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ORIGINAL ARTICLE

Phytophthora: an underestimated threat to agriculture, forestry, and natural ecosystems in sub-Saharan Africa

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Abstract

Phytophthora species are highly destructive plant pathogens and pose a significant threat to plants in various ecosystems, including agriculture, forest plantations, and natural environments. In sub-Saharan Africa, a total of 77 *Phytophthora* species have been identified and this review aims to provide an overview of the species diversity and progress of *Phytophthora* research in this region. Numerous important studies have been carried out in this region, contributing significantly to our understanding of *Phytophthora* in various research fields. However, compared to global data, the advancement of *Phytophthora* research in sub-Saharan Africa has been relatively slow. This is evident from the fact that some countries in the region have yet to report the presence of *Phytophthora* species. Thus, this review also highlights critical research gaps, particularly concerning the potential impacts of climate change, and suggests specific studies to address these gaps. The identified research studies are of utmost urgency as they not only aim to safeguard the iconic floral biodiversity of the region but also play a crucial role in enhancing the economy and ensuring food security.

Keywords Aquatic *Phytophthora* · Black pod disease of cacao · Cape Floristic Region · Foot and root rot of citrus and avocado · Late blight of potatoes · Taro leaf blight

Introduction

Phytophthora species are among the most damaging plant pathogens known (Ribeiro 2013). The discovery of *Phytophthora infestans*, the first described species of the genus, dates to the mid-nineteenth century Irish potato famine (De Bary 1876). In the 1840s, the pathogen was introduced into Europe from Mexico via the USA (Goss et al. 2014). Subsequently, *P. infestans* infected and killed most potato crops in Europe, causing the hunger-driven migration of millions of people from the European continent to America, and colonies in Africa and Asia (Ristaino 2002). Ironically, these migrants unknowingly introduced *P. infestans*, the underlying reason for their displacement, to their new settlements throughout the world via infected propagation material (Yoshida et al. 2013). For example, *P. infestans* was first reported in the South African Cape Peninsula, a vibrant settlement on the Europe-India trade route, in 1890 (Blersch 1890). Later, in 1913 and 1922, it was also reported in various locations in the interior of South Africa (Wager 1941). It is thought that many other *Phytophthora* species were introduced into sub-Saharan Africa together with their crop hosts in a similar manner (Santini et al. 2018).

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Numerous *Phytophthora* species have been reported from sub-Saharan Africa. In this region, *Phytophthora* can be found in almost all climatic zones and ecosystems. The severity of *Phytophthora* diseases varies widely among different environmental gradients and in the growing regions of different crop hosts. Several *Phytophthora* species have been documented to cause diseases in plantation trees, including pines, *Eucalyptus*, and *Acacia* (Linde et al. 1994a, b; Roux et al. 2005; Maseko et al. 2007). In addition, *Phytophthora* causes important diseases on fruit trees such as avocado, cocoa, and citrus as well as on several different vegetable crops, including potato and taro (Nagel et al. 2013a; Akrofi 2015; Njoroge et al. 2019; Saville and Ristaino 2021). There have also been reports of *Phytophthora* diseases in natural ecosystems, such as in the Cape Floristic Region in the Western Cape Province of South Africa (Van Wyk 1973b; Von Broembsen 1984a; Bezuidenhout et al. 2010).

In the twentieth century, improvements in isolation techniques (Jung et al. 1996; Drenth and Sendall 2001) and the development of selective media (Tsao and Guy 1977; Tsao and Ocana 1969; Hüberli et al. 2000) have substantially increased the discovery rate of new and described *Phytophthora* species from various ecosystems. With the advancement of molecular technologies such as high-throughput sequencing in the twenty-first century, the discovery rate of *Phytophthora* species has increased exponentially around the world (Bose et al. 2018, 2021b; Català et al. 2015, 2017). However, except for South Africa, where new species of *Phytophthora* are being reported at regular intervals (Nagel 2013; Nagel et al. 2015; Oh et al. 2013; Bose et al. 2018, 2021a, b), there are very few reports from sub-Saharan Africa (Nagel et al. 2013a; Scott et al. 2013; Marcot et al. 2023).

Forestry and agriculture form the backbone of the economy and food security of most countries in sub-Saharan Africa (Whiteman and Lebedys 2006; OECD 2016). Based on global data, *Phytophthora* species (and various other *Oomycota*) continue to be major impediments to these industries (Abad et al. 2022). For example, in South Africa, there has been an exponential increase in the root rot disease of cold-tolerant *Eucalyptus* species caused by *Phytophthora alticola* (Bose et al. 2023). Similarly, new lineages of *P. infestans* have been detected in sub-Saharan Africa (Pule et al. 2013; Njoroge et al. 2016). Apart from South Africa, however, novel research revealing the previously unknown diversity of *Phytophthora* species from the region is scarce (Oh et al. 2013; Nagel et al. 2013b, 2015; Bose et al. 2018, 2021a, b; Hulbert et al. 2019; Bose and Hammerbacher 2023). However, this knowledge is crucial to limiting the impact of these pathogens, whether introduced or native, in the region.

In this review, we summarise the reported diversity of *Phytophthora* species and key advancements in this field of research in sub-Saharan Africa. We discuss the known species diversity of *Phytophthora* in various environmental settings, such as plantation forests, natural ecosystems, and agriculture (Table 1; Fig. 1). In addition, we propose strategies for bridging present knowledge gaps about *Phytophthora* in sub-Saharan Africa.

Acquisition of *Phytophthora* distribution data for sub-Saharan Africa

The primary dataset for *Phytophthora* species recorded from sub-Saharan Africa was sourced from the USDA Fungus-Host Database (Farr and Rossman 2021). To enhance and refine this dataset, additional published lists and literature were consulted. Furthermore, records of *Phytophthora* strains from sub-Saharan African countries were incorporated from the CBS collection at the Westerdijk Fungal Biodiversity Institute (https://wi.knaw.nl/), the Herb IMI database maintained by Kew Royal Botanical Gardens (http://www.herbimi.info/herbimi/home.htm), and the World *Phytophthora* Collection (WPC) housed at the University of California, Riverside (https://microplantpath.ucr.edu/world-phytophthora-collection-university-california-riverside). Whenever possible, the current names of species that had undergone taxonomic revision were used. No differentiation was made between records supported by molecular data and those based solely on morphological data. The resulting dataset is available through Mendeley Data (https://doi.org/10.17632/8khwwsn3xx.1) and as Supporting data with this article.

Vegetable crops

Several *Phytophthora* species, including *P. capsici*, *P. drechsleri*, *P. medicaginis*, and *P. nicotianae*, have been reported to cause disease in vegetable crops in sub-Saharan Africa (Table 1). Nevertheless, the two most important *Phytophthora* species on vegetable crops in this region are *P. infestans* and *P. colocasiae*, which cause late blight of potatoes and leaf blight of taro, respectively.

