Chapter 1

Biology and ecology of *Ceratocystis* species with an emphasis on their insect associations

1.1. INTRODUCTION

The genus *Ceratocystis* Ell. & Halst. includes many pathogens of mostly woody and some herbaceous plant species, globally. These fungi result in a variety of disease symptoms, including branch and stem cankers, vascular staining, wilting and root disease, often leading to mortality of infected plants (Kile 1993). Some of the well known tree pathogens include *C. fagacearum* (Bretz) Hunt, the causal agent of oak wilt (Bretz 1952, Sinclair *et al*. 1987), *C. fimbriata sensu stricto* (*s.s.*) Ell. & Halst. that causes black rot of sweet potato (Halstead 1890, Engelbrecht & Harrington 2005), *C. albifundus* M. J. Wingf., De Beer & M. J. Morris the cause of Ceratocystis wilt of Australian wattle trees (Morris *et al*. 1993, Wingfield *et al.* 1996), *C. laricicola* Redfern & Minter infecting larch (Redfern *et al*., 1987), *C. polonica* (Siem) Moreau that results in blue stain of Norway spruce (Solheim 1986) and *C. platani* (Walter) Engelbrecht & Harrington which is the cause of an important canker stain disease of plane trees (Mook 1940, Walter 1946, Ferrari & Pichenot 1975, Tsopelas & Angelopoulos 2004, Engelbrecht & Harington 2005).

Ceratocystis spp. pose and increasing threat to plantation forestry based on hardwood species in the tropics and Southern Hemisphere. Whereas before the 1980's there were no reports of hardwood tree species being affected by *Ceratocystis* spp., a number of reports of such diseases have emerged in the last 20 years particularly form Africa (Wingfield 1990, Morris *et al*. 1993, Roux *et al.* 2000, Roux *et al.* 2001a,b, Roux *et al.* 2004b, Roux *et al.* 2005) and South America (Ribeiro *et al*. 1985, Barnes *et al*. 2003a, Rodas *et al*. 2008). These reports have included the description of previously unknown *Ceratocystis* spp., thus also illustrating the limited information currently available regarding the species diversity of this genus.

Information pertaining to *Ceratocystis* spp. in Africa is limited. Apart from the few records from plantations there are reports of these fungi from agricultural crops and indigenous plants (Kihurani *et al*. 2000, Crous *et al*. 2000). Studies in the last five years have resulted in a number of reports of *Ceratocystis* spp. from native trees in southern and eastern Africa, including the description of previously unknown species (Roux *et al.* 2005, 2007, Kamgan *et al*. 2008). This highlights the lack of information regarding these fungi on the continent and emphasising the fact that many important pathogens still await description and study.

The taxonomic history of the genus *Ceratocystis* is complex and has been debated extensively in the past (De Hoog & Scheffer 1984, Upadyay 1993, Samuels 1993, Wingfield 1993). Numerous species concepts have been applied since the establishment of the genus and only with the use of the phylogenetic species concept have the most crucial issues been resolved. However, problems still persist for emerging groups now recognised to reside in the genus, as neither the morphological, nor the phylogenetic species concepts are sufficiently robust to delineate species with certainty (Engelbrecht & Harrington 2005, Wingfield *et al*. 2006). Currently, a combination of the morphological, biological and phylogenetic species concepts is necessary to delineate species (Engelbrecht & Harrington 2005, Wingfield *et al*. 2006).

Ceratocystis spp. have evolved several characteristics to ensure successful dispersal and infection of plants. These specifically include characteristics making them suitable for insect dispersal (Leach *et al*. 1934, Ingold 1961, Griffin 1968, Lanza & Palmer 1977). The insects either create wounds, or visit fresh wounds on plants, thus disseminating *Ceratocystis* spp. Species in the genus can have casual vectors such as nitidulid beetles (Coleoptera: Nitidulidae) (Jewell 1956, Moller & DeVay 1968, Harrington 1987) and flies (Griswold 1953, Moller & DeVay 1968, Hinds 1972) or mutualistic vectors such as bark beetles (Coleoptera: Scolytidae) (Kirschner 2001). Both the fungal and insect associates have a number of chemical and physical adaptations to facilitate the association between them (Leach *et al*. 1934, Ingold 1961, Lanza & Palmer 1977).

The aim of this review is to briefly summarise the taxonomic history of the genus *Ceratocystis*, to provide a review of knowledge pertaining to the biology of these fungi and most importantly to consider their symbiotic relationships with insects. Other important issues, such as the economic importance of these fungi and their requirement for wounds as infection sites are also highlighted using key examples. The intention here is to provide a foundation for the studies presented in the thesis that follows the review. The latter product focuses specifically on expanding the knowledge base regarding species of *Ceratocystis* on non-native plantation tree species in Africa.

1.2. TAXONOMIC HISTORY OF THE GENUS *CERATOCYSTIS*

The taxonomic history of the genus *Ceratocystis* is complex and has encompassed many changes during the course of the past 120 years (Figure 1). The genus was first established by Ellis & Halsted in 1890 for the species *Ceratocystis fimbriata*, after it was found associated with black rot of sweet potato in the United States of America (USA) (Halsted 1890). During subsequent years, *C. fimbriata* was treated in many different genera, including *Ophiostoma* Sydow & Sydow, *Sphaeronema* Sacc., *Endoconidiophora* Münch, *Rostrella* Zimm. and *Ceratocystiopsis* H.P. Upadhyay & W.B. Kendr. (Upadhyay 1981).

Much of the confusion surrounding the taxonomy of *Ceratocystis* and similar genera was due to the similarity of morphological structures of these fungi. Fungi in the above mentioned genera typically all have long, beaked ascomata with spores produced at their apices in sticky masses. Ascospores are generally produced in evanescent asci (Elliot 1923). It is thus not surprising that today, morphology is not used as the only technique for species identification and new descriptions in these genera.

Numerous techniques and criteria have been applied to clarify the taxonomy of the genus *Ceratocystis*. One of the first techniques to be used was the separation of genera based on their associated anamorphs (Melin & Nannfeldt 1934, Bakshi 1951, Kendrick 1971, Nag Raj & Kendrick 1975, Upadhyay 1981). Another technique commonly applied was to distinguish between genera based on ascospore morphology (Bakshi 1951, Olchowecki & Reid 1974, Upadhyay & Kendrick 1975). Biochemical characteristics, such as the composition of the cell walls and sensitivity and tolerance to antibiotics, were also distinguishing factors for genera (Fergus 1956, Smith *et al*. 1967, Jewell 1974, Weijman & De Hoog 1975, Harrington 1981). Ultrastructural differences, for example, the development of teleomorph structures, types of cells present and the construction of the cell walls were also used to distinguish between genera in *Ceratocystis sensu lato* (Benny & Kimbrough 1980, Van Wyk *et al*. 1991, Van Wyk *et al*. 1993). More recently, DNA sequence data have been utilized to distinguish between genera and species (Hausner *et al*. 1992, 1993a, b, c, Spatafora & Blackwell 1993, 1994, Wingfield *et al*. 1994, 1996, Witthuhn *et al*. 1998, 1999, Barnes *et al.* 2003a, Johnson *et al.* 2005, Van Wyk *et al.* 2004a, b, 2006). The latter approach that has applied the phylogenetic species complex has contributed substantially to resolving confusion regarding the taxonomic position of *Ceratocystis*.

The difficulty with the morphological description of *Ceratocystis* and the species accommodated in the genus is well illustrated from the first description of *Ceratocystis*. Halsted & Fairchild (1891), incorrectly identified the ascocarps of *C. fimbriata* as pycnidia and the ascospores as conidia. This was perhaps understandable given the fact that the asci delequese very early in the development of the ascomata. Saccardo (1892), unaware of the oversight of Ellis & Halsted, transferred *C. fimbriata* to *Sphaeronema* as *S. fimbriatum*. In 1918, *S. fimbriatum* was transferred to *Linostoma* (Fr.) Hohn., a genus split from *Ceratostomella* Sacc., based on its dark coloured perithecia with long necks and ovoid asci containing spores arranged in several rows (Von Höhnel 1918). However, the name *Linostoma* had previously been assigned to a genus of flowering plants in the *Thymeleacaeae* Juss., forcing Sydow and Sydow (1919) to establish the genus *Ophiostoma.* They relegated all the species previously in *Linostoma* to this newly established genus, separate from *Ceratostomella*.

Approximately three decades after *Ceratocystis* was first described, Elliott (1923), not accepting the changes made by Von Hönel (1918), found that the incorrectly identified pycnidia of *C. fimbriata* were in fact perithecia with ascospores emerging from deliquescent asci. He transferred *O. fimbriatum* to *Ceratostomella* (Elliot 1923). Later, Melin & Nannfeldt (1934), reduced the genus *Endoconidiophora*, which was established for species that formed conidia endogenously, to synonymy with *Ceratostomella*. They also transferred *Ceratostomella fimbriata*, *Ce. paradoxa* (Dade) Moreau and *Ce. adiposa* Butl. back to *Ophiostoma*, due to the fact that they had *Chalara* (Corda) Rabenh. conidial states (Melin & Nannfeldt 1934). Melin & Nannfeldt (1934), stated that the oldest genus name, *Endoconidiophora,* should be used, but this name would be confusing and thus they suggested the genus name *Ophiostoma,* until a more suitable name could be found.

