species have uncertain status in the genus *Ophiostoma* (De Beer & Wingfield 2013). The number of *Ophiostoma* species is increasing rapidly due to ongoing research efforts on the interactions between fungi and bark beetles in China (Chang *et al.* 2017, 2019, 2020, 2021, Wang *et al.* 2018b, 2019b, 2020f) and Europe (Linnakoski *et al.* 2010, 2016, Aas *et al.* 2018, Jankowiak *et al.* 2019a, b, c).

Most members of *Ophiostoma* are commonly associated with forest trees, causing the economically important blue-stain in freshly exposed sapwood of softwood species (Seifert 1993, Uzunović & Byrne 2013, Roy *et al.* 2014, Gomdola *et al.* 2022). However, *O. novo-ulmi* is an example of a highly virulent tree pathogen responsible for Dutch elm disease (Brasier 1991). In addition, *O. piceae* was recorded to cause a disseminated infection involving the lung and the brain in a patient with lymphoblastic lymphoma (Bommer *et al.* 2009). *Ophiostoma* species are commonly associated with bark- and wood-dwelling beetles and their mites. They include bark- and ambrosia beetles, cerambycid beetles, nitidulid beetles and weevils (Juzwik *et al*. 1998, Kirisits 2004, Jankowiak & Kolařík 2010, Kamgan Nkuekam *et al.* 2012, Jankowiak & Bilański 2013a, b). The association between the pathogenic pine wood nematode (PWN) *Bursaphelenchus xylophilus* vectored by *Monochamus* spp. and *Ophiostoma* species has also been documented (Wingfield 1987, Wang *et al.* 2018b).

The genus *Ophiostoma* has a wide geographic distribution, including records for Africa, Asia, Europe, Oceania (including Australia), North and South America. They are abundant in the Northern Hemisphere, especially in conifer ecosystems in Asia, Europe, and North America (Table 103). *Ophiostoma ips*, *O. piceae*, *O. piliferum* and *O. quercus* are globally widespread, likely due to human activity and the movement of wood products around the globe (Taerum *et al*. 2018). *Ophiostoma* species can colonise a wide diversity of host tree species, including angiosperms and gymnosperms. Most of the formally described species of *Ophiostoma* are known only from conifers (96 species), including those in the genera *Abies*, *Larix*, *Picea*, *Pinus*, *Pseudotsuga*, and *Tsuga.* Only 38 *Ophiostoma* species are recorded from hardwoods, although these fungi can infect a wide diversity of hardwood hosts, especially *Eucalyptus*, *Fagus*, *Nothofagus*, *Quercus* and *Ulmus* trees (Table 103).

Ecological and economic significance

Ophiostoma species cause a serious wilt disease on elms plus many *Ophiostoma* species are economically important blue-stain agents of pines worldwide. Some bark beetle species are linked to many serious tree diseases and they are commonly associated with *Ophiostoma* species. These three aspects are detailed below.

Blue-stain is the discoloration of tree sapwood caused by the growth of blue-stain, typically from ophiostomatoid (as defined by Malloch & Blackwell 1993) genera such as *Ceratocystis*, *Endoconidiophora*, *Grosmannia*, *Ophiostoma*, *Leptographium* and also from non-ophiostomatoid genera, *e.g.*, *Sphaeropsis* (*Diplodia*) and *Lasiodiplodia* (Seifert 1993, Uzunović & Byrne 2013). Blue-stain is caused by pigmented fungal hyphae usually growing in the ray parenchyma cells, resin ducts and later in the tracheids (Seifert 1993). Discoloration is due to melanin, a dark pigment existing inside the cell walls of the hyphae, and not due to staining of the sapwood tissues (Zink & Fengel 1989). *Ophiostoma* species, which are commonly carried by bark- and wood-dwelling beetles and mites, usually colonise freshly felled logs and freshly sawn lumber, causing a dark bluish discolouration in the sapwood that is difficult to remove or reduce in intensity (Kirisits 2004). Discoloration by blue-stain fungi reduces the value of wood and wood products, limiting export opportunities, and thus affecting the timber trade and markets. Blue-stain is considered a serious problem in softwoods in the Northern Hemisphere but hardwoods are also affected (Seifert 1993, Butin 1996, Uzunović & Byrne 2013). Due to the large proportion of sapwood, *Pinus* wood is very highly susceptible to fungal staining (Seifert 1993). *Ophiostoma ips*, *O. floccosum*, *O. piliferum*, *O. minus*, *O. peregrinum*, *O. piceae*, *O. pluriannulatum*, and *O. setosum* are the most important *Ophiostoma* blue-stain agents of pines in Europe, New Zealand, North America, and Patagonia (Seifert 1993, Uzunović *et al.* 1999, Thwaites *et al.* 2005, De Errasti *et al.* 2018, Jankowiak *et al.* 2021).

Dutch elm disease (DED) caused by *Ophiostoma himal-ulmi*, *O. ulmi*, and *O. novo-ulmi* is one of the most destructive diseases of woody trees across Europe, North America, and Central Asia. The causal agents of DED are among the most devastating plant pathogens studied in the 20th century that have dramatically altered the urban and native forest composition in Europe and North America. Dutch elm disease was first noticed in 1919 by the Dutch

Phytopathological Service when it was spread over large areas of Benelux and part of Northern France. There were two large DED pandemics, which caused severe losses among native elms in Europe and North America. The first pandemic caused by *O. ulmi* first appeared in Europe in the 1910s and, 20 years later, in North America leading to a loss of between 10 and 40 % of elms in various European countries (Brasier 2000, Santini & Faccoli 2014). Around 1940, the disease disappeared in Europe. A second wave followed in the 1960s, causing a more destructive outbreak of the disease in Europe, North America, and Central Asia. The second pandemic, which is still ongoing, was caused by the highly virulent *O. novo-ulmi*, which almost totally replaced *O. ulmi*, and has killed most mature elm trees on the three continents (Brasier 2000, Santini & Faccoli 2014). *Ophiostoma ulmi* and *O. novo-ulmi* most likely originated from Asia (Brasier 2000), where native elm trees are more resistant to these fungi (Santini & Faccoli 2014). Two distinct subspecies within *O. novo-ulmi* populations are recognised: *O. novo-ulmi* ssp. *novo-ulmi*, previously known as the Euro-Asian race (EAN), and *O. novo-ulmi* ssp. *americana*, previously known as the North American race (NAN) (Brasier 1979, Brasier & Kirk 2001). A third species, *O. himal-ulmi* can infect *Ulmus wallichiana* and its distribution is limited to the Himalayas (Brasier & Mehrotra 1995). Dutch elm disease is mainly spread by the bark beetles *Scolytus* spp. and *Hylurgopinus rufipes* (Webber 1990, 2000, Jacobi *et al.* 2007, 2013, Jankowiak *et al.* 2019a, b, c), but the infection can also spread via root grafts (Webber & Brasier 1984). Initial symptoms of DED include wilting and discoloration of the leaves at the tip of shoots. Dieback continues and the wilt continues throughout the entire crown and the tree eventually dies. A diagnostic symptom of DED is the browning of the water-conducting vessels (visible by peeling off the outer bark) of the whole outer growth ring due to the formation of tyloses and gels in the xylem of affected branches (Rioux *et al.* 1998, Ouellette *et al.* 2004, Kirisits 2013). The DED fungi produce a unique, phytotoxic, low molecular weight protein known as ceratoulmin (Takai 1974, 1978). Ceratoulmin is produced by the DED pathogens in xylem vessels of stems and branches and is involved in the development of DED symptoms in elms infected with *O. novo-ulmi* (Del Sorbo *et al*. 2002).

Bark beetle-fungus symbioses are a classic model of symbiosis in nature. Insects have a widespread association with fungi, especially with members of *Microascales* and *Ophiostomatales* that cause blue staining of wood and serious tree diseases. Associations between insects and fungi are very diverse, ranging from farming-like nutritional ambrosia symbioses to looser associations of beetles with fungal hitchhikers (Six 2012, Hulcr & Stelinski 2017). Most species carry fungi, either in specialised structures of the integument called mycangia or phoretically on the exoskeleton (Six 2012). *Ophiostoma* species are mainly associated with phloem-feeding bark beetles (*Coleoptera*, *Scolytinae*) and, to a lesser extent, with ambrosia beetles (*Coleoptera*, *Solytinae* and *Platypodinae*) that cultivate and feed on fungal gardens along the walls of their galleries in sapwood. The precise role of *Ophiostoma* species within bark beetles-fungi systems and the specificity of these associations, are yet to be clearly defined (Wingfield *et al*. 2017b). Some *Ophiostoma* species are highly specific and maintain close relationships with one or a few beetle species on one host tree. A good example is the association of *O. canum* with *Tomicus minor* or *O. pityokteinis* with *Pityokteines* spp. Other fungi have non-specific associations with bark beetles and have larger ranges of insects and host trees, such as *O. piceae* or *O. quercus* (Kirisits 2004). *Ophiostoma* species are morphologically well-adapted for dispersal by beetles. Sexual structures of these fungi are mostly ascomata with elongated necks, exuding sticky spores at their apices and are often surrounded by ostiolar hyphae that attach easily to the bodies of passing insects. Asexual structures are in most cases erect conidiophores with sticky spores at their apices (Malloch & Blackwell 1993). Species of *Ophiostoma* have been noted on more than 100 species of arthropods including bark- and ambrosia beetles and their mites, weevils (Coleoptera, Molytinae) and cerambycid beetles (*Coleoptera*, *Cerambycidae*) (Table 103). Sap-feeding (nitidulid) beetles (*Coleoptera*, *Nitidulidae*) visiting fresh wounds on hardwood trees have been also recognised as vectors of *Ophiostoma* species (Juzwik *et al.* 1998, Kamgan Nkuekam *et al.* 2012, Jankowiak *et al.* 2019a, b, c). Based on the available literature, *Ips typographus* vectored 24 species of *Ophiostoma*, followed by *Ips subelongatus* (15 species), and *Pityogenes chalcographus* (13 species).

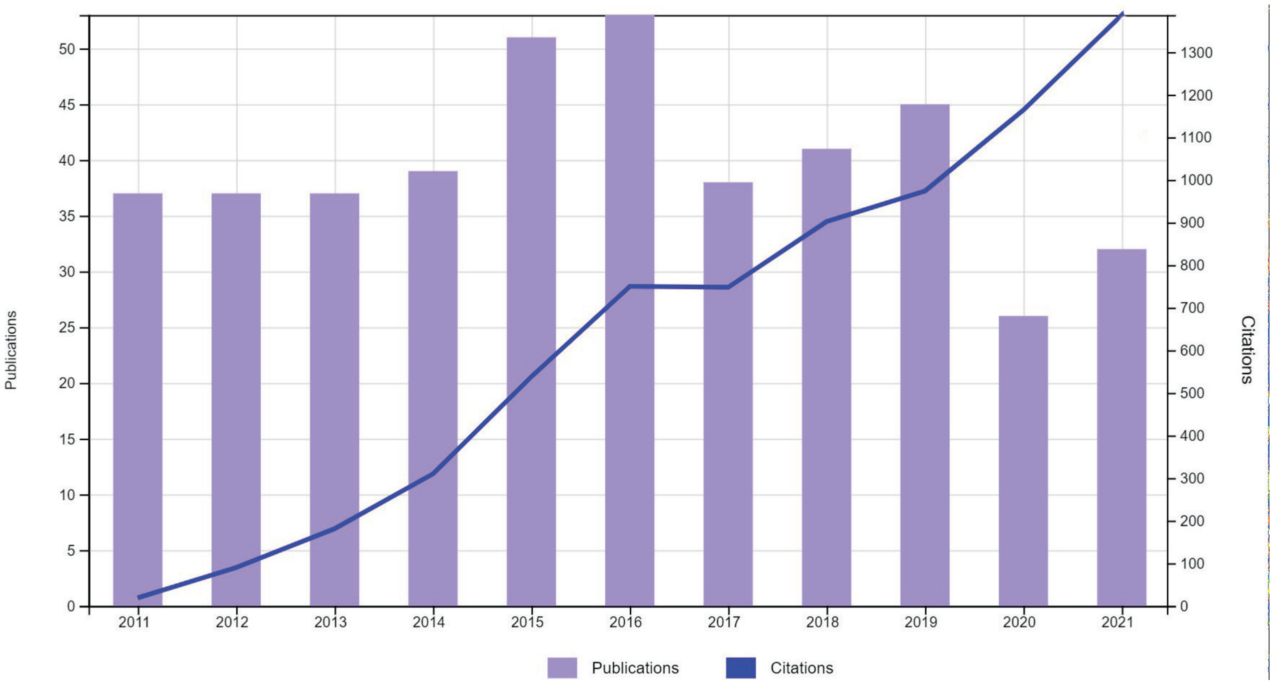

Fig. 127. Trends in research of *Ophiostoma* in the period 2011–2021.

Table 102. Top 10 cited articles related to Ophiostoma published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	The role of phytopathogenicity in bark beetle-fungus symbiosis: A challenge to the classic paradigm	181	Six *et al.* (2011)
2	Redefining *Ceratocystis* and allied genera	162	De Beer *et al.* (2014)
3	Hydraulic limits preceding mortality in a pinon-juniper woodland under experimental drought	139	Plaut e*t al.* (2012)
4	The family *Narnaviridae*: Simplest RNA viruses	137	Hillman & Cai (2013)
5	Virus world as an evolutionary network of viruses and capsidless selfish elements	130	Koonin *et al.* (2014)
6	Bacteria associated with a tree-killing insect reduce concentrations of plant defense compounds	117	Boone *et al.* (2013)
7	The divorce of *Sporothrix* and *Ophiostoma*: solution to a problematic relationship	113	De Beer *et al.* (2016a)
8	Increasing forest loss worldwide from invasive pests requires new trade regulations	107	Roy *et al.* (2014)
9	Isolations from the redbay ambrosia beetle, *Xyleborus glabratus*, confirm that the laurel wilt pathogen, *Raffaelea lauricola*, originated in Asia	71	Harrington *et al.* (2011)
10	The genome and transcriptome of the pine saprophyte *Ophiostoma piceae*, and a comparison with the bark beetle-associated pine pathogen *Grosmannia clavigera*	48	Haridas *et al.* (2013)

Mites have multiple effects on insect-fungus associations (Lombardero *et al.* 2000, Hofstetter & Moser 2014), using the beetles for dispersal and access to tree species and access to fungi as many mites are mycetophagous. Many mites transport *Ophiostoma* species (Chang *et al*. 2017, 2020), for example, *Tarsonemus* mites associated with the southern pine beetle, *Dendroctonus frontalis* carry the ascospores of *O. minus* (Moser 1985), whereas mites associated with conifer-infesting beetles in China vectored *O. ips* (Chang *et al.* 2017).