Late blight of potatoes

In Africa, potato is the fourth most important crop after wheat, maize, and rice because it is an important source of carbohydrates (Ezekiel et al. 2013; Dreyer 2017). Between 2002 and 2021, potato production in Africa experienced significant growth, with reports indicating that it expanded across approximately two million hectares of cultivated land in 42 countries (FAOSTAT 2022). On this continent, potatoes are grown by smallholder and commercial growers for both

Table 1 *Phytophthora* taxa identified from various ecosystems of sub-Saharan Africa. This list includes well-described species, informal species, hybrids, and phylotypes (suffixed with asterisks). The table only includes taxa that were at least provisionally identified up to the species level. For taxa without a publication record, accession numbers from databases were included. For more information, please refer to the dataset available through Mendeley Data (https://doi.org/10.17632/8khwwsn3xx.1)

Phytophthora taxa	Ecosystems							References
	Vegetable crops	Fruit crops	Plantation forestry	Natural woodland and velds	Botanical gardens	Plant nurseries	Aquatic ecosystems	
P. aff. *meadii**			×	×				Bose et al. (2018)
P. afrocarpa				×				Bose et al. (2021a)
P. alticola			×	×				Maseko et al. (2007); Bose et al. (2017); Bose et al. (2018)
P. amnicola			×		×		×	Hulbert et al. (2019); Bose et al. (2021b)
P. amnicola × *P. chlamydospora*					×		×	Nagel et al. (2013b); Hulbert et al. (2019)
P. arecae	×							Maseko et al. (2007)
P. asparagi			×	×	×			Bose et al. (2018); Hulbert et al. (2019)
P. boehmeriae			×					Linde et al. (1994b); Roux and Wingfield (1997); Maseko et al. (2007)
P. cactorum	×					×		Mes (1934); Wijers (1937); Van der Merwe et al. (1972); Bumbieris (1974); Gorter (1977); Marais (1979); Oudemans and Coffey (1991); Erwin and Ribeiro (1996); Crous et al. (2000)
P. cambivora				×				Bose et al. (2018)
P. capensis		×	×	×	×			Bezuidenhout et al. (2010); Bose et al. (2018); Hulbert et al. (2019)
P. capsici	×							Thompson et al. (1994); Meitz et al. (2010)
P. castaneae		×						Cooke et al. (2000)
P. chlamydospora			×		×		×	Oh et al. (2013); Nagel et al. (2015); Hulbert et al. (2019)
P. cinnamomi	×	×	×	×	×	×	×	Wager (1941); Van der Merwe et al. (1972); Van der Merwe and Van Wyk (1973); Von Broembsen (1984a); Von Broembsen and Kruger (1985); Lübbe and Geldenhuys (1990); Linde et al. (1994b); Crous et al. (2000); Maseko et al. (2007); Oh et al. (2011); Crous et al. (2004); Bahramisharif et al. (2014); Bezuidenhout et al. (2010); Mbaka et al. (2010); Nagel et al. (2013a); Nesamari et al. (2017); Bose et al. (2018)
P. citricola	×		×	×				Wager (1941); Erwin and Ribeiro (1996); Bose et al. (2018)
P. citrophthora		×						Doidge (1925); Wager (1931); Hector and Loest (1937); Gorter (1977); Meitz-Hopkins et al. (2014)
P. cocois		×						Weir et al. (2015)

Table 1 (continued)

Phytophthora taxa	Ecosystems							References
	Vegetable crops	Fruit crops	Plantation forestry	Natural woodland and velds	Botanical gardens	Plant nurseries	Aquatic ecosystems	
P. colocasiae				×				Maseko et al. (2007); Bandyopadhyay et al. (2011)
*P. constricta**			×					Bose et al. (2021b)
*P. crassamura**			×					Bose et al. (2021b)
P. cryptogea		×	×	×		×		Wager (1941); Doidge (1950); Bumbieris (1974); Marais (1979); Mills et al. (1991); McLeod and Coertze (2007); Bezuidenhout et al. (2010); Bose et al. (2018)
P. drechsleri	×		×	×		×		Thompson (1987); Thompson and Phillips (1988); Bezuidenhout et al. (2010); Bose et al. (2018)
*P. elongata**			×	×				Bose et al. (2018)
P. emzansi				×		×		Bezuidenhout et al. (2010); Bose et al. (2021a)
P. fragariae		×						IMI 353558
P. frigida			×	×	×			Maseko et al. (2007); Bose et al. (2018)
P. gondwanense			×					Bose et al. (2018)
P. gregata complex*			×	×				Bose et al. (2018)
P. heveae		×						Nagel et al. (2013a)
P. hibernalis		×						Erwin and Ribeiro (1996)
*P. humicola**			×					Bose et al. (2018)
P. hydropathica × *P.* sp. Maryland					×			Hulbert et al. (2019)
P. infestans	×					×		Nobbs (1903); Doidge and Bottomley (1931); McLeod and Coertze (2006)
*P. inundata**				×				Bose et al. (2018)
*P. kwongonina**			×	×				Bose et al. (2021b)
P. lacustris					×		×	Nagel et al. (2015)
*P. litchi**				×				Bose et al. (2018)
P. meadii			×					Roux and Wingfield (1997)
P. medicaginis	×							Thompson (1987)
P. megakarya		×						Guest (2007)
P. megasperma	×							Förster and Coffey (1993)
P. multivesiculata						×		Bose and Hammerbacher (2023)
P. multivora			×	×		×		Jung and Burgess (2009); Bezuidenhout et al. (2010); Meitz-Hopkins et al. (2014); Bose et al. (2018); Hulbert et al. (2019)
P. nicotianae	×	×	×	×				Doidge (1924); Wager (1931, 1935, 1941); Zeijlemaker (1971); Gorter (1977); Marais (1979); Thompson (1981); Thompson and Naudé (1992); Botha (1993); Linde et al. (1994a); Crous et al. (2000); Maseko et al. (2001); Bezuidenhout et al. (2010); Nagel et al. (2013a); Meitz-Hopkins et al. (2014); Bose et al. (2018)

Table 1 (continued)

Phytophthora taxa	Ecosystems							References
	Vegetable crops	Fruit crops	Plantation forestry	Natural woodland and velds	Botanical gardens	Plant nurseries	Aquatic ecosystems	
P. niederhauserii		×	×	×				Abad et al. (2014); Bose et al. (2018)
P. palmivora		×		×				Bose et al. (2018); Erwin and Ribeiro (1996)
P. parvispora			×	×		×		Bezuidenhout et al. (2010); Bose et al. (2018)
P. phaseoli	×							Erwin and Ribeiro (1996)
P. plurivora			×	×			×	Nagel et al. (2015); Bose et al. (2018)
P. porri	×							Von Maltitz and Von Broembsen (1983)
*P. pseudocryptagea**			×	×				Bose et al. (2018)
P. pseudocryptogea × *P. cryptogea*					×			Hulbert et al. (2019)
*P. rosacearum**			×					Bose et al. (2021b)
*P. rubi**			×					Bose et al. (2021b)
P. sp. × WS							×	Oh et al. (2013)
P. sp. AUS2A*				×				Bose et al. (2018)
P. sp. canthium				×				Oh et al. (2013)
P. sp. Kelmania*				×				Bose et al. (2018)
P. sp. Kununurra				×				Oh et al. (2013)
P. sp. nov. 3A*			×					Bose et al. (2021b)
P. sp. nov. 9A*				×				Bose et al. (2018)
P. sp. RSA10A*				×				Bose et al. (2018)
P. sp. RSA1A*			×	×				Bose et al. (2018)
P. sp. RSA2A*			×					Bose et al. (2018)
P. sp. RSA3A*			×	×				Bose et al. (2018)
P. sp. RSA5A*			×	×				Bose et al. (2018)
P. sp. RSA7A*			×	×				Bose et al. (2018)
P. sp. stellaris			×				×	Oh et al. (2013)
P. sp. Umtamvuna							×	Oh et al. (2013)
P. sp. xHennops			×	×			×	Oh et al. (2013); Bose et al. (2018)
P. syringae		×						Wager (1941)
P. taxon raspberry*				×				Bose et al. (2018)
P. taxon Sisulu-river		×					×	Meitz-Hopkins et al. (2014); Nagel et al. (2015)
*P. thermophila**			×	×				Bose et al. (2021b)
P. thermophila × *P. amnicola*							×	Nagel et al. (2013b)
P. tropicalis			×					Hulbert et al. (2019)

