RESEARCH
SIGNPOST

The Xylariaceae as phytopathogens

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Abstract

This paper outlines the diseases caused by members of the Xylariaceae a large and well known ascomycete family with worldwide distribution. The significance of water stress in host trees in relation to development of canker disease following latent invasion is considered with examples from Europe, U.S.A, Australia, and Thailand. Root infections caused mainly by species of Rosellinia are reviewed and the implication of toxins produced by certain of these fungi is addressed. Reference to a third group of diseases, needle blights, is made.

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Introduction

Although our studies over the past 25 years on the ascomycete family the Xylariaceae have concentrated on taxonomic aspects we have accumulated considerable data on their metabolites, distribution, general ecology and as causative agents of *Pl. Dis.*s. More recently molecular techniques have been applied to aid taxonomic decision making and for the identification of ecological samples. This review concentrates on the Xylariaceae as plant pathogens, an area of their activity which is frequently underestimated or is generally neglected, and is based on findings from our collaborative studies.

The family

The Xylariaceae is a large and well known ascomycete family which is distributed throughout the world. Although representatives occur widely in the temperate zone the family has greater representation in the tropics [1,2,3]. The family is usually thought of as being wood inhabitants but many taxa occur in dung, litter, soil and even insects [3,4] There is no consensus as to the number of genera which can be accommodated within the family. Ju and Rogers [1] and Whalley [3] although not in complete agreement on all of the genera indicated an upper figure of around 40 genera but since then the description of new genera raises this total to 50 or more depending on individual views.

These genera are circumscribed mainly on features of their teleomorphs which include form of stroma, pigmentation, shape and dimensions of ascospores, ascospore wall ornamentation, length and position of the germination slit, a type of ascus apical apparatus [1,3]. However the realization that the anamorphic state provides a previously unused source of taxonomic characters which are useful for the separation of closely related taxa [5,6] has resulted in the widespread use of the anamorph for the delimitation of many xylariaceous genera [1,7]. Secondary metabolites produced in liquid culture have also been used to aid in the establishment of a more satisfactory systematic arrangement in the Xylariaceae [8].

Xylariaceae as phytopathogens

Although the Xylariaceae are not usually regarded as important plant pathogens [4,9] an increasing number of members of the family are becoming recognised as the cause of a number of diseases of economic significance [3]. These diseases occur both under agricultural conditions and in natural ecosystems and can be grouped as canker diseases, root rots, and needle blights.

Canker diseases

Many of the canker causing species of Xylariaceae are associated with stress conditions in their hosts and this in turn has led authors to suggest that they are 'latent' invaders only becoming aggressive and invasive in trees which are exhibiting water stress [3,7,10]. Although the Xylariaceae appear to be common endophytes in many plants, especially in the tropics [11] there is some argument as to their exact status. Rogers [7] expressed the view that "an endophyte is a fungus that leads a cryptic life that does not normally disrupt the host. i.e. a parasite that is not pathogenic or not highly so." Further more he stated, "At first examination, the *Xylariaceae* would seem to be an

Table I. Canker diseases caused by members of the Xylariaceae

Species	Principal hosts
Biscogniauxia atropunctata (Schwein.: Fr.). Pouzar	*Quercus*
B. mediterranea (De Not.) Kuntze	*Quercus*
B. nothofagi Whalley, Læssoe & Kile	*Nothofagus cunninghamii*
B. nummularia (Bull.:Fr.) Kuntze	*Fagus*
B. uniapiculata (Penz. & Sacc.) Whalley & Læssoe apud Whalley, Læssoe & Kile	*Eucalyptus camaldulensis*
Camillea punctulata (Berk.) & Rav.) Læssoe, J.D. Rogers & Whalley	*Quercus*
C. tinctor (Berk.) Læssoe, J.D. Rogers & Whalley	*Acer, Platanus*
Daldinia concentrica (Bolton : Fr.) Ces. & De Not.	*Fraxinus*
Entoleuca mammata Wahlenberg : Fr.) J,D. Rogers & Y.-M. Ju	*Populus, Salix, Alnus, Betula*
Hypoxylon rubiginosum (Pers.: Fr.) Fr.	*Catalpa, Hevea*
Xylaria arbuscula Sacc.	*Macadamia*

unlikely group to contain a large number of endophytes. Their widespread capacity to destroy lignocellulosic substrates and to cause various types of diseases largely based on extensive tissue degradation would tend to lead to the conclusion that the general lifestyle of the *Xylariaceae* is that of a facultative parasite or facultative saprophyte" [7].