Research interests

There are 436 publications and 5 912 citations from 2011–2021 in the Web of Science (Fig. 127), with the top 10 most cited articles displayed in Table 102. Most of the publications focused on fungal/insect relationships, blue-stain management (forestry) and research on double-stranded RNA viruses associated with DED-causing fungi (potential biocontrol agents). Double-stranded RNA viruses (non-encapsulated) that belong to the genus *Mitovirus* of the family *Narnaviridae* have been recovered from the mitochondria of many fungi including the DED pathogens, although technical difficulties in genetically manipulating the mitochondria of filamentous fungi so far have limited the potential exploitation of these RNA viruses as a means of introducing an engineered version into DED pathogen populations that could induce hypovirulence (Hillman & Cai 2013, Hintz *et al.* 2013, Koonin & Dolja 2014).

Bark beetle fungus interactions

Dendroctonus ponderosae (mountain pine beetle, MPB) has been reported to form multipartite symbiotic associations with several species of blue stain fungi and the fungal symbionts provide a source of nutrients, enhance conditions for brood development and possibly enhance the beetle's capacity to invade trees (Six & Wingfield 2010, Six 2012, Ploetz *et al.* 2013, Vanderpool *et al.* 2018). However, these fungi insect associations are quite complex, for example, the multiple fungal symbionts for MPB may provide plasticity with regards to which symbiont can provide adaptive benefits under certain environmental conditions, or the fungal symbionts can act in a complementary fashion to allow survival under adverse conditions or when the MPB invades new host species (Ojeda Alayon *et al.* 2017). In addition to fungi, there are also bacteria associated with MPB that can reduce the concentrations of various plant defense compounds (Boone *et al.* 2013). It has also been noted that in bark beetle-fungus symbiosis the fungal partner may not always promote phytopathogenicity, in some instances the fungal associate could be potentially antagonistic towards the beetle and in some instances, beetles carry bacteria that are antagonistic towards the fungal associates (reviewed in Six & Wingfield 2011). A rather complex picture emerges for bark beetle-fungus symbiosis that can involve bacterial symbionts, fungal associates/mutualists, and mites that can feed on some fungal associates and in turn the mites can parasitise the beetle (Six & Wingfield 2010). These complex interactions need to be assessed in the future to gain a better understanding of how beetles move into new geographic regions and invade new host species.

Diversity and systematics

Many members of the *Ophiostomatales* are fungal associates of ambrosia and bark beetles and these fungi can be agents of blue stain or tree diseases, therefore there is considerable interest in the fungi vectored by these insects. Major strides have been achieved with the aid of various molecular markers that have resulted in considerable taxonomic revisions for the order *Ophiostomatales*. This order includes two families, *Kathistaceae* and *Ophiostomataceae* (Hyde *et al.* 2020d). Within *Ophiostomataceae*, De Beer *et al.* (2022) recognized the following genera: *Aureovirgo*, *Ceratocystiopsis*, *Dryadomyces*, *Esteya*, *Fragosphaeria*, *Graphilbum*, *Grosmannia*, *Harringtonia*, *Hawksworthiomyces*, *Heinzbutinia*, *Jamesreidia*, *Leptographium*, *Masuyamyces*, *Ophiostoma*, *Raffaelea*, and *Sporothrix*. In addition, De Beer *et al.* (2022) were able to define 24 possible lineages that could represent additional genera based on extensive sampling. Members of *Ophiostoma* can be identified based on morphological and molecular criteria. Typically, several molecular markers are applied for species identification or for designating new taxa; these markers are rDNA ITS, rDNA LSU, and segments of protein-coding genes such as *tub*, *tef*1 and *cal* (Zipfel *et al.* 2006, De Beer *et al.* 2013, 2016a, Yamaoka 2017, Yin *et al.* 2016). Table 103 demonstrates that species of *Ophiostoma*

Table 103. Distribution of *Ophiostoma* spp. worldwide. Species in bold belong to *Ophiostoma s. str.* based on ITS or LSU sequences (113 species); *North America (N.A.) = 54 species; South America (S.A.) = 13 species; Africa (Af.) = 11 species; Europe (E.) = 59 species; Asia (As.) = 67 species; Oceania (O.) = 17 species. Four species distributed worldwide: *O. ips*, *O. piecae*, *O. piliferum* and *O. quercus*. 🌲 on conifers = 109 species (96 only on conifers); 🌿 on hardwoods = 53 species (only on hardwoods = 38 species). 🌿 on conifers and hardwood = 14 species; 🐜 species in association with insects = 114 species; 🌲🪵 typically wood-associated species = 16 species.

Species	N. A.*	S. A.	Af.	E.	As.	O.
Ophiostoma ainoae H. Solheim 🌲🐜				🟩	🟩	
Ophiostoma acarorum R.Chang & Z.W.de Beer 🌲🐜					🟩	
=*Masuyamyces acarorum* (R. Chang & Z.W. de Beer) M. Procter & Z.W. de Beer						
Ophiostoma adjuncti (R.W. Davidson) Harrington 🌲	🟩					
Ophiostoma aggregatum H. Wang, Q. Lu & Z. Zhang 🌲🐜					🟩	
Ophiostoma album Wang & Lu 🌲🐜					🟩	
Ophiostoma allantosporum (Griffin) M. Villarreal 🌲🐜	🟩					
Ophiostoma ambrosium (Bakshi) Hausner, J. Reid & Klassen 🌿🐜				🟩		
=*Masuyamyces ambrosius* (B.K. Bakshi) M. Procter & Z.W. de Beer						
Ophiostoma angusticollis (E.F. Wright & H.D. Griffin) M. Villarreal 🌲	🟩					🟩
Ophiostoma araucariae (Butin) de Hoog & Scheffer 🌲		🟩		🟩		
Ophiostoma arborea (Olchow. & J. Reid) Yamaoka & M.J. Wingf. 🌲	🟩					
Ophiostoma arduennense F.-X. Carlier, Decock, K. Jacobs & Maraite 🌲🌿🐜	🟩			🟩		
Ophiostoma australiae (Kamgan, K. Jacobs & M.J. Wingf.) Z.W. de Beer & M.J. Wingf. 🌿🪵						🟩
Ophiostoma bacillisporum (Butin & G. Zimm.) de Hoog & Scheffer 🌿🐜				🟩		
Ophiostoma bicolor R.W. Davidson & D.E. Wells 🌲🐜	🟩			🟩	🟩	
Ophiostoma borealis Kamgan, H. Solheim & Z.W. de Beer 🌲🌿🐜🪵				🟩		
Ophiostoma botuliforme Masuya 🌲🐜					🟩	
=*Masuyamyces botuliformis* (Masuya) Z.W. de Beer & M. Procter						
Ophiostoma brevipilosi R.Chang & Z.W.de Beer 🌲🐜					🟩	
Ophiostoma breviusculum Chung, Yamaoka, Uzunovic & Kim 🌲🐜					🟩	
Ophiostoma brunneociliatum Math.-Käärik 🌲🐜				🟩	🟩	
Ophiostoma brunneolum Linnakoski, Z.W. de Beer & M.J. Wingf. 🌲🐜				🟩	🟩	
Ophiostoma brunneum (R.W. Davidson) Hausner & J. Reid 🌲🐜	🟩					
Ophiostoma californicum (DeVay, R.W. Davidson & Moller) Hausner, J. Reid & Klassen 🌿	🟩					
Ophiostoma canum (Münch) Syd. 🌲🐜	🟩			🟩	🟩	
Ophiostoma carpenteri J. Reid & Hausner 🐜	🟩					
Ophiostoma castaneae (Vanin & Solovjev) Nannf. 🌿				🟩		
Ophiostoma catonianum (Goid.) Goid. 🌿				🟩		
Ophiostoma clavatum Math. 🌲🐜				🟩	🟩	
Ophiostoma columnare (Olchow. & J. Reid) Seifert & G. Okada 🌲	🟩					
Ophiostoma conicola Marm. & Butin 🌲🐜	🟩					
Ophiostoma coronatum (Olchow. & J. Reid) M. Villarreal 🌲🌿🐜	🟩					🟩
=*Jamesreidia coronata* (Olchow. & J. Reid) M. Procter & Z.W. de Beer						
Ophiostoma crenulatum (Olchow. & J. Reid) Hausner & J. Reid 🌲	🟩					
Ophiostoma cupulatum (McNew & Harrington) Z.W. de Beer & M.J. Wingf. 🌲	🟩					
Ophiostoma denticiliatum Linnakoski, Z.W. de Beer & M.J.Wingf. 🌿🐜🪵				🟩		
Ophiostoma denticulatum (R.W. Davidson) Z.W. de Beer &M.J. Wingf. 🌲🐜	🟩					
Ophiostoma fasciatum (Olchow. & J. Reid) Hausner, J. Reid & Klassen 🌲🐜	🟩					🟩
Ophiostoma flexuosum H. Solheim 🌲🐜				🟩		
Ophiostoma floccosum Math. 🌲🌿🐜🪵	🟩		🟩	🟩	🟩	🟩
Ophiostoma fuscum Linnakoski, Z.W. de Beer & M.J. Wingf. 🌲🐜				🟩	🟩	
Ophiostoma genhense Z. Wang & Q. Lu 🌲🐜					🟩	
Ophiostoma gilleteae Marinc., Z.W. de Beer, M.J. Wingf. 🐜	🟩					

Table 103. (Continued).

Species	N. A.*	S. A.	Af.	E.	As.	O.
Ophiostoma gmelinii R.L. Chang, Z.W. de Beer & M.J. Wingf.					🟩	
Ophiostoma grande Samuels & E. Müll		🟩				
Ophiostoma grandicarpum (Kowalski & Butin) Rulamort				🟩		
=*Heinzbutinia grandicarpa* (Kowalski & Butin) Z.W. de Beer & M. Procter						
Ophiostoma himal-ulmi Brasier & M.D. Mehrotra					🟩	
Ophiostoma hongxingense Z. Wang & Q. Lu					🟩	
Ophiostoma huangnanense Z. Wang and Q. Lu					🟩	
Ophiostoma hyalothecium (R.W. Davidson) Hausner, J. Reid & Klassen	🟩					
Ophiostoma hylesinum T. Aas, H. Solheim & R. Jankowiak				🟩		
Ophiostoma introcitrinum (Olchow. & J. Reid) Hausner, J. Reid & Klassen	🟩			🟩		
Ophiostoma ips (Rumbold) Nannf.	🟩	🟩	🟩	🟩	🟩	🟩
Ophiostoma japonicum Yamaoka & M.J. Wingf.				🟩	🟩	
Ophiostoma jiamusiensis R. Chang, Z.W. de Beer & M.J. Wingf.					🟩	
Ophiostoma jilinense R. Chang, Z.W. de Beer & M.J. Wingf.					🟩	
=*Masuyamyces jilinensis* (R. Chang et al.) M. Procter & Z.W. de Beer						
Ophiostoma karelicum Linnakoski, Z.W. de Beer & M.J. Wingf.				🟩		
Ophiostoma kryptum K. Jacobs & Kirisits				🟩		
Ophiostoma kunlunense R.L. Chang & Z.W. de Beer					🟩	
Ophiostoma leucocarpum (R.W. Davidson) Z.W. de Beer & M.J. Wingf.	🟩			🟩		
Ophiostoma lignorum (Wollenw.) Goid.				🟩		
Ophiostoma longicollum Masuya			🟩		🟩	
Ophiostoma longiconidiatum Kamgan, K. Jacobs & Jol. Roux						
Ophiostoma longirostellatum (Bakshi) Arx & E. Müll.				🟩		
Ophiostoma lotiforme Z. Wang & Q. Lu					🟩	
=*Masuyamyces lotiformis* (Z. Wang & Q. Lu) M. Procter & Z.W. de Beer						
Ophiostoma macroclavatum Linnakoski, Z.W. De Beer & M.J. Wingf.				🟩		
Ophiostoma macrosporum (Francke-Grosm.) Z.W. deBeer & M.J. Wingf.				🟩		
Ophiostoma maixiuense Z. Wang and Q. Lu					🟩	
Ophiostoma manchongi R.L. Chang & Z.W. de Beer					🟩	
Ophiostoma massoniana Wang & Lu					🟩	
=*Masuyamyces massonianae* (Wang & Lu) M. Procter & Z.W. de Beer						
Ophiostoma megalobrunneum (R.W. Davidson & Toole) de Hoog & Scheffer	🟩					
Ophiostoma micans M.L. Yin, Z.W. de Beer & M.J. Wingf.					🟩	
Ophiostoma microsporum Arx	🟩					
=*Heinzbutinia microspora* (Arx) Z.W. de Beer & M. Procter						
Ophiostoma minus (Hedgc.) Syd.	🟩			🟩	🟩	
Ophiostoma montium (Rumbold) Arx	🟩					
Ophiostoma multiannulatum (Hedgc. & R.W. Davidson) Hendrix	🟩					
Ophiostoma multisynnematum Z. Wang & Q. Lu					🟩	
Ophiostoma nigricarpum (R.W. Davidson) de Hoog	🟩				🟩	🟩
=*Jamesreidia nigrocarpa* (R.W. Davidson) M. Procter & Z.W. de Beer						
Ophiostoma nikkoense Yamaoka & Masuya					🟩	
Ophiostoma nitidum M.L. Yin, Z.W. de Beer & M.J. Wingf.					🟩	
Ophiostoma noisomeae Musvuugwa, LL. Dreyer & F. Roets			🟩			
Ophiostoma novo-ulmi Brasier	🟩			🟩	🟩	🟩
Ophiostoma novae-zelandiae (L.J. Hutchison & J. Reid) Rulamort						🟩
Ophiostoma olgensis Wang & Lu					🟩	
Ophiostoma pallidulum Linnakoski, Z.W. de Beer & M.J. Wingf.				🟩		🟩

Table 103. (Continued).

