Research review

Diseases of Pines and Eucalypts in South Africa Associated with *Pythium* and *Phytophthora* Species

C. Linde, G.H.J. Kemp and M.J. Wingfield

Department of Microbiology and Biochemistry, University of the Orange Free State, P.O. Box 339, Bloemfontein 9300.

SYNOPSIS

This review covers diseases of *Pinus* and *Eucalyptus* spp. associated with *Pythium* and *Phytophthora* spp. The relative importance of these fungi is discussed and their host range is described. It is shown that the most important species are *Phytophthora cinnamomi* and to a lesser extent *Phytophthora cryptogea*. Diseases associated with *Pythium* and *Phytophthora* spp. in South Africa have been inadequately studied in the past. This review emphasises the occurrence and importance of *Pythium* and *Phytophthora* in forestry in South Africa and attempts to place it in perspective.

The forestry industry in South Africa depends largely on exotic species of *Pinus* and *Eucalyptus*. Species of these hosts are planted in more or less equal proportions and together, they cover an area of approximately 1,2 million hectares (Anonymous, 1990). Forestry is based on a monoculture system and this has led to a concern regarding the potential threat of diseases to this industry (Wingfield *et al.*, 1991). Oomycetous fungi, and particularly species of *Phytophthora,* are known to cause serious damage to woody plants in many parts of the world (Crandall, 1936; Crandall, 1950; Evans, 1968; Firman, 1974; Katsura, 1976; Liyanage, 1989; Opeke and Gorenz, 1974; Tidball and Linderman, 1990). Little attention has, however, been given to the occurrence and importance of *Pythium* and *Phytophthora* spp. in forestry in South Africa.

Phytophthora and *Pythium* spp. are serious pathogens with a wide host range. *P. cinnamomi* for example has a host range of over a 1 000 plant species (Zentmyer, 1980). Various symptoms such as root rot, die-back, blight, cankers, fruit rot, pod rot, collar rot, and necrosis of feeder roots are associated with infection by *Phytophthora* spp. (Gallegly, 1983; Zentmyer, 1980). In contrast, *Pythium* spp. are usually confined to nursery diseases such as pre- and post-emergence damping-off of various *Eucalyptus* and *Pinus* spp. (Marks and Kassaby, 1974; Vaartaja, 1967; Vaartaja and Salisbury, 1961). Species of *Pythium* and *Phytophthora* associated with root diseases of *Eucalyptus* and *Pinus* spp. are summarised in *Table 1*. The aim of this review is to summarise the knowledge regarding the most important *Pythium* and *Phytophthora* spp. and the diseases they cause to *Eucalyptus* and *Pinus* spp. Special reference is given to the disease situation in South Africa.

DISEASES ASSOCIATED WITH *PHYTOPHTHORA* AND *PYTHIUM* ON ESTABLISHED TREES

a) Diseases caused by *Phytophthora*

Phytophthora cinnamomi and *Phytophthora cryptogea* are considered to be the most important species pathogenic to *Eucalyptus* and *Pinus* spp. (Bumbieris, 1976; Hamm and Hansen, 1982; Heather *et al.*, 1977; Marks and Kassaby, 1974; Newhook, 1959; Podger, 1978; Podger and Batini, 1971). *P. cryptogea* is less widespread than *P. cinnamomi* and appears to be a pathogen of minor significance (Shepherd and Halsall, 1977; Weste, 1975). *P. cryptogea* also appears to vary in pathogenicity and Shepherd and Pratt (1973) were able to recognise distinct northern and southern ecotypes of the fungus in Australia. *Phytophthora drechsleri* associated with seedling deaths is considered to be a synonym of *P. cryptogea* (Bumbieris, 1974). The conspecificity of the two species was unfortunately not recognised by some researchers prior to 1978 (Podger, 1978).

Phytophthora cinnamomi has been regarded by some as the most destructive plant pathogen ever discovered (Wolstenholme, 1979; Zentmyer, 1980). A classic example of a devastating disease associated with *P. cinnamomi* is the well-known Jarrah (*Eucalyptus marginata* Sm.) die-back in western Australia, which is undoubtedly the most serious forest disease associated with an Oomycetous fungus (Podger *et al.*, 1965). *P. cinnamomi* is also associated with die-back of *Eucalyptus* spp. other than *E. marginata* in Australia (Marks *et al.*, 1972; Podger, 1972; Pratt *et al.*, 1973; Weste and Taylor, 1971). In

pines, it is associated with littleleaf disease of *Pinus echinata* Mill. (shortleaf pine) and *Pinus taeda* L. (loblolly pine) on poorly-drained soils in south-eastern USA (Campbell, 1948; Campbell, 1949; Fraedrich *et al.*, 1989; Zak and Campbell, 1958). A root disease similar to littleleaf disease also occurs on *P. radiata* D. Don. in New Zealand. *P. cinnamomi* and *Phytophthora cactorum* were the two pathogens consistently associated with the *P. radiata* decline and appear to be of equal importance (Newhook, 1959). This disease is essentially the same as the littleleaf disease of *P. echinata* in south-eastern USA, except that symptoms develop far more rapidly (Newhook, 1959).