Regardless of their exact status there are many examples of members of the Xylariaceae associated with canker diseases (Table I). Undoubtedly *Entoleuca mammata* (Wahlenberg: Fr.) J.D. Rogers & Y.-M. Ju (=*Hypoxylon pruinatum* (Klotz.) Cke.=*H.mammatum* (Wahl.) J.H. Miller) is the best known and economically the most important. It has long been recognised as the cause of serious stem canker disease in aspen [12,13]. *Populus tremuloides* Michx. is the main host in North America and *P. tremula* L. in Europe [13,14,15]. Marty [16] calculated that in 1971 '*Hypoxylon*' canker (*E. mammata*) in Minnesota, eastern Upper Michigan, and south western Wisconsin was responsible for an annual loss of $4.4 million at time of harvest. It has also been estimated that this fungus results in the death of 1-2% of aspen grown in the U.S.A. [17]. *Entoleuca mammata* also infects *Acer, Alnus, Betula, Carpinus, Fagus, Picea, Pyrus, Salix, Sorbus*, and *Ulmus* but it is only on *Populus* that it appears to be an important pathogen (Figs 1-2) [13]. In North America the disease is common throughout the northeast, the Great Lakes region, and the north western prairies. Although aspen is abundant and the fungus is present in the northern Rocky Mountains and Alaska canker disease is apparently absent [18]. Pinon [15] considered the disease to have been present in the Alps for over 30 years. The source of infection is uncertain but ascospores have always been assumed to be the main route although ascospore inoculations have proved to be unreliable [13,19].

The economic importance of '*Hypoxylon*' canker has resulted in considerable research into the site of infection and the growing conditions of the trees which subsequently become infected [13, 20]. A number of conditions have been related to infection with good correlation being shown between natural cankers and one or two year old lateral branches [21] and with branch galls caused by the insect *Saperda inornata* Say [22]. There is evidence, in spite of conflicting data, to relate water stress in trees with higher incidence of canker [23,24]. Under water stressed conditions the proline content of aspen has been shown to increase dramatically and that radial growth

rates of *E. mammata* isolates were stimulated to a greater extent by proline than other amino acids [25]. Later it was found that there is clonal variation in the amino acid contents of aspen induced by diurnal drought stress and that this might influence susceptibility to the canker disease [26]. Chapela [27] demonstrated that *E. mammata* (as *Hypoxylon mammatum*) is an endophyte of aspen and therefore the importance of water stress in the host in relation to invasion and canker development is highly significant. Hubbes [28] first suggested that a toxin or toxins might be implicated in the disease symptoms caused by *E. mammata*. Early attempts to isolate and purify the toxin known as mammatoxin demonstrated the presence of several compounds all active in bioassays [29,30]. Studies in our laboratories have resulted in the isolation of the dihydroisocoumarins, 5-methylmellein, 5-methoxycarbonylmellein and 5-carboxymellein [31] and cytochalasin D [32] from North American and European isolates of *E. mammata*. Although 5-carboxymellin and cytochalasin D exhibited bioactivity in leaf and shoot assays they proved not to be the toxic factors involved in the disease process although the cytochalasins are well known for their tissue toxicity in plants [33,34]. Two families of toxins have now been identified, one a diterpene (hymatotoxin) which is structurally similar to momilactones and the second as tetralones [35,36]. The momilactones were originally isolated from rice (*Oryza sativa* cv. Koshihikan) husk and they inhibit the growth of rice roots and the germination of lettuce seeds [37,38]. Tetralones are similar to juglone which is toxic to many plants as well as bacteria, fungi, fish, and mice [39]. There appears to be a complex host-parasite relationship between *E. mammata* and aspen host with pyrocatechol and other bark compounds inhibiting its growth [28,40,41,42]) followed by post-infection production of phytoalexins which inhibit ascospore germination but not mycelial growth [43].

Although the '*Hypoxylon*' canker of aspen has received the most attention a number of species of *Biscogniauxia* and *Camillea* cause significant canker diseases but usually only in trees which have become stressed through drought, injury or fire damage [4,9,3]. *Biscogniauxia mediterranea* is well known as causing coal canker in cork oak (*Quercus suber* L.) and it is considered to be the main cause of the decline of the oak in southern Europe (figs 3-4) [44,45]. During a survey in 1974 of Portuguese cork oak stands 41.5% of the trees were found to be diseased with *B. mediterranea* considered to be the principal pathogen [45]. Surveys of cork oak trees in the Lagos region of Portugal between 1989 and 1994 again indicated a high association between diseased trees and *B. mediterranea* with in the region of 30% of all trees exhibiting signs of decline (Santos, Pers. Comm.). Canker of oak also occurs in Spain, France, Italy, and in North Africa where it has been reported to reach epidemic proportions [46]. Most reports, and from our own observations, canker is more prevalent and damaging in trees which are water stressed following periods of hot dry weather. It is of interest to note that in the first report of *B. mediterranea* in the UK the host was *Castanea sativa* Mill. and not a species of *Quercus* and that it was suggested that the tree involved may have suffered from drought stress during the previous dry summers [47]. The relationship between water stress and ability of *B. mediterranea* to cause canker disease was clearly shown by a series of inoculation experiments of *Quercus cerris* L. where only those trees maintained under water stress conditions succumbed to the disease [48].