Species	N. A.*	S. A.	Af.	E.	As.	O.
=*Masuyamyces pallidulus* (Linnak. et al.) M. Procter & Z.W. de Beer						
Ophiostoma palustre J.A Osorio, Z.W. de Beer & Jol. Roux			🟩			
Ophiostoma patagonicum de Errasti & Z.W. de Beer		🟩				
Ophiostoma pehueninum M. Zapata, M.A. Palma & E. Piontelli		🟩				
Ophiostoma peniculi Z. Wang & Q. Lu					🟩	
Ophiostoma peregrinum de Errasti & Rajchenb.		🟩		🟩		
Ophiostoma perfectum (R.W. Davidson) de Hoog	🟩					
Ophiostoma persicinum Govi & Di Caro				🟩		
Ophiostoma piceae (Münch) Syd.	🟩	🟩	🟩	🟩	🟩	🟩
Ophiostoma piliferi H.M. Wang and Q. Lu					🟩	
Ophiostoma piliferum (Fr.: Fr.) Syd.	🟩	🟩	🟩	🟩	🟩	🟩
Ophiostoma pityokteinis R. Jankowiak & P. Bilański				🟩		
Ophiostoma pluriannulatum (Hedgc.) Syd., In Sydow & Sydow	🟩	🟩	🟩	🟩		🟩
Ophiostoma poligraphi M.L. Yin, Z.W. de Beer & M.J. Wingf.					🟩	
Ophiostoma ponderosae (T.E. Hinds & R.W. Davidson) Hausner	🟩					
Ophiostoma populicola (Olchow. & J. Reid) Z.W. de Beer	🟩					
Ophiostoma populinum (T.E. Hinds & R.W. Davidson) de Hoog & Scheffer	🟩					
Ophiostoma pseudobicolor Z. Wang & Q. Lu					🟩	
Ophiostoma pseudocatenulatum Jankowiak, R. Linnakoski & Z.W. De Beer				🟩		
Ophiostoma pseudokarelicum T. Aas, H. Solheim & R. Jankowiak				🟩		
Ophiostoma pseudominus (Olchow. & J. Reid) Hausner, J. Reid & Klassen	🟩					
Ophiostoma pseudonigrum (Olchow. & J. Reid) Hausner & J. Reid	🟩					
Ophiostoma pseudotsugae (Rumb.) von Arx	🟩					
Ophiostoma pulvinisporum X.D. Zhou & M.J. Wingf.	🟩					
Ophiostoma pusillum Masuya					🟩	
Ophiostoma qinghaiense M.L. Yin, Z.W. de Beer & M.J. Wingf.					🟩	
Ophiostoma quercus (Georgev.) Nannf.	🟩	🟩	🟩	🟩	🟩	🟩
Ophiostoma rachisporum Linnakoski, Z.W. de Beer & M.J. Wingf.				🟩		
Ophiostoma retusi (R.W. Davidson & T.E. Hinds) Hausner, J. Reid & Klassen	🟩					
Ophiostoma roraimense Samuels & E. Müll		🟩				
Ophiostoma rostrocoronatum (R.W. Davidson & Eslyn) de Hoog & Scheffer	🟩					
=*Jamesreidia rostrocoronata* (R.W. Davidson & Eslyn) M. Procter & Z.W. de Beer						
Ophiostoma rufum R. Jankowiak & P. Bilański				🟩	🟩	
Ophiostoma sanum Z. Wang and Q. Lu					🟩	
Ophiostoma saponiodorum Linnakoski, Z.W. de Beer & M.J. Wingf.				🟩		
=*Masuyamyces saponiodorus* (Linnak. et al.) M. Procter & Z.W. de Beer						
Ophiostoma sejunctum M. Villarreal, Arenal, V. Rubio & M. de Troya				🟩		
Ophiostoma setosum Uzunovic, Seifert, S.H. Kim & C. Breuil	🟩				🟩	🟩
Ophiostoma shangrilae M.L. Yin, Z.W. de Beer & M.J. Wingf.					🟩	
Ophiostoma shanziensis Marinc., Z.W. de Beer, M.J. Wingf.					🟩	
Ophiostoma shennongense T. Wang & Q. Lu					🟩	
Ophiostoma signatum T. Aas, H. Solheim & R. Jankowiak				🟩		
Ophiostoma simplex K. Jacobs & M.J. Wingf.	🟩			🟩		
Ophiostoma solheimii B. Strzałka & R. Jankowiak				🟩		
=*Heinzbutinia solheimii* (Strzałka & Jankowiak) Z.W. de Beer & M. Procter				🟩		
Ophiostoma songshui R. Chang, Z.W. de Beer & M.J. Wingf.					🟩	
Ophiostoma sparsiannulatum Zanzot, Z.W. de Beer and M.J. Wingf.	🟩			🟩		
Ophiostoma spinosum P. Cannon				🟩		

Table 103. (Continued).

Species	N. A.*	S. A.	Af.	E.	As.	O.
Ophiostoma ssiori Masuya, Kubono & Ichihara					🟩	
Ophiostoma subalpinum Ohtaka & Masuya					🟩	
Ophiostoma subannulatum Livingston & R.W. Davidson	🟩					
Ophiostoma subelongati Z. Wang & Q. Lu					🟩	
Ophiostoma sugadairense J. Li, Yamaoka & Masuya					🟩	
Ophiostoma taizhouense G. H. Zheng & Q. Lu					🟩	
Ophiostoma taphrorychi B. Strzałka & R. Jankowiak				🟩		
Ophiostoma tapionis Linnakoski, Z.W. de Beer & M.J. Wingf.				🟩		
Ophiostoma tasmaniense Kamgan-Nkuek, Jol.Roux & Z.W.de Beer			🟩			🟩
Ophiostoma tenellum (R.W. Davidson) M. Villarreal	🟩					
=*Jamesreidia tenella* (R.W. Davidson) Z.W. de Beer & M. Procter						
Ophiostoma tetropii Math.	🟩			🟩	🟩	
Ophiostoma tingens (Lagerb. & Melin) Z.W. de Beer & M.J. Wingf.				🟩	🟩	
Ophiostoma tonghuaense H.M. Wang and Q. Lu					🟩	
Ophiostoma torticiliata (Olchow. & J. Reid) Seifert & G. Okada	🟩					
Ophiostoma torulosum (Butin & G. Zimm.) Georg Hausner, J. Reid & Klassen				🟩		
Ophiostoma tremulo-aureum (R.W. Davidson & T.E. Hinds) de Hoog & Scheffer	🟩					
Ophiostoma triangulosporum Butin		🟩				
Ophiostoma trinacriforme (A.K. Parker) T.C. Harr.	🟩					
Ophiostoma tsotsi Grobbelaar, Z.W. de Beer & M.J. Wingf.			🟩		🟩	
Ophiostoma typographi R. Chang, Z.W. de Beer & M.J. Wingf.					🟩	
Ophiostoma ulmi (Buism.) Nannf.	🟩			🟩	🟩	
Ophiostoma undulatum Kamgan-Nkuek, M.J.Wingf. & Jol.Roux						🟩
Ophiostoma valachicum Georgescu, Teodoru & Badea				🟩		
Ophiostoma valdivianum (Butin) Rulamort		🟩				
Ophiostoma villosum T. Aas, H. Solheim & R. Jankowiak				🟩		
Ophiostoma wuyingense R. Chang, Z.W. de Beer & M.J. Wingf.					🟩	
Ophiostoma xinganense Z. Wang & Q. Lu					🟩	
Ophiostoma yaluense H.M. Wang and Q. Lu					🟩	

have a worldwide distribution and can occur on a variety of host trees and in association with various insect vectors. Future efforts including surveying under-sampled tree/plant species and new geographical regions combined with new methodologies such as eDNA (environmental DNA) and metagenomic approaches (Hermans *et al.* 2017) may uncover new species and identify other organisms (such as insects and bacteria) that are associated with these fungi.

Genomics of the Ophiostomatales and Dutch Elm Disease

To infect and proliferate in their hosts, blue-stain fungi had to evolve strategies to combat host defence mechanisms along with biochemical pathways that provide efficient means for nutrient uptake and for pathogenic species, virulence factors towards the plant hosts (Six 2013, Lah *et al.* 2017). Genomics, transcriptomics, and proteomics are offering new tools to investigate saprophyte or pathogen-host interactions and fungal insect interactions among members of the *Ophiostomatales* (Khoshraftar *et al.* 2013, Forgetta *et al.* 2013, Haridas *et al.* 2013, Comeau *et al.* 2015, Nigg *et al.* 2015, Perdiguero *et al.* 2015, Ojeda Alayon *et al.* 2017, Wingfield *et al.* 2017a, Ibarra Caballero *et al.* 2019). With regards to Dutch elm disease, comparative genomics has shown that hybridisation among *O. ulmi*, *O. novo-ulmi* subsp. *novo-ulmi* and *O. novo-ulmi* subsp. *americana* resulted in the introgression of adaptive genes that promoted the success of the invasive species that comprise the DED fungi (Hessenauer *et al.* 2020). Attention has also been placed on the biosynthetic gene clusters that produce secondary metabolites and among the DED pathogens, comparative genomics identified a unique fujikurin-like gene cluster (OpPKS8) (Sbaraini *et al.* 2017). In addition, various genes involved in plant toxin neutralisation such as terpenes have been noted in their genomes (Haridas *et al.* 2013, Lah *et al.* 2017, Ibarra Caballero *et al.* 2019). Although genomics has provided a wealth of information and identified candidate genes that could be involved in pathogenicity or maintaining fungus insect interactions, genetics tools such as RNAi and CRISPR/Cas9 need to be applied in future studies to validate these findings (Carneiro *et al.* 2010, Dort *et al.* 2020).

Auhors: G. Hausner and R. Jankowiak

97. **Neofusicoccum** Crous *et al.*, Stud. Mycol. 55: 247. 2006.

Type species: *Neofusicoccum parvum* (Pennycook & Samuels) Crous *et al.*

Classification: *Ascomycota*, *Pezizomycotina*, *Dothideomycetes*, *Botryosphaeriales*, *Botryosphaeriaceae.*

Background

Neofusicoccum includes 64 species listed in Index Fungorum (2022), the sequence data of all, except one species, *Neofusicoccum sichuanense* (Xu *et al.* 2022b), are available at NCBI's GenBank nucleotide database. Species of *Neofusicoccum* are endophytes; however, similar to other members of *Botryosphaeriales*, they will cause disease when their hosts are under stress. The pathway of infection for *Neofusicoccum* varies from endophytic colonisation in plant tissues to infection via wounds caused naturally, mechanically or by insects (Slippers & Wingfield 2007). The spores can be dispersed by rain, wind and soil from the infected substrate such as pruned or fallen wood, twigs, fruit and leaf litter. The spores can persist in infected substrates for a few years and cause infection when weather conditions are suitable (Mehl *et al.* 2013).

The main disease symptoms caused by *Neofusicoccum* include canker, die-back, fruit rots, blossom blight and eventually tree death (Slippers & Wingfield, 2007). The species diversity of *Neofusicoccum* in association with canker on almond (Gramaje *et al.* 2012), avocado (McDonald & Eskalen 2011, Guarnaccia *et al.* 2016), citrus (Adesemoye *et al.* 2014), *Eucalyptus* (Chen *et al.* 2011b), grapevine (Pitt *et al.* 2013, Linaldeddu *et al.* 2015), mango (Marques *et al.* 2013), oak (Linaldeddu *et al.* 2014), olives (Carlucci *et al.* 2013), pear (Cloete *et al.* 2011), pistachio panicle and shoot blight (Chen *et al.* 2014c) and walnut (Chen *et al.* 2014b) has been well studied.

Neofusicoccum species have broad host ranges with worldwide distribution (Abeywickrama *et al.* 2023). They have been reported from a wide range of climate conditions, although they occur more in areas with a temperate climate (Burgess *et al.* 2019, Batista *et al.* 2022, Jami *et al.* 2022). Some species are not favoured by particular climatic conditions perhaps due to the dominancy of a specific host cultivar or differences in the soil climate (Lazzizera *et al.* 2008). Although *Neofusicoccum* species cause disease on a broad host range (Slippers *et al.* 2017), they are mainly pathogenic on *Anacardiaceae*, *Cupressaceae*, *Ebenaceae*, *Fagaceae*, *Juglandaceae*, *Lauraceae*, *Moraceae*, *Myrtaceae*, *Oleaceae*, *Pinaceae*, *Proteaceae*, *Rosaceae*, *Rutaceae*, *Vitaceae* and *Lamialesi* families (Marin-Felix *et al.* 2017a).

Ecological and economic significance

Neofusicoccum species cause severe economically important diseases on mainly woody plants. For example, *Neofusicoccum* species are among the main causal agents of grapevine trunk disease (GTD). This is one the most destructive diseases on grapes worldwide with a high economic impact. It has been estimated to cause a loss of 1 billion euros in France, 260 million US dollars in California and 8.3 billion US dollars in Australia (Úrbez-Torres & Gubler 2011, Mondello *et al.* 2018a).

Neofusicoccum species are latent pathogens: they have endophytic life stages in their hosts (asymptomatic) but when their hosts are subjected to a stress condition such as hail, drought, frost or insect attack, they cause severe damage (Slippers & Wingfield 2007). The movement of plants from their natural environment to a new environment is another source of stress (Burgess & Wingfield 2017).