domestic consumption and export (Gildemacher et al. 2009; Haverkort et al. 2013). By far, the most damaging potato disease is late blight caused by *Phytophthora infestans*, which has been reported in all potato-growing regions of the world (Fry et al. 2015; Saville and Ristaino 2021).

Phytophthora infestans was introduced into Europe via the USA before 1840. From there, it migrated to the African continent together with European settlers (Yoshida et al. 2013). In consequence, this disease was first reported in Africa as early as 1890, from South Africa (Blersch 1890). The pathogen, however, was identified considerably later by Ethel Doidge (Wager 1941). In addition to potatoes, *P. infestans* affects various other hosts, including tomatoes and brinjal in Africa and around the world (McLeod and Coertze 2006; Pule et al. 2013; Seidl Johnson and Gevens 2014; Fry et al. 2015).

The genetic diversity of *P. infestans* in sub-Saharan Africa is low (Ghislain et al. 2019). This is because seed potatoes from locations with significantly higher pathogen diversity, such as Europe or North America, are not freely interchanged (Ghislain et al. 2019). The vast majority of *P. infestans* isolates from this area were categorised as US-1 (old lineage), with some belonging to the novel lineage 2_A1, formerly known as KE-1 (Pule et al. 2013). This new 2_A1 lineage has substantially displaced the US-1 in many regions of sub-Saharan Africa to a point where both lineages are rarely reported from the same area (Njoroge et al. 2016). Both lineages represent the A1 mating type; however, the A2 mating type (lineage EU_33_A2) was recently reported in Nigeria (Nnadi et al. 2019). The further spread of this lineage and additional introductions of the A2 mating type in sub-Saharan Africa can lead to the establishment of sexually reproducing populations in this region. Sexual reproduction can have an important impact on the occurrence and management of late blight not only through the production of oospores that can survive in soil without a living host, but also by generating new lineages that have new phenotypes (Fry 2020).

In sub-Saharan Africa, annual losses due to late blight are estimated at 15–30% with losses of up to 57% being reported in some cases (Ghislain et al. 2019). Furthermore, climate change is expected to slightly increase the severity of late blight in sub-Saharan Africa (Sparks et al. 2014). This slight increase in disease incidence may not pose a threat to potato production. Still, controlling this disease in sub-Saharan Africa is essential for the food security of this region, as potato is an important staple crop for small growers and subsistence farmers.

Various approaches have been used globally to control late blight, including seed certification, integrated management, fungicide sprays, early planting, elimination of disease sources, and planting resistant cultivars (Fry 2016; van der Waals and Krüger 2020). Among these, the use of fungicides is losing popularity due to environmental concerns and the development of resistance in some strains of the pathogen (Ghislain et al. 2019). Introducing natural resistance into

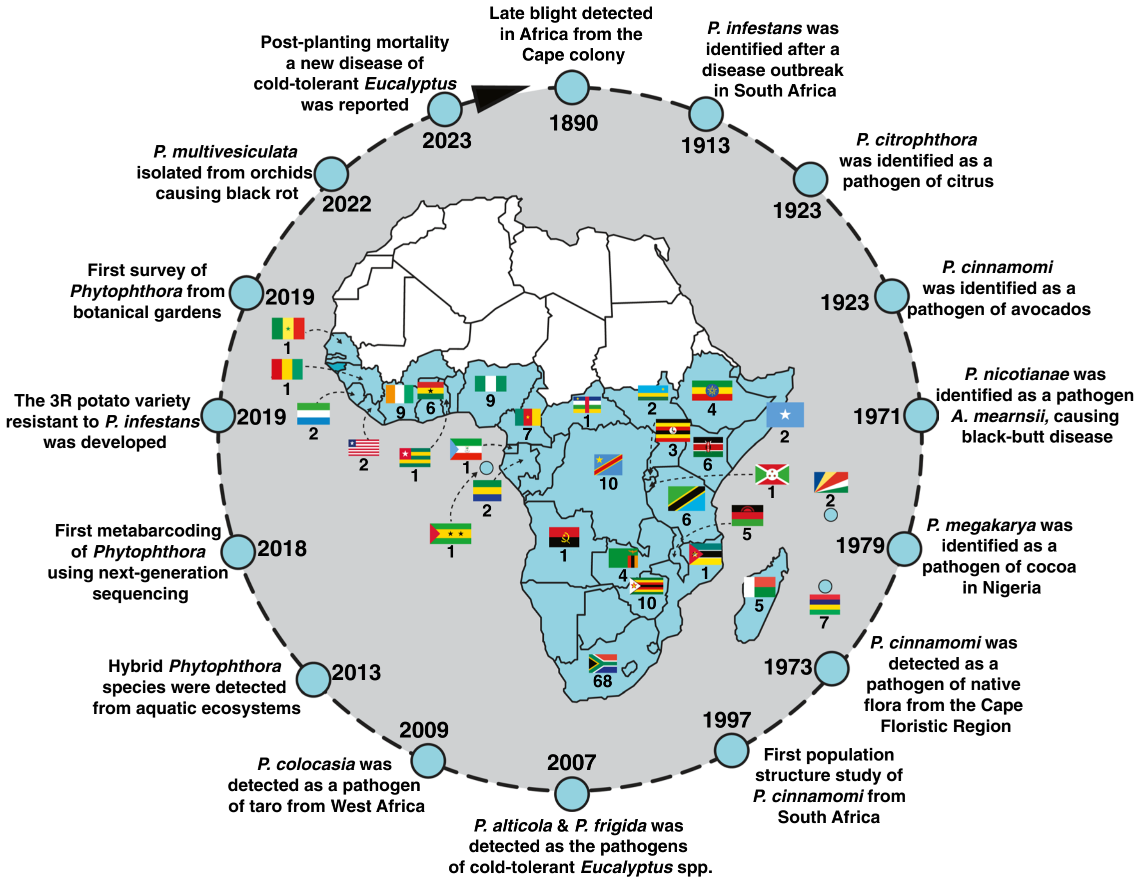

Fig. 1 The number of *Phytophthora* taxa recorded from each country in sub-Saharan Africa. The timeline around the continent of Africa displays significant scientific achievements from the region. The Figure only includes taxa that were at least provisionally identified up to the species level. For more information, please refer to the dataset available through Mendeley Data (https://doi.org/10.17632/8khwwsn3xx.1)

potato cultivars is a sustainable method for controlling this disease. Nevertheless, *P. infestans* rapidly overcomes the cultivar resistance (Haverkort et al. 2009). To address this, three resistance genes were introduced into potatoes from their wild relatives (Ghislain et al. 2019). These introduced resistance genes are providing long-lasting resistance to multiple strains of *P. infestans* in sub-Saharan Africa (Ghislain et al. 2019).