In New South Wales, Australia, *P. cryptogea* has been regarded as a pathogen of *P. radiata* (Davison and Bumbieris, 1973; Heather and Pratt, 1975). However, most of the isolations of *P. cryptogea* associated with declining *P. radiata*, occurred during years when abnormally wet conditions persisted until spring. The affected trees in the field varied from one to 44 years old, but most were between 31 and 44 years old (Davison and Bumbieris, 1973).

Shearer *et al.* (1987) compared the pathogenicity of *P. cryptogea* on established *Eucalyptus* with that of *P. cinnamomi.* Although both species were pathogenic, *P. cinnamomi* was more virulent than *P. cryptogea*. The latter fungus can also cause pre- and post-emergence damping-off of various *Pinus* and *Eucalyptus* spp. (Hamm and Hansen, 1982; Heather *et al.*, 1977; Marks and Kassaby, 1976). Nevertheless, *P. cryptogea* is geographically less widespread than *P. cinnamomi* and is, therefore, less significant than the world-wide distributed *P. cinnamomi* (Pratt and Heather, 1973b; Shepherd and Halsall, 1977; Weste, 1975).

b) Diseases caused by *Pythium* spp.

Some controversy exists regarding the importance of *Pythium* spp. as pathogens of mature forest trees. They are generally not considered as important pathogens of *Eucalyptus* and *Pinus* trees (Marks and Kassaby, 1974; Marks and Kassaby, 1976). Pratt and Heather (1973a) suggested that *Pythium* and *Phytophthora* spp., other than *P. cinnamomi*, can act either singly or in combination with *P. cinnamomi* to cause die-back of *Eucalyptus* trees. Lorio (1966) also suggested that *Pythium splendens, Pythium vexans* and *Pythium irregulare* in association with *P. cinnamomi,* may play an important role in *P. taeda* decline in Louisiana. It is often the case that soil in pine sites with high concentrations of, e.g., *P. irregulare* and *Pythium debaryanum,* lead to higher mortalities of *P. echinata,* than soil with low concentrations of *Pythium* spp. (Otrosina and Marx, 1975). However, the effect that *Pythium* infection has on the trees is, apparently, related to tree vigour (Lorio, 1966).

NURSERY DISEASES CAUSED BY *PYTHIUM* AND *PHYTOPHTHORA*

Pythium spp. have a wide host range but infect mainly juvenile or succulent tissues of annual plants (Hendrix and Campbell, 1973). They are most commonly associated with pre- and post-emergence damping-off of pines and eucalypts in nurseries (Marks and Kassaby, 1974; Vaartaja, 1967; Vaartaja and Salisbury, 1961). In contrast, *Phytophthora* spp., especially *P. cinnamomi* and *P. cryptogea,* are well-known pathogens of established trees, but are also serious pathogens of *Eucalyptus* and *Pinus* spp. under nursery conditions (Hamm and Hansen, 1982; Marks and Kassaby, 1974; Marks and Tippett, 1978; Newhook, 1959; Podger and Batini, 1971). Other species of *Pythium* causing diseases of *Eucalyptus* include *Pythium deliense* and *Pythium myriotylum,* associated with post-emergence damping-off (Sharma *et al.*, 1985) and *P. cactorum, Phytophthora citricola* and *Pythium anandrum* which cause a stem disease of various *Eucalyptus* spp. in Tasmanian nurseries (Wardlaw and Palzar, 1985).

Various other *Pythium* and *Phytophthora* spp. have been associated with root diseases of *Pinus* and *Eucalyptus* trees under field and nursery conditions (*Table 1*). These species may contribute to the development of root diseases, but in most cases, pathogenicity has not been established (Campbell and Hendrix, 1967; Davison and Bumbieris, 1973; Hocking, 1968; Lorio, 1966; Marks and Kassaby, 1974; Newhook, 1959; Otrosina and Marx, 1975; Pratt and Heather, 1973a). They are, however, not associated with specific disease problems, but more frequently form part of complex interactions with other pathogenic fungi (Lorio, 1966; Newhook, 1959; Podger, 1978).

DISEASE SITUATION IN SOUTH AFRICA

a) Diseases caused by *Phytophthora* spp.

A number of *Phytophthora* spp. have been associated with destructive plant diseases in South Africa. These diseases include a root rot of avocado (*Persea americana* Mill.) associated with *P. cinnamomi* (Doidge and Bottomley, 1931; Von Broembsen, 1984a; Wager, 1941; Wager, 1942), fruit rot and trunk gummosis of citrus associated with *P. citricola, P. cinnamomi, P. citrophthora* (Sm. & Sm.) Leon. and *P. cactorum* (Mes, 1934; Wager, 1931; Wager, 1941), root and crown rot of apple associated with *P. cactorum* (Van der Merwe and Matthee, 1973), stem rot of passion fruit (*Passiflora edulis* Sims.) associated with *P. nicotianae* var. *parasitica* (Van den Boom and Huller, 1970), and root and crown rots of a variety of other plants associated with both *Phytophthora* and *Pythium* spp. (Darvas *et al.*, 1984; Von Broembsen, 1984a; Wager, 1941). *Phytophthora cinnamomi* is a common pathogen of grapes (*Vitis vinefera* L.) and commercially cultivated *Protea* spp. (Van der Merwe

et al., 1972; Von Broembsen and Brits, 1985). *P. parasitica* is responsible for a black-butt disease of *Acacia mearnsii* de Wild. (Zeijlemaker, 1971), an important forest tree species used for the production of tannins and high quality paper.