Neofusicoccum parvum is the most dominant and aggressive species (Amponsah *et al.* 2011). Various factors such as propagation materials, microclimate conditions and the emergence of alternative hosts influence *N. parvum* to be a dominant species (Linaldeddu *et al.* 2015). Plant material can appear healthy but moving such material around the world is repeatedly introducing *N. parvum* to new environments. One of the many examples is the movement of *N. parvum* with *Eucalyptus* and *Vitis vinifera* across

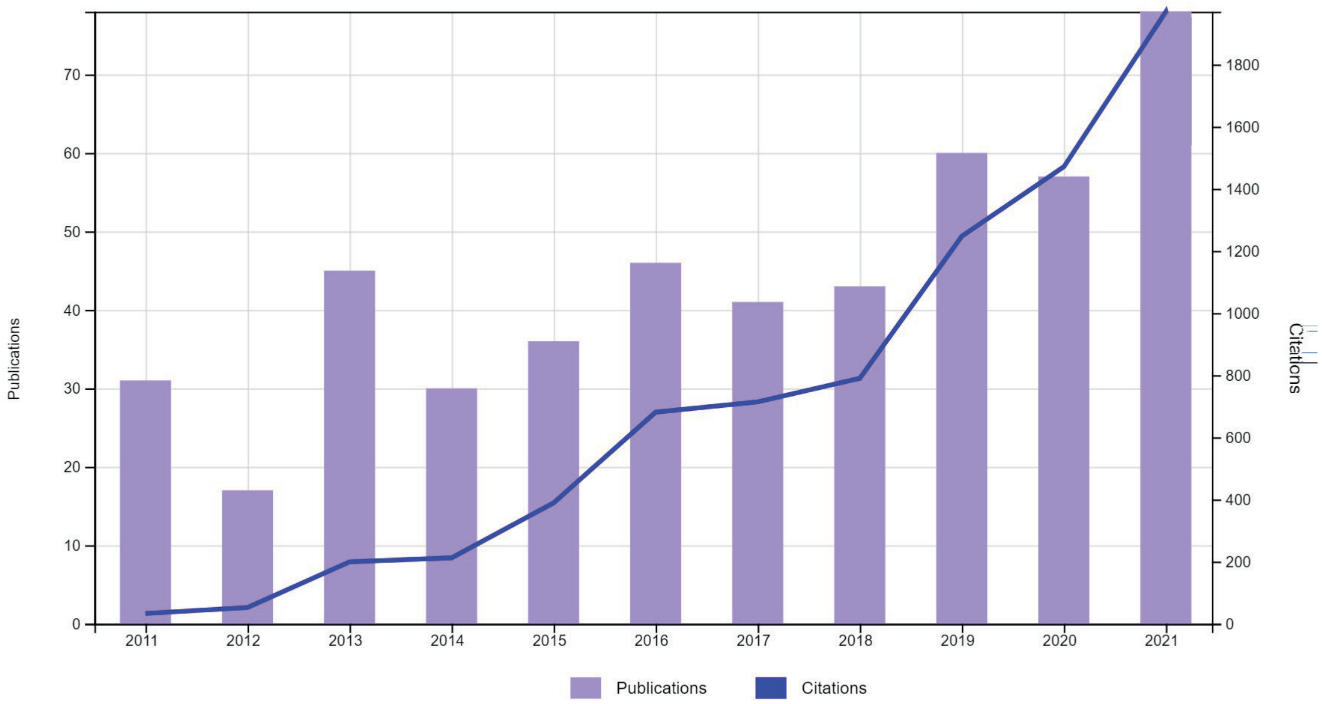

Fig. 128. Trends in research of *Neofusicoccum* in the period 2011–2021.

Table 104. Top 10 cited articles related to *Neofusicoccum* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	The *Botryosphaeriaceae*: genera and species known from culture	515	Phillips *et al.* (2013)
2	One stop shop: backbones trees for important phytopathogenic genera: I (2014)	235	Hyde *et al.* (2014)
3	Genera of phytopathogenic fungi: GOPHY 1	185	Marin-Felix *et al.* (2017a)
4	Grapevine trunk diseases: a review of fifteen years of trials for their control with chemicals and biocontrol agents	131	Mondello *et al.* (2018b)
5	Families, genera, and species of *Botryosphaeriales*	113	Yang *et al.* (2017)
6	Characterization of fungal pathogens associated with grapevine trunk diseases in Arkansas and Missouri	106	Urbez-Torres *et al.* (2012)
7	*Botryosphaeriaceae*: Current status of genera and species	102	Dissanayake *et al.* (2016)
8	Fungal trunk pathogens associated with wood decay of almond trees on Mallorca (Spain)	100	Gramaje *et al.* (2012)
9	Phylogeny, morphology, distribution, and pathogenicity of *Botryosphaeriaceae* and *Diaporthaceae* from English walnut in California	82	Chen *et al.* (2014b)
10	Species of *Botryosphaeriaceae* involved in grapevine dieback in China	75	Yan *et al.* (2013)

the world (Sakalidis *et al.* 2013). *Neofusicoccum parvum* was first identified from kiwifruits in New Zealand (Pennycook & Samuels 1985), but since then it has been reported from 223 hosts in 50 countries (Batista *et al.* 2022).

Research interests

There are 484 publications and 5 591 citations from 2011–2021 in the Web of Science (Fig. 128), with the top 10 most cited articles listed in Table 104. Most of the publications focused on the taxonomy of *Neofusicoccum* species as well as disease management.

Taxonomy and phylogeny

Neofusicoccum was introduced by Crous *et al.* (2006b) for *Botryosphaeria* species with *Fusicoccum* asexual morph, based on LSU sequences. It is difficult to distinguish *Botryosphaeria* and *Neofusicoccum* based on morphology. Although a *Dichomera* synasexual structure in *Neofusicoccum* can differentiate it from *Botryosphaeria*, not all *Neofusicoccum* spp. have this structure (Phillips *et al.* 2013). Paraphyses occur in *Botryosphaeria* but are not present in *Neofusicoccum*. However, it is difficult to distinguish them from sterile hyphae among conidiogenous cells (Phillips *et al.* 2013). Crous *et al.* (2006b) introduced 13 new combinations in *Neofusicoccum*. Later Phillips *et al.* (2013) recognised 22 species based on ITS and *tef*1 sequences. They created a key based on conidial morphology and dimensions, cultural characteristics, host association and geographic distribution that could separate all 22 described *Neofusicoccum* species. Dissanayake *et al.* (2016) introduced 29 species based on ITS, *tef*1 and LSU sequences. Hyde *et al.* (2014) suggested the combination of *tef*1, ITS and *tub* is sufficient to distinguish *Neofusicoccum* species. Marin-Felix *et al.* (2017a) and Yang *et al.* (2017a) used a combination of ITS, *tef*1, *tub* and *rpb2* sequence data to resolve 34 species. Interestingly, Jayawardena *et al.* (2019) resolved 43 species in *Neofusicoccum* by using the same combination. Wanasinghe *et al.* (2018) and Tibpromma *et al.* (2018b) listed 44 species based on Index Fungorum. There are 64 species known for *Neofusicoccum*. Of the 64 species, there are a few species of which the species names need to be updated in the NCBI's GenBank nucleotide database: *Neofusicoccum versiforme* is presented with its basionym (*Dichomera versiformis*) (Crous *et al.* 2019b), while five recently described species, *N. hyperici*, *N. miyakoense*, *N. okinawaense* (Hattori *et al.* 2021a), *N. cruenta* and *N. hamamelidis* (Zhang *et al.* 2021e) are presented as *Neofusicoccum* sp.

Some species of *Neofusicoccum* are closely related such as *N. parvum* and *N. ribis* (Slippers *et al.* 2004c, Crous *et al.* 2006b). Despite broadly using ITS for fungal barcoding, ITS does not distinguish cryptic species. In these cases, the application of genealogical concordance phylogenetic species recognition (GCPSR) was recommended to distinguish all species. Therefore, by 2011, five species, namely *N. umdonicola*, *N. cordaticola*, *N. kwambonambiense*, *N. batangarum* and *N. occulatum* (Pavlic *et al.* 2009, Begoude *et al.* 2010, Sakalidis *et al.* 2011) were identified in the *N. parvum*/*N. ribis* complex. Currently 17 species belong to this species complex (Hattori *et al.* 2021b).

Disease management

Grapevine diseases caused by *Neofusicoccum* species are among the most cited papers. Mondello *et al.* (2018b) reviewed 15 years of practices on disease management of grapevine trunk diseases including applying pruning wound protection, resistant cultivars (Travadon *et al.* 2013), chemical (Pitt *et al.* 2012) and biocontrol (Kotze *et al.* 2011). Resistant cultivars (Guan *et al.* 2016) and pruning wound treatments have been successful against *Neofusicoccum* die-back (Úrbez-Torres & Gubler 2011). The xylem morphology differs in each cultivar. *Neofusicoccum* is a vascular pathogen and studies have shown that there is a correlation between the xylem morphology and disease susceptibly (Pouzoulet *et al.* 2014). It is crucial to understand the mechanism of virulence to detect the most effective disease management. Morales-Cruz *et al.* (2015) studied grapevine trunk pathogens and showed distinct mechanisms of virulence such as specific cell wall oxidative functions and secondary metabolic pathways in *N. parvum.*

Neofusicoccum studies on crops such as grapevine (Cloete *et al.* 2011, Úrbez-Torres & Gubler 2011, White *et al.* 2011, Pitt *et al.* 2012, 2013, Urbez-Torres *et al.* 2012, Yan *et al.* 2013, Linaldeddu *et al.* 2015, Wanasinghe *et al.* 2018), almond (Gramaje *et al.* 2012), olive (Úrbez-Torres *et al.* 2013a, Abdelfattah *et al.* 2015), walnut (Chen *et al.* 2014a, Xu *et al.* 2022b), avocado (McDonald & Eskalen 2011, Guarnaccia *et al.* 2016) and eucalyptus (Chen *et al.* 2011b) are among the most cited studies. On grapevines, *Neofusicoccum* species are among the most virulent pathogens causing cankers

(Urbez-Torres *et al.* 2012, 2013). In 2008, severe almond tree decline was observed in Spain with *N. australe* and *N. parvum* being among the destructive pathogens (Gramaje *et al.* 2012).

Antifungal and phytotoxin activities play important roles in causing disease. For example, Lambert *et al.* (2012) showed the level of some phenolic compounds in grapevine increases in response to the presence of fungi. Although some fungi have shown susceptibility to these compounds, *Neofusicoccum* species including *N. parvum* show less susceptibility (Lambert *et al.* 2012). This may be because *N. parvum* produces 13 metabolites belonging to four chemical families. Abou-Mansour *et al.* (2015) identified two of those toxins from grapevines with die-back symptoms and showed that these metabolites are phytotoxic and allow this fungus to adapt to any environmental conditions and cause disease such as die-back.

Author: F. Jami

98. ***Hericium*** Pers., Neues Mag. Bot. 1: 109. 1794.

Type species: *Hericium coralloides* (Scop.) Pers.

Classification: *Basidiomycota*, *Agaricomycotina*, *Agaricomycetes*, *Russulales*, *Hericiaceae.*

Background

Hericium is an edible and medicinal mushroom belonging to the family *Hericiaceae*, order *Russulales*, of the class *Agaricomycetes*. *Hericium* is a small genus with 34 species listed in Index Fungorum (2022). Species of *Hericium* are commonly associated with traditional food and folk medicines in China (Shao *et al*. 2019), are found in the wild in East Asia and India (Das *et al*. 2011) and are native to North America.

Hericium species are white and fleshy and grow on dead or dying wood. The sporocarp resembles a fragile icicle-like thorn. They do not have caps and consist of amyloid spores and fibres filled with oil mist. Spores are spherical to ellipsoidal, smooth, or covered with warts (Kuo 2014). *Hericium* originated in North America and is widely distributed in East Asia, India, and Europe (Das *et al*. 2011) being typically found in all temperate latitudes of the Northern Hemisphere (Grace & Mudge 2015). Sporulation of *Hericium* is from early summer to late autumn under temperatures between 18 °C and 24 °C. The *Hericium* sporocarp is called lion's mane in English, hóutóugū in Chinese, and yamabushitake in Japanese (Sangtitanu *et al*. 2020). It is also known as monkey's head, pom pom, bear's head, hog's head fungus, white beard, old man's beard, and bearded tooth (Thongbai *et al*. 2015).

Hericium mushrooms have long been investigated for their therapeutic potential. Recently, several bioactive compounds with immune-stimulating properties have been extracted from this mushroom (Sheng *et al*. 2017). There have been many comments about its bioactive secondary compounds (Chen *et al*. 2017b). *Hericium* is a great source of novel therapeutic compounds that have effects on nerve and brain targets. Most of the neurotrophic compounds have effects on the human nerve cells and neurogenerative diseases such as Alzheimer's disease and Parkinson's disease (Zhang *et al*. 2016b, Ratto *et al*. 2019, Chong *et al*. 2020, Ryu *et al*. 2021).

Ecological and economic significance

In general, *Hericium* species occur in the highlands, sub-mountains, and mountains, but it is also found in many types of lowland forests (Kujawska *et al*. 2021). The genus *Hericium* includes white rot fungi that grow on the trunks, branches, and stumps of deciduous and coniferous trees (Larsson & Larsson 2003). *Hericium* species on old trees and dead wood are usually reported as signs of forests that are expanding naturally.

Hericium is an important source of nutrients and is used medicinally, thus making this mushroom significant and economically valuable (Rahi & Malik 2016). *Hericium* mushrooms can greatly enhance the effects of medications to relieve symptoms (Li *et al*. 2018a). Also, the cultivation of these mushrooms generates additional revenue for farmers (Park *et al*. 2004).