Taro leaf blight

Taro is an edible aroid and one of the world's top five root crops. This plant is native to Southeast Asia and southern India (USDA ARS 2023) and was introduced to various humid, subtropical, and temperate areas of the world, such as Africa (Alexandra et al. 2020). According to the FAO, Africa accounts for more than 70% of global taro production (FAOSTAT 2022). Taro is produced in Africa by smallholder and subsistence farmers in Nigeria, Ethiopia, Cameroon, Ghana, Burundi, Madagascar, Rwanda, and the Central African Republic (Oladimeji et al. 2022; https://www.tridge.com/). However, taro yields have decreased over the last few years, with the lowest production recorded in Africa in 2020 (FAOSTAT 2022). A substantial part of this decrease in taro productivity can be attributed to the emergence of taro leaf blight, caused by *Phytophthora colocasiae*, in West Africa in 2009 (Bandyopadhyay et al. 2011). This disease affected taro crops in Nigeria, Cameroon, Ghana, and other neighbouring countries, causing an economic loss of about USD 1.4 billion annually (Onyeka 2014).

Phytophthora colocasiae is a heterothallic species that was initially identified on the Indonesian island of Java (Raciborski 1900) and is believed to have an Asian origin (Zhang et al. 1994). This disease is now causing substantial losses on taro crops throughout the world (Miyasaka et al. 2013). As a result, it has been designated as one of the most serious pathogens threatening food security in the tropics (Alexandra et al. 2020; Oladimeji et al. 2022). *Phytophthora colocasiae* is mostly transmitted in the field by asexual spores carried by water to susceptible hosts via rain splashes. Symptomatic plants have water-soaked lesions that exude fluid that changes colour from a bright yellow to dark purple when dry. The lesions enlarge as the disease progresses, with a zonate appearance and are brownish to purplish brown in colour. Sporangia arise from leaf lesions in clusters, causing leaf senescence. The disease colonises the corms as well and causes root and corm rot (Miyasaka et al. 2013).

Three mating types, A1, A2, and A0, have been identified in *P. colocasiae*. All three mating types have been reported from various Asian and Pacific regions (Tyson and Fullerton 2007). However, the global distribution of these mating types is not homogeneous (Tyson and Fullerton 2007). In Hawaii, for example, most isolates were initially reported to be A1 (Ko 1979), although the A2 mating type has since been discovered there (Shrestha et al. 2014). On the other hand, in Taiwan, only the A2 type is known (Ann et al. 1986; Zhang et al. 1994). However, the mating types of *P. colocasiae* in West and Central Africa are largely unknown. Knowledge of the genetic diversity of the host is equally limited (Oladimeji et al. 2022). Therefore, taro breeding for disease resistance in sub-Saharan Africa has not progressed extensively. In this scenario, based on the economic losses incurred by the farmers in this region, research involving the mitigation of this pathogen and the selection of tolerant cultivars is urgently needed.

Fruit crops

Various species of *Phytophthora* have been isolated from symptomatic fruit trees in sub-Saharan Africa (Table 1), for example, *P. cactorum* from apples, citrus, and grapes; *P. cinnamomi* from pineapples, apples, and grapes; *P. cryptogea* from citrus and grapes; and *P. megasperma* from grapes. However, here we consider the three main hosts of *Phytophthora* occurring in sub-Saharan Africa, namely, avocado, cocoa, and citrus.

Root rot and dieback of avocado

Avocado (*Persea americana*) is one of the most widely planted fruit crops in sub-Saharan Africa. Hence, it is often referred to as "green gold." Kenya and South Africa are the two most important avocado producers in the region, followed by the Democratic Republic of the Congo, Ethiopia, and Cameroon. The first large-scale production of avocado in Africa started in Tzaneen and Louis Trichardt in South Africa in 1938 (Bezuidenhout 2018). Soon after, dieback was reported and the causal organism was identified as *P. cambivora*, which was later corrected to *P. cinnamomi* (Doidge and Bottomley 1931; Wager 1941), a pathogen originating from Southeast Asia (Ko et al. 1978). Root rot and dieback caused by *P. cinnamomi* are now among the most damaging diseases of avocados in this region although its current estimated economic impact in various avocado-growing regions of sub-Saharan Africa is unavailable. Due to high summer rainfall and soil temperatures, the severity of this disease is exceptionally high in South Africa (Bekker 2011). Thus, phosphorous acid (phosphite) treatments, foliar sprays, trunk paints, soil drenches, and *Phytophthora*-tolerant rootstocks are used to manage this disease (Bezuidenhout 2018).

Phytophthora cinnamomi is a heterothallic species. When compared to A2 mating type isolates, the A1 isolates have a high level of genetic diversity (Dobrowolski et al. 2002;

Arentz 2017). The A2 mating type is more aggressive and the dominant type in various areas of the world, including South Africa (Linde et al. 1997; Kamoun et al. 2015; Arentz 2017). Nevertheless, both mating types of *P. cinnamomi* have been reported in South Africa (Linde et al. 1997; Oh et al. 2011) and in Kenya (Mbaka et al. 2010) in various ecosystems. However, sexual reproduction in nature has not been reported in South Africa or elsewhere in Africa. A recent population genetic study using 15 microsatellite markers indicated that *P. cinnamomi* from natural vegetation in the Western Cape had the highest level of genotypic diversity and the number of unique alleles, indicating this could be the point of introduction of *P. cinnamomi* to South Africa. Shared genotypes were detected between isolates from avocado orchards and natural vegetation, indicating the movement of isolates between these areas (Engelbrecht et al. 2022).

Black pod disease of cacao

Cacao black pod rot is the most damaging disease of *Theobroma cacao* in the world. Depending on the geographic region, various species of *Phytophthora* have been reported as causal agents of this disease (Drenth and Guest 2013). *Phytophthora* species that have been linked to this disease include *P. botryosa*, *P. capsici*, *P. citrophthora*, *P. heveae*, *P. katsurae*, *P. megakarya*, *P. megasperma, P. palmivora*, *P. theobromicola* along with several other species (Decloquement et al. 2021). Among these, *P. palmivora* and *P. megakarya* are the most damaging pathogens (Erwin and Ribeiro 1996; Guest 2007). *Phytophthora palmivora* has a global distribution, whereas *P. megakarya* is restricted to African countries (Guest 2007). *Phytophthora megakarya* is considered to have evolved in Nigeria, near the Cameroonian border, and currently consists of two genetically distinct populations occurring in Central and Western Africa (Nyassé et al. 1999).