Bakshi (1951), not accepting the taxonomic placement of *Ceratocystis* and other genera at that time, reduced *Ceratostomella, Linostoma*, *Ophiostoma* ,*Grosmannia, Rostrella* Zimmermann, *Ceratocystis* and *Endoconidiophora* to three, namely *Ceratostomella* (including only *Ceratostomella*), *Ophiostoma* (including *Linostoma*, *Ophiostoma* and *Grosmannia*) and *Ceratocystis* (including of *Rostrella*, *Ceratocystis* and *Endoconidiophora*). The type species, *O. fimbriatum,* was also transferred to *Ceratocystis* as *C. fimbriata* (Bakshi 1951). This caused considerable debate amongst mycologists working with these fungi with some authors not accepting this classification (Moreau 1952, Von Arx 1952, Von Arx & Műller 1954). Upadhyay (1981), chose to synonymise all the above genera and treated them as one genus, namely *Ceratocystis*. However, together with this genus he established *Ceratocystiopsis* based on the differences in the morphology between these fungi and *Ceratocystis* (Upadhyay & Kendrick 1975).

Species of *Ceratocystis* have been noted to have distinct differences based on morphology, physiology and molecular data when compared to *Ceratocystiopsis* and *Ophiostoma* (Smith *et al*. 1967, Weijman & De Hoog 1975, Harrington 1981, De Hoog & Scheffer 1984, Hausner *et al*. 1993a), while common characteristics are often shared between *Ceratocystiopsis* and *Ophiostoma* (De Hoog & Scheffer 1984, Hausner *et al*. 1993a, Wingfield 1993). Wingfield (1993), therefore synonymised the genus *Ophiostoma* with *Ceratocystiopsis*. The taxonomic debate was muted when Hausner *et al*. (1993a, b, c) utilized DNA sequence data for distinction between *Ceratocystis* and *Ophiostoma*.

The emergence of DNA-based techniques has had a significant impact on the taxonomic status of *Ceratocystis* and other fungi. These techniques, and particularly DNA sequence-based phylogenies, have shown clearly that *Ceratocystis* represents a very distinct genus and resides in a different order (Microascales) from the morphologically similar genera with which it had been confused in the past (Hausner *et al*. 1993a, b, c, Spatafora & Blackwell 1994). Several studies using DNA sequence data of the large sub-unit (LSU), ribosomal RNA (rRNA) (Hausner *et al*., 1993a,b, Wingfield *et al*. 1994) and the small sub-unit (SS) rRNA (SSrRNA) (Hausner *et al*.

1992, 1993a, b) have confirmed the uniqueness of the genus *Ceratocystis*. Recently, this was supported by Blackwell and co-authors (2006).

An important result of using DNA sequence data to elucidate the taxonomy of the genus *Ceratocystis* was the discovery by Witthuhn *et al*. (1998) that two distinct phylogenetic groups could be recognised within the genus. These two groups were referred to as the Fimbriata group and the Coerulescens group (Witthuhn *et al*. 1998). However, due to the similarity of some of the species at a single gene, multiple gene geneologies have become a necessity in studying *Ceratocystis* spp. (Van Wyk *et al.* 2004a, b, Engelbrecht & Harrington 2005, Johnson *et al*. 2005, Van Wyk *et al*. 2006, 2007a, b, Kamgan *et al*. 2008). Commonly used genes in multi gene phylogenies include, the Transcription Elongation Factor 1-α (EF1-α), the Internal Transcribed Spacer Region including the 5.8S rRNA operon (ITS), the Beta-tubulin gene regions and Mating type genes (Barnes *et al.* 2003a, Marin *et al*. 2003, Johnson *et al.* 2005, Van Wyk *et al.* 2004a, b, 2006, 2007a, b). Using multi gene phylogenies, it has been found that *Ceratocystis* in fact represent at least three distinct genera (Wingfield *et al.* 2006). However, this distinction has not yet been formalised and currently, *Ceratocystis* is best thought of as including three phylogenetic groups, namely the Fimbriata, Coerulescens and Moniliformis groups (Wingfield *et al*. 2006).

Within some of the groups in the genus *Ceratocystis*, the phylogenetic species concept is not sufficient to delineate between species. Due to this insufficiency, Engelbrecht & Harrington (2005), applied a combination of the morphological and biological species concepts to separate species within the *C. fimbriata s.l.* species complex. In the study, the authors separated *C. fimbriata s.s*. from other taxa in what has now become known as the *C. fimbriata s. l.* species complex. The complexity of the *C. fimbriata s.l.* group, however, requires considerable additional work and new species are being described within this complex annually. In future studies, a combination of the morphological, biological and phylogenetic species concepts will prove necessary to clarify the taxonomic status of species complexes in the genus *Ceratocystis*.

1.3. IMPORTANCE OF *CERATOCYSTIS* SPP.

The genus *Ceratocystis* includes both saprophytes and important primary plant pathogens of angiosperms and gymnosperms. The saprophytic fungi are usually known for their sap staining ability (Von Shrenck 1903, Kile 1993). Although these fungi do not have a detrimental effect on their hosts, they decrease the value of the timber products produced from them (Davidson 1935). The pathogenic species include fungi causing diseases of agronomic crops, fruit trees and timber trees including conifers and hardwood species (Kile 1993, Roux & Wingfield 2007). *Ceratocystis* spp. infect roots, stems and fruit, causing a range of symptoms from rot and canker to stains, wilt and death of their hosts. Species in the genus includes some of the best known tree pathogens including *C. fagacearum*, the cause of oak wilt in the USA (Bretz 1952, Sinclair *et al*. 1987), *C. cacaofunesta* Engelbrecht & Harrington the cause of canker disease of *Theobroma cacao* L. (cacao) (Desrosiers 1958, Malaguti 1952, Idrobo 1958, Goberdhan 1959, Havord 1962, Schieber 1969, Bezerra 1997, Delgado & Suarez 2003) and *C. platani*, the cause of canker of plane trees (Mook 1940, Walter 1946, Walter *et al*. 1952, McCracken & Burkhardt 1977, Panconesi 1981, Matasci & Gessler 1997, Panconesi 1999, Tsopelas & Angelopoulos 2004).

In the following section a number of the most important examples of *Ceratocystis* spp. causing diseases of agricultural crops and trees are highlighted. As the focus of this review is on *Ceratocystis* spp. and their role in forest species, we only present a short overview of some of the most important *Ceratocystis* spp. on agricultural plants and forestry species, with emphasis on examples of *Ceratocystis* spp. causing diseases of forest trees, to present some background for the rest of the chapters presented in this dissertation. For more information on diseases of agricultural crops reference can be made to publications by Harrington (2004). An extensive list of *Ceratocystis* spp. that are proven tree pathogens (Table 2) and those which are considered saprophytes and staining agents or for which no clear role as pathogens have been established (Table 3) in forests and plantations are presented at the end of this review.

1.3.1. *Ceratocystis* spp. infecting agricultural crops

Ceratocystis cacaofunesta

Ceratocystis cacaofunesta, previously part of the *C. fimbriata s.l* species complex, was first reported infecting cacao (*Theobroma cacao*), as *C. fimbriata,* in 1918 from South America (Desrosiers 1958, Delgado & Suarez 2003) and has since then been recorded killing trees in numerous countries (Malaguti 1952, Idrobo 1958, Goberdhan 1959, Havord 1962, Schieber 1969, Bezerra 1997). Although *C. cacaofunesta* has had an impact on cacao production, the disease currently has little effect as it is managed by the use of resistant planting stock (Simmonds 1994).

Ceratocystis fimbriata s.s.

Ceratocystis fimbriata s.s. was the first *Ceratocystis* sp. reported to infect an agricultural crop. It was first reported causing black rot of sweet potatoes (*Ipomoea batatas* L.) in the USA in 1890 (Halsted 1890). One year after its first discovery, almost all sweet potato growers in the main sweet potato production area in the USA were affected by black rot (Halsted & Fairchild 1891). Although black rot of sweet potato had a destructive impact on the production of the crop, it is today relatively uncommon as a result of the implementation of integrated disease control (Kihurani *et al.* 2000).

Ceratocystis paradoxa

Ceratocystis paradoxa was first reported from pine-apple (*Ananas comosus* (L.) Merr.) in France in 1886 (De Seynes 1886). Since then, the fungus has been reported from coconut palm (*Cocos nucifera* L.) (Dade 1928), oil palm (*Elaeis guineensis*), date palm (*Arecu cathecu* L.) (Kile 1993) and sugar cane (*Saccharum officinarum* L.) (Lewton-Brain 1907, McMartin 1937, Chang & Jensen 1974). The disease occurs in the tropics (Ploetz *et al*. 2003) and has been reported from approximately 40 countries (Wismer 1961).

A number of modes of transmission have been reported for *C. paradoxa*. Numerous authors feel the most common mode of transmission is by means of insects. These include *Carpophilus hemipterus* L., *Urophorus humeralis* F., *Haptoncus ocularis* Fairmaire (Chang & Jensen 1974) and flies (Chi 1949). It has also been reported that the fungus can be dispersed by means of infected soil and cuttings, and via air dispersal (Wismer 1961). Similar to a number of *Ceratocystis* spp., *C. paradoxa* requires wounds for infection. These wounds could be created by insects, rats and mechanical damage (Fawcett 1931, Wismer 1961, Chan & Jensen 1974) or silvicultural practices such as the preparation of cuttings (Wismer 1961).

Symptoms associated with pineapple disease include butt rot and leaf spot of pineapples and rot of pineapple fruits (De Seynes 1886, Ploetz *et al*. 2003), germination failure sugar cane seeds, rot of sugar cane cuttings and stems and death of pineapple stalks and wilting of leaves (Wismer 1961). The disease affects all sugar cane growing areas (Wismer 1961) and has been reported to lead to serious crop failure (McMartin 1944, Chi 1949, Antoine 1956).

Crop losses of between 20 and 80% have been reported (Dickson *et al*. 1931). To date, a number of control strategies have been developed for pineapple disease which include cultural techniques such as selection of cutting size and planting stock and seed treatment (Wismer 1961), selecting the correct planting time as well as the use of fungicides (Wakker & Went 1898, Ploetz *et al.* 2003).