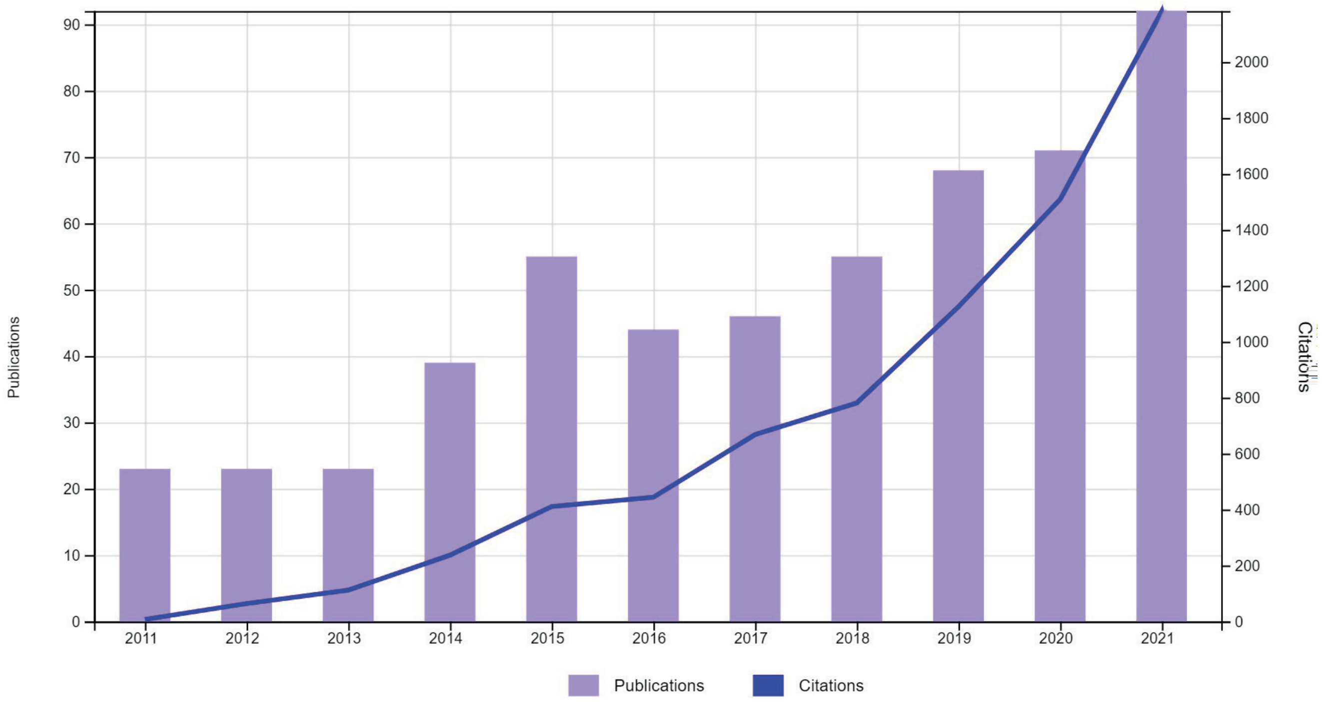

Fig. 129. Trends in research of *Hericium* in the period 2011–2021.

Table 105. Top 10 cited articles related to *Hericium* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Chemistry, nutrition, and health-promoting properties of *Hericium erinaceus* (Lion's Mane) mushroom fruiting bodies and mycelia and their bioactive compounds	115	Friedman (2015)
2	Assessment of heavy metals in some wild edible mushrooms collected from Yunnan Province, China	105	Zhu *et al*. (2011a)
3	Optimization of enzyme-assisted extraction and characterization of polysaccharides from *Hericium erinaceus*	99	Zhu *et al*. (2014)
4	Structures, biological activities, and industrial applications of the polysaccharides from *Hericium erinaceus* (Lion's Mane) mushroom: A review	98	He *et al*. (2017b)
5	Chemical composition and nutritional and medicinal value of fruit bodies and submerged cultured mycelia of culinary-medicinal higher basidiomycetes mushrooms	97	Cohen *et al*. (2014)
6	Medicinal mushrooms: Valuable biological resources of high exploitation potential	87	Gargano *et al*. (2017)
7	Evaluation of selected culinary-medicinal mushrooms for antioxidant and ACE inhibitory activities	84	Abdullah *et al*. (2012)
8	Antioxidant and hepatoprotective potential of endo-polysaccharides from *Hericium erinaceus* grown on tofu whey	83	Zhang *et al*. (2012e)
9	Polysaccharide of *Hericium erinaceus* attenuates colitis in C57BL/6 mice via regulation of oxidative stress, inflammation-related signaling pathways and modulating the composition of the gut microbiota	79	Ren *et al*. (2018a)
10	Composition and mechanism of antitumor effects of *Hericium erinaceus* mushroom extracts in tumor-bearing mice	74	Kim *et al*. (2011)

Research interests

There are 539 publications and 5 458 citations from 2011–2021 in the Web of Science (Fig. 129), with the top 10 most cited articles listed in Table 105. Most publications focused on chemical composition, bioactive compounds, medicinal properties, mushroom cultivation, as well as taxonomy and phylogeny.

Chemical composition research

Most fresh basidiomes and mycelium of *Hericium* species are rich in protein and dietary fibre, while some are also rich in polysaccharides and crude fibre (Friedman 2015). Rodrigues *et al*. (2015) reported that *He. erinaceus* is a good source of protein, sugar, and fat contents. It also contains copper, iron, and zinc, suggesting mushrooms as a potential source of multiple macro- and micronutrients.

Bioactive compounds research

Bioactive compounds have been found in both mushrooms and mycelium, with mycelium reported to have more bioactive compounds than the sporocarp (Sullivan *et al*. 2006, Sokoł *et al*. 2016, Chen *et al*. 2017b, Wang *et al*. 2019). *Hericium* mushrooms are rich sources of polysaccharides and polyketides (Thongbai *et al*. 2015), as well as phenolic acid and generally bioactive secondary compounds from *Hericium* incorporate alkaloids and pyrone such as erinapyron A-C, hericene A-D, herierin III (Corana *et al*. 2019); terpenoid such as cyatha-3,12-diene, erinacines A-E; sterol compounds; volatile aromatic compounds such as erinaceolactone A, C; and nonribosomal peptides such as fumitremorgin C and methylthiogliotoxin (Chen *et al*. 2017b). Medicinal properties/therapeutic effects include antioxidant (Gupta *et al*. 2018, Jiang *et al*. 2019), anticancer (Lee *et al*. 2014, AM 2017), antidiabetic (Wu & Xu 2015, Gupta *et al*. 2018), antihyperglycemic (Liang *et al*. 2013, Yao *et al*. 2021), hypolipidemic properties (Liang *et al*. 2013), anti-inflammatory (Shao *et al*. 2019, Hetland *et al*. 2020), antimicrobial (Shen *et al*. 2017, Vamanu & Voica 2017), antiviral (Liu *et al*. 2019d), antifungal (Gargano *et al*. 2017, Song *et al*. 2020), and hepatoprotective (Zhang *et al*. 2012, Wang *et al*. 2019).

Antioxidant activities of Hericium

A mushroom-derived preparation from *Hericium* protects against oxidative damage to cellular DNA (Chang & Miles 2004). Kim *et al*. (2013a) found that *He. erinaceus* water extracts possess significant antioxidant activities. Park *et al*. (2018) reported that the wild type of *Hericium* was useful for breeding genetic sources or processed food materials with high antioxidant activity. Jiang *et al*. (2019) reported that the effects of *Hericium* extraction on antioxidant activities are varied, possibly because the different components obtained under different extraction states have various antioxidant mechanisms.

Hepatoprotective activities of Hericium

Endo-polysaccharides from *He. erinaceus* fractions grown on tofu whey protected mice from liver damage *in vivo* caused by carbon tetrachloride. The strong hepatoprotective effect and potent hepatoprotective effect *in vivo* may be due to its potent antioxidant capacity (Zhang *et al*. 2012). Cui *et al.* (2016a) reported that extracellular polysaccharides and intracellular polysaccharides of *He. erinaceus* were protective against liver injury.

Anticancer activities of Hericium

Cancer is the world's leading cause of death and *Hericium* has many medicinal properties such as anticancer activity. Younis (2017) evaluated different polar and non-polar extracts of *He. erinaceus* for anticancer activity against different human cancer cells and suggested that *He. erinaceus* can be a good source of natural anticancer compounds. *Hericium* extracts (HTJ5 and HTJ5A) are active against liver cancer, colon cancer, and gastric cancer *in vitro* and tumour xenografts bearing in mice *in vivo*. The compounds have the potential to be developed as anticancer agents for the treatment of gastrointestinal cancer used alone or in combination with chemotherapeutic drugs that are used clinically (Li *et al*. 2014c).

Antidiabetic, antihyperglycemic, and hypolipidemic properties

Liang *et al*. (2013) reported that the water extract of *He. erinaceus* (AEHE) in streptozotocin (STZ) resulted in a decrease in blood glucose and an increase in blood insulin levels in diabetic rats; AEHE treatment reduces lipid disorders. AEHE dispensation increased the activities of catalase, glutathione peroxidase and glutathione levels, and decreased malondialdehyde level in the liver tissue. Moreover, *He. erinaceus* has antidiabetic effects, that may be used as therapeutics against diabetes (Wu & Xu 2015, Gupta *et al*. 2018).

Anti-inflammatory activities of Hericium

According to Hetland *et al*. (2020), the anti-inflammatory mechanisms cause a reduction of cytokines that cause inflammation, oxidative stress, alteration of the gut microorganisms, and the anti-allergic mechanism to rebalance the helper T cells. Anti-inflammatory mechanisms induced by *Hericium* were reduced pro-inflammatory cytokines, and increased nerve growth to protect against neuron death in cerebrovascular disease (Lee *et al*. 2014). Diling *et al.* (2017) reported the growth of beneficial gut microorganisms that prevent mucosal inflammation caused by inflammatory bowel disease and improve host immunity (Ren *et al.* 2018a).

Cultivation of Hericium species

Hericium mushrooms are widely cultivated for medicinal properties, also for culinary reasons and are common in Japan and North America, but are rarely found in Europe (Boddy *et al*. 2011, Atila 2019). Han *et al*. (2005) reported that the artificial cultivation of *He. americanum* and *He. coralloides* is possible. *Hericium cirrhatum*, *He. coralloide*, and *He. erinaceus* are rarely recorded in Europe, but *He. erinaceus* is easily cultivated for mushroom products (Boddy *et al.* 2011). Most sporocarps of *Hericium* mushrooms are collected in the wild (Song *et al*. 2020). In general, the mycelium of *Hericium* grows best at 25 °C and produces sporocarps between 16 °C and 28 °C (Han *et al*. 2005, Bunroj *et al*. 2017). Indoor production of *Hericium* mushrooms is energy and resource-intensive, involving processed substrates such as sawdust and climate-controlled growing facilities. However, outdoor (forest farming) cultivation on totem logs has been reported (Grace & Mudge 2015).

Taxonomy and phylogeny

The morphology of *Hericium* species has been thoroughly investigated (Venturella *et al.* 2016, Ouali *et al.* 2020). Hallenberg *et al.* (2013) reported the evolutionary analysis of *Hericium* based on ITS sequences. Most phylogenetic studies of *Hericium* species use SSU, LSU, and ITS sequence data. Due to high interspecific sequence gene divergence within *Hericium*, additional support from morphological and ecological characters is required (Das *et al.* 2013, Jumbam *et al.* 2019, Singh & Das 2019, Khan *et al.* 2021).

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99. ***Phakopsora*** Dietel, Ber. Deutsch. Bot. Ges. 13: 333. 1895.

Type species: *Phakopsora punctiformis* (Barclay & Dietel) Dietel

Classification: *Basidiomycota*, *Pucciniomycotina*, *Pucciniomycetes*, *Pucciniales*, *Phakopsoraceae.*

Background

Phakopsora is a large genus of fungi that causes rust diseases in plants, especially in humid tropical and subtropical regions (Berndt *et al*. 2007). Over 150 epithets are listed in Index Fungorum and 112 species are recognised (Bánki *et al.* 2023). Their host plants encompass a wide range of phylogenetically distantly related families (Ono *et al*. 1992), and at least 31 plant families are hosts of *Phakopsora* species (Farr & Rossman 2022). All rust fungi share an obligate biotrophic lifestyle which means they can only feed, grow and reproduce in association with living host plants (Primiano *et al.* 2017). Rust fungi attack mostly leaves and stems and rust infections usually appear as numerous rusty, orange, yellow, or even white-coloured spots that rupture the epidermis (Agrios 2005). The pathogen reduces carbon sequestration by reducing the photosynthetic potential of its hosts and by diverting and metabolising photosynthetic products for their benefit (Helfer 2014).

Rust fungi have complex and variable life cycles that may include up to five spore stages produced in different types of fruiting structures (spermogonia, aecia, uredinia, telia and basidia) and in some cases, two unrelated hosts may be required for the production of different spore stages and completion of their life cycle (Aime *et al.* 2017). However, many species have reduced life cycles that lack one or more of these spore stages. This happens in most *Phakopsora* species where the spermogonial and aecial stages are not known (Buriticá 1999, Berndt *et al*. 2007, Ono 2015). The life cycle of *Phakopsora pachyrhizi* appears to be microcyclic, producing only uredinia and telia and is completed on one host, soybean or other legumes. Uredinia produce urediniospores that are spread by wind and can cause infection, while the telia produce teliospores, which, for *Phak. pachyrhizi* has never been shown to germinate in the field (Agrios 2005).

Phakopsora pachyrhizi causes one of the most destructive soybean diseases with severe losses in yield. Unlike most rust fungi that have a restricted host range, range, *Phak. pachyrhizi* has a wide host range, mainly in the family *Fabaceae* (Ono *et al.* 1992, Farr & Rossman 2022). In soybean, the infection process starts when an asexual urediniospore germinates on the host surface to form a single germ tube that results in an appressorium and infects by direct, cuticular penetration. Haustoria are formed in mesophyll and epidermal cells. Then, intense colonisation of the mesophyll tissue occurs, and the intercellular spaces of the leaves become filled with fungal mycelium. A domed-shaped eruption occurs in the host epidermis to form uredinia producing urediniospores that are spread by wind (Koch *et al.* 1983). Temperatures between 18 to 26.5 ºC and a minimum of 6–7 hr of continuous leaf wetness are favourable conditions for the development of rust lesions in soybean (Melching *et al.* 1989).

Phakopsora was introduced by Dietel (1895) with telia subepidermal in origin, usually remaining covered with host epidermis but sometimes becoming erumpent, crustose, hemispherical or lenticular, often dark chestnut-brown to blackish brown. Teliospores are one-celled, and arranged irregularly or in vertical rows, in several compact spore strata. The teliospores are equally thin to moderately thick-walled, slightly to conspicuously thickened apically in uppermost cells, almost colourless to cinnamon-brown or chestnut-brown, usually darker above and paler below. Evaluation of their taxonomic characters based on all spore stages has not been possible for many *Phakopsora* species due to a lack of knowledge concerning their full life cycles. The taxonomic acceptance or distinctness of most species named under *Phakopsora* has been done by a first approximation (Ono *et al.* 1992).