Both *P. megakarya* and *P. palmivora* are heterothallic, and for both species, the A1 and A2 mating types have been reported in sub-Saharan Africa (Akrofi 2015). The majority of *P. megakarya* isolates infecting cocoa are mating type A1. Yet, both mating types have been reported from Equatorial Guinea, Cameroon, Ghana, and Nigeria (Appiah et al. 2003). In contrast, mating type A2 of *P. palmivora* predominates in Africa, although both mating types have been observed in Ghana and Togo (Appiah et al. 2003). This asymmetry in mating type distribution may favour interspecific hybridization, but not sexual reproduction (Brasier and Griffin 1979). Fortunately, although the two species are closely related and coexist in cocoa farms, no hybrids have been observed, possibly due to differences in chromosome numbers in *P. megakarya* and *P. palmivora* (Akrofi 2015).

Cocoa trees affected by *Phytophthora megakarya* and *P. palmivora* exhibit overlapping symptoms. Cacao black pod rot starts with the emergence of a small, firm, and dark lesion on the cocoa pod. Within days, the lesions rapidly expand to cover the entire surface of the pod and internal tissue, eventually giving the pods a mummified appearance (Dennis and Konam 1994; Drenth and Guest 2013). A single infected pod can yield an inordinate number of zoospores under favourable conditions, which are disseminated by rain, insect vectors, contaminated soil, and farming equipment. In addition to infecting pods, both pathogens infect bark, leaves, and flowers. Stem cankers are concealed by the bark but frequently discharge a reddish exudate (Guest 2007).

Phytophthora megakarya was first identified in Nigeria in 1979 (Brasier et al. 1981) and thereafter, from Togo (Djekpor et al. 1982), Ghana (Dakwa 1988), La Côte d'Ivoire (Luterbacher and Akrofi 1993; Nyassé et al. 1999; Risterucci et al. 2003), and Cameroon (Nyassé et al. 1999). *Phytophthora megakarya* is a more aggressive pathogen than *P. palmivora* (Akrofi et al. 2003; Opoku et al. 2000). For example, *P. palmivora* was the only recognised causative agent of the black pod disease of cocoa in Ghana before 1985, resulting in 30% crop loss (Akrofi et al. 2003). After 1985, with the emergence of *P. megakarya* in that country, the impact of this malady increased substantially (Dakwa 1988).

The management of black pod rot is complicated by the fact that both *P. megakarya* and *P. palmivora* can successfully survive within alternative hosts, which are often intercropped with cocoa. Throughout West and Central Africa, cocoa is intercropped with various shade plants, including citrus, papaya, banana, and cassava, to name a few. This approach offers numerous advantages, including better soil fertility, drought and bushfire resistance, and the opportunity for additional income. Several of these intercropped plant species may function as alternate hosts for pod rot pathogens. *Phytophthora megakarya* has been isolated from an assortment of alternative host plants, such as *Funtumia elastica*, *Sterculia tragacantha*, *Dracaena manii*, *Ricinodendron heudelotii* (Opoku et al. 2002), *Xanthosoma sagittifolium*, *Musa paradisiaca*, *Elaeis guineensis*, *Persea americana*, *Carica papaya*, *Mangifera indica*, *Colocasia esculenta*, *Athyrium nipponicum*, *Ananas comosus* on cacao farms in Ghana (Akrofi et al. 2015), and the native tree, *Irvingia gabonensis*, in Cameroon (Holmes et al. 2003). *Phytophthora palmivora* also has a very wide host range that includes citrus, papaya, and other species intercropped with cocoa (Erwin and Ribeiro 1996).

Studies have shown that *P. megakarya* has displaced *P. palmivora* in cocoa plantations in Cameroon and Nigeria (Nyassé et al. 1999). This is likely to also happen in other parts of West and Central Africa. *Phytophthora palmivora* can survive in a wider temperature range than *P. megakarya* (Puig et al. 2018). However, the optimal growth temperature for *P. megakarya* overlaps with the cocoa production conditions in the region (Puig et al. 2018). This and its ability to sporulate profusely may be the reason why *P. megakarya* is highly successful and is projected to increase in abundance in West Africa (Teixeira 2021). At the same time, there is a significant potential for the global spread of this pathogen to other important cocoa-growing regions, as observed for *P. ramorum* (Grünwald et al. 2012). However, strict quarantine measures can prevent this pathogen from spreading, and more research is needed to reduce its economic impact in Africa.

Phytophthora diseases of citrus

South Africa is one of the largest exporters of citrus worldwide. Since 1891, gummosis disease on citrus was known to occur in the Cape Colony (Hector and Loest 1937), but it was only in 1930 that the cosmopolitan *Phytophthora citrophthora* was isolated and identified from such symptoms in South Africa (Wager 1941). This pathogen was also identified by Doidge (1925), as the causal agent of brown rot of citrus fruit during an epidemic that affected parts of the Transvaal (Gauteng, Limpopo, and Mpumalanga) and the Cape Province (Western, Eastern, and Northern Cape). Subsequently, *P. citrophthora* was reported from the Mpumalanga, Eastern Cape, and Limpopo provinces on a variety of citrus hybrids (Doidge and Bottomley 1931; Hector and Loest 1937).

In addition to *P. citrophthora*, Gorter (1977) identified *P. nicotianae* as the pathogen of citrus causing root and collar rot. Following this, Von Maltitz and Von Broembsen (1985) reported *P. citricola* from the Western Cape Province. Consequently, three surveys of *Phytophthora* species linked with citrus orchards and nurseries in South Africa were published. The initial investigation, from 1982 to 1984, exclusively detected *P. nicotianae* in citrus nurseries in the Eastern Cape and the Transvaal region (currently Limpopo, Mpumalanga, North West, and Gauteng). This finding was subsequently supported in the study by Thompson et al. (1995) where the authors also detected *P. nicotianae* in root and soil samples from orchards in the Transvaal. Maseko et al. (2002) also showed that *P. nicotianae* was the most abundant species associated with citrus orchards in Mpumalanga and Limpopo, while *P. citrophthora* was less common within these provinces. Later, Schutte and Botha (2010), while investigating the causal agent of trunk and branch canker on clementine mandarins in the Western Cape, concluded that *P. citrophthora* was the predominant species in that province.

Recently, Meitz-Hopkins et al. (2014) surveyed all major citrus-producing regions of South Africa spanning seven provinces, Eastern Cape, Kwazulu-Natal, Limpopo, Mpumalanga, Northern Cape, North West, and Western Cape. Their PCR-RFLP analyses of the ITS region for all 162 isolates confirmed *P. nicotianae* as the most abundant species (mostly A1 mating type), followed by *P. citrophthora* which included both G1 and G2 subgroups. The authors also isolated *P. multivora* and an unknown species with high similarity to *P.* taxon Sisulu-river, an undescribed species detected from a riparian ecosystem in South Africa (Nagel et al. 2015).