1.3.2. *Ceratocystis* spp. infecting fruit-tree crops

Ceratocystis fimbriata s.l.

Numerous fungi that resembles *C. fimbriata* s.s. in morphology have been lumped together as *C. fimbriata s.l.* These fungi have been reported from a multitude of hosts and from most continents. Their impact on agricultural crops is significant, causing diseases such as canker of stone fruit (*Prunus* spp. L.) (DeVay *et al*. 1963), canker wilt and death of coffee (*Coffea* L.) (Obregon 1936, Pontis 1951, Szkolnik 1951, Echandi & Segall 1956) and citrus (*Citrus* L.) (Contreras & Marmelioz 1984, Instituto Colombiano Agropecuario 1993). The fungus has been reported to be the most serious pathogen of coffee and has affected approximately 800 000 hectares of coffee cultivating areas in South America (Castro 1998). *Ceratocystis fimbriata s.l.* infection of citrus has had a significant affect on the citrus industry. Since its report in 1981 to 1994, the disease had lead to the death of 10% of lemon trees in Colombia

(Mourichon 1994).

Ceratocystis manginecans

Ceratocystis manginecans M. van Wyk, A. Al Adawi & M. J. Wingf. was first reported as *C. fimbriata* in 2005, infecting mango trees in Oman (Van Wyk *et al*. 2005, Al Adawi *et al*. 2006). In 2007, the fungus infecting mango was re-described as a distinct species namely *C. manginecans* (Van Wyk *et al*. 2007a). This pathogen leads to gummosis as well as vascular discolouration, cankers and wilting of leaves (Van Wyk *et al*. 2005, Al Adawi *et al*. 2006). Tree mortality was observed to occur six months after the appearance of symptoms (Al Adawi *et al*. 2006).

1.3.3. *Ceratocystis* spp. as pathogens of forest and plantation trees

Ceratocystis albifundus

Ceratocystis albifundus, the causal agent of Ceratocystis wilt of Australian *A. mearnsii* in Africa, is considered one of the most important pathogens of non-native *A. mearnsii* trees on the continent (Morris *et al*. 1993, Roux & Wingfield 1997, Roux *et al*. 1999, Roux *et al*. 2005). Infection by *C. albifundus* leads to wilting and finally mortality of trees (Roux *et al*. 1999). This pathogen affects trees of all ages and is able to kill trees ao all ages under field conditions. The fungus has also been shown to lead to wilting and mortality of mature trees within six weeks after artificial inoculation (Roux *et al*. 1999). The fungus has also been reported on eight native host genera from the African continent (Roux *et al*. 2007). Although *C. albifundus* produces lesions after artificial inoculation on native tree species, mortality has not been observed in the native vegetation (Roux *et al*. 2007).

Ceratocystis fagacearum

Ceratocystis fagacearum causes oak wilt (Bretz 1952, Sinclair *et al*. 1987) of *Quercus* spp. L. in the USA. Other known hosts of this fungus are *Castanea mollissima* Blume, *C. sativa* Mill., *Lithocarpus densiflorus* (Hook. & Arn.) Rehd., *Castanopsis sempervirens* (Kellogg) Hjelmqvist and most genera in the Fagaceae (Bretz 1952). In 1944, a survey of oak trees in Wisconsin revealed that more than half the trees in a localised area of 40.4 ha had been killed by *C. fagacearum* (Rexrode & Brown 1983).

A second study investigating eight counties in Wisconsin reported that approximately 11% of the annual growth increase of oak forests was offset by mortality of the trees caused by oak wilt (Rexrode & Brown 1983).

Ceratocystis fagacearum seems to have a loose association with a number of insect species that are not known to be primary pests and are not able to create wounds on the host trees (Gibbs 1980, Juzwik & French 1983). These insects include *Carpophilus dimidiatus, Ca. sayi, Euporaea labilis* and *E. peltoides*. Transmission of *C. fagacearum* by nitidulid beetles is significant in overland spread of the fungus and the establishment of new infection centres (Cease & Juzwik 2001). The beetles are attracted to sporulating mats on recently killed oak trees, and after feeding on these mats, they are covered in fungal propagules which they subsequently spread to other trees (Juzwik & French 1983). These insects only disseminate the fungus to fresh wounds and do not seem to benefit from the association.

Ceratocystis fimbriata s.l.

Species in the *C. fimbriata s.l.* species complex have been reported to cause death of several plantation grown tree species. Hosts include rubber trees (*Hevea brasiliense* Muell.) (Olson & Martin 1949), *Eucalyptus* spp. (Roux *et al*. 2000) and *Acacia* spp. (Ribeiro *et al.* 1985). This fungus was first reported to cause disease and mortality of non-native hardwood tree species in the late 1980's when it was reported from *A. decurrens* Willd. in South America (Ribeiro *et al.* 1985). It was later reported from *Eucalyptus* spp. growing in the Republic of Congo (Roux *et al*. 2000), where infection leads to rapid wilting, discoloration of the xylem and mortality of trees ranging from six months to four years (Roux *et al*. 2000). Shortly thereafter, the fungus was also reported as the cause of disease of *Eucalyptus* spp. in Uganda and Uruguay (Roux *et al*. 2001a, Barnes *et al*. 2003b).

In 2004, *C. fimbriata s.l.* was reported to infect wounds of *Eucalyptus* spp. in South Africa (Roux *et al*. 2004b). It is, however, interesting to note that to date, *C. fimbriata s.l.* has not been reported to be associated with disease of *Eucalyptus* spp. in South Africa. This could be due to the influence of climate as the areas where *C. fimbriata s.l.* has been reported to cause disease of *Eucalyptus* spp., is more tropical than the areas where *C. fimbriata s.l.* has not been reported to cause disease. Another explanation for the difference in the pathology of the fungus on these hosts in the different areas could be due to the presence of resistant plant material in the areas where the fungus does not lead to severe disease problems.

Ceratocystis fujiensis

Ceratocystis fujiensis M. J. Wingf., Yamaoka & Marin is a pathogen of *Larix kaempferi* (Lamb.) Carrière that has recently been described from Japan (Marin *et al*. 2005). This species was reported during a study of two closely related species, *C. polonica* and *C. laricicola* in Europe and Japan (Marin *et al*. 2005). *Ceratocystis fujiensis* is morphologically indistinguishable from *C. laricicola* but has been shown to be a distinct species based on DNA sequence comparison and ecological aspects. The ecological aspects include the insect associates of these two species, as *C. laricicola* is associated with *Ips cembrae* Heer, and *C. fujiensis* is associated with *I. subelongatus* Motsch. (Marin *et al*. 2005). *Ceratocystis fujiensis* is currently restricted to Asia and in association with its insect vector, is able to kill *Larix* spp., thus posing a substantial quarantine threat to forestry in the Northern Hemisphere (Marin *et al*. 2005) as neither *C. fujiensis* nor its associated insects occur in these regions.

Ceratocystis laricicola

Ceratocystis laricicola was first reported to infect European larch (*Larix decidua* Miller) in 1972 and is vectored by the larch bark beetle *I. cembrae* (Redfern *et al*. 1987). It is generally accepted that beetle attacks alone could in some cases lead to tree mortality, however, inoculation trials have shown that *C. laricicola* is an aggressive pathogen of larch and most probably an important component of tree death (Redfern *et al*. 1987). To date, the fungus has been reported from numerous countries including Europe (Pfeffer 1995), Scotland, Denmark (Crooke & Bevan 1957, Redfern *et al*. 1987, Stauffer *et al*. 2001) and Germany (Crooke & Bevan 1957, Redfern *et al*. 1987).

Ceratocystis pirilliformis

Ceratocystis pirilliformis was first reported colonising wounds on *Eucalyptus* spp. in Australia (Barnes *et al*. 2003a). Shortly after the report of this fungus from Australia, a study was performed to investigate *Ceratocystis* spp. infecting wounds of *Eucalyptus* spp. in South Africa. Similar to the study in Australia, *C. pirilliformis* was frequently isolated from wounds (Roux *et al*. 2004b, Kamgan *et al*. 2009). Although *C. pirilliformis* has not been associated with disease of *Eucalyptus* spp. under natural conditions, it was shown to be able to produce lesions after being inoculated onto *Eucalyptus* seedlings under greenhouse conditions and ~10cm diameter trees under field conditions (Roux *et al*. 2004b). In that study, it was also found that *C. pirilliformis* displayed the same levels of pathogenicity as *C. fimbriata* on *Eucalyptus* spp. (Roux *et al*. 2004b).

Ceratocystis polonica

Ceratocystis polonica, first reported from Poland in the 1930's, is an important insect-associated pathogen of *Picea* Dietrich spp. (Siemaszko 1939). It has been reported to cause severe damage to these trees in Norway (Christiansen & Bakke 1988) and destructive outbreaks during which millions of *Picea* trees were killed have been documented from North and Central Europe (Postner 1974, Christiansen & Bakke 1988). From 1985 to 1994, *C. polonica* and its insect associate, *Ips typographus* L., have been responsible for the loss of approximately 14.1 million cubic meters of *Picea* wood in Austria, Switzerland and Germany (Führer 1996). The most recent outbreak of *I. typographus* in central and Western Europe started around 1992 and has been reported to be triggered by adverse climatic conditions (Führer 1996, Kirisits 2001a).