Familial classification of rust fungi is now largely done using DNA sequences in phylogenetic studies. The LSU and SSU of the nuclear ribosomal RNA sequences are most often used in phylogenetic studies at the infrageneric and infrafamilial levels in rust fungi. Single-copy nuclear genes are used less for phylogenetic studies of rust fungi than in *Ascomycota* because of the limiting amounts of DNA and the high frequency of amplification of other fungi with nonspecific primers. However, *tef1*, *tub*, *rpb2* and cytochrome *c* oxidase subunit 3 (*CO3*) have been successfully applied at the species level for discerning relationships within specific genera of rust fungi (Aime *et al.* 2017).

Ecological and economic significance

Phakopsora species cause rust diseases on important crops and two are detailed below.

Rust of soybean (*Glycine max*) caused by either *Phakopsora pachyrhizi* and/or *Phak. meibomiae* is the most severe soybean disease and is one of the most economically important plant diseases in South America (Amorim *et al.* 2016). Rust disease caused by *Phak. pachyrhizi* is known as Asian soybean rust and is more severe than American rust caused by *Phak. meibomiae*. *Phakopsora pachyrhizi* is among the main fungal plant pathogens (Sconyers *et al.* 2006, Dean *et al*. 2012) and can infect all aerial parts (stems, leaves, pods and petioles) of soybean (Chander *et al. 2019)*. The most common symptoms are small tan to dark brown or reddish brown lesions on leaves, leaf chlorosis, necrosis and reduction of photosynthetic area. High infection levels lead to premature defoliation and early maturity, resulting in high yield losses (Hartman *et al.* 2015). The symptoms can vary according to the interaction between the host genotype and the fungal isolate. Asian soybean rust causes severe losses in humid tropical and subtropical regions. Yield losses ranging from 80 to 90 % are reported in the absence of control measures (Hartman *et al.* 2015, Amorim et *al.* 2016). In Brazil, *Phak. pachyrhizi* causes over 2.80 billion US dollars in losses per year, since the first outbreak of Asian soybean rust in 2001, the losses are estimated at 40 billion US dollars based on the costs of control measures and reductions in crop yield (Consórcio Antiferrugem 2022). A critical factor for the management of soybean rust is the many hosts that *Phak. pachyrhizi* and *Phak. meibomiae* have in addition to soybean (Agrios 2005, Amorim *et al.* 2016). Control measures for soybean rust include the elimination of soybean plants in the off-season, avoiding planting of soybeans in climatic conditions favourable to the disease, the use of resistant or early cycle soybean varieties, and the use of appropriate fungicides preferably multisite fungicides, due to the risk of *Phak. pachyrhizi* isolates developing multiple resistance to the modes of action utilised (Amorim *et al.* 2016, Müller *et al.* 2021).

Asian grapevine leaf rust (on *Vitis* spp.) caused by *Phakopsora euvitis* is a major foliar disease of grapevine in Asia and is considered the main threat to viticulture in North America (Chatasiri & Ono 2008). The rust causes tiny yellow spots on the adaxial side of mature leaves, a spot corresponds to a pustule on the abaxial side of the leaf tissue, as the disease progresses, the pustules coalesce, and the spots become necrotic lesions that vary in shape and size (Primiano *et al.* 2017). The high severity of the disease leads to premature defoliation, thus reducing the storage of assimilated carbon in the rootstock and affecting the yield in subsequent years (Nogueira Júnior *et al*, 2017). Disease control is based on the use of fungicides in a preventive way after fruit harvest (Amorim et *al.* 2016, Primiano *et al.* 2017).

Other *Phakopsora* species cause rust disease on economically important plants. For example, *Phak. cherimoliae* causes rust on fruit trees of *Annona* species (Farr & Rossman 2022); *Phak. gossypi* causes tropical rust of leaves on cotton (Amorim *et al.* 2016), *Phak. crotonis* causes rust on species of ornamental plants of *Croton* (Farr & Rossman 2022).

Research interests

There are 438 publications and 5 143 citations from 2011–2021 in the Web of Science (Fig. 130), with the top 10 most cited

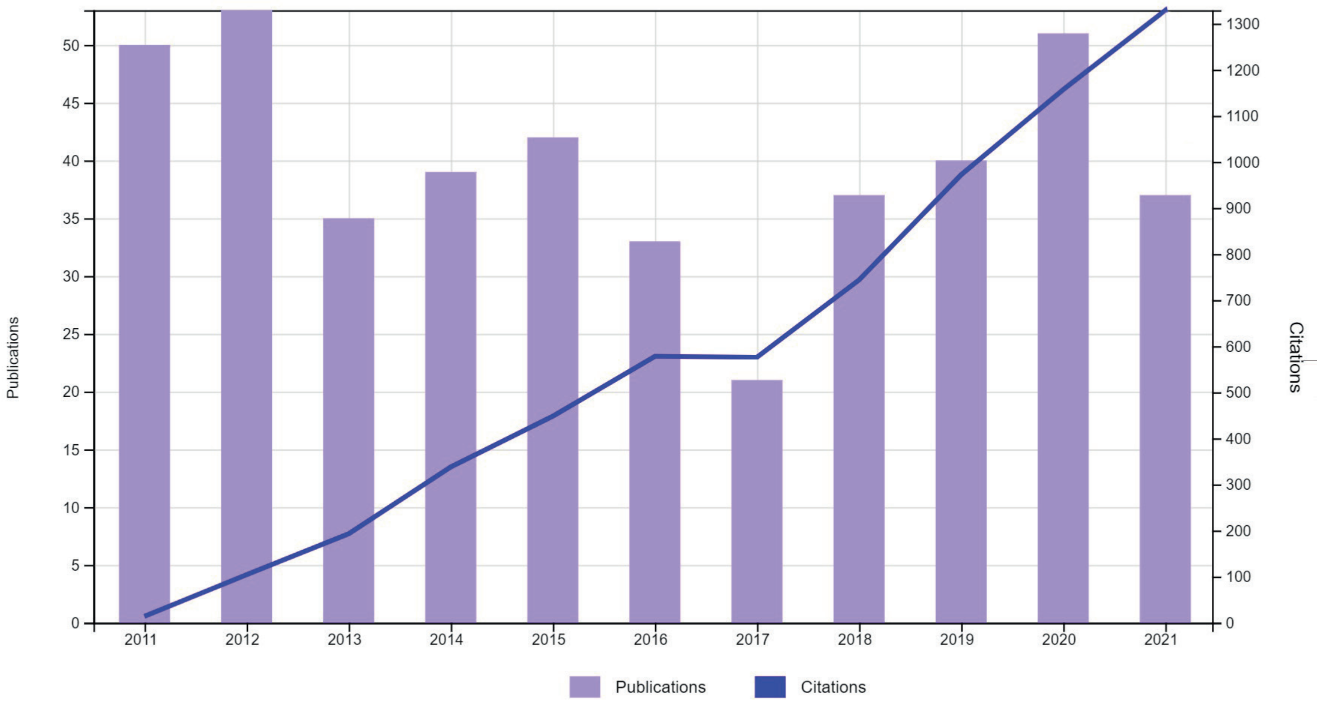

Fig. 130. Trends in research of *Phakopsora* between 2011–2021.

Table 106. Top 10 cited articles related to *Phakopsora* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Crops that feed the World 2. Soybean-worldwide production, use, and constraints caused by pathogens and pests	238	Hartman *et al.* (2011)
2	Identification of novel soybean microRNAs involved in abiotic and biotic stresses	222	Kulcheski *et al.* (2011)
3	Asian soybean rust in Brazil: past, present, and future	121	Godoy *et al.* (2016)
4	Identification of a new soybean rust resistance gene in PI 567102B	77	Li *et al.* (2012b)
5	Loss of abaxial leaf epicuticular wax in *Medicago truncatula* irg1/palm1 mutants results in reduced spore differentiation of anthracnose and nonhost rust pathogens	73	Uppalapati *et al.* (2012)
6	Plant pathogenic fungi	70	Doehlemann *et al.* (2017)
7	The ins and outs of rust haustoria	62	Garnica *et al.* (2014)
8	A pigeonpea gene confers resistance to Asian soybean rust in soybean	60	Kawashima *et al.* (2016)
9	Sensitivity of *Phakopsora pachyrhizi* towards quinone-outside-inhibitors and demethylation-inhibitors, and corresponding resistance mechanisms	57	Schmitz *et al.* (2014)
10	Dissecting the economic impact of soybean diseases in the United States over two decades	43	Bandara *et al.* (2020)

articles listed in Table 106. The publications focused mainly on the economic and social impact, control and epidemiology of Asian soybean rust.

Economic and social impact

Soybean is a major oilseed crop produced and consumed worldwide and one of the most important agricultural commodities for international trade. Brazil and the USA are the main soybean producers and together they export over 50 billion US dollars per year (FAO 2022, USDA 2022). Asian soybean rust causes significant losses in soybean yield. In addition to economic losses, *Phakopsora* infection in soybeans may have implications for food security because of world dependence on the soybean crop, directly and indirectly for food products (Hartman *et al.* 2011). The emergence of more aggressive *Phakopsora* populations or fungicide resistance may favour the emergence of epidemics negatively impacting soybean production and increase the pesticide burden on disease control.

Disease management

Strategies for the management of rust caused by *Phakopsora* are mostly aimed at genetic resistance and chemical control. Genetic resistance has mainly looked for sources/genes of resistance and mechanisms associated with resistance against *Phak. pachyrhizi.* In soybean, the eight major resistance loci that confer resistance to Asian soybean rust are *Rpp1*, *Rpp2*, *Rpp3*, *Rpp4*, *Rpp5*, *Rpp6*, *Rpp1b* and *Rpp* (*Hyuuga*) (Hyten *et al.* 2007, Monteros *et al.* 2007, Garcia *et al*. 2008, Silva *et al.* 2008, Meyer *et al.* 2009, Hyten *et al.* 2009, Li *et al.* 2012b, Kim *et al.* 2012, Yu *et al.* 2015b). Legume species related to soybean are possible sources of resistance to Asian soybean rust, the loci *CcRpp1* in *Cajanus cajan* confer full resistance to *Phak. pachyrhizi* in soybean (Kawashima *et al.* 2016). In grape breeding programmes genotypes of *Vitis* with high resistance against *Phak. euvitis* has been identified; however, there is still little information about the nature of genetic resistance (Patil *et al*. 1999, Hennessy *et al*. 2007, Angelotti *et al*. 2008). Site-specific demethylation inhibitors (DMI), quinone outside inhibitors (QoI) and succinate dehydrogenase inhibitors (SDHIs) are the most frequent group of fungicides utilised to control Asian soybean rust (Amorim *et al.* 2016, Müller *et al.* 2021). The efficacy of DMI, QoI and SDHIs has decreased over time (Godoy *et al.* 2014, 2017). Studies report point DNA mutations in *Phak. pachyrhizi* isolates that result in a reduction of sensitivity to DMI (Schmitz *et al.* 2014), QoI (Klosowski *et al.* 2016), SDHIs (Simões *et al.* 2018). Knowledge about pathogen biology, genetic resistance, efficacy and sensitivity to fungicides are important and will support the development of efficient strategies for the management of diseases caused by *Phakopsora* species.

Epidemiology

Knowledge of favourable and predisposing conditions for the development of a disease is essential to adopt effective management strategies. Rust diseases caused by *Phakopsora* species are more common in humid and hot regions (Berndt *et al*. 2007) and temperature is one of the key factors affecting rust spore viability. *Phakopsora pachyrhizi* appears to maintain the ability to cause infection even following extended winter conditions (Park *et al*. 2008). However, Patil *et al*. (1997) reported that urediniospores of *Phak. pachyrhizi* lost their viability when they were kept at 4 to 5 °C or below for 5 d. The introduction of *Phakopsora* species into new areas usually happens through spores spread by the wind (Agrios 2005). Unlike many other rust fungi, *Phak. pachyrhizi* has a wide host range (Farr & Rossman 2022) that can be an inoculum source for infections in soybeans. Young *et al*. (2011b) studied *Phak. pachyrhizi* rust epidemics in Florida, and observed that precipitation was the principal factor affecting disease progress, where disease increased rapidly after rain events and was suppressed during dry periods. Studies on the biology and life cycle of *Phakopsora* species have helped to understand disease progression in the field and the development of management strategies.

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100. ***Leptosphaeria*** Ces. & De Not., Comment. Soc. Crittog. Ital. 1(fasc. 4): 234. 1863.

Type species: *Leptosphaeria doliolum* (Pers.) Ces. & De Not.

Classification: *Ascomycota*, *Pezizomycotina*, *Dothideomycetes*, *Pleosporales*, *Leptosphaeriaceae*.