Citrus diseases caused by *Phytophthora* have also been documented in a few other countries from sub-Saharan Africa. *Phytophthora citrophthora* has been found to infect a variety of citrus species in Liberia (Nagel et al. 2013a). In investigating the aetiology of citrus tree decline in Cameroon, Ndo et al. (2019) identified *Phytophthora* as one of the primary causal agents. However, species identification was not undertaken. In studying the *Phytophthora* species responsible for citrus gummosis in Kenyan orchards, Mounde et al. (2012) found that *P. citrophthora* was the most prevalent species, followed by *P. nicotianae.*

Plantation forestry

Forests are important for solving current global socio-environmental problems such as biodiversity loss, climate change, and substantially support resource-based livelihoods. In this regard, sub-Saharan Africa is recognized as a key player in the dynamics of the global carbon cycle (Bombelli et al. 2009). Commercial forestry in sub-Saharan Africa is mostly based on exotic tree species because the region lacks sufficient indigenous timber resources (Zwolinski and Bayley 2001). In 1876, the first commercial *Eucalyptus* plantation was established in South Africa (Zobel et al. 1987). Today, *Eucalyptus* is the most planted tree in the region, followed by *Pinus*, *Hevea*, *Acacia*, and *Tectona*. A plethora of pests and pathogens have been identified in the plantations of these exotic trees (Wingfield et al. 2001a, 2013). However, our understanding of the *Phytophthora* diversity and susceptibility of these exotic trees to this pathogen is largely limited to South Africa (Fig. 1).

The three most important exotic plantation trees in South Africa include species of *Pinus*, *Eucalyptus* and *Acacia mearnsii*. Among these, more than 90% of the plantation land area is dedicated to *Pinus* and *Eucalyptus*. Several native and introduced *Phytophthora* species cause damage to these trees (Wingfield and Knox-Davies 1980; Wingfield and Swart 1994; Linde et al. 1994a, b; Roux and Wingfield 1997; Roux et al. 2012; Wingfield et al. 2001b) (Table 1). *Phytophthora cinnamomi*, for example, causes root and collar rot in some *Pinus* and *Eucalyptus* species (Linde et al. 1994b). Until the early 1990s, *P. cinnamomi* was the only known species associated with these trees. *Phytophthora boehmeriae* and *P. nicotianae* were later isolated from symptomatic *Eucalyptus* species in South Africa (Linde et al. 1994b). In the last decade, two new *Phytophthora* species, *P. alticola* and *P. frigida*, were found to cause collar rot on cold-tolerant eucalypts (Maseko et al. 2007; Bose et al. 2017). Besides this, *P. alticola*, a species of unknown origin, is most likely also responsible for the recent outbreak of post-planting mortality of *E. nitens*, a previously unknown disease that reduced the commercial deployment of this tree in South Africa (Bose et al. 2023).

The most prevalent *Phytophthora* disease of *A. mearnsii* is "black butt," which is caused by *P. nicotianae* (Zeijlemaker and Margot 1970; Zeijlemaker 1971) (Fig. 1). The disease is characterized by the darkening of the bark at the base of the tree, followed by bark cracking and gummosis (Zeiljemaker 1967, 1971; Roux et al. 1995; Roux and Wingfield 1997). Later, *P. boehmeriae* and *P. meadii* were also isolated from symptomatic *A. mearnsii* (Roux and Wingfield 1997). A disease with comparable symptoms was identified in Kenya and Tanzania (Roux et al. 2005). The severity of the disease was greatest in southwestern Tanzania. However, species identification was not conducted (Roux et al. 2005).

All the studies listed above are based on isolation from infected tissue or soil baiting. Therefore, species identification was limited. To address this, Bose et al. (2018) conducted the first study in Africa to catalogue *Phytophthora* diversity from *E. grandis* and *A. mearnsii* plantations (and adjacent native forests) using high-throughput sequencing. In this study, the authors detected 22 *Phytophthora* taxa in the plantation soils, including 12 new reports and many new phylotypes. In a subsequent study, Bose et al. (2021b) also catalogued *Phytophthora* diversity from the roots of these two non-native tree species. In this study, the authors detected 27 *Phytophthora* species, which included seven new reports (Table 1). These two investigations significantly expanded the number of *Phytophthora* species known from South Africa and sub-Saharan Africa as a whole (Fig. 1).

Natural woodlands and veld

The natural woodlands and veld of Africa are iconic. These sub-Saharan ecosystems provide important habitats for both plants and animals. Thus, it is imperative to preserve this ecosystem against both native and invasive pests and pathogens. Various invasive *Phytophthora* species are important pathogens of native plants, particularly in woody ecosystems (Rizzo and Garbelotto 2003; Hansen et al. 2012; Bradshaw et al. 2020; Jung et al. 2020). However, surveys considering *Phytophthora* diversity in natural ecosystems are scarce in sub-Saharan Africa, except for South Africa.

In South Africa, the Cape Floristic Region in the Western Cape Province has received the greatest attention due to its extraordinary floral diversity. The most common *Phytophthora* in the Cape Floristic Region is *P. cinnamomi* (Von Broembsen 1984a; Von Broembsen and Kruger 1985). In this region, this pathogen is known to cause collar- and root-rot of several native plant species from the families *Ericaceae*, *Proteaceae*, and *Bruniaceae* (Von Broembsen 1984a; Von Broembsen and Kruger 1985). *Phytophthora cinnamomi* is one of the most damaging pathogens of various plants from *Proteaceae*, such as species of *Protea*, *Leucospermum*, and *Leucadendron*, including the iconic silver tree, *Leucadendron argenteum* (Van Wyk 1973a, b; Knox-Davies 1975; Von Broembsen 1984a). Subsequently, trials confirmed that species of *Leucadendron* and *Leucospermum* have a higher susceptibility to *P. cinnamomi* than *Protea* (Von Broembsen and Brits 1985). This invasive pathogen was recently identified causing collar and root rot in *Sorocephalus imbricatus*, a critically endangered *Proteaceae* endemic to this region (Paap et al. 2023). Besides this, *P. cinnamomi* was also detected as a pathogen of commercially cultivated proteas in the Southwestern Cape (Von Broembsen and Brits 1985).

Ocotea bullata (stinkwood) is an endemic tree native to South Africa in the family *Lauraceae*. *Phytophthora cinnamomi* was found responsible for the dieback of *O. bullata* in the Eastern Cape Province (Von Broembsen et al. 1986; Lübbe and Geldenhuys 1990; Lübbe and Mostert 1991). Both A1 and A2 mating types of *P. cinnamomi* were recovered from the region. The A2 mating type was primarily associated with the declining trees, whereas the A1 mating type was isolated from asymptomatic trees, seedlings, and soil from undisturbed plots. Hence, it was predicted that the *P. cinnamomi* A2 mating type was pathogenic to *O. bullata* (Von Broembsen et al. 1986).

Several other *Phytophthora* species have been reported from indigenous hosts in the Cape Floristic Region, such as *P. capensis*, *P. citricola*, *P. cryptogea*, *P. drechsleri*, and *P. emzansi* (Von Broembsen 1984a; Nagel et al. 2013a) (Table 1). Among these, *P. emzansi* and *P. capensis* were found infecting cultivated *Agathosma* species, *Curtisia dentata*, and *Olea capensis* (Bezuidenhout et al. 2010). Recently, Bose et al. (2021a) also recovered *P. emzansi* from the rhizosphere soil of *Afrocarpus falcatus*, *Podocarpus elongatus*, and *Rapanea melanophloeos* through surveys conducted by the Cape Citizen Science programme. The authors also isolated a novel species, *Phytophthora afrocarpa*, from the rhizosphere soil of *A. falcatus*, a keystone tree species of the South African afrotemperate forest.