A serious decline of beech (*Fagus sylvatica* L.) in the lower region of a beech wood on the Nebrodi mountain range was reported by the Forestry Commission of Messina in
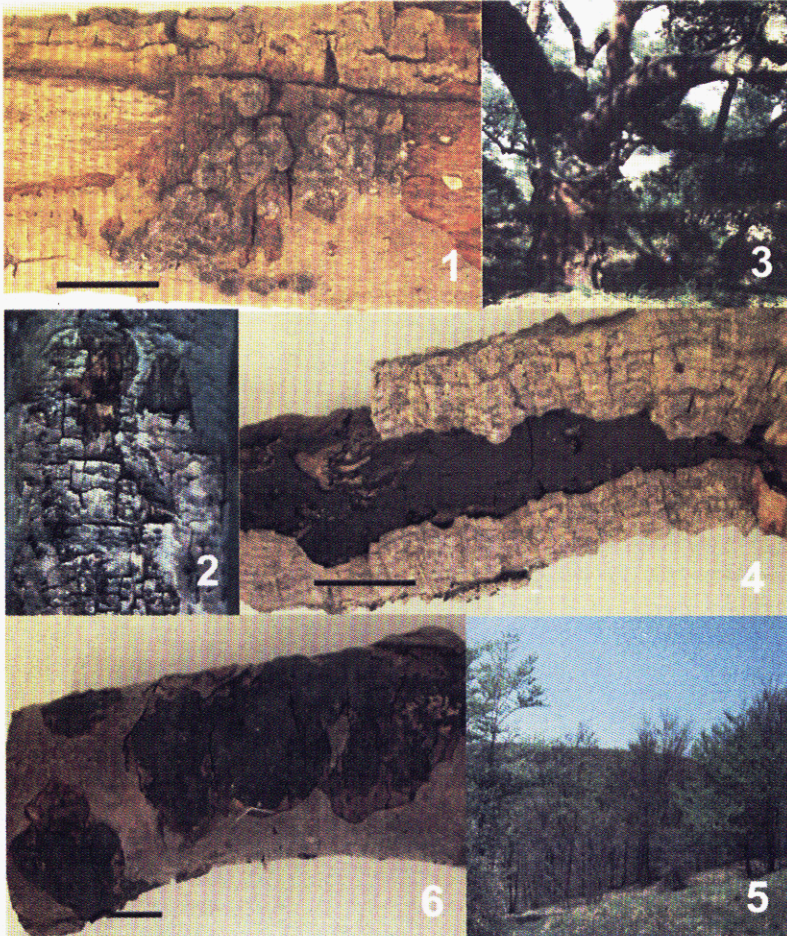
Figure 1. *Entoleuca mammata* stromata. Bar = 10mm. **Figure 2.** *E. mammata* causing canker on *Salix*. **Figure 3.** Mature *Quercus suber* (cork oak) tree showing bark stripped from the trunk. **Figure 4.** *Biscogniauxia mediterranea* on *Q. suber*. Bar = 10mm. **Figure 5.** *Fagus sylvatica* trees in Sicily killed by *B. nummularia*. **Figure 6.** *B. nummularia* stromata on *Fagus*. Bar = 10mm.

Sicily in 1990 (Fig. 5). Initially it was thought that *B. mediterranea* was likely to be the culprit since it was widespread in mainland Italy although on oak and not on beech trees [48]. Subsequent field surveys and examination of diseased branches revealed that *B. nummularia* and not *B. mediterranea* was the cause (Figs 6-7) [49]. It was also apparent that in the Nebrodi range most of the trees badly affected were those growing on steep slopes or on areas with shallow soil where poor water retention could lead to drought conditions during the summer months. They concluded that "probably the prolonged drought and high temperatures over the last ten years have caused conditions of stress in the beech trees and made them susceptible to this disease [49]. Our investigations of the

Xylariaceae in the UK have shown *B. nummularia* to occur widely as an endophyte in beech trees in southern England and parts of Wales. Stromata only develop on freshly detached branches or dying branches still attached to the tree although the fungus is present in healthy branches and twigs. Rogers [7] referred to such xylariaceous fungi as 'sneaky' preferring to think of them as latent invaders developing as the host becomes weakened rather than as endophytes in the usual sense [50]. In their recent monograph of *Biscogniauxia* Ju *et al.* [51] stated that "all experimental and observational evidence indicates that *Biscogniauxia* species are adapted to dry or at least seasonally dry habitats. Development within the bark probably buffers developing stromata from drying. Sufficient water for the activities of these fungi in dead or dying trees is probably via the decomposition of cellulose and the consequent production of water molecules". Lonsdale [52] emphasized the close relationship between water stress and strip canker development caused by *B. nummularia* and later Hendry, Boddy & Lonsdale [53] concluded that the *Biscogniauxia* possesses some pathogenic ability and does not simply invade dead tissue. It is likely that a number of other *Biscogniauxia* species behave in similar fashion to *B. mediterranea* and *B. nummularia* and when their host tree suffers from water stress become invasive developing their stromata and causing die back in the branches and canker as the disease progresses. *Biscogniauxia nothofagi* fits this pattern. It was first described from Tasmania (Australia) where southern beech trees (*Nothofagus cunninghamii* (Hock.) Oerst.) which had been previously attacked by *Chalara australiensis* Kile & J. Walker were found to have developed canker caused by the *Biscogniauxia* [54] (Figs 8-10) . The *Chalara* causes a severe vascular disease resulting in crown wilt and general water stress [55] thus enabling the previously symptomless *B. nothofagi* to invade.

In another drought/water stress situation *B. uniapiculata* has recently been linked with die back and canker in *Eucalytpus camaldulensis* Dehn. in a plantation in Saraburi Province in Thailand. Three mature trees which had recently died were found to have extensive development of the applanate stromata of *B. uniapiculata* when a survey of the plantation was carried out on 16 June 1999 (Figs 11-12) [56]. This plantation site is subject to dry spots during the hot season and trees in these areas are therefore likely to suffer from water shortage. Although *B. uniapiculata* has been reported from *Eucalyptus* in Hawaii there is no account of it causing disease [51].