It has been suggested that *I. typographus* is the primary cause of mortality of *P. abies* trees (Christiansen & Bakke 1988) and that after attack by the beetles, *C. polonica* establishes in the galleries of these insects. In order to overcome the biochemical and structural defence mechanisms of the trees, these beetles will mass attack the living trees, thereby causing mortality (Raffa & Klepzig 1992). Evidence has been provided to suggest that *I. typographus* is in fact not the primary cause of *P. abies* mortality, but that mortality is caused by *C. polonica*. Mass inoculation trials with *C. polonica* simulating attacks by *I. typographus* resulted in tree death (Horntveldt *et al*. 1983, Christiansen 1985, Christiansen *et al*. 1987, Solheim 1988, Croise *et al*. 1998, Kirisits 1998, Krokene & Solheim 1998, Yamaoka *et al.* 2000, Kirisits & Offenthaler 2002).

1.3.4. Staining and/or saprophytic *Ceratocystis* spp. on forest trees

Saprophytic and sap stain fungi do not lead to tree mortality or negatively effect the wood structure, but does lead to the decrease in timber value. In the past, the term staining fungi was in some cases used to refer to fungi that are also pathogenic in nature and could lead to tree mortality (Gibbs 1993). Staining fungi has also been described as generalists (Seifert 1993) with more that one species occurring on a single piece of timber (Davidson 1935, Campbell 1960, Olchowecki & Reid 1974, Seifert 1993).

The discoloration caused by *Ceratocystis* spp. varies from blue, grey to black (Seifert 1993) and is due to the darkly pigmented hyphae that colonise the wood (Hartig 1878, Hedgcock 1906, Munch 1907, Croan & Highley 1995). Hyphae that cause the discolouration are concentrated in the parenchyma and resin ducts of colonised wood and often occur in the tracheids, but are in general unable to enter wood cell walls (Seifert 1993, Croan & Highley 1995). These *Ceratocystis* spp. do not lead to mortality or to structural damage of the timber (Boyce 1961, Chow 1983, Blanchette *et al*. 1992, Seifert 1993). Some of the effects staining fungi in the genus *Ceratocystis* have on wood include minor dry weight loss (Eslyn & Davidson 1976), minor strength loss (Seifert 1993) and toughness loss (Findlay & Pettifor 1937, Chapman & Scheffer 1940). The wood production quality damage caused by staining fungi have in the past been controlled by chemical treatment and the use of antagonistic fungi exhibiting antagonism targeted metabolites (Benko & Henningson 1986, Croan & Highley 1991, 1994, Hiratsuka *et al*. 1994).

Staining fungi in the genus of *Ceratocystis* are dispersed by numerous means. They are generally associated with insects and rely on them for dispersal (Leach *et al*. 1934, Leach 1940, Mathiesen 1950, Mathiesen-Käärik 1953). These associations have been noted to be either a close or a loose association (Gibbs 1993). Mathiesen-Käärik (1953), also stated that air dispersal is possible in species such as *C. coerulescens*. Dowding (1969) showed that air dispersal is possible as long as the air conditions were not to dry.

Ceratocystis coerulescens is common on *Pinus* spp. and *Piceae* spp. in Europe (Munch 1907, Bakshi 1950, Griffen 1968, Olchowecki & Reid 1974, Upadhyay 1981). It has been reported to be associated with a number of insects including *Ips schmutzenhofferi*, *Orthotomicus proximus* and *Pityogenus chacographus* (Mathiesen 1950, Mathiesen-Käärik 1953). *Ceratocystis coerulescens* commonly infects recently cut logs and broken roots (Seifert 1993) and has been referred to as a saprophyte or wound coloniser (Wingfield *et al*. 1997) and has not been reported to be a pathogen of *Pinus* or *Picea* spp. Interestingly, *C. coerulescens* has however been reported as a severe pathogen on a single host genus namely *Acer* spp. (Kile 1993).

1.4. WOUNDS AS INFECTION SITES FOR *CERATOCYSTIS* SPP.

It is documented that *Ceratocystis* spp. require wounds for infection (DeVay *et al*. 1963, Kile 1993). These wounds can originate from various sources including wind and hail damage, growth cracks, insect feeding, animals and human activities such as grafting, pruning and harvesting practices. Fresh wounds attract sap-feeding insects that may carry *Ceratocystis* spp. to these substrates and disperse ascospores from diseased to healthy hosts (Moller & DeVay 1968). Spores can also be spread to wounds in wind-borne frass (Iton 1960, Kile 1993).

A species in the *Ceratocystis fimbriata s.l.* species complex commonly infects peach trees wounded during harvesting of the fruit as the fruit is broken from the stem (DeVay *et al*. 1963). A species in this complex has also been reported to infect coffee plants in Colombia through stem wounds made by workers who support themselves against the stems of the plants to prevent slipping on the steep hills on which the coffee plants are grown (Marin *et al*. 2003). Pruning wounds are also common entry points for members of the *C. fimbriata s.l* species complex, and the fungus can be carried on machetes or other pruning tools (Walter 1946, Teviotdale & Harper 1991).

It has been reported that *C. platani* can infect trees via underground root grafts in perennial plants (Walter 1946, Kile 1993). This occurrence is common in areas where trees of the same species grow in close proximity and where root systems graft in native ecosystems (Walter 1946, Kile 1993). This form of dispersal has also been reported for *C. fagacearum* in natural and urban forests (Accordi 1986, Kile 1993).

Natural forces commonly cause wounds that can be infected by *Ceratocystis* spp. Strong winds and hail are common sources of wounds. *Ceratocystis albifundus*, for example, has been shown to infect several native tree species after strong winds damaged stems and branches (Roux *et al*. 2007). Similarly, *C. albifundus* has also been isolated from hail and insect damage on *A. mearnsii* in South Africa (Roux & Wingfield 1997).

Insects such as bark beetles (Coleoptera: Scolytinae) make wounds that facilitate the infection of host trees by *Ceratocystis* spp. Beetles bore through the bark to excavate egg galleries in the underlying phloem. During this process, the wound is directly inoculated with fungi (Bramble & Holst 1940, Leach 1940). Examples of fungi that are specifically vectored by bark beetles include *C. laricicola* associated with *I. cembrae* (Redfern *et al*. 1987), *C. polonica* associated with the bark beetle *I. typographus* (Horntvedt 1988, Solheim 1986, Krokene & Solheim 1996), *C. fujiensis* associated with *I. subelongatus* (Yamaoka *et al*. 1998), *C. fagacearum* associated with *Pseudopityophthorus minutissimus* Zim. (Ambourn *et al*., 2005) and *C. rufipennis* associated with *Dendroctonus rufipennis* Kirby (Harrington & Wingfield 1998).

Recently *C. atrox* M. van Wyk & M.J. Wingf. was reported from tunnels of the wood-boring insect *Phoracantha acanthocera* Macleay (Cerambicydae: Coleoptera) (Macleay) (Van Wyk *et al*. 2007b). These, insects, although not necessarily associated with specific *Ceratocystis* spp., greatly assist these fungi in infection of suitable hosts through the wounds that they create. Another example of this is *C. polychroma* associated with *Hexamitodora semivelutina* Hell. (Coleoptera: Cerambycidae) on *Syzygium aromaticum* L. Merr. & Perry (Van Wyk *et al*. 2004a).

It has been well documented that *Ceratocystis* spp. infect artificially made wounds on trees. In this regard, two species, *C. eucalypti* and *C. pirilliformis* were first discovered in trials where *Eucalyptus* spp. in Australia had been intentionally wounded (Kile 1996, Barnes *et al*. 2003). Similarly, *C. fimbriata s.l.* and *C. moniliformis* are well-known from wounds on *Eucalyptus* spp. in South Africa (Roux *et al*. 2004b). The use of artificial wounds has in recent years been used widely to collect *Ceratocystis* spp. from trees on which they do not necessarily cause disease. Two studies investigating *Ceratocystis* spp. infecting medicinal bark harvesting wounds on native tree species in Africa, isolated *C. albifundus* (Roux *et al*., 2004a), and two previously undescribed species, *C. savannae* Kamgan & Jol. Roux and *C. tsitsikammensis* Kamgan & Jol. Roux (Kamgan *et al*. 2008). Likewise, a study in Colombia yielded a previously undescribed species, *C. neglecta* M. van Wyk, Jol. Roux & C. Rodas from artificially made wounds on *Eucalyptus* spp. (Rodas *et al*. 2008). A number of other wounding studies are underway in various parts of the world and these will most likely yield numerous other undescribed species from hosts and countries not previously surveyed.

Successful infection of wounds by *Ceratocystis* spp. is dependant on a number of physical and environmental factors. Species in the *C. fimbriata s.l.* species complex, for example, are able to infect their hosts when viable fungal propagules are deposited onto relatively superficial bark wounds (DeVay *et al.* 1968). In contrast, *C. fagacearum* can only infect the host tree if viable fungal propagules come into contact with freshly exposed wood (xylem) of the host (Kuntz & Drake 1957).

Temporal factors have been shown to affect the success of infection by *Ceratocystis* spp. (Bostock & Middleton 1987, Biggs 1989, Teviotdale & Harper 1991). Numerous studies have shown that *C. fagacearum* could not cause infection when wounds were older than 24 hours (Morris *et al*. 1955, Kuntz & Drake 1957, Gibbs 1980). It has been reported that this loss of susceptibility of wounds over time could be attributed to the loss of the thin film of moisture present on fresh wounds, along with the formation of a periderm after wounding. Biggs (1989), attributed the increase in resistance of wounds to infection over time to the accumulation of suberin. Wound infection by other microorganisms has been shown to influence infection success of pathogens. It has been reported that the colonization of wounds by the saprophytic fungus, *Ophiostoma piceae* (Munch) H. Sydow & Sydow, prior to the artificial inoculation of the wound with *C. fagacearum*, prevented colonization and infection by the pathogen (Gibbs 1980). A similar influence has been observed for bacteria with the inhibition of *Botrytis cinerea* (De Bary) Whetzel by a bacterial species in the genus *Pseudomonas* Migula (Barka *et al*. 2002).