The first disease of forest trees in South Africa was noted as early as 1893 on *Pinus pinea* L., *P. radiata* and *E. marginata* in the western and southern Cape Province (Hutchins, 1893). The causal agent was, however, never identified. *P. radiata* is highly susceptible to *P. cinnamomi* in South Africa (Von Broembsen, 1984a; Wingfield and Knox-Davies, 1980) and *E. marginata* is known for its susceptibility to this fungus elsewhere in the world (Podger *et al.*, 1965). Furthermore, studies on *P. cinnamomi* have shown that the fungus is widespread in the southern and western Cape Province (Von Broembsen, 1984a,b). It is therefore probable that the first recorded disease of forest trees in South Africa was caused by *P. cinnamomi.*

Evidence that *P. cinnamomi* is indigenous to South Africa was presented when the A1 mating type was recovered from rivers and indigenous hosts (Knox-Davies, 1975; Von Broembsen, 1984b; Von Broembsen and Kruger, 1985; Von Broembsen *et al.*, 1986). Only the A2 mating type of *P. cinnamomi* occurs in managed forestry areas which are distant from the indigenous flora of the Cape where the A1 mating type is commonly found. This suggests that *P. cinnamomi* was introduced into exotic forestry areas (Wingfield *et al.*, 1989).

Phytophthora cinnamomi has caused serious losses in pine nurseries in the Cape Province. At the Witelsbos (south-eastern Cape) nursery, it was necessary to quarantine the whole nursery (Anonymous, 1979/1980). At the Kluitjieskraal (south-western Cape) nursery, *P. cinnamomi* necessitated the destruction of 130 000 seedlings (Anonymous, 1980/1981). A forestry nursery at Grabouw suffered severe losses due to *P. cinnamomi,* favoured by poor drainage (Donald and von Broembsen, 1977). The annual mortality of *P. radiata* seedlings produced in that nursery, ranged from 26 to 57 % for the period 1971 to 1975.

Eucalyptus fastigata Deane & Maid. and *Eucalyptus fraxinoides* Deane & Maid. have been severely affected by *P. cinnamomi* in South Africa (Wingfield and Knox-Davies, 1980). Mortality of *E. fastigata* is limited to individual trees and occurs scattered in plantations. Death of *E. fraxinoides* has been high and it appears to be the most susceptible *Eucalyptus* species planted in South Africa (Wingfield *et al.*, 1989). The cultivation of both species has been stopped owing to their high level of susceptibility to *P. cinnamomi* associated root diseases.

Phytophthora cinnamomi has been recovered from dying 19 to 20-year-old *P. radiata* trees in the southern and western Cape Province (Von Broembsen, 1984a). This is in contradiction with the reported susceptibility of *P. radiata* in USA which is at its highest when the trees are over 20 and especially over 30 years old (Newhook, 1959). However, this age-related susceptibility was determined for littleleaf disease and it is uncertain whether the trees examined by Von Broembsen (1984a) suffered from this disease or not. Furthermore, differences in climatic conditions and soil type could play a role in this variation in age-related susceptibility, as these factors influence both host and pathogen (Marks *et al.*, 1972).

Phytophthora cinnamomi has occasionally been isolated from mature (40–50 year) *P. radiata* as well as from *Pinus clausa* Chapm. on wet or nutritionally poor sites (Wingfield and Knox-Davies, 1980). *P. radiata* and *P. clausa* are the most susceptible *Pinus* spp. under field and nursery conditions in South Africa. However *P. clausa* is not widely planted and its susceptibility is therefore of minor significance. *Pinus elliottii* Engelm., *Pinus pinaster* Ait., *Pinus halepensis* Mill. and *Pinus patula* Schlecht & Cham. were also susceptible to *P. cinnamomi* in nurseries, but to a lesser extent (Von Broembsen, 1984a). Species of *Phytophthora* other than *P. cinnamomi* have not been reported from *Eucalyptus* and pine plantations in South Africa.

b) *Pythium*-related diseases

Various *Pythium* spp. have been isolated occasionally from coniferous seedlings in South African forest nurseries (Darvas *et al.*, 1978). No serious losses were recorded and *Pythium* spp. have, therefore, not been considered as important pathogens of *Eucalyptus* and *Pinus* spp. in South Africa. However, *P. splendens* has recently been associated with mortalities of one to two-year-old *Eucalyptus grandis* seedlings in northern Natal (Linde *et al.*, 1992). Furthermore, *P. irregulare* has been associated with establishment deaths of *P. patula* on previously cultivated lands in the north-eastern Cape (Linde *et al.*, 1993). In both cases, mortalities were high with great economically importance. It was also the first time that *Pythium* spp. have been associated with mortality of *Eucalyptus* and *Pinus* trees under field conditions (Linde *et al.*, 1992; Linde *et al.*, 1993).

CONCLUSIONS

Oomycetous fungi, particularly *Phytophthora* spp., include some of the most notorious pathogens of forest trees. Although *P. cinnamomi* has been associated with occasional death and die-back of mature eucalypt and pine trees in South Africa, it does not, however, appear to be amongst the most serious pathogens of forest trees in the country.