The recognition that water stress in the host might be associated with canker disease caused by *Biscogniauxia* species is not new. *Biscogniauxia atropunctata* (as *Hypoxylon atropunctatum* (Schwein.: Fr.) Cooke) has long been recognised as causing a serious drought related disease on oaks in the southern states of North America (Fig. 13) [57,58,59,60,61]. In what can be seen as a classical pattern Bassett *et al.* [59] reporting on drought related oak mortality in Arkansas stated that "Arkansas experienced its worst drought in 30 years during the summer of 1980. In the spring of 1981, a marked increase was observed in the death of oak trees and the incidence of *Hypoxylon* canker. This disease is caused by the fungus *Hypoxylon atropunctatum* which invades the phloem and sapwood causing tissue death and eventual decay". They later state that "*Hypoxylon* canker was considered of minor importance, but is now widespread throughout the oak forests of Arkansas". Tainter *et al.* [60] had noted a similar situation in South Carolina and Van Arsdel [58] for Texas. Bassett *et al.* [59] also reported that the *Hypoxylon* canker occurred on dead trees of black/red oaks at 65.1%, in blackjack oaks at 56.3% but in post oaks at only 18.2%. It therefore
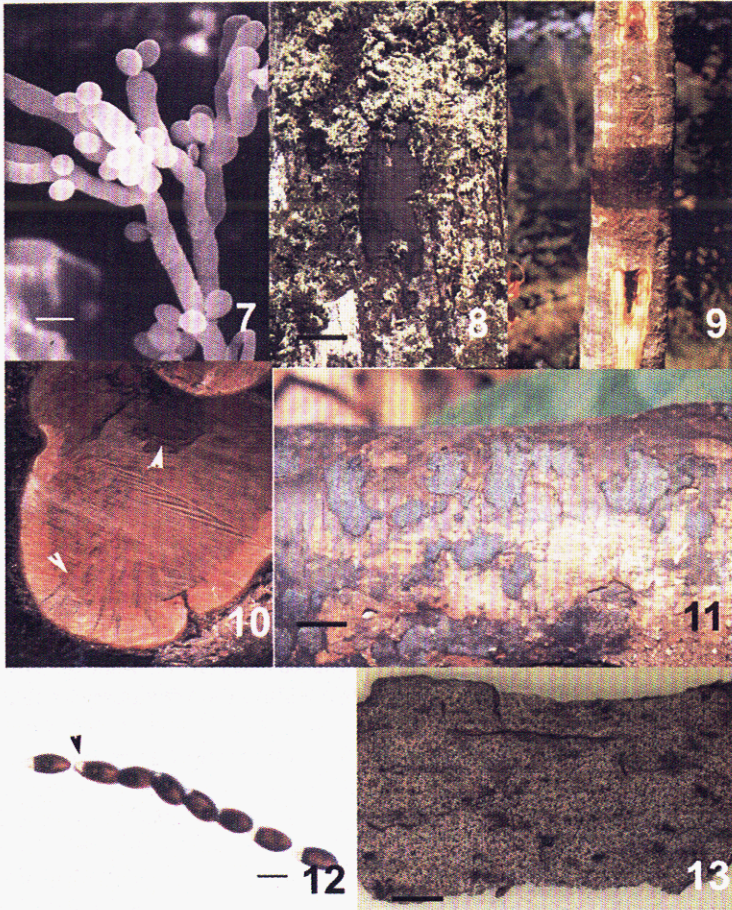
Figure 7. *B. nummularia* anamorph. Bar = 10μm. **Figure 8.** *B. nothofagi* stroma. Bar = 15mm. **Figure 9.** Young stem canker of *Nothofagus cunninghamii* caused by *B. nothofagi*. **Figure 10.** Cross section of trunk of young *N. cunninghamii* exhibiting early stages of canker development (arrowed). **Figure 11.** *B. uniapiculata* stromata on Eucalyptus in Thailand. Bar = 10mm. **Figure 12.** *B. uniapiculata* ascospores showing appendage (arrowed). Bar = 10μm. **Figure 13.** *B. atropunctata* stromata on southern red oak in Tennessee, U.S.A. Bar = 15mm.

appears that there are probably species differences in relation to drought and therefore canker development in the same way that there are clonal differences in aspen in relation to canker caused by *E. mammata* [26]. Furthermore it was calculated that *B. atropunctata* resulted in a loss of 7.1% volume of black/red oak in Northwest Arkansas in 1981 [59].

Camillea Fr. is another genus of the Xylariaceae which has similarities to *Biscogniauxia* both in general morphological appearance and in lifestyle favouring more open, sun exposed positions in tropical and subtropical forests [62] *Camillea punctulata* causes a stem canker of *Quercus* in the southeastern U.S.A (Fig 14) [63] and has been

linked with trees which are water stressed through prior infection with the oak wilt fungus, *Ceratocystis fagacearum* (Bretz) J. Hunt [64]. The related *C. tinctor* is associated with canker in American sycamore (Figs 15-19) [65] and also in plane (*Platanus occidentalis* L. and *P. acerifolia* (Ait.) Willd.) [66].