Apart from the Cape Floristic Region, Oh et al. (2013) detected many previously described and potentially novel *Phytophthora* species associated with asymptomatic vegetations while surveying natural forests in five South African provinces. *Phytophthora multivora* emerged as a frequently identified species in this study. Furthermore, a recent population genetics study indicated South Africa as a potential place of origin for *P. multivora* (Tsykun et al. 2022).

Similarly, Bose et al. (2018, 2021b) detected a remarkable diversity of *Phytophthora* from natural forest plots in KwaZulu-Natal and Mpumalanga using high-throughput sequencing technology. The diversity of *Phytophthora* reported in these studies included numerous novel phylotypes, such as *Phytophthora* RSA1A, RSA5A, RSA7A, and RSA10A, as well as species previously unknown from South Africa (Table 1).

Botanical gardens

Botanical gardens are *ex situ* conservation sites. Hence, they curate remarkable plant collections, frequently comprising both native and exotic plant species. Botanical gardens are also an important trade centre for ornamental plants. These activities promote the introduction of new pests and pathogens, as well as natural microbes that infect the exotic plants maintained in the garden. Globally, botanical gardens are frequently seen as an excellent venue for the early detection of pests and pathogens, such as *Phytophthora* species (Britton et al. 2010; Paap et al. 2017; Wondafrash et al. 2021). Nevertheless, there is only one survey from sub-Saharan Africa that studied *Phytophthora* species in botanical gardens.

Hulbert et al. (2019) surveyed three botanical gardens and one urban garden in the Western Cape Province of South Africa. Through this study, the authors detected nine previously described species: *P. amnicola*, *P. asparagi*, *P. capensis*, *P. cinnamomi*, *P. chlamydospora*, *P. emzansi*, *P. lacustris*, *P. multivora*, and *P. tropicalis*, along with three potential hybrids: *P. amnicola* × *P. chlamydospora*, *P. hydropathica* × *P.* sp. Maryland, and *P. pseudocryptagea* × *P. cryptogea*. Of the species discovered in this study, *P. amnicola*, *P. asparagi*, and *P. tropicalis*, as well as the three potential hybrids, are the first to be recorded from South Africa. This research demonstrates the need to conduct comparable investigations in sub-Saharan African botanical gardens to strengthen the plant quarantine system and expand our knowledge of the diversity of *Phytophthora* from this region.

Plant nurseries

Plant nurseries serve as an important gateway for the introduction of exotic plant pathogens, such as *Phytophthora* species. This is because nurseries provide an optimal environment for the reproduction and hybridization of these invasive *Phytophthora* species, as well as facilitating their dispersal and establishment in various ecosystems (Brasier 2008). Numerous studies in Europe and North America have thoroughly investigated the role of nurseries in spreading *Phytophthora* diseases (Reichard and White 2001; Jones and Baker 2007; Jung et al. 2016). Such research from sub-Saharan Africa, on the other hand, is sparse. A few studies, however, have been undertaken in South Africa. Marais (1980) reported five *Phytophthora* species from grapevine nurseries, including *P. cactorum*, *P. cinnamomi*, *P. cryptogea*, *P. megasperma*, and *P. nicotianae*. However, about 30 years later, Spies et al. (2011) and Langenhoven et al. (2018) only found *Phytophthora niederhauserii* in such nurseries. This pathogen is a polyphagous species that has also been detected in various plant nurseries globally (Abad et al. 2014). *Phytophthora cinnamomi* has also been isolated from forest and buchu (*Agathosma* species) nurseries in South Africa (Donald and von Broembsen 1977; Bezuidenhout et al. 2010), which may have played a role in its dispersal to natural vegetation in the Western Cape Province. In the South African citrus industry, nursery plants were identified as a major pathway for the dispersal of *Phytophthora* to established orchards in South Africa. The Citrus Improvement Scheme (CIS) was subsequently introduced to improve the quality and pathogen status of citrus nursery plants supplied to producers. Recommendations from the CIS resulted in a reduction of the incidence of *Phytophthora* in nursery samples from 78% to less than 2.5% (Pretorius 2019). Recently, *Phytophthora multivesiculata* was identified by Bose and Hammerbacher (2023) from an orchid nursery in Gauteng Province causing black rot of ornamental *Cymbidium* hybrids and *Ansellia africana*, a native species. Follow-up research revealed that *P. multivesiculata* is not exclusively limited to orchid nurseries in Gauteng and also affects numerous other orchid species in the subfamily Epidendroideae (Bose unpublished).

When comparing the diversity of *Phytophthora* species between soil and roots in plantations using next-generation sequencing, Bose et al. (2021b) identified four species that were exclusively present in the roots of *Eucalyptus grandis* and *Acacia mearnsii*. These were *P. constricta, P. rosacearum*, *P. kwongonina*, and *P. thermophila*. This data showed that there could be an alternative source of *Phytophthora* inoculum other than plantation soil infecting these non-native plantation trees, which could have been introduced from nurseries. However, rigorous surveys are necessary to prove this hypothesis. The absence of these surveys might have irreversible implications in future, as demonstrated by *Fusarium circinatum*. This fungus was first detected in a nursery in South Africa (Viljoen et al. 1994) and is now an established pathogen of pines in plantations, causing substantial economic losses (Mitchell et al. 2012; Mitchell et al. 2011). A similar trend has been echoed by various *Phytophthora* species elsewhere in the world (Moralejo et al. 2009; Bienapfl and Balci 2014), including the infamous *P. ramorum* (Grünwald et al. 2012).

Aquatic ecosystems

Phytophthora species are ideally adapted to water environments, which provide these organisms with suitable living conditions as well as an easy pathway to propagate and reach suitable plant hosts, hence promoting the expansion of their habitat. *Phytophthora* research in aquatic environments indicates that this ecosystem can be used for the early detection of new species and hybrids (Man in't Veld et al. 1998; Jung et al. 2011; Reeser et al. 2011; Hüberli et al. 2013; Yang et al. 2014; Burgess 2015; Jung et al. 2016; Stamler et al. 2016). Three *Phytophthora* diversity studies have been undertaken from aquatic environments in sub-Saharan Africa, all from South Africa.

The first survey was conducted by Nagel et al. (2013b). In this study, the authors detected eight *Phytophthora* species, including a novel taxon, *P.* taxon Sisulu-river, as well as two hybrid species from the Crocodile River in the Gauteng Province of South Africa. Clade 6 *Phytophthora* species were the most abundant and included *P. chlamydospora* and *P. lacustris*. *Phytophthora multivora*, *P. plurivora*, and *P. citrophthora* represented the clade 2 species. Clade 6 hybrids included T-A (*P. thermophila* × *P. amnicola*) and A-PG (*P. amnicola* × *P. chlamydospora*). Both these hybrids were distinguished by a highly polymorphic ITS region (Nagel et al. 2015). Following this study, putative hybrids from clade 9, *P.* sp. ×WS and *P.* sp. × Hennops were also discovered in South African streams (Oh et al. 2013). In addition to these two studies, Bezuidenhout et al. (2010) identified *Phytophthora capensis* from both plant samples from endemic shrubs as well as stream water in Western Cape Province, and Von Broembsen (1984b) identified *P. cinnamomi* from all major rivers of this province. Nevertheless, subsequent studies failed to confirm the latter's observation.