A wide variety of *Pythium* spp. contribute to severe disease losses in forest nurseries worldwide. Although commonly associated with mature diseased *Euca-lyptus* and *Pinus* spp., their importance as pathogens of those trees is uncertain. In South Africa, *Pythium* spp. have, in the past, been associated with nursery diseases only, and they appear to be of minor significance. However, with the discovery of *P.*

splendens and *P. irregulare* as pathogens of trees under field conditions, it is likely that similar disease complexes would be identified elsewhere in the world.

Improvement of nursery practices in recent years includes the use of composted bark as a growth medium instead of soil which is often infested with pathogens. Bark medium has almost completely eliminated damping-off caused by *Pythium* spp. in pine seedlings. The acid nature of this medium is unfavourable for disease development (Hoitink and Fahy, 1986; Huang and Kuhlman, 1991; Spencer and Benson, 1982). Nursery diseases associated with *Pythium* and *Phytophthora* spp. are, therefore, unlikely to be a problem in the future.

Species of *Phytophthora* and *Pythium* include some of the world's most destructive plant pathogens and their impact on economically important crops has been well documented (Gregory, 1983). However, the presence of these fungi, especially those associated with *Eucalyptus* and *Pinus* spp. under field conditions, has been inadequately studied in the past. A detailed survey of forestry plantations is therefore necessary to establish which *Pythium* and *Phytophthora* spp. are involved, and what role they play in the root disease complex.

TABLE 1. Occurrence and pathogenicity of Pythium *and* Phytophthora *spp. associated with* Eucalyptus *and* Pinus *spp.*

Species	Host[x]	Pathogenity[y]	References
Phytophthora boehmeriae Saw.	P	F+	Oxenham and Winks, 1963
" *cactorum* (Lehb. & Cohn) Schroet.	E	F+	Shearer *et al.*, 1988
	E	N+	Wardlaw and Palzar, 1985
	P	F+	Newhook, 1959
	P	N+	Newhook, 1959
" *cinnamomi* Rands	E	F+	Malajczuk *et al.*, 1977; Marks and Kassaby, 1974; Marks *et al.*, 1972; Podger, 1972; Podger *et al.*, 1965; Pratt *et al.*, 1973; Weste and Taylor, 1971
	E	N+	Podger and Batini, 1971
	P	F+	Campbell, 1948; Cambell, 1949; Lorio, 1966; Newhook, 1959; Zak and Campbell, 1958
	P	N+	Hamm and Hansen, 1982; Heather *et al.*, 1977; Newhook, 1959
" *citricola* Saw.	E	F-	Pratt and Heather, 1973a; Shearer *et al.*, 1987
	E	N+	Wardlaw and Palzar, 1985
	P	F-	Davison and Bumbieris, 1973; Newhook, 1959
	P	N-	Davison and Bumbieris, 1973
" *cryptogea* Pethybr. & Laff.	E	F-	Shearer *et al.*, 1987
	E	F+	Shearer *et al.*, 1988
	E	N+	Marks and Kassaby, 1974
	P	F+	Bumbieris, 1976; Davison and Bumbieris, 1973
	P	F-	Newhook, 1959
	P	N-	Davison and Bumbieris, 1973
	P	N+	Hamm and Hansen, 1982
" *drechsleri* Tucker	E	F-	Campbell and Hendrix, 1967; Marks and Kassaby, 1974; Pratt and Heather, 1973a; Shepherd and Pratt, 1973
	E	N+	Marks and Kassaby, 1974
	P	F+	Heather and Pratt, 1975
	P	N+	Heather *et al.*, 1977
" *megasperma* Drechs.	E	N+	Marks and Kassaby, 1976
	P	N-	Gilmour, 1966

