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Phytophthora

A Global Perspective

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