Climatic factors such as temperature and relative humidity also influence the germination of spores and infection of *Ceratocystis* spp. (Cole & Fergus 1956). In this study, the authors reported that fungi could survive at extremely low temperatures for a period of time under laboratory conditions, as spores withstood freezing at -10°C after 83 days (Cole & Fergus 1956). The authors also observed differences in the response of conidia compared to that of ascospores. The thermal death point of the ascospores (42°C - 44°C) were higher than that of the conidia (40°C - 42°C). They also found that relative humidity and temperature had a significant influence on the germination and survival of fungi.

In forestry operations, wounding of trees is common. In operations such as pruning, a fresh, open wound is created when the branches are cut or sawn off, or where double stems are reduced. Accidental wounds are also often created when timber is removed in thinning operations. Furthermore, timber is often infected by *Ceratocystis* spp. after harvesting, resulting in blue stain of the harvested product. This is especially common where timber is not debarked immediately, allowing insects and fungi to survive under the bark. Management operations that reduce the occurrence of wounds and that involve the speedy removal of bark could, therefore, reduce infection of timber by *Ceratocystis* spp.

1.5. INSECT ASSOCIATIONS WITH *CERATOCYSTIS* SPP.

It is a well established fact that *Ceratocystis* spp. are dispersed by arthropods (Sinclair *et al*. 1987). Hartig (1878), first recognised the interrelationship between insect damage, discolouration of wood and fungi during his study of blue-stain in the sapwood of conifers. Münch (1907, 1908), also observed that blue-stain in living trees and lumber is associated with attack by bark beetles. Since these reports, a number of studies have been compiled regarding various aspects of the association of fungi with bark beetles and numerous reports of such associations have been made for *Ceratocystis* spp. (Table 1).

Ceratocystis spp. have associations with three broad categories of insects. These categories are (1) Bark beetles (phloeophagous insects), (2) nitidulid beetles and (3) more general insects (Harrington 1987, Kirisits 2004). These associations can be very specific, such as those with bark beetles, or general. In the following section, the various groups of insects associated with *Ceratocystis* spp. will be discussed and the different types of associations between *Ceratocystis* spp. and insects as well as the various adaptations by *Ceratocystis* spp. to facilitate these relationships will be considered.

1.5.1. Interdependence of insects and their associated *Ceratocystis* spp.

There is considerable debate regarding the interdependence of *Ceratocystis* spp. and their associated insects. A point of much debate is whether the fungus or the insect is the primary cause of tree death, or whether it is a combination of the two. Examples where the interdependence has been studied include *C. fagacearum*, *C. polonica* (Christiansen 1985, Solheim 1988, Kirisits 1998, Krokene & Solheim 1998, Yamaoka *et al.* 2000, Kirisits & Offenthaler 2002) and *C. laricicola* (Crooke & Bevan 1957, Redfern *et al*. 1987, Yamaoka *et al.* 1998, Stauffer *et al*. 2001, Kirisits 2001a, b).

The symbiosis involving *Ips typographus* and *C. polonica* aptly illustrates the differing opinions regarding the nature of the interaction between bark beetles and their fungal associates. It has been suggested that *I. typographus* is the primary cause of mortality of *P. abies* trees (Christiansen & Bakke 1988) and that after attack by the beetles, *C. polonica* establishes in the galleries of these insects. In order to overcome the biochemical and structural defence mechanisms of the trees, these beetles will mass attack the living trees, thereby causing mortality (Raffa & Klepzig 1992). On the other hand, evidence has been provided to suggest that *I. typographus* insects are in fact not the primary cause of *P. abies* mortality, but that mortality is caused by *C. polonica*. Experiments in which trees have been mass inoculated with *C. polonica*, to simulate the situation when trees are attacked by *I. typographus*, has resulted in considerable blue stain and also tree death (Horntveldt *et al*. 1983, Christiansen 1985, Christiansen *et al*. 1987, Solheim 1988, Croise *et al*. 1998, Kirisits 1998, Krokene & Solheim 1998, Yamaoka *et al.* 2000, Kirisits & Offenthaler 2002). It is thus hypothesised that *C. polonica* increases the effect of *I. typographus* infestation and makes the host more suitable for attack and reproduction of its insect vector (Whitney 1982, Harrington 1993, Paine *et al.* 1997).

Tree infesting insects and *Ceratocystis* spp. may exist in symbiotic relationships. *Ceratocystis* spp. are dependent on insects for dissemination, while the insects in some cases rely on these *Ceratocystis* spp. to lower the defences of the trees (Raffa & Klepzig 1992, Krokene 1996, Paine *et al*. 1997). An important pathogen, *C. laricicola* seems to have such an association with its insect symbiont, *I. cembrae* (Redfern *et al*. 1987, Yamaoka *et al.* 1998, Stauffer *et al*. 2001, Kirisits 2001b). *Ips cembrae* is regarded as a secondary pest of larch, and has played a significant role in the establishment of *C. laricicola* in Scotland, after it was introduced in the 1950's (Crooke & Bevan 1957, Redfern *et al.* 1987). The insect involved in the symbiosis benefits from the association in the sense that the fungus lowers the defence mechanisms of the host tree, thus allowing the beetles to colonise the trees (Redfern *et al*. 1987).

Insects have been reported to assist their associated fungi with "transport" as in the case of *C. fagacearum*, the causal agent of oak wilt (Bretz 1952, Sinclair *et al*. 1987). *Ceratocystis fagacearum* seems to have a loose association with a number of insect species (*Carpophilus dimidiatus, Ca. sayi, Euporaea* spp.) that are not known to be primary pests and are not able to create wounds on the host trees (Juzwik & French 1983). Therefore, the insects only transport/disseminate the fungus to fresh wounds, that act as suitable sites for infection by the fungus, and they do not seem to benefit from the association.

1.5.2. Adaptations of *Ceratocystis* spp. for the purpose of insect dispersal

Insect associated *Ceratocystis* spp. possess a number of adaptations to ensure the success of the symbiosis. One of these adaptations is the production of fruity odours that attract insects (Lanza & Palmer 1977). Not all *Ceratocystis* spp., however, produce fruity aromas. Species of *Ceratocystis* spp. that produce fruity odors include species in the *C. fimbriata s.l* species complex, *C. pirilliformis*, *C. fagacearum* and *C. moniliformis* Hedgcock (Mathiesen-Kräökik 1953, Kirschner 2001, Barnes *et al*., 2003a). Numerous studies have identified a number of monoterpenes to play a role in the production of these fruity odors. These are citronellol, geraniol, nerol, linalool, alphaterpiniol and neral (Lanza *et al.* 1976, Lanza & Palmer 1977).

The ascospores of *Ceratocystis* spp. are presented in slimy (mucilaginous) masses at the apices of long ascomatal necks (Ingold 1961). These long necks lift the spores of *Ceratocystis* spp. above competing fungi (Leach *et al*. 1934, Griffin 1968, Malloch & Blackwell 1993). Some species, however, do not produce long necks and have adapted by producing their spore masses in thread-like tendrils (Wingfield 1993). The slimy spore masses produced at the apices of long ascomatal necks increases the possibility for the spores to adhere to the bodies of insects due to an adhesive layer around the spores (Leach *et al*. 1934, Griffin 1968, Malloch & Blackwell 1993). Ascospore shape has also been reported to have an influence on the adhesion of these spores to the insects (Malloch & Blackwell 1993). It has been hypothesised that the concave shape of the spores produced by *Ceratocystis* spp., facilitates the spores coming into contact with the insects at more than one point, and that the numerous expanded contact areas could assist in the spores not being dislodged from the insect body during transmission (Malloch & Blackwell 1993). Spores also poses protective sheaths than enable them to be ingested by insects and pass unharmed through their intestinal tracts (Leach 1940, Moller & DeVay 1968).

1.5.3 Categories of insects associated with *Ceratocystis* spp.

1.5.3.1 Bark Beetles

Bark beetles (Coleoptera: Scolytidae) create wounds that facilitate infection by *Ceratocystis* spp. and assist in the dissemination of these fungi from one host to another. Beetles bore through the bark to excavate egg galleries in the underlying phloem. During this process, the wounds are directly inoculated with fungi carried on the exoskeleton of the beetles, as well as through spores in the digestive tracts of some beetles (Bramble & Holst 1940, Leach 1940).

Tree infecting *Ceratocystis* spp. associated with bark beetles include *C. laricicola, C. polonica, C. fujiensis* and *C. rufipenni* M. J. Wingf., T. C. Harr. & H. Solheim. *Ceratocystis laricicola* is specifically associated with *I. cembrae* in Europe (Redfern *et al*. 1987). Research has shown that *C. laricicola* is highly pathogenic to larch trees, lowering the defence mechanisms of the host tree and thus allowing the beetle to colonise the trees (Redfern *et al*. 1987). This fungus/beetle association has been well studied and is known from Europe (Pfeffer 1995), Scotland, Denmark (Crooke &

Bevan 1957, Redfern *et al*. 1987, Stauffer *et al*. 2001) and Germany (Crooke & Bevan 1957, Redfern *et al*. 1987).

Ceratocystis polonica is known to infect *Picea abies* (Bruegger) P. Schmidt and is associated with the bark beetle *I. typographus* (Horntvedt 1988, Solheim 1986, Krokene & Solheim 1996). Since the 1970's, it has lead to significant damage in Europe (Christiansen & Bakke 1988, Fűhrer 1996). Furniss *et al*. (1990), reported that the spores of *C. polonica* are disseminated on the exoskeleton, or in the guts of the insects. The fungus will infect the phloem of the tree after the beetles attack healthy trees (Krokene & Solheim 2001). Mass attack by the beetles and subsequent infection by the fungus ultimately leads to mortality of the host trees (Christiansen & Bakke 1988). However, the pathogenicity of *C. polonica* without the interaction of the beetles has been established during mass inoculation tests, where the fungus alone was inoculated into small wounds on the tree and proved to be pathogenic (Horntvedt *et al*. 1983, Krokene & Solheim 1998, Harrington *et al*. 2002).