There is an urgent need to catalogue aquatic *Phytophthora* species from sub-Saharan Africa, as has been done elsewhere in the world. This is because several *Phytophthora* hybrids are emerging plant pathogens, such as *P. alni* and its variants (Brasier et al. 1999), *Phytophthora* × *pelgrandis* (Bonants et al. 2000; Faedda et al. 2013; Hurtado-Gonzales et al. 2009; Man in't Veld et al. 2012; Nirenberg et al. 2009), and *Phytophthora* × *serendipita* (Man in 't Veld et al. 2007, 2012). These hybrids, such as those from ITS clades 8 (Bertier et al. 2013; Jafari et al. 2020) and 1 (Ersek et al. 1995; Man in 't Veld et al. 2007), have expanded their host ranges and evolved novel virulence factors with isolates becoming more aggressive while overcoming the limitations of their parental species by obtaining and recombining alleles or genes from both parents, followed by rapid evolution (Brasier 2000, 2001; Bertier et al. 2013). Meanwhile, among the four clade 6 hybrids, A-PG and T-A were detected from South Africa (Nagel et al. 2013b). Isolates of these hybrid *Phytophthora* species obtained from South Africa were also found in soils of declining vegetation in Western Australia, indicating that they may pose a risk to plant health. However, no further investigation into their pathogenicity on native South African plant species and crops was conducted.

How can we bridge the current knowledge gaps?

This review summarised both the historic and the current *Phytophthora* species diversity and research in sub-Saharan Africa. In the last decade, several important studies have been conducted that partially filled the knowledge gaps on *Phytophthora* research in this region, with a significant number of them being carried out in South Africa. These studies focused on species diversity, population genetics, and developing disease-resistant crop varieties. Still, there is a paucity of *Phytophthora* research in various parts of sub-Saharan Africa. In the future, this pitfall might have irreversible effects on the floral biodiversity, food security, and economy of this region.

Except for South Africa, large-scale *Phytophthora* biodiversity studies are currently missing from the remainder of sub-Saharan Africa (Fig. 1). This is evident from the species lists from this article with that of Nagel et al. (2013a), Scott et al. (2013), and Marcot et al. (2023). Previously, 22 *Phytophthora* species had been recorded from South Africa (Scott et al. 2013); this number has now grown to 68. These additional species include new reports, species, hybrids, and phylotypes. However, the species list remained the same for most other countries in the region (Scott et al. 2013; Marcot et al. 2023) (Fig. 1). *Phytophthora* has not been documented in a few sub-Saharan countries, including Namibia, Botswana, Benin, and a few others (Fig. 1). As exemplified by the Cape Citizen Science programme (https://citsci.co.za/), diversity studies can be performed inexpensively and with the involvement of local communities (Hulbert 2016; Hulbert et al. 2023). Through this programme, diversity studies were conducted in the Greater Cape Floristic Region, allowing the detection of novel species, previously unreported species, and potential new hybrids (Hulbert et al. 2019; Bose et al. 2021a). Furthermore, this programme trained amateur science enthusiasts with skills to detect plant diseases, collect samples, isolate microbes, and much more. Similar approaches and platforms could be employed to address the current lack of diversity studies from other countries in sub-Saharan Africa. Besides this, data emerging from such diversity studies will also provide crucial information that can be utilized by future studies, such as the one recently conducted by Marcot et al. (2023) as well as by governments to increase the efficacy of current quarantine measures in the region.

In this century, several *Phytophthora* species have been described from Sub-Saharan Africa and many previously known species have been isolated from new hosts and environments. However, in most cases, the pathogenicity of these *Phytophthora* species has not been determined. An important example of this is *Phytophthora multivora*, a recently described species with a broad host range (Scott et al. 2009; Migliorini et al. 2019). This species, although previously reported as *P. citricola*, is an emerging pathogen that has featured increasingly in reports of *Phytophthora* in South Africa, both from agricultural and natural environments (Bezuidenhout et al. 2010; Oh et al. 2013; Meitz-Hopkins et al. 2014; Bose et al. 2018, 2021b; Hulbert et al. 2019; Spies unpublished). Consequently, the impact of this species on food safety and security in sub-Saharan Africa and the conservation of local flora is largely unknown. Studies to investigate the pathogenicity of newly reported species, as well as newly discovered species such as *P. afrocarpa* (Bose et al. 2021a), should be prioritised to elucidate the extent to which they threaten crop production and the indigenous vegetation in sub-Saharan Africa.

Achieving food security continues to be a challenge in Africa. In this scenario, our knowledge of *Phytophthora* species affecting agriculture in sub-Saharan Africa is predominantly restricted to *P. cinnamomi*, *P. infestans,* and *P. nicotianae*. However, other *Phytophthora* species have comparable effects on various other crops from the region, such as *P. megakarya* and *P. colocasiae*. The impact of *P. megakarya* on cacao production is affecting the economies of West and Central Africa through reduced yield (Akrofi et al. 2015). Similarly, taro leaf blight is a major constraint to taro production in Central and West Africa. However, our current knowledge of this pathosystem is sparse (Oladimeji et al. 2022). These shortfalls can be addressed by launching population genetic studies involving both hosts and pathogens as well as selective breeding programmes for developing disease-resistant crop varieties, as has been done for potatoes and avocados.

Sub-Saharan Africa is particularly vulnerable to the negative effects of climate change (Pereira 2017). In sub-Saharan Africa, the average temperature has increased by 0.5 °C over the past century (Kotir 2011) and is projected to increase by more than 2 °C by the end of 2100 (Niang et al. 2014). At the same time, the region has limited financial resources and a lack of advanced infrastructure and technology, which further increases its vulnerability (Di Falco 2014; Fisher et al. 2015; Mall et al. 2017). Simultaneously, we know that climate change will positively influence the distribution, invasiveness, and pathogenicity of various *Phytophthora* species globally, such as *P. cinnamomi* (Burgess et al. 2017), *P. infestans* (Sparks et al. 2014), and *P. ramorum* (Venette and Cohen 2006). In this scenario, it is essential to estimate the impact of climate change on native *Phytophthora* species from the region, such as *P. alticola, P. colocasiae* and *P. megakarya*. For example, *P. alticola*, which was previously a minor pathogen in South Africa, is now causing significant post-planting mortality of *E. nitens* (Bose et al. 2023). Since *E. nitens* is adapted to cold climates, it was hypothesised that warming temperatures might be the cause of its increased susceptibility to *P. alticola*.

Conclusions

Phytophthora research in sub-Saharan Africa has gained some momentum in the last decade. Nonetheless, a substantial portion of this research was undertaken in South Africa. This is because a majority of sub-Saharan Africa includes developing nations, with inadequate resources and funding for performing basic research. In an era of globalisation, the negative impact of *Phytophthora* and other understudied plant diseases on Africa's food security, economy and sustainability will extend beyond the continent's boundaries. Furthermore, currently, unknown and undescribed *Phytophthora* species and hybrids from the African continent may pose a significant risk to global crop production and plant health. Therefore, global research funding organisations should strongly consider supporting plant protection research in sub-Saharan Africa.

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Declarations

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