Although *E. mammata* and species of *Biscogniauxia* and *Camillea* are the most frequently reported xylariaceous fungi in relation to canker diseases a number of taxa in other genera are worthy of note. A number of species of *Hypoxylon* have been reported as traumatic parasites of tea bushes (*Camellia sinensis* (L.) Kuntze) by Agnihothrudu [67,68] *Hypoxylon rubiginosum* is linked with a most unusual association with catalpa (*Catalpa bignonioides* Walt.) where it was reported to cause canker in trees on the campus of the University of Georgia, U.S.A. Local fishermen beat the trunks of the catalpa with clubs to dislodge the Catalpa worm (*Ceratomia catalpae* Boisduval.) to use as bait resulting in localized injury to the trees with the subsequent the development of canker caused by *H rubiginosum* [69]. Another interesting situation concerns *R. diathrausta* (Rehm) L.E. Petrini which in the European Alps only occurs at high altitude growing on branches of *Pinus montana* Miller ssp. *prostata* Tubeuf. Furthermore it only occurs on trees in extremely exposed situations and then appears to be restricted to branches subjected to wind burn [9].

Daldinia is another genus which can be regarded as adapted to dry conditions [70]. *Daldinia concentrica* is associated with a condition known as calico wood of ash (*Fraxinus excelsior* L.) and occurs as a frequent endophyte in leaves and branches [71]. It also produces its stromata for several years once its host tree has died and has been implicated in the weakening of ash trees making them susceptible to storm damage (Fig. 20) [72]. Our recent studies on *D. concentrica* show that following inoculations in young ash trees with ascospores those which were deliberately water stressed soon exhibited signs of die back associated with the spread of *Daldinia* whilst those trees which were kept fully watered remained healthy and *Daldinia* was rarely isolated from living tissue.

In Poland an interesting link has been reported between *H.fuscum* (Pers.) Fr. and alder (*Alnus incana* (L.) Moench) which had been weakened by industrial pollutants (Fig. 21) [73]. Under these conditions *H. fuscum* became a serious pathogen resulting in a very destructive white pocket rot in wood of dead alders. Miller [74] considered *H. fuscum* to be saprotrophic on members of the Betulaceae but Rogers indicated that it might be parasitic on *Alnus tenuifolia* Nutt. in North America [75]. In the U.K. *H. fuscum* is common on *Corylus avellena* L. and is frequently found on recently dead or dying stems and branches still attached to living trees.

Agnihothrudu [67,68] drew attention to a number of species of *Hypoxylon* and related Xylariaceae as traumatic parasites on tea, coffee and rubber in India stating that "It is most likely that many are weak, secondary parasites attaching wood as traumatic pathogens" [68] A number of the species listed were said to be involved in wood rot following sun scorch or trauma. This would clearly fit the pattern of water stress leading to latent invasion and canker as already referred to above.