Ceratocystis fujiensis is associated with *I. subelongatus* in Japan (Yamaoka *et al*. 1998, Stauffer *et al*. 2001). The beetle infests larch trees (*Larix kaempferi*) (Koizumi 1990, Yamaoka *et al*. 1998), inoculating *C. fujiensis* into the trees and resulting in tree death (Yamaoka *et al*. 1998, Stauffer *et al*. 2001). *Ceratocystis fujiensis* has been proven to be highly pathogenic, resulting in tree mortality within 100 days after mass inoculation of 30 year-old Japanese larch (Yamaoka *et al*. 1998).

Ceratocystis rufipenni is associated with *Dendroctonus rufipennis* Kirby (Harrington & Wingfield 1998). This beetle has been described as a weak to moderately aggressive pest of *Picea* spp. in Canada and the U.S.A. (Harrington & Wingfield 1998, Six & Klepzig 2004). A number of species associated with *D. rufipennis* has been reported to cause symptoms on *Picea* spp. during inoculation trials, however, *C. rufipenni* seems to be the most aggressive (Horntvedt *et al*. 1983, Solheim 1988, Solheim & Safranyik 1997). Once the fungus has infected its host, it colonises the sapwood and phloem (Solheim 1995). The fungus colonises new hosts rapidly and is often found at the leading edge of fungal growth spreading towards the sapwood of *D. rufipennis* infested trees (Solheim 1995).

1.5.3.2. Nitidulid beetles

Nitidulid beetles, or sap-feeding beetles (Coleoptera: Nitidulidae), have been reported as vectors of a number of *Ceratocystis* spp., including *C. fagacearum*, *C. moniliformis*, *C. fimbriata* (Collins & Kalnins 1965, Moller & DeVay 1968, Juzwik *et al*. 1998) and *C. paradoxa* (Dade) Moreau (Chan & Jensen 1974). Some authors view Nitidulids as the most important insect vector group of *Ceratocystis* spp. in the nort and central states of the USA (Juzwik 2001). Nitidulid beetles do not make wounds but visit wounds made by other factors such as insect or animal feeding as well as, natural forces or mechanical damage (Connell 1956, Juzwik *et al*. 1999). The adults of these beetles are attracted to, and live in fermenting plant sap, decaying fruit, or fungi (Downie & Arnett 1996). These beetles and their larvae actually feed off the sap of the host trees as well as on the fungal mats (Moller & DeVay 1968, Cease & Juzwik 2001). As these beetles feed on the fungal mats, viable pathogen propagules attach to their bodies and are spread with them (Juzwik & French 1983, Apple *et al*. 1990). In this manner, they assist in the establishment of new oak wilt infection centres, either within the same stands or in adjacent or more distant stands (Juzwik 2001).

1.5.3.3. Generalist organisms

A number of generalist organisms, including insects other than bark beetles and Nitidulid beetles, transmit *Ceratocystis* spp. These include phoretic mites (Himelick & Curl 1958, Moller & DeVay 1968, Moser *et al*. 1985, 1997), nematodes (Vovlas *et al*. 1994) and flies (Diptera) (Himelick & Curl 1958, Moller & DeVay 1968, Bridges & Moser 1983, Moser 1997). As early as the late 1950's the mite, *Garmania bulbicola* Oudemans was identified to be able to transmit *C. fagacearum* to artificial wounds (Hemlick & Curl 1958). Similarly, a species of the mite *Tarsonemus* has been reported in studies of a member of the *C. fimbriata s.l.* species complex (Moller & DeVay 1968) and more recently *C. fujiensis* (Moser *et al*. 1997).

Flies (Diptera) have been reported to be associated with *Ceratocystis* spp. (Collins & Kalnins 1965, Moller & DeVay 1968). Already in the mid 1960's *Drosophila* spp. were reported to be an important associate of the well known *C. fagacearum* (Collins & Kalnins 1965). Similarly, in a study by Moller & DeVay (1968), the authors also reported two fly species to be associated with *C. fimbriata* including, *Drosophila* *melanogaster* Meigen and *Chymomyza procnemoides* Wheeler. The authors, however, felt the association of these two species with *C. fimbriata* was a casual one.

A limited number of studies have identified more general organisms as associates of *Ceratocystis* spp. In a study of banana diseases and pests, *C. paradoxa* was reported to be associated with nematodes (Vovlas *et al*. 1994). In this study, *C. paradoxa* was found to be transmitted by the nematode *Helicotylenchus multicinctus* Cobb associated with root systems of declining bananas. There are also single reports of *Ceratocystis* species associated with organisms such as ants (Greiff & Currah 2007) and mice (Goto *et al*. 1954).

1.5.4. Association levels between insects and *Ceratocystis* spp.

There are two distinct categories of associations between *Ceratocystis* spp. and insects. Some species, such as those in the *C. fimbriata s.l* complex and *C. moniliformis* clades, have a casual relationship with insects. These are the species that tend to produce fruity odours which attract many species of flies (Diptera) and sap beetles (Nitidulidae) (Himelick & Curl 1958). Another group of *Ceratocystis* spp., mostly those in the *C. coerulescens* group tend not to produce fruity odours. These species rely on very close relationships with specific insects, particularly bark beetles, for their dispersal (Harrington & Wingfield 1998).

Some *Ceratocystis* spp. have been associated with a number of different insect species, forming no specific relationships with particular insect species. These *Ceratocystis* spp. are all characterized by the production of fruity volatiles that attract generalist insects (Moller & DeVay 1968, Kirisits 2004). Species of *Ceratocystis* that have this loose form of relationship with insects include *C. fimbriata s.l.*, *C. fagacearum* and *C. moniliformis* (Mathiesen-Kräärik 1953, Kirschner 2001). *Ceratocystis fagacearum*, for example, has been reported from nitidulid beetles (Bretz 1952, Collins & Kalnins 1965, Juzwik *et al*. 1998) and flies (Hemelick & Curl 1958). Similarly, a species in the *C. fimbriata s.l* species complex has been reported from nitidulid beetles, flies and mites (Moller & DeVay 1968).

A number of *Ceratocystis* spp. have associations with specific insect species. In these cases, one insect species is associated with only one fungus. If these relationships did not exist or failed, the fungi involved would not be able to disseminate effectively. These *Ceratocystis* spp. do not produce the same fruity volatiles as those produced by *Ceratocystis* spp. with loose associations with insects. Examples here are *C. laricicola,* associated with the bark beetle *I. cembrae* (Redfern *et al*. 1987), *C. fujiensis* associated with *I. subelongatus* (Yamaoka *et al*. 1998), *C. rufipenni* associated with *D. rufipennis* (Solheim & Safranyik 1997, Wingfield *et al*. 1997) and *C. polonica* which is associated with *I. typographus* (Solheim 1986, Christiansen & Solheim 1990, Krokene & Solheim 1996, Harrington & Wingfield 1998, Kirisits *et al*. 2000).

Ceratocystis laricicola is specifically associated with *I. cembrae* in Europe (Redfern *et al*. 1987). This fungus/beetle association has been well studied and is known from various countries (Crooke & Bevan 1957, Redfern *et al*. 1987, Pfeffer 1995, Stauffer *et al*. 2001). *Ceratocystis laricicola* has not been reported being associated with any other insects and is involved in a symbiotic relationship with *I. cembrae*.

The close association between *C. polonica* and the bark beetle *I. typographus* (Horntvedt 1988, Solheim 1986, Krokene & Solheim 1996) has led to significant losses of *P. abies* trees in Europe (Christiansen & Bakke 1988, Fűhrer 1996). In this association, spores of *C. polonica* are disseminated on the exoskeleton, or in the intestinal tract, of the beetle (Furniss *et al*. 1990) and infects the *Picea* trees after mass attack by the beetles, ultimately leading to trees death (Christiansen & Bakke 1988).

Ceratocystis fujiensis, associated with *I. subelongatus*, is inoculated into its host tree when the beetle infests larch trees (Koizumi 1990, Yamaoka *et al*. 1998). Similar to *C. polonica*, *C. fujiensis* has been proven to be highly pathogenic to its host, but is not able to infect the host tree without the assistance of its insect associate (Yamaoka *et al*. 1998, Stauffer *et al*. 2001).

Ceratocystis rufipenni, associated with *D. rufipennis,* is an example of a close association of a fungus with an insect, but not the reciprocal situation (Harrington & Wingfield 1998, Six & Klepzig 2004). *Ceratocystis rufipenni* has only been found associated with *D. rufipennis* (Six & Klepzig 2004). *Ceratocystis rufipenni* has been shown to be the most aggressive fungus associated with *D. rufipennis* (Horntvedt *et* *al*. 1983, Solheim 1988, Solheim & Safranyik 1997) and is usually found at the leading edge of fungal growth (Solheim 1995). This indicates that *C. rufipenni* is directly dependent on *D. rufipennis* for dissemination and could suggest that *C. rufipenni* assists *D. rufipennis* to overcome the tree's defence mechanisms.