" *megasperma* var. *sojae*	E	F-	Shearer *et al.*, 1987; Davison and Bumbieris, 1973
	P	N-	Davison and Bumbieris, 1973
" *nicotianae* Breda de Haan	E	F-	Shearer *et al.*, 1987
var. *nicotianae*	E	F+	Belisario, 1990; Shearer *et al.*, 1988
	P	N-	Davison and Bumbieris, 1973
" *nicotianae* var. *parasitica* Dast.	E	F-	Pratt and Heather, 1973a
	E	F+	Shearer *et al.*, 1988
" *syringae* (Kleb.) Kleb	P	F-	Newhook, 1959
	P	N-	Newhook,1959
Pythium acanthicum Drechs.	P	F-	Davison and Bumbieris, 1973; Hocking, 1968
	P	N+	Vaartaja and Salisbury, 1961
" *acanthophoron* Sid.	E	F-	Pratt and Heather, 1973a
	P	N-	Darvas *et al.*, 1978
" *anadrum* Drechs.	E	N+	Wardlaw and Palzar, 1985
	P	F-	Davison and Bumbieris, 1973
" *aphanidermatum* (Edson) Fitzp.	P	N+	Huang and Kuhlman, 1990
" *debaryanum* de Bar.	E	F-	Marks and Kassaby, 1974
	E	N+	Marks and Kassaby, 1974
	E	N-	Vaartaja, 1967
	P	F-	Otrosina and Marx, 1975
	P	N-	Darvas *et al.*, 1978; Vaartaja, 1967
	P	N+	Vaartaja and Salisbury, 1961
" *deliense* Meurs	E	F-	Pratt and Heather, 1973a
	E	N+	Sharma *et al.*, 1985
" *echinulatum* Matt.	E	N-	Vaartaja, 1967
	P	N-	Vaartaja, 1967
" *helicoides* Drechs.	P	N-	Campbell and Hendrix, 1967
" *hemmanianum* Hesse	P	N-	Darvas et al., 1978
" *hypogynum* Middl.	P	N-	Darvas *et al.*, 1978
" *intermedium* de Bar.	E	N+	Vaartaja, 1967
	P	N+	Vaartaja, 1967
" *iwayamai* S. Ito	E	N+	Vaartaja, 1967
	P	N+	Vaartaja, 1967
" *irregulare* Buis.	E	F-	Marks and Kassaby, 1974
	E	N+	Marks and Kassaby, 1974; Vaartaja, 1967
	P	F-	Davision and Bumbieris, 1973; Lorio, 1966; Ostosina and Marx, 1975
	P	F+	Linde *et al.*, 1993
	P	N+	Vaartaja, 1967
" *mamillatum* Meurs	E	F-	Marks and Kassaby, 1974
	E	N+	Vaartaja, 1967
	P	F-	Davison and Bumbieris, 1973
	P	N+	Vaartaja, 1967
" *mastophorum* Drechs.	P	F-	Davision and Bumbieris, 1973
" *middletoni* Spar.	E	F-	Pratt and Heather, 1973a
" *myriotylum* Drechs.	E	N+	Sharma *et al.*, 1985
	E	N-	Vaartaja, 1967
	P	N-	Vaartaja, 1967

" *oedochilum* Drechs.	E	F-	Pratt and Heather, 1973a
" *oligandrum* Drechs.	P	F-	Davison and Bumbieris, 1973
" *periplocum* Drechs.	E	N+	Vaartaja, 1967
	P	N+	Vaartaja, 1967
" *pyrilobum* Vaart.	E	N+	Vaartaja, 1967
	P	N+	Vaartaja, 1967
" *rostratum* Butl.	E	N-	Vaartaja, 1967
	P	N-	Vaartaja, 1967
" *spinosum* Saw.	P	N-	Campbell and Hendrix, 1967
" *splendens* Braun	E	F-	Pratt and Heather, 1973a
	E	N+	Vaartaja, 1967
	E	F+	Linde *et al.*, 1992
	P	F-	Lorio, 1966
	P	N+	Campbell and Hendrix, 1967; Vaartaja, 1967
" *sylvaticum* Camp. & Hendr.	P	N+	Campbell and Hendrix, 1967
" *ultimum* Trow	E	F-	Marks and Kassaby, 1974
	E	N+	Marks and Kassaby, 1974; Vaartaja, 1967
	P	N+	Vaartaja, 1967; Vaartaja and Salisbury, 1961
" *ultimum* var. *sporangiiferum* Drechs.	E	F-	Pratt and Heather, 1973a
" *vexans* de Bar.	E	F-	Marks and Kassaby, 1974
	P	F-	Davison and Bumbieris, 1973; Lorio, 1966
" *violae* Chest. & Hickm.	E	N+	Vaartaja, 1967
	P	F-	Davison and Bumbieris, 1973
	P	N+	Vaartaja, 1967

[x]P = *Pinus* spp.
E = *Eucalyptus* spp.
[y]F = Forest
N = Nursery
+ = pathogenic
- = non-pathogenic

REFERENCES

ANONYMOUS, 1990. The South Africa forestry and forestry products industry. Leaflet: Facts 88/89.

ANONYMOUS, 1979/1980. Annual report of the Department of Forestry 1979/1980.

ANONYMOUS, 1980/1981. Annual report of the Department of Forestry 1980/1981.

BELISARIO, A., 1990. A new *Phytophthora* disease of the aerial parts of *Eucalyptus* species. *Bulletin OEPP/EPPO* 20: 129–132.

BUMBIERIS, M., 1974. Characteristics of two *Phytophthora* species. *Australian Journal of Botany* 22: 655–660.

BUMBIERIS, M., 1976. The role of *Phytophthora cryptogea* and waterlogging in a decline of *Pinus radiata*. *Australian Journal of Botany* 24: 703–709.

CAMPBELL, W.A., 1948. *Phytophthora cinnamomi* associated with the roots of littleleaf-diseased pine. *Plant Disease Reporter* 32: 472.

CAMPBELL, W.A., 1949. Relative abundance of *Phytophthora cinnamomi* in the root zones of healthy and littleleaf-diseased shortleaf pine. *Phytopathology* 39: 752–753.

CAMPBELL, W.A., and HENDRIX, F.F., Jr., 1967. *Pythium* and *Phytophthora* populations in southern forest tree nurseries. *Phytophathology* 57: 457.

CRANDALL, B.S., 1936. Root diseases of some conifers and hardwoods caused by *Phytophthora cambivora (Phytophthora cinnamomi). Plant Disease Reporter* 20: 202–204.

CRANDALL, B.S., 1950. The distribution and significance of the chestnut root rot Phytophthoras, *P. cinnamomi* and *P. cambivora. Plant Disease Reporter* 34: 194–196.