One species of *Xylaria*, *X. arbuscula* has been shown to be responsible for a quick decline of macadamia (*Macadamia integrifolia* Maiden & Betche) in a commercial orchard in Hawaii [76]. The disease appeared to originate from trunk infections and a number of the diseased trees were found to have the typical club-shaped stromata of the *Xylaria* growing on the trunk with extensive decay of the bark tissues beneath.
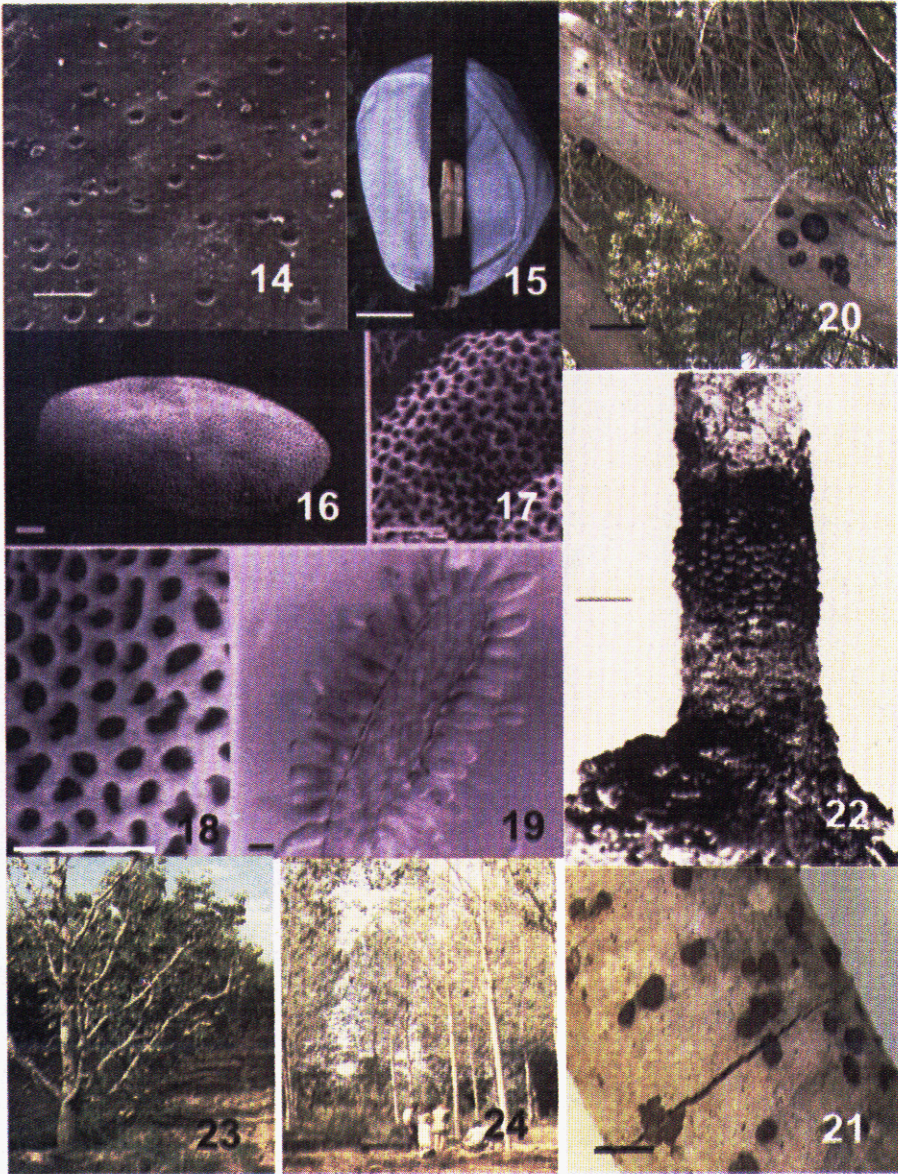
Figure 14. *Camillea punctulata* stromata. Bar = 2.5mm. **Figure 15.** *C. tinctor* on branch showing characteristic yellow staining. Bar = 40mm. **Figure 16.** *C. tinctor* ascospore. Bar = 1µm. **Figure 17.** *C. tinctor* ornamented ascospore. Bar = 1µm. **Figure 18.** *C. tinctor* ornamented ascospore. Bar = 1µm. **Figure 19.** *C. tinctor Xylocladium* anamorph. Bar = 1µm. **Figure 20.** *Daldinia concentrica* stroma on *Fraxinus*. Bar = 120mm. **Figure 21.** *Hypoxylon fuscum* stroma on *Betula*. Bar = 1mm. **Figure 22.** *Rosellinia necatrix* perithecia. Bar = 30mm. **Figure 23.** Dead apple trees killed by *R. necatrix* in Alcobaca, Portugal. **Figure 24.** Dead *Populus* killed by *R. necatrix* in Portugal.

Root infections

Although a diverse selection of xylariaceous fungi are implicated in root infections it is species of *Rosellinia* and *Kretzschmaria* which are the most important (Table II). *Rosellinia necatrix* is a plurivorous international pathogen of considerable economic importance (Fig. 22) [4,77, 78]. It has been reported to infect over 170 plant species from 63 genera and 30 families [79] and Teixeira de Sousa [80] pointed out that herbaceous plants can also be infected and should be regarded as a potential source of inoculum. *Rosellinia necatrix* rarely produces ascocarps in nature so that most identifications are based on vegetative features, the development of its *Dematophora* anamorph and disease symptoms resulting in some uncertainty concerning its reported wide host range and geographical distribution [78]. There are indications that *R. necatrix* is probably more prevalent in temperate areas with the closely related *R. arcuata* Petch being more common in the tropics [81]. Petrini [82] noted that macroscopically *R. arcuata* resembles *R. necatrix* but that its ascospores are statistically significantly larger. Although it has been possible to induce ascocarp production in the laboratory the method is long term and comparison of temperate and tropical isolates using molecular techniques needs to be undertaken to examine the precise relationship between *R. necatrix* and *R. arcuarta* [78]. There is an impressive array of reports of major problems caused by *R. necatrix* on economically important plants in Europe, including apple, grape vine, pear, plum, sweet cherry, poplar, jasmine and scented geranium [80,83,84,85,86,87,88]. In Portugal 42% of the apple orchards in the Alcobaca area were infected with 14% of the trees exhibiting advanced disease symptoms and are either dead or dying (Fig 23) [88]. In France, although apple and wild cherry (*Prunus avium* L.) are badly affected, jasmine (which is important in the perfume industry), together with carnation, narcissus and paeony are all subject to major loss [85]. In Italy "*R. necatrix* is considered to be one of the most dangerous agents of root-rot in Poplars" and is responsible for a loss of between 0.5-1% in total production [84]. In some regions this loss may reach 5-10% with some plantations suffering a loss of as high as 20-25% [87]. Investigations into conditions which favour *R. necatrix* infection in poplars found that *R. necatrix* spread readily on a loose soil with a high sand content [89]. They also reported that soil moisture content near to field capacity encouraged mycelial spread from tree to tree but under dry conditions trees were more liable to attack. The importance in removing from the soil any woody or organic debris which might have had contact with *Rosellina* was recommended as part of a control strategy [89,90]. *Populus deltoides* Marsh. grown in plantations for match production in the Coimbra region of Portugal, has also proved to be susceptible to white root rot with *R. necatrix* being isolated from the diseased roots. Trees of 15 years and approximately 10 metres tall were killed within one season following the onset of leaf yellowing and premature defoliation (Figs 24-25) [88].