Not all associations between insects and *Ceratocystis* spp. are easily defined. An example of this is the association between *C. rufipenni* and *D. rufipennis*. Although a close relationship between *C. rufipenni* and *D. rufipennis* was reported by Wingfield *et al*. (1997), the fungus was not isolated from these beetles in later studies (Six & Bentz 2003, Six & Klepzig 2004). These contradictions in results could be due to difficulties in isolating the fungus or the incubation temperature (Solheim 1995). It could also be due to fungal succession. *Ceratocystis rufipenni* is usually only isolated from the leading edge of the lesions on freshly infected wood (Solheim 1995, Six & Bentz 2003). It could be that when the insects emerge from the wood (1-2 years after attack), saprophytic fungi had colonised the wood where the beetles developed and that *C. rufipenni* was not present at the time of emergence (Solheim 1995). It could also be that the main mode of dissemination of *C. rufipenni* by *D. rufipennis* is in the intestinal tract of the insect (Harrington *et al*. 1996), thereby also explaining the limited success in isolating the fungus from the insect. Although the biology of *C. rufipenni* is very similar to that of *C. polonica* (Christiansen 1985, Solheim & Safranyik 1997), their association with their respective insects differs significantly. Both these fungi are highly pathogenic on their respective hosts and are commonly isolated from the leading edges of the infections. *Ceratocystis polonica* is, however, frequently isolated from its associated beetle *I. typographus*, whereas *C. rufipenni* is not frequently isolated from *D. rufipennis*.

The fact that bark beetles are important forest pests, and that many of their fungal associates cause destructive tree diseases, emphasizes the need for further and detailed investigation into these associations. Although a vast number of studies have been reported on the relationships between insects and *Ceratocystis* spp., the limited knowledge of these in Africa creates a void in research in this field. Understanding the interactions between these organisms will inevitably help combat these forest pests and pathogens. For example, the wilt pathogen *C. albifundus,* one of the most threatening pathogens of plantations of non-native *A. mearnsii*, is hypothesised to be native to the African continent (Roux *et al.* 2001c, Barnes *et al.* 2005) and has not been studied regarding its possible insect vectors. Knowledge pertaining to the biology and ecology of the insect vectors of these pathogens could assist in the control of the insect as well as the pathogens.

1.6. CONCLUSIONS

Ceratocystis spp. include many economically important plant pathogens including a group that cause diseases of trees and sap-stain of timber worldwide. Losses incurred by these pathogens include tree mortality, growth reduction and the decrease in value of timber. Wounds and the insects that form part of a symbiotic relationship with these fungi are important factors for the dispersal and infection of these pathogens. However, very little information is available on these fungi in Africa. As the forestry industry in a number of African countries have entered a dramatic growth and development stage, the recent reports of a number of wilt pathogens in the genus *Ceratocystis* in some African countries emphasize the need for further studies on this group of fungi on the continent.

Effective management of tree diseases and pests rely on a number of factors. These include comprehensive information of the threatening organism's biology, ecology and origin. Once the origin of a pathogen is known, risk assessment could be improved and centres can be identified for possible research into control measures (Linde *et al*. 2002). At a deeper level, knowledge of pathogenic fungi's genetic structure is also important role. With globalisation and the increasing movement around the world of people and commodities, the possibility of new introductions of plant diseases and pests increase. Although a pathogen or pest is present in a country, the introduction of new genotypes could pose a greater threat than the one that currently exists. Therefore, to reduce the threat of pests and pathogens, it is necessary to have a comprehensive understanding about their genetic diversity and movement.

Answering the many questions pertaining to the origin and dispersal of *Ceratocystis* spp. between countries and continents could assist in the restriction of further spread of these pathogens and the threat they pose to the forestry industry and natural ecosystems. In similar fashion, knowledge pertaining to their symbiotic relationships with insects could also assist in the formulation of management strategies. Studies in the thesis that follow this review, focus on *Ceratocystis* spp. infecting wounds on non-native plantation hardwood tree species in southern and eastern Africa. These studies will focus mainly on the morphology, phylogeny and pathogenicity of these fungi. Furthermore, the insect vectors associated with these fungi and the role they play in the dissemination and biology of the fungi isolated are considered. Use is made of population diversity studies with polymorphic DNA markers to obtain knowledge pertaining to the possible origin of the most important fungi obtained during the studies. This knowledge should be valuable in the development of management and quarantine strategies against these pathogens.

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TABLE 1. List of reported associations of *Ceratocystis* spp. and their associated insects.

***Ceratocystis* spp.**	**Insect spp.**	**Host**	**Country**	**Reference**
C. atrox	*Phorocantha acanthocera*	*Eucalyptus* spp.	Australia	VanWyk *et al*. 2007b
C. bhutanensis	*Ips schmutzenhofferi*	*P. spinulosa*	Bhutan	Van Wyk *et al.* 2004a
C. coerulescens	*I. acuminatus*	*Pinus sp*		Mathiesen 1950, Mathiesen-Käärik 1953
	Orthotomicus proximus	*P. sylvestris*		Mathiesen 1950, Mathiesen-Käärik 1953
	Pityogenus chalcographus	*P. sylvestris*		Mathiesen 1950, Mathiesen-Käärik 1953
C. fagacearum	*Carpophilus brachypterus*	Unknown		Henry 1944, Bretz 1952, Juzwik & French 1983
	Ca. dimidiatus	Unknown		Henry 1944, Bretz 1952, Juzwik & French 1983
	Ca. sayi	Unknown		Cease & Juzwik 2001, Juzwik *et al*., 2004
	Epuraea labilis	Unknown		Henry 1944, Bretz 1952, Juzwik & French 1983
	E. peltoides	Unknown		Henry 1944, Bretz 1952, Juzwik & French 1983
C. fimbriata	*Ca. freemani*	Unknown		Moller & DeVay 1968
	Chymomyza procnemoides	Unknown		Moller & DeVay 1968
	Euporea spp.	Aspen		Hinds 1972
C. fujiensis	*I. subelongatus*	*Larix kaempferi*	Japan	Yamaoka *et al.* 1998, Marin *et al*. 2005
C. laricicola	*I. cembrae*	*L. deciduas*	Europe	Redfern *et al*. 1987, Kirisits *et al*. 2000, Stauffer *et al.* 2001
C. manginecans	*Hypocryphalus mangiferae*	*Mangifera indica*	Oman	Al-Adawi *et al*. 2006
C. moniliformopsis	*Eucryphia lucia*	*Eucalyptus oblique*	Australia	Yuan & Mohammed 2002
	Nothofagus cunninghamii	*E. oblique*	Australia	Yuan & Mohammed 2002
C. paradoxa	*Urophorus humeralis*	Sugar cane	USA	Chang & Jensen 1974
	Carpophilus hemipterus	Sugar cane	USA	Chang & Jensen 1974

	Haptoncus ocularis	Sugar cane	USA	Chang & Jensen 1974
***Ceratocystis* spp.**	**Insect spp.**	**Host**	**Country**	**Reference**
C. polonica	*I typographus*	*P. abies*	Europe	Siemaszko 1939, Mathiesen 1950, Mathiesen 1951, Mathiesen Käärik 1953, Harding 1985, 1989, 1995, Solheim 1986, Furniss *et al.* 1990, Solheim 1992a, b, 1993a, b, Virri & Von Weisenberg 1995, Krokene & Solheim 1996, Viiri 1997, Grubelnik 1998, Harrington & Wingfield 1998, Kirschner 1998, Kirisits *et al*. 2000, Kirschenr 2001, Salle *et al.* 2003, Jankowiak 2005, Viiri & Lieutier 2004
	I. amitinus	*Pi. Cembra*		Kirisits *et al*. 2000
	I. duplicates			Valkama 1995, Krokene & Solheim 1996
	H. palliates	*P. abies*		Krokene & Solheim 1996
	H. palliates	*Pi. Sylvestri*		Krokene & Solheim 1996
	H. palliates	*L. kaempveri*		Krokene & Solheim 1996
	Pityogenus chalcographus	*P. abies*		Kirisits 1996, Krokene & Solheim 1996, Kirisits *et al*. 2000
	Polygraphus polygraphus	*P. abies*		Krokene & Solheim 1996
C. polychroma	*Hexamitodera semivelutina*	*Syzygium aromaticum*	Sulawesi	Van Wyk *et al*. 2004
C. rufipenni	*D. rufipennis*	*P. engelmannii*	Canada	Harrington & Wingfield 1998

TABLE 2. List of *Ceratocystis* spp. reported as the causal agents of forest and plantation tree diseases under field and/or greenhouse conditions.

***Ceratocystis* spp.**	**Host**	**Country**	**Reference**
C. albifundus	*Acacia mearnsii*	South Africa	Morris *et al*. 1993, Roux *et al*. 1997, 199b
	A. mearnsii	Kenya	Roux *et al*. 2005
	A. mearnsii	Tanzania	Roux *et al*. 2005
	A. mearnsii	Uganda	Roux *et al*. 2001
C. coerulescens	*Acer* spp.	USA	Kile 1993
C. fagacearum	*Quercus* spp.	USA	Henry 1943, Bretz 1952, Hunt 1956, Upadhyay 1981
C. fimbriata s.l.	*A. decurrens*	Brazil	Ribeiro *et al*. 1985
	Eucalyptus spp.	Brazil	Laila *et al*. 1999
	Eucalyptus spp.	Republic of Congo	Roux *et al*. 2000
	Eucalyptus spp.	Uganda	Roux *et al*. 2001b
	Eucalyptus spp.	Uruguay	Barnes *et al.* 2003
	Eucalyptus spp.	South Africa	Roux *et al*. 2004
C. fujiensis	*L. kaempferi*	Japan	Yamaoka *et al.* 1998
	Piceae spp.	Japan	Marin *et al*. 2005
C. laricicola	*L. deciduas*	Europe	Redfern *et al*. 1987, Kirisits *et al*. 2000, Stauffer *et al.* 2001
	Larix spp.	Scotland	Harrington & Wingfield 1998
C. pirilliformis	*Eucalyptus* spp.	South Africa	Roux *et al*. 2004
C. platani	*Platanus* spp.	USA	Mook 1940, Walter 1946,
	Platanus spp.	France	Ferrari & Pichenot 1975
	Platanus spp.	Southern Europe	Panconesi 1999
	Platanus spp.	Greece	Tsopelas & Angelopoulos 2004
	Platanus spp.	Italy	Panconesi 1981
C. polonica	*P. abies*	Europe	Mathiesen 1950, Mathiesen-Käärik 1953, Postener 1974, Harding 1985, Christiansen & Bakke 1988, Harding 1995, Solheim 1986, Furniss *et al.* 1990, Krokene & Solheim 1996, Grubelnik 1998, Harrington & Wingfield 1998, Salle *et al.* 2003, Jankowiak 2005
	P. abies	Austria	Führer 1996
	P. abies	Switzerland	Führer 1996
	P. abies	Germany	Führer 1996
	Piceae spp.	Poland	Siemaszko 1939, Mathiesen 1951, Hunt 1956
	Piceae spp.	Sweden	Siemaszko 1939, Mathiesen 1951, Hunt 1956
	Pi. Cembra	Norway	Harrington & Wingfield 1998
	Pi. Sylvestri		Kirisits *et al.* 2000
C. polonica	*L. kaempveri*		Valkama 1995, Krokene & Solheim 1996
C. populicola	*Populus tremuloides*	Canada & USA	Johnson *et al*., 2005