DARVAS, J.M., SCOTT, D.B., and KOTZÉ, J.M., 1978. Fungi associated with damping-off in coniferous seedlings in South African nurseries. *South African Forestry Journal* 104: 15–19.

DARVAS, J.M., TOERIEN, J.C., and MILNE, D.L., 1984. Control of avocado root rot by trunk injection with phosetyl-Al. *Plant Disease* 68: 691–693.

DAVISON, E.M., and BUMBIERIS, M., 1973. *Phytophthora* and *Pythium* spp. from pine plantations in South Australia: *Australian Journal of Biological Science* 26: 163–169.

DOIDGE, E.M., and BOTTOMLEY, A.M., 1931. A revised list of plant diseases occurring in South Africa. *Botanical Surveys of the South African Memoirs* 11: 1–78.

DONALD, D.G.M., and VON BROEMBSEN, S.L., 1977. The control of *Phytophthora cinnamomi* Rands in a South African forest nursery. *South African Forestry Journal* 100: 50–55.

EVANS, S.G., 1968. *Phytophthora cinnamomi* causing a basal rot of *Chamaecyparis lawsoniana* and its varieties. *Plant Pathology* 17: 142–144.

FIRMAN, I.D., 1974. Cocoa canker. In: GALLEGLY, P.H., (Ed.)