In New Zealand *R. necatrix* was reported to be responsible for a serious white root rot in Walnut (*Juglans regia* L.) and the importance of removing remains of dead trees, especially their roots, was seen to be important for the restriction of the disease [91] Teixeira de Sousa [80] and Sztejnberg *et al.* [92] recommended solarization of soil prior to planting, or exposure of infected roots to air, light and summer heat combined with treatment of the soil with a 0.1-0.2% suspension of benomyl or thiabendazole compounds as the best chance for control.
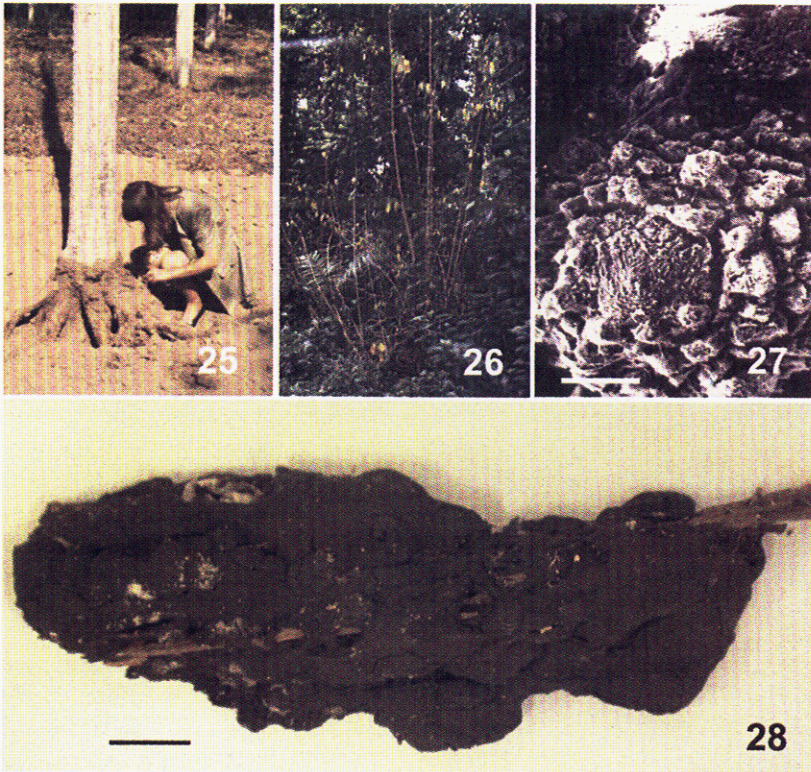
Figure 25. Sampling of *Populus* roots infected with *R. necatrix.* **Figure 26.** Dead *Hibiscus* infected with *R. bunoides.* **Figure 27.** *R. bunoides* stroma. Bar = 1 μm. **Figure 28.** Stromata of *Kretzschmaria deusta.* Bar = 5mm.

In spite of its economic importance little is known about the pathogenicity of *R. necatrix* but it is suspected that toxins are involved. It has been found to produce a number of secondary metabolites in culture including rosellinic acid [93,94], cytochalasin E [8,95], rosellichalasin [96] and rosenectrone [97]. Examination of fluorescence emission spectra and fluorescence decay time following uptake of cytochalsin E in young leaves of apple (*Malus domestica* L.) indicated a direct effect on photosynthesis which might contribute to the pathogenicity of the fungus and it was also suggested that *in vivo* chlorophyll fluorescence may be used to monitor early damage by fungal toxins [98]. *Rosellinia arcuata* is a pathogen mainly of tea (*Camellia sinensis* (L.) Kuntze) and coffee (*Coffea arabica* L.) and has long been considered to be the tropical equivalent of *R. necatrix* [81]. Petrini [82] pointed out that there are several species of pathogenic *Rosellinia* with ascospores similar to both *R. arcuata* and *R. necatrix* but she disagreed with Francis [81] who considered *R. arcuarta* and *R. bothrina* (Berk. & Br.) Sacc.) to be conspecific. She also noted that the Petch collections of *R. arcuarta* are from a mountainous region of Sri Lanka and that in New Zealand *R. arcuata* was mainly

collected in the northern part of North Island with subtropical vegetation. Furthermore *R. arcuata* has not been reported from cultivated trees in New Zealand [82].

Rosellinia bunodes is an important tropical species and is reported to be widespread in tropical America, Central Africn Republic, India, Indonesia, Malaysia, Philippines, Sri Lanka, Zaire and parts of Central America [99]. It causes black root rot of tropical and subtropical woody plants (Fig. 26) but is most frequent on cacao (*Theobroma cacao* L.), quinine (*Chincona* spp.), coffee (*Coffea* spp.), rubber *(Hevea brasiliensis* Muell.) and tea (*Camellia sinensis* (L.) Kuntze) [99]. Unlike *R. necatrix* it readily produces mature ascocarps in nature which develop a distinctive wart-like ornamentation and have ascospores with characteristically long tapering ends (Fig. 27). It is transmitted though mycelium impregnated organic litter or woody debris [99]. There is no evidence that toxins are involved and cytochalasin E and other phytotoxic compounds found in *R. necatrix* are absent [100]. Another tropical species, *R. pepo* appears to be restricted to Central America, the West Indies and West Africa [101]. Coffee is the economically important host but it is said to be plurivorous [101]. In the UK a ring-die back in creeping willow (*Salix repens* L.) has been linked to *R. desmazieresii* which attacks the roots and underground stems causing chlorosis, wilting and in some cases plant death [102]. It also appears that environmental conditions that coincide with development of new disease rings are similar to those conditions which favour growth of the *Rosellinia* in vitro [103]. *Rosellinia desmazieresii* produces cytochalasin D in laboratory culture but it is not known if this has any implications in the disease process [8].