***Ceratocystis* spp.**	**Host**	**Country**	**Reference**
C. populicola	*Populus tremuloides*	Poland	Gremmen & De Kam 1977, Przybyl 1984, Johnson *et al*. 2005
	Populus tremuloides	Quebec	Vujanovic 1999, Johnson *et al*. 2005
C. rufipenni	*P. engelmannii*	Canada	Harrington & Wingfield 1998
C. smalleyi	*Carya cordiformis*	USA	Johnson *et al*. 2005

TABLE 3. List of *Ceratocystis* spp. reported from forest and plantation tree species but with no clear association with disease or mortality of these trees.

Ceratocystis spp.	**Host**	**Country**	**Reference**
C. albifundus	*Acacia cafra*	South Africa	Roux *et al*. 2007
	Burkea africana	South Africa	Roux *et al*. 2007
	Combretum molle	South Africa	Roux *et al*. 2007
	Co. zeyheri	South Africa	Roux *et al*. 2007
	Faurea saligna	South Africa	Roux *et al*. 2007
	Ocna pulcra	South Africa	Roux *et al*. 2007
	Ozoroa paniculosa	South Africa	Roux *et al*. 2007
	Terminalia sericia	South Africa	Roux *et al*. 2007
	Brachystegia speciformis	Zambia	Roux *et al*. 2004
	Tulbergia nitidula	Zambia	Roux *et al*. 2004
	Parinari curatelifolia	Zambia	Roux *et al*. 2004
	Julbinardia spp.	Zambia	Roux *et al*. 2004
	Brachystegia busei	Malawi	Roux *et al*. 2004
C. atrox	*Eucalyptus* spp.	Australia	VanWyk *et al*. 2007b
C. bhutanensis	*P. spinulosa*	Bhutan	Van Wyk *et al.* 2004b
C. caryae	*Carya* spp.	USA	Johnson *et al*. 2005
	Ulmus spp.	USA	Johnson *et al.* 2005
	Ostrya virginiana	USA	Johnson *et al.* 2005
C. coerulescens	*Acer* spp.	Canada	Griffin 1968
	Pinus spp.	Scotland	Bakshi 1950
	Pinus spp.	Sweden	Lagerberg *et al.* 1927
	Piceae spp.	USA	Upadhyay 1981, Olchowechi & Reid 1974
	Piceae spp.	Germany	Munch 1907, Hunt 1956
	Pseudotsuga spp.	Germany	Upadhyay 1981, Davidson 1935
	Quercus spp.	Germany	Upadhyay 1981
	Fagus spp.	-	Upadhyay 1981
C. douglasii	*Pseudotsuga* spp.	USA	Wingfield *et al*. 1997
C. eucalypti	*Eucalyptus* spp.	Australia	Kile *et al*. 1996
C. moniliformis	*Liquidamber* spp.	USA	Hedgcock 1906
	Quercus spp.	Scotland	Bakshi 1951
	Quercus spp.	Japan	
	Pycnanthus komba	Cameroon	Luc 1952
	Calamus maximus	Philippines	Roldan 1962
	Endospermum peltatum	Philippines	Roldan 1962
	Parkea javanica	Philippines	Roldan 1962
	Fagus grenata	Japan	Kitajima 1936
	Eucalyptus spp.	South Africa	Roux *et al.* 2004
C. moniliformopsis	*E. oblique*	Australia	Yuan & Mohammed 2002
	E. oblique	Australia	

Ceratocystis spp.	Host	Country	Reference
C. pinicola	*Pinus* spp.	England	Harrington & Wingfield 1998
C. pirilliformis	*Eucalyptus* spp.	Australia	Barnes *et al*. 2003a
C. resinifera	*Piceae* spp.	Norway	Harrington & Wingfield 1998
C. resinifera	*Piceae* spp.	Scandinavia	Lagerberg *et al*. 1927, Roll-Hansen & Roll-Hansen 1980, Harrington &Wingfield 1998
C. savannae	*Acxacia nigrescens*	South Africa	Kamgan *et al*. 2008
	Combretum zeyheri	South Africa	Kamgan *et al*. 2008
	Terminalia sericea	South Africa	Kamgan *et al*. 2008
	Sclerocarya birrea	South Africa	Kamgan *et al*. 2008
	Burkea Africana	South Africa	Kamgan *et al*. 2008
C. tsitsikammensis	*Rapanea melanophloeos*	South Africa	Kamgan *et al*. 2008
	Ocotea bulata	South Africa	Kamgan *et al*. 2008
C. tribiliformis	*P. merkusii*	Indonesia	Van Wyk *et al*. 2006
C. variospora	*Quercus* spp.	USA	Davidson 1944
	Betula platyphylla	Japan	Johnson *et al*. 2005
C. virescens	*Liquidambar* spp.	USA	Davidson 1944
	Lirodendron spp.	USA	Davidson 1944
	Nassa spp.	USA	Davidson 1944
	Fagus spp.	USA	Davidson 1944
	Magnolia spp.	USA	Davidson 1944
	Quercus spp.	USA	Davidson 1944

Appendix 1

- 1878 — *Ceratostomella* established (Saccardo) Type: *C. piliferum*
- 1890 — *Ceratocystis* established (Ellis & Hallstead) Type: *C. fimbriata*
- 1892 — *Ceratocystis* transferred to *Sphaeronema* (Saccardo)
- 1908 — *Endoconidiophora* established (Münch)
- 1918 — *Ceratostomella* split into *Ceratostomella* & *Linostoma* (Von Höhnel), *C. fimbriata* to *Linostoma*
- 1918 — *Ceratocystis* transferred to *Linostoma* (Von Höhnel)
- 1919 — *Ophiostoma* established (Sydow & Sydow) Linostoma transferred to *Ophiostoma*
- 1923 — *Ophiostoma fimbriatum* transferred to *Ceratostomella* (Elliot)
- 1932 — *Ophiostomataceae* established for *Ophiostoma* (Nannfeldt)
- 1934 — *Endoconidiophora* reduced to synonymy with *Ceratostomella* (Mellin & Nannfeldt)
- 1934 — *Ceratostomella fimbriata* and other species transferred to *Ophiostoma* (Mellin & Nannfeldt)
- 1950 — Some *Endoconidiophora* transferred back to *Ceratocystis* (Bakshi)
- 1951 — *Ceratocystis* and *Ophiostoma* separated (Bakshi)
- 1952 — *Endoconidiophora* and *Ceratostomella* synonymised with *Ophiostioma* (Von Arx)
- 1954 — *Ceratocystis* synonymised with *Ophiostoma* (Von Arx & Muller)
- 1956 — *Endoconidiophora* and *Ophiostoma* synonymised with *Ceratocystis* (Hunt)
- 1967 — *Ceratocystis* and *Ophiostoma* separated based on cell wall composition (Smith *et al.*)
- 1974 — Separate *Ophiostoma* and *Ceratocystis* based on anamorph state (Von Arx)
- 1974 — *Ophiostoma* and *Ceratocystis* synonymised. *Ceratocystis* subdivided into four groups nl. Minuta, Ips, Fimbriata and
- 1975 — *Ceratocystiopsis* established. *Ceratocystis* and *Ophiostoma* synonymised. Tranfered Minuta group to *Ceratocystis* and *Ophiostoma* divided based on types of cells present in inner perithecium. (Benny & Kimbrough)
- 1980 — *Ceratocystiopsis*, Pilifera group to *Endoconidiophora* and Fimbriata group to *Ceratocystis* (Upadhyay & Kendrick)
- 1981 — *Ceratocystis* and *Ophiostoma* divided based on sensitivity to Cyclohexamide (Harrington)
- 1988 — *Ceratocystiopsis* and *Ophiostoma* synonymised. (Wingfield *et al*)
- 1992 — *Ceratocystis* and *Ophiostoma* divided based on DNA sequence data. (Hausner *et al*)
- 1993 — *Ceratocystis* placed in Microascales and *Ophiostoma* in Ophiostomatales. (Hausner *et al*)
- 2002 — *Chalara* transferred to *Thielaviopsis* (*Ceratocystis* anamorph*). Ophiostoma* anamorphs recognised as *Sporothrix, Leptographium, Pesotum* and *Hyalorhinocladiella*. (Paulin-Mahady *et al*)
- 2006 — *Ophiostoma separated into Ophiostoma, Grosamannia and Ceratocystiopsis* (Zipfel *et al*)