Background

Leptosphaeria was introduced by Cesati & De Notaris (1863) with 26 species and *Lep. doliolum* was chosen as the lectotype for the genus (Shearer *et al.* 1990). Species of *Leptosphaeria* are characterised by papillate, immersed or erumpent, perithecial ascomata, with somewhat thick peridia, bitunicate cylindrical asci and hyaline to brown, transversely septate ascospores (Hyde *et al.* 2013). The asexual morphs of *Leptosphaeria* are coniothyrium- and phoma-like, and comprise depressed, globose conidiomata, with a flattened base and cylindrical necks (Zhang *et al.* 2012, Alves *et al.* 2013, De Gruyter *et al.* 2013, Hyde *et al.* 2013). The conidiomata wall comprises scleroplectenchymatous cells and conidia are ellipsoidal to subcylindrical (Hyde *et al.* 2011). Crane & Shearer (1991) described *Leptosphaeria* as comprising hyaline to dark brown, ellipsoid or fusoid ascospores with one to many septa. *Leptosphaeria doliolum* previously known as *Sphaeria doliolum* was lectotypified by Persoon (1800), based on the collection of 12 specimens of *S. doliolum*. Höhnel (1909) separated *Leptosphaeria* based on centrum features into three genera, namely *Leptosphaeria*, *Nodulosphaeria* and *Scleropleella* (Zhang *et al.* 2012c). Müller (1950) further subdivided *Leptosphaeria* into four sections and this treatment was revised by Munk (1957) who termed these sections as section I (*Eu-Leptosphaeria*), section II (*ParaLeptosphaeria*), section III (*Scleropleella*) and section IV (*Nodulosphaeria*). *Leptosphaeria* was previously placed in *Phaeosphaeriaceae* by Eriksson & Hawksworth (1986) and later accommodated in *Leptosphaeriaceae* (Barr 1987, Eriksson & Hawksworth 1991). Recent studies have reported that the taxonomy of *Leptosphaeria* is complex with various subspecies and varieties (Câmara *et al.* 2002, Eriksson & Hawksworth 2003, Wunsch & Bergstrom 2011, De Gruyter *et al.* 2013). *Leptosphaeria* resembles other genera such as *Amarenomyces*, *Bricookea*, *Diapleella*, *Entodesmium*, *Melanomma*, *Nodulosphaeria*, *Paraphaeosphaeria*, *Passeriniella*, *Phaeosphaeria* and *Trematosphaeria* but differs in forming ascomata on dicotyledonous hosts, in having cylindrical asci with short pedicels and smooth-walled, ellipsoid or fusoid, septate ascospores. *Leptosphaeria* has a widespread distribution and is particularly predominant in temperate regions. *Leptosphaeria* species are either saprobic or grow as necrotrophs on the stems or leaves of herbaceous or woody plants in terrestrial habitats (Hyde *et al.* 2013). The dark brown, 3-septate ascospores were previously considered as a primitive character, as compared to more newly evolved species characterised by paler, longer and narrower ascospores with more than three septa (Wehmeyer 1946). De Gruyter *et al.* (2013) reported that the subspecies of *Lep. doliolum* are closely related based on LSU and ITS phylogenetic evidence and postulated that *Lep. doliolum* represents a species complex. De Gruyter *et al.* (2013) provided a detailed multi-gene phylogenetic tree based on ITS, *act*, *tub* and *chs* genes, and showed that the subspecies of *Lep. doliolum* represent two subclades in the *Lep. doliolum* species complex. In recent studies based on multi-gene analyses, *Leptosphaeria* formed a paraphyletic clade sister to *Neophaeosphaeria* with moderate bootstrap support in *Leptosphaeriaceae* (Schoch *et al.* 2009, Zhang *et al.* 2012c, Hyde *et al.* 2013). Ariyawansa *et al.* (2015b) provided a backbone tree for *Leptosphaeria* and allied genera based on 18S nrDNA, 28S nrDNA, ITS, *rpb2*, *tef1* and *act* multigene phylogenetic analyses. Currently, *Leptosphaeria* comprises 605 species (Hongsanan *et al.* 2020).

Ecological and economic significance

Leptosphaeria species cause several economically important plant diseases and five are detailed below.

***Leptosphaeria* leaf spot of maize** caused by *Leptosphaeria maydis* has been commonly reported in the United States (Illinois) (Stout 1930, Farr *et al.* 1989). This disease is also of economic significance in Nepal (De Leon 1984) but there are no reports of it being seed-borne. Symptoms include tiny lesions that become big and concentric, covering major areas of the leaves. It is most visible on the lower part of leaves during the blossoming period (Stout 1930, De Leon 1978). *Leptosphaeria maydis* is often associated with *Septoria zeae* which suggests that these two species may be different morphs of the same fungus (Stout 1930). *Leptosphaeria maydis* is also in the quarantined pest list of Sudan (IPPC 2016). Based on recent statistics, the total maize production in the United States and Canada (Ontario), from 2016 to 2019 was 1.5 billion metric tons, which is equal to 210.7 billion US dollars (USDA-NASS 2020). The mean economic loss caused by maize disease in the United States and Canada (Ontario) from 2016 to 2019 was 55.90 US dollars per acre (138.13 US dollars per hectare) (Mueller *et al*. 2020). Grain damage caused by maize diseases results in declined availability of food, feed, and fuel. The most economical way to control maize disease is the use of resistant or tolerant cultivars but in practice, resistance might not usually occur in a single cultivar for all diseases. Hence, chemical control is the most feasible method to ensure productivity (Chaube & Singh 1991). There are many other *Leptosphaeria* species which cause leaf spots on maize but in the past years, there have been several intergeneric transfers of *Leptosphaeria* species by dividing them into new groups such as *Paraphaeosphaeria* or existing genera for instance *Entodesmium* and *Phaeosphaeria* (Zhao *et al.* 2021b). Also, one of the most challenging aspects is the huge diversity of asexual morphs attributed to this genus, therefore a thorough revision is needed to ensure which species belong to *Leptosphaeria*.

Diseases of hemp (*Cannabis sativa*) caused by *Leptosphaeria cannabina* were first found in irregularly-shaped leaf spots of wilted *Cannabis sativa* near Alba, Italy by Ferraria & Massa (1912). Leaf spots were broadly whitish in the center with an ochreous margin measuring about 3–5 mm diam. The fungus also infects Russian hemp (Gitman & Boytchenko 1934, Dobrozrakova *et al.* 1956). Ferraris & Massa (1912) suggested *Lep. cannabina* as a possible sexual morph of *Septoria cannabis* but this was not confirmed in culture. *Cannabis sativa* is a high value crop, and is used in construction (hemp fibre), food and feed (hemp seeds), cosmetics (oils, creams, shampoos, *etc*.), energy production (biofuels), paper production (hemp fibre) and textile industry (hemp fibre) (Visković *et al*. 2023). As stated by industry reports in the United States, the hemp market is rising at a yearly rate of 34 %, from 4.6 billion US dollars in 2019 to 26.6 billion US dollars in 2025 (Zhu *et al.* 2020b). The average world import of hemp products is about 42 million US dollars in 2020 (UNCTAD 2022). During hemp production, diseases may cause farmers to lose their profits up to 11 % of hemp production value (Zhu *et al.* 2020a). According to Brightfield Group (2021) estimates, 115 000 hectares (ha) of industrial hemp were planted in the United States in 2020, with 300 000 ha projected to be planted in 2021 and 930 000 ha by 2023. Basic approaches for hemp disease management comprise the elimination of the pathogen, control of the environment and host resistance (Punja 2021). Currently, using disease-resistant cultivars is one of the most efficient methods to manage diseases of hemp (Hansen *et al.* 2020). Presently no conventional fungicides are available for hemp disease.

Nettle rash is caused by *Leptosphaeria acuta*, a plant pathogen prevalent on the stems of common nettle (*Urtica dioica*).

Leptosphaeria acuta is characterised by black, smooth ascomata with shiny cones which are at first immersed in its host and later break through to the surface, usually in large numbers (Nature Spot, Koukol *et al.* 2020). The ascomata mature in late winter and spring (Nature Spot 2020). They have protruding central ostioles through which ascospores are released and form part of the group of unresolved species in *Leptosphaeriaceae* with six and more transverse septa and fusoid ascospores measuring up to 50 µm long, lacking an appendage and gelatinous sheath (Müller 1950). *Urtica dioica* (*Urticaceae*) is a herbaceous flowering plant native to Asia, Europe, North Africa and Northern America (Viotti *et al.* 2022). Leaves of *U. dioica* are commonly used as a form of medicinal tea or as diuretic and antidiabetic treatments in Libya (Zovko Končić & Bljajić 2019). In Europe, nettles have been widely cultivated during the 19th century as a fibre plant (Vogl & Hartl 2003). As stated by Bredemann (1959), a nettle crop can produce efficient yields for 4 years and, based on recent data, fibre yield was 1 696 kg/ha in Tuscany (Italy) (Bacci *et al*. 2009). There are no statistics regarding yield loss due to nettle rash.

Apart from being pathogens of economically important plants, some *Leptosphaeria* species have biological control properties such as *Lep. faullii* on certain *Hypodermataceae* (Darker 1964) or produce antifungal polyketides such as leptosphaerins that may have biocontrol properties (Lin *et al.* 2017).

Research interests

There are 257 publications and 5 133 citations from 2011–2021 in the Web of Science (Fig. 131), with the top 10 most cited articles listed in Table 107. Most of the publications focused on disease management (fungicide resistance, disease resistance), and research on pathogenic *Leptosphaeria* species as well as taxonomy.

Disease management

Disease management for *Leptosphaeria* includes mostly chemical, cultivation and cultural control. These are explained below.

Chemical control **involves** a fungicide program which is important in reducing the effect of *Leptosphaeria* in cropping systems (Richard *et al*. 2002). Currently, there are more than 200 fungicides registered for use in food processing (Yoon *et al.* 2013). The frequent use of fungicides to control *Leptosphaeria* may cause resistance therefore it should be used in a timely manner (Walters 2012). The discovery and development of new fungicides is predicted to take about 10 years and might cost nearly 260 million US dollars, hence it is important to reduce fungicide resistance (Van de Wouw *et al.* 2017). Fungicides work as protectants so it needs to be applied at the first sign of disease (McGrath 2004). Studies carried out by OSU and WSU have revealed Coronet and Mertect as very effective treatments for seed-borne *Leptosphaeria* and other fungi (Ocamb 2023).

Cultivation techniques are also important in controlling *Leptosphaeria* diseases. Residues from previous crops in the surroundings of where new plants are being established must be buried to reduce the risk of spores spreading to the current cropping area (Fu *et al*. 2021).

Cultural control for *Leptosphaeria* disease involves modifying the growing environment to decrease the prevalence of the fungus (Walters 2009). For example, plant seeds must be certified free of *Leptosphaeria*, susceptible weeds must be managed and plants rotated for at least three years, infested seed should be treated in water at 50 °C and germination rate should be evaluated to check their viability, residues must be buried after harvest or plant debris eliminated to reduce the population of *Leptosphaeria* spp. and seedbeds and seed fields must be checked regularly for presence of the disease (Ocamb 2003). Seed treatment must also be

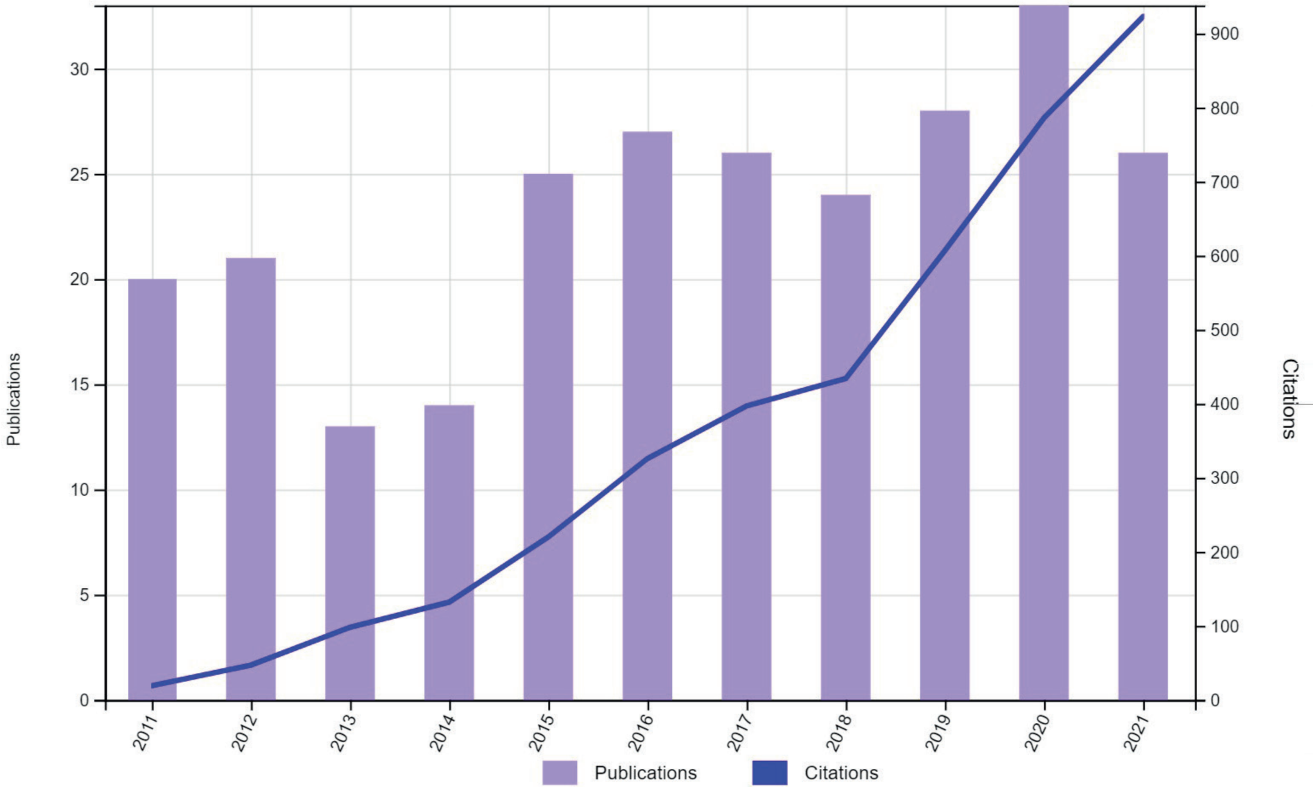

Fig. 131. Trends in research of *Leptosphaeria* in the period 2011–2021.

Table 107. Top 10 cited articles related to *Leptosphaeria* published in the period 2011–2021.

Rank	Article title	No. of citations	References
1	Redisposition of phoma-like anamorphs in *Pleosporales*	332	De Gruyter *et al.* (2013)
2	Revision of the *Massarineae* (*Pleosporales*, *Dothideomycetes*)	312	Tanaka *et al.* (2015)
3	Phylogenic diversity of fungal endophytes in Spanish stands of *Pinus halepensis*	134	Botella & Diez (2011)
4	Refined families of *Dothideomycetes*: *Dothideomycetidae* and *Pleosporomycetidae*	131	Hongsanan *et al.* (2020a)
5	Evolution and genome architecture in fungal plant pathogens	121	Möller & Stukenbrock (2017)
6	Diversity and antimicrobial activities of the fungal endophyte community associated with the traditional Brazilian medicinal plant *Solanum cernuum* Vell. (*Solanaceae*)	96	Vieira *et al.* (2012)
7	Revision of agents of black-grain eumycetoma in the order *Pleosporales*	79	Ahmed *et al.* (2014)
8	Dark septate endophytes isolated from a xerophyte plant promote the growth of *Ammopiptanthus mongolicus* under drought condition	71	Li *et al.* (2018c)
9	Potential of endophytic fungi isolated from cotton roots for biological control against verticillium wilt disease	71	Yuan *et al.* (2017)
10	Phylogenetic insights resolve *Dacampiaceae* (*Pleosporales*) as polyphyletic: *Didymocyrtis* (*Pleosporales*, *Phaeosphaeriaceae*) with Phoma-like anamorphs resurrected and segregated from *Polycoccum* (*Trypetheliales*, *Polycoccaceae fam. nov.*)	61	Ertz *et al.* (2015)

considered and seeds of crops should be treated for *Leptosphaeria* after testing (Sharma *et al.* 2015a).