Phytophthora disease of cocoa. Great Britain, Aberdeen University Press, pp. 141–148.
FRAEDRICH, S.W., TAINTER, F.H., and MILLER, A.E., 1989., Zoospore inoculum density of *Phytophthora cinnamomi* and the infection of lateral root tips of shortleaf and loblolly pine. *American Phytopathological Society* 79: 1109–1113.
GALLEGLY, G.A., 1983. The world of *Phytophthora*. In: ERWIN, D.C., BARTNICKI-GARCIA, S., and TSAO, P.H., (Eds.). *Phytophthora: Its Biology, Taxonomy, Ecology and Pathology*. The American Phytophatological Society, St. Paul, Minnesota, pp. 1–7.
GILMOUR, J.W., 1966. The pathology of forest trees in New Zealand. The fungal, bacterial and algal pathogens. *New Zealand Forestry Survey Technical Papers* 48, 82 pp.
GREGORY, P.H., 1983. Some major epidemics caused by *Phytophthora*. In: ERWIN, D.C., BARTNICKI-GARCIA, S., and TSAO, P.H., (Eds.). *Phytophthora: Its Biology, Taxonomy, Ecology and Pathology*. The American Phytopathological Society, St. Paul, Minnesota, pp. 271–278.
HAMM, P.B., and HANSEN, E.M., 1982. Pathogenicity of *Phytophthora* species to Pacific Northwest USA conifers. *European Journal of Forest Pathology* 12: 167–174.
HEATHER, W.A., and PRATT, B.H., 1975. Association of *Phytophthora drechsleri* Tucker with death of *Pinus radiata* D. Don in southern New Wales. *Australian Journal of Botany* 23: 285–288.
HEATHER, W.A., PRATT, B.H., and CHIN, T.Y., 1977. Pre- and post-emergence damping-off seedlings of *Pinus* species by *Phytophthora cinnamomi* and *Ph. drechsleri*. *Australian Journal of Botany* 25: 358–359.
HENDRIX, F.F., Jr., and CAMPBELL, W.A., 1973. *Pythiums* as plant pathogens. *Annual Review of Phytopathology* 11: 77–98.
HOCKING, D., 1968. Fungi associated with damped-off and healthy pine seedlings and with seed in east African pine nurseries. *Transactions of the British Mycological Society* 51: 221–226.
HOITINK, H.A.J., and FAHY, P.C., 1986. Basis for the control of soilborne plant pathogens with composts. *Annual Review of Phytopathology* 24: 93–114.
HUANG, J.W., and KUHLMAN, E.G., 1990. Fungi associated with damping-off of slash pine seedlings in Georgia. *Plant Disease* 74: 27–30.
HUANG, J.W., and KUHLMAN, E.G., 1991. Formulation of a soil amendment to control damping-off of slash pine seedlings. *Phytopathology* 81: 163–170.
HUTCHINS, D.E., 1893. *Tree-planting, 1893 – A descriptive catalogue of the best trees to plant in Cape Colony, with brief instructions of planting*. Cape Town, Government Printer, 68 pp.
KATSURA, K., 1976. Two new species of *Phytophthora* causing damping-off of cucumber and trunk rot of chestnut. *Transactions of the British Mycological Society* 17: 238–242.
KNOX-DAVIES, P.S., 1975. Decline of silver trees and other indigenous species. *Veld & Flora* 61: 20–22.
LINDE, C., KEMP, G.H.J., and WINGFIELD, M.J., 1993. *Pythium irregulare* associated with establishment deaths of *Pinus patula* on old agricultural lands. *Proceedings of the 31st Annual Plant Pathology Congress*, Langebaan, South Africa, p. 26.
LINDE, C., WINGFIELD, M.J., and KEMP, G.H.J., 1992. A new and serious root disease of *Eucalyptus* associated with a species of *Pythium*. *Phytophylactica* 24: 126.
LIYANAGE, N.I.S., 1989. *Phytophthora citricola* on rubber in Sri Lanka. *Plant Pathology* 38: 438–439.
LORIO, P.L., Jr., 1966. *Phytophthora cinnamomi* and *Pythium* species associated with loblolly pine decline in Louisiana. *Plant Disease Reporter* 50: 596–597.
MALAJCZUK, N., McCOMB, A.J., and PARKER, C.A., 1977. Infection by *Phytophthora cinnamomi* Rands of roots of *Eucalyptus calophylla* R. Br. and *Eucalyptus marginata* Donn. ex. Sm. *Australian Journal of Botany* 25: 483–500.
MARKS, G.C., and KASSABY, F.Y., 1974. Pathogenicity of *Pythium* spp. and *Phytophthora drechsleri* to *Eucalyptus* spp. *Australian Journal of Botany* 22: 661–668.
MARKS, G.C., and KASSABY, F.Y., 1976. Pathogenicity of 9 species of *Phytophthora* to *Eucalyptus sieberi*. *Australian Forestry Research* 7: 59–63.
MARKS, G.C., and TIPPETT, J.T., 1978. Symptom development and disease escape in *Eucalyptus obliqua* growing in soils infected with *Phytophthora cinnamomi*. *Australian Forestry Research* 8: 47–56.
MARKS, G.C., KASSABY, F.Y., and REYNOLDS, S.T., 1972. Die-back in the mixed hardwood forests of eastern Victoria, a preliminary report. *Australian Journal of Botany* 20: 141–154.
MES, M.G., 1934. A wilt of snapdragon (*Antirrhinum majus*) in South Africa. *South African Journal of Science*, pp. 281–287.
NEWHOOK, F.J., 1959. The association of *Phytophthora* spp. with mortality of *Pinus radiata* and other conifers. *New Zealand Journal of Agricultural Research* 2: 808–843.
OPEKE, L.K., and GORENZ, A.M., 1974. Phytophthora pod rot: Symptoms and economic importance. In: P.H. GALLEGLY (Ed.). *Phytophthora disease of cocoa*. Great Britain, Aberdeen University Press, pp. 117–124.
OTROSINA, W.J., and MARX, D.H., 1975. Populations of *Phytophthora cinnamomi* and *Pythium* spp. under shortleaf and loblolly pines in littleleaf diseased sites. *Phytopathology* 65: 1224–1229.
OXENHAM, B.L., and WINKS, B.L., 1963. Phytophthora root rot of pines in Queensland. *Queensland Journal of Agricultural Science* 20: 355–366.
PODGER, F.D., 1972. *Phytophthora cinnamomi*, a cause of lethal disease in indigenous plant communities in Western Australia. *Phytopathology* 62: 972–981.
PODGER, F.D., 1978. Biology of the pathogens and its relevance to forest management. In: K.M., OLD, (Ed.). *Phytophthora and forest management in Australia. Report of a conference held at CSIRO Division of Forest Research, Canberra*, pp. 14–26.
PODGER, F.D., and BATINI, F., 1971. Susceptibility to *Phytophthora cinnamomi* root-rot of thirty six species of *Eucalyptus*. *Australian Forestry Research* 5: 9–20.
PODGER, F.D., DOEPEL, R.F., and ZENTMYER, G.A., 1965. Association of *Phytophthora cinnamomi* with a disease of *Eucalyptus marginata* forest in Western Australia. *Plant Disease Reporter* 49: 943–947.
PRATT, B.H., and HEATHER, W.A., 1973a. Recovery of potentially pathogenic *Phytophthora* and *Pythium* spp. from native vegetation in Australia. *Australian Journal of Biological Science* 26: 575–582.
PRATT, B.H., and HEATHER, W.A., 1973b. The origin and distribution of *Phytophthora cinnamomi* Rands in Australian native plant communities and the significance of its association with particular plant species. *Australian Journal of Biological Science* 26: 559–573.
PRATT, B.H., HEATHER, W.A., and SHEPHERD, C.J., 1973. Recovery of *Phytophthora cinnamomi* from native vegetation in a remote area of New South Wales. *Transactions of the British Mycological Society* 60: 197–204.
SHARMA, J.K., MOHANAN, C., and FLORENCE, E.J.M., 1985. Disease survey in nurseries and plantations of forest tree species grown in Kerala. *Research Report* 36, 268 pp.
SHEARER, B.L., MICHAELSEN, B.J., and WARREN, H.J., 1987. Comparative behaviour of *Phytophthora* species in the secondary phloem of stems and excised roots of *Banksia grandis* and *Eucalyptus marginata*. *Australian Journal of Botany* 35: 103–110.
SHEARER, B.L., MICHAELSEN, B.J., and SOMERFORD, P.J., 1988. Effects of isolate and time of inoculation on invasion of secondary phloem of *Eucalyptus* spp. and *Banksia grandis* by *Phytophthora* spp. *Plant Disease* 72: 121–126.
SHEPHERD, C.J., and HALSALL, D.M., 1977. Studies on *Phytophthora* species associated with forest die-backs. In: *CSIRO Division of Plant Industry, Annual Report 1976*, pp. 26–30.
SHEPHERD, C.J., and PRATT, B.HY., 1973. Separation of two ecotypes of *Phytophthora drechsleri* Tucker occurring in Australian native forests. *Australian Journal of Biological Science* 26: 1095–1107.
SPENCER, S., and BENSON, D.M., 1982. Pine bark, hardwood bark compost, and peat amendment effects on development of *Phytophthora* spp., and lupine root rot. *Phytopathology* 72: 346–351.
TIDBALL, C.J., and LINDERMANN, R.G., 1990. *Phytophthora* root and stem rot of apple rootstocks from stool beds. *Plant Disease* 74: 141–146.
VAARTAJA, O., 1967. Damping-off pathogens in South Australian nurseries. *Phytopathology* 57: 765–768.
VAARTAJA, O., and SALISBURY, P.J., 1961. Potential pathogenicity of *Pythium* isolates from forest nurseries. *Phytopathology* 51: 505–507.
VAN DEN BOOM, T., and HULLER, I.M., 1970. *Phytophthora* stem rot of passion fruit, *Passiflora edulis*, in South Africa. *Phytophylactica* 2: 71–74.