Kretzchmaria deusta (Fig. 28) has long been recognized as an important pathogen of a range of tree species being associated with the base of trunks but infecting through the roots [104,105]. There are accounts of between 11-20% of beech trees infected by this fungus in Czechoslovakian forests [106] in the Sara mountains in Yugoslavia an infection rate of up to 42% has been reported [107]. *Kretzchmaria zonata,* sometimes seen as the tropical equivalent, is responsible for an inportant root rot in rubber (*H. brasiliensis* Muell.) in India [68] and Malaysia [108]. In Hawaii *K. clavus* has been shown to be a major cause of root rot in Macadamia [109] and it was later suggested that as most of the infected macadamia orchards are located near forests of *Metrosideros collina* (Forst.) Gray subsp. polymorpha (Gang) Rock where *K. clavus* is a common inhabitant then these trees provided the source of the infection [110]. Infection of macadamia in Taiwan by *K. clavus* has also been reported but the source of the infection was not known [111]. Rogers & Ju [112] in their monograph of *Kretzschmaria* noted the ability of many species to survive on dead material and considered them to be parasites of opportunity.

Xylaria mali is the only *Xylaria* species of note to be associated with root infections. It is responsible for a serious, but geographically restricted, black root rot of apple trees in Virginia and the Carolinas of North America [113]. *Xylaria polymorph* is a common and widespread species which has been reported as a weak pathogen which enters through wounds causing disease in *Acer rubrum* L., *Coffea Arabica* L., *Platanus acerifolia* (Ait) Willd and other woody hosts [114].

Needle blight diseases

There are a number of reports of needle blight diseases of conifers from Europe and N. America caused by species of *Rosellina* [115]. *Rosellinia herpotrichiodes* Hepting & R.W. Davidson is usually considered to be the main antagonist causing outbreaks on

Table II. Root infections caused by members of the Xylariaceae

Species	Host
Kretzschmaria clavus (Fr.) Sacc.	*Macadamia*
K. deusta (Hoffm.: Fr.) P. Martin	*Fagus* and many deciduous trees
K. zonata (Lev.) P. Martin	*Hevea*
Rosellinia arcuata Petch	*Camellia sinensis, Coffea*
R. bunodes (Berk. & Broome) Sacc.	*Coffea*
R. desmazieresii (Berk. & Broome) Sacc.	*Salix*
R. necatrix Prill.	Many
R. pepo Pat.	*Coffea*
Xylaria mail Fromme	*Malus*
X. polymorpha Pers.:Fr.	*Acer, Coffea, Platanus*

young plants of Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) in forest nurseries [116,117], on Sitka spruce seedlings (*Picea sitchensis* (Bong.) Carr), [118] and on three-year old plants of *Picea abies* (L.) Karsten [119]. Francis following taxonomic studies on *Rosellinia* species concluded that all of the infections in young conifer seedlings were caused by *R. minor* (Hohn.) S.M. Francis and not by *R. herpotrichioides* [115]. However she recognized *R. herpotrichioides* to be a distinct species in its own right noting that as well as taxonomic differences its occurrence on lower branches of mature hemlock (*Tsuga canadensis* (L.) Carr. growing nearest to the stream banks along coves in the Pisgah National Forest in N. Carolina, S.A [120] was an entirely different situation to that of the nursery beds where *R. minor* occurred [115]. Other reports on *Rosellinia* causing disease in conifers [121,122,123] were all considered by Francis [115] to be caused by *R. minor*. It appears that *R. minor* can cause serious loss in forest nursery beds [122] especially through overcrowding, prolonged high humidity and when growth results in a dense lower canopy of foliage [115,124] Although *R. thelena* has been associated with conifer foliage in Denmark it appears to occur only on pruned branches resulting from thinning out of the trees and did not appear to be the cause of any disease [125].

Conclusions

The Xylariaceae can be seen to cause canker, root rot and needle blight diseases although they are rarely considered to be of significance. Canker caused by *Entoleuca mammata*, species of *Biscogniauxia* and *Camillea* are associated with water stressed conditions in woody hosts. The fungi appear to be common in the living tissue of these hosts and only become invasive once water stress conditions have developed. *Entoleuca* in particular is well known as the cause of severe loss of aspen in North America. Root infections leading to white or black root rot depending on the species are a major characteristic of *Rosellinia* and *Kretzschmaria* species. There are also examples of other xylariaceae causing root infections such as *X. arbuscula* and *X. polymorpha*. Cytochalasin E and rosenectrone can cause similar disease symptoms in apple cuttings to those occurring under field conditions following infection by *R. necatrix*. This species occurs widely and infects an exceptionally wide range of plants, many of commercial importance but because of the lack of perithecial material and its close similarity to *R. arcuata* molecular studies on these species should be undertaken to determine the exact situation.

Acknowledgements

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