Toxins

Studies related to toxins production are mostly from *Leptosphaeria maculans* which is no longer in the genus *Leptosphaeria s. str*. *Leptosphaeria maculans* was previously named *Sphaeria lingam* (Henderson 1918) and then renamed *Phoma lingam* by Desmazières (1849). Tulasne & Tulasne (1863) suggested that the sexual morph of *P. lingam* is *Leptosphaeria maculans* (Desm.) Ces. & De Not. Several strains of *Leptosphaeria maculans* (sexual morph of *P. lingam*) grouped in a distinct clade and were renamed *Plenodomus lingam* (De Gruyter *et al.* 2009, 2013). Two compounds have been reported from endophytic *Leptosphaeria* species. Takahashi et al. (1994) reported leptosins A, B, C, D, E and F from the mycelium of a strain of *Leptosphaeria* sp. attached to the marine alga *Sargassum tortile.* Lin et al. (2010) discovered leptosphaerins A–G from solid cultures of *Leptosphaeria* sp. Lin *et al.* (2017) found antifungal polyketides leptosphaerins A–G from a strain of *Leptosphaeria* sp. isolated from the soil sample on the surface of the sporocarp of *C. sinensis* in China. Luo *et al.* (2017) reported isobenzofuranones and isochromenones from a culture of a deep-sea sediment derived *Leptosphaeria* sp. SCSIO 41005. However, whether these compounds exhibit any significant toxicity is not known and warrants further research.

Taxonomy and phylogeny

Sequences of the entire ITS region separated *Phaeosphaeria* from *Leptosphaeria s. str.* The taxonomy of *Leptosphaeria* has been problematic due to inadequate morphological characters used to distinguish taxa and a lack of reference strains (Ariyawansa *et al.* 2015c, Doilom *et al.* 2021). Câmara *et al.* (2002) reported that peridial wall morphology, characters of the asexual morph, and to a lesser extent hosts, are phylogenetically significant at the generic level while ascospore and conidial morphology are taxonomically significant at the species level. Sequences of the entire ITS region separated *Phaeosphaeria* from *Leptosphaeria s. str.* and seems to be a strong candidate for species delimitation in *Leptosphaeria* (Câmara *et al.* 2002). Ariyawansa *et al.* (2015b) sequenced the SSU, LSU, ITS, *rpb2*, *tef1* and *act* gene regions and provided a multi-locus phylogeny of *Leptosphaeria*. Hence, ITS provides better resolution for species delimitation in *Leptosphaeria* when supplemented with other protein genes such as *rpb2*, *tef1* and *act*. There are currently 605 morphological species but only 15 species have molecular data (Hongsanan *et al*. 2020). In recent years, several species of *Leptosphaeria* have been transferred to other genera hence, its taxonomy is unstable. *Leptosphaeria s. str.* comprises several possibly host-specific, pathogenic species and DNA sequence data are essential for accurate species delimitation. Recollection and epitypification of the described taxa and sequence data from several gene regions are needed to ensure a stable taxonomy.

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DISCUSSION AND CONCLUSIONS

In this study, we have reviewed the general background of the 100 most cited genera. Some of these genera have been studied for decades for their economic and ecological importance. *Saccharomyces* and *Botrytis*, for example, are highly cited as the species are important model organisms. The high number of citations could also be attributed to the large number of species. Among the top 10 most cited genera, several genera have over 100 species. For example, *Candida* has about 300 species, *Trichoderma* has over 450 species, *Penicillium* and *Alternaria* with over 500 species. However, despite having only eight species, *Saccharomyces* is the most cited genus while *Phakopsora* with over 100 species is the least cited of the 100 most cited genera. This highlights the importance of *Saccharomyces* as a model organism and an agent of fermentation.

The majority of the highly cited genera include important pathogens. *Candida* ranks number two in the list of most cited genera mainly due to the large number of opportunistic infections (Brown *et al*. 2012). *Pichia* is the fifth most common cause of candidemia (Cooper 2011) and ranks number eight on the list.

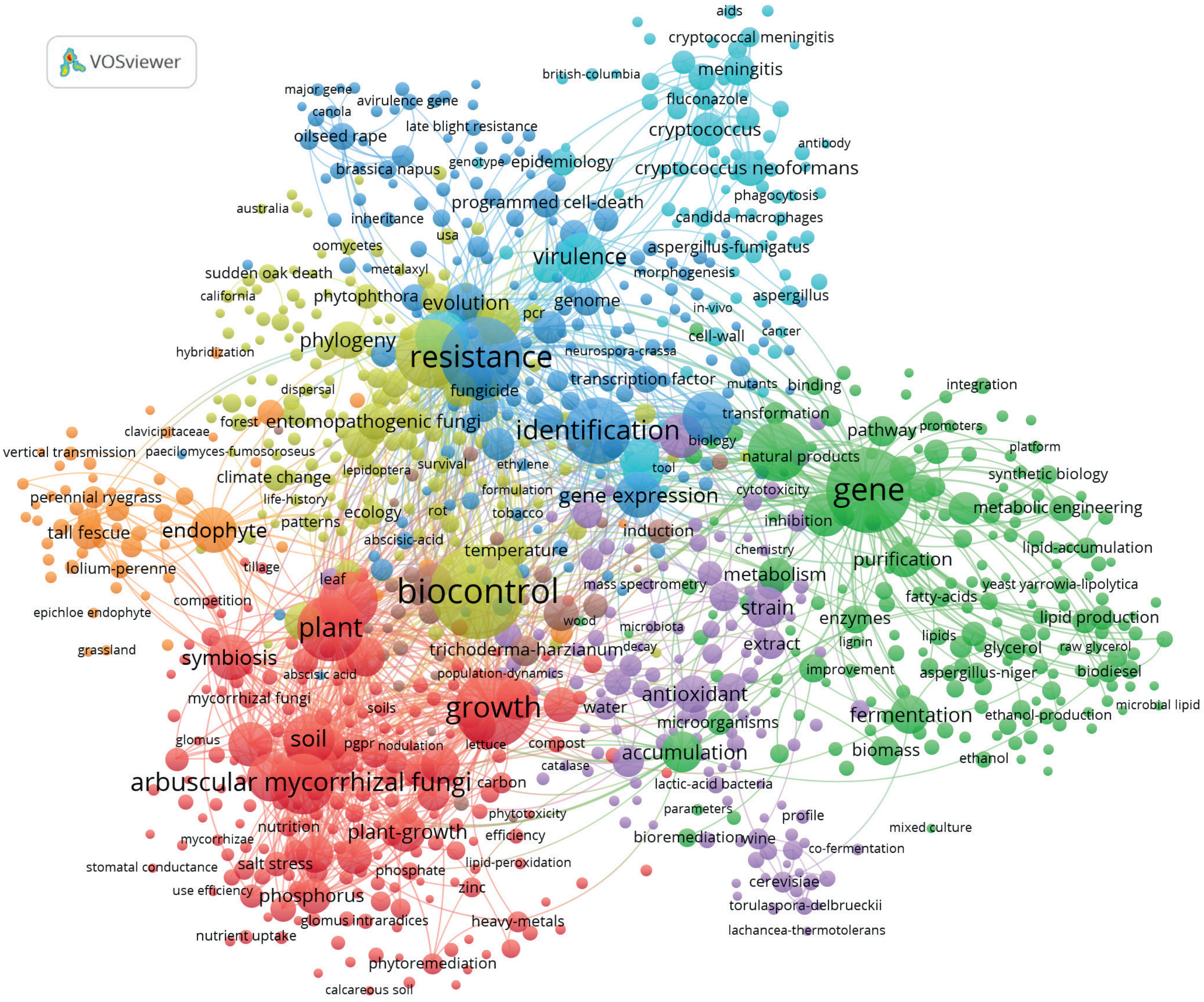

Fig. 132. Network visualisation of keywords of the publications related to all the 100 most cited genera. The larger the text and the circle the more often the subject has been cited.

Five of the world's most feared fungi are also listed as the most cited genera with *Candida* (2nd), *Aspergillus* (3rd), *Malassezia* (41st), *Talaromyces* (48th) and *Amanita* (80th) (Hyde *et al.* 2018a). Several most cited genera are also listed as the top 10 fungal pathogens in molecular plant pathology (Dean *et al.* 2012), such as *Botrytis* (7th), *Colletotrichum* (14th), *Fusarium* (4th), *Melampsora* (87th), *Puccinia* (29th) and *Ustilago* (35th).

The most commonly used keywords for the 100 most cited genera include "arbuscular mycorrhizal fungi", "biocontrol", "gene", "growth", "identification" and "resistance" (Fig. 132). These are also some of the main aspects of the research associated with these genera which demonstrates that numerous studies focused not only on the identification of fungi but also on their application. This trend is likely to continue for fungal research considering fungi can be further exploited as potential new sources of food and novel metabolites with biotechnological, industrial and pharmaceutical applications.

Research citation bias

This paper provides valuable insights into the importance of the most cited genera. To minimise the potential effect of citation bias, the Web of Science database was used and self-citations were excluded. When compiling the list of the top 10 cited articles, we discarded papers that correspond to taxonomic compilations of a large number (usually 100) of various new fungal taxa as the number of citations does not account for only one genus. These include for example the exclusion of Crous *et al.* (2015) for *Ophiostoma*; Ariyawansa *et al.* (2015a), Li *et al.* (2016a) and Liu *et al.* (2015b) for *Agaricus*; Crous *et al.* (2014a, b), Liu *et al.* (2015b) and Hyde *et al.* (2016) for *Diaporthe*; Ariyawansa *et al.* (2015a), Li *et al.* (2016a), Tibpromma *et al.* (2017), Crous *et al.* (2018) and Hyde *et al.* (2020b) for *Amanita.* However, citation bias still influences this study. If we take the genus *Pichia* for example, most citations in Fig. 17 refer to species that are no longer members of that genus. The number of citations referring to obsolete names of yeasts, for example, names of presently non-*Pichia* species, is large because the genus was reclassified more than a decade ago (Kurtzman *et al.* 2008, Kurtzman 2011a).

Conclusions

The list of the 100 most cited genera started from information compiled from the PubMed database. The highly researched phyla are *Ascomycota* (63 genera), *Basidiomycota* (27 genera), *Mucoromycota* (5 genera), *Oomycota* (3 genera) and *Glomeromycota* (2 genera). *Ascomycota* is highly researched possibly due to the extent of the biodiversity of the group. Among *Ascomycota*, 51 genera belong to the subphylum *Pezizomycotina* and 12 genera are classified in the *Saccharomycotina. Pezizomycotina* has received significant research interest as some species serve as model organisms. *Pezizomycotina* also includes edible fungi that are highly prized in culinary traditions worldwide. *Pezizomycotina* can form mycorrhizal associations with plants but are also important plant pathogens. They are also used in biotechnological processes, including the production of enzymes, biofuels, and biodegradable plastics. *Saccharomycotina* includes species with ecological importance and also includes opportunistic pathogens. As *Saccharomycotina* exhibits considerable genomic diversity, their study provides valuable information for evolutionary and functional contexts. Twenty-one of the basidiomycete genera are classified in *Agaricomycotina*, four in *Pucciniomycotina* and two in *Ustilaginomycotina*. *Agaricomycotina* is one of the largest and most diverse fungal groups. *Agaricomycotina* is economically significant as a food source globally as it includes button mushrooms, shiitake, and portobello. *Pucciniomycotina* includes rust fungi which are important in terms of their impact on agriculture and our understanding of host-pathogen interactions. Four of the *Mucoromycota* genera are classified in *Mucoromycotina* and one in *Mortierellomycotina*. *Mucoromycotina* serve as model organisms and are important for several biotechnological processes. *Mortierellomycotina* species are extremophiles which can enhance our understanding of adaptability and survival strategies in extreme conditions. Both *Glomeromycota* genera are classified in *Glomeromycotina*. *Glomeromycotina* includes arbuscular mycorrhizal fungi which have significant implications for agriculture and environmental resilience. In terms of classes, the *Agaricomycetes* (19 genera) and *Sordariomycetes* (18 genera) were the best represented in the highly cited list, closely followed by *Dothideomycetes* (16 genera) and then *Eurotiomycetes* (11 genera). Interestingly, most genera belong to *Pleosporales* (eight genera; *Dothideomycetes*) and *Hypocreales* (seven genera; *Sordariomycetes*), followed with six genera each by *Agaricales*, *Eurotiales* and *Saccharomycetales* (*Agaricomycetes*, *Eurotiomycetes* and *Saccharomycetes*, respectively). Although *Botryosphaeriaceae* (*Botryosphaeriales*, *Dothideomycetes*) is the family represented by the largest number of genera (five genera) in the list, the order is not in the top three orders with the most represented genera. *Pleosporaceae* (*Pleosporales*, *Dothideomycetes*) and *Saccharomycetaceae* (*Saccharomycetales*, *Saccharomycetes*) both represent the next highest number of four genera included in the list, followed by *Aspergillaceae* (*Eurotiales*, *Eurotiomycetes*) and *Sclerotiniaceae* (*Helotiales*, *Leotiomycetes*) with three genera each included in the list. Ninety-one out of the 100 most cited genera have genome data available in the FungiDB and MycoCosm databases (Grigoriev *et al.* 2014, Amos *et al.* 2022). The top 33 genera have genome data available, which is likely an important factor in their high research interest as genome data contributes significantly to our understanding of biology, ecology, evolution, and applications. Therefore, these data suggest that the ranking of the 100 most cited genera is based on several factors including their importance as a model organism, their economic importance and their importance in industrial applications. This indicates that genera with molecular and genome data as well as data on their application are likely to warrant significant research interest.

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DECLARATION ON CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

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