VAN DER MERWE, J.J.H., and MATTHEE, F.N., 1973. *Phytophthora* crown and root rot of apple trees in South Africa. *Phytophylactica* 5: 55–58.

VAN DER MERWE, J.J.H., JOUBERT, D.J., and MATTHEE, F.N., 1972. *Phytophthora cinnamomi* root rot of grapevines in the Western Cape. *Phytophylactica* 4: 133–136.

VON BROEMBSEN, S., 1984a. Occurrence of *Phytophthora cinnamomi* in indigenous and exotic hosts in South Africa, with special reference to the south-western Cape Province. *Phytophylactica* 16: 221–225.

VON BROEMBSEN, S.L., 1984b. Distribution of *Phytophthora cinnamomi* in rivers of the south-western Cape Province. *Phytophylactica* 16: 227–229.

VON BROEMBSEN, S.L., and BRITS, G.J., 1985. *Phytophthora* root rot on commercially cultivated proteas in South Africa. *Plant Disease* 69: 211–213.

VON BROEMBSEN, S.L., and KRUGER, F.J., 1985. *Phytophthora cinnamomi* associated with mortality of native vegetation in South Africa. *Plant Disease* 69: 715–717.

VON BROEMBSEN, S.L., LUBBE, W.A., and GELDENHUYS, C.J., 1986. *Phytophthora cinnamomi* associated with decline of stinkwood (*Ocotea bullata*) in southern Cape indigenous forests. *Phytophylactica* 18: 44.

WAGER, V.A., 1931. Diseases in South Africa due to members of the Pythiaceae. *Union of South Africa Department of Agriculture, Bulletin* 105: 1–43.

WAGER, V.A., 1941. Descriptions of the South African Pythiaceae with records of their occurrence. *Bothalia* 5: 3–35.

WAGER, V.A., 1942. *Phytophthora cinnamomi* and wet soil in relation to the dying-back of avocado trees. *Hilgardia* 14: 519–532.

WARDLAW, T.J., and PALZAR, C., 1985. Stem diseases in nursery seedlings caused by *Phytophthora cactorum*, *P. citricola* and *Pythium anandrum*. *Australasian Plant Pathology* 14: 57–59.

WESTE, G.M., 1975. *Phytophthora drechsleri* and *Eucalyptus viminalis*. *Australian Plant Pathology Society Newsletter* 4: 1–38.

WESTE, G.M., and TAYLOR, P., 1971. The invasion of native forest by *Phytophthora cinnamomi* I. Brisbane Ranges, Victoria. *Australian Journal of Botany* 19: 281–294.

WINGFIELD, M.J., and KNOX-DAVIES, P.S., 1980. Observations on diseases in pine and eucalyptus plantations in South Africa. *Phytophylactica* 12: 57–60.

WINGFIELD, M.L., SWART, W.J., and KEMP, G.H.J., 1991. Pathology considerations in clonal propagation of *Eucalayptus* with special reference to the South African situation. *Proceedings of the 1991 IUFRO Symposium – Intensive Forestry, the Role of Eucalyptus*, pp. 811–820.

WINGFIELD, M.J., SWART, W.J., and VON BROEMBSEN, S.L., 1989. Root diseases of pines and eucalypts in South Africa. In: D.J. MORRISON, (Ed.). *Proceedings of the IUFRO Seventh International Conference on Root and Butt Rots, Canada*, pp. 563–569.

WOLSTENHOLME, B.N., 1979. *Horticultural report: Australian research on biological control of* Phytophthora cinnamomi, *the world's most destructive plant pathogen: Report on a study tour of Australia*. Department of Horticultural Science, University of Natal, South Africa, 45 pp.

ZAK, B., and CAMPBELL, W.A., 1958. Susceptibility of southern pines and other species to the littleleaf pathogen in liquid culture. *Forest Science* 4: 156–161.

ZEIJLEMAKER, F.C.J., 1971. Black-butt disease of black wattle caused by *Phytophthora nicotianae* var. *parasitica*. *Phytophathology* 61: 144–145.

ZENTMYER, G.A., 1980. *Phytophthora cinnamomi and the diseases it causes. Monograph 10*. American Phytopathological Society, St. Paul, Minnesota, 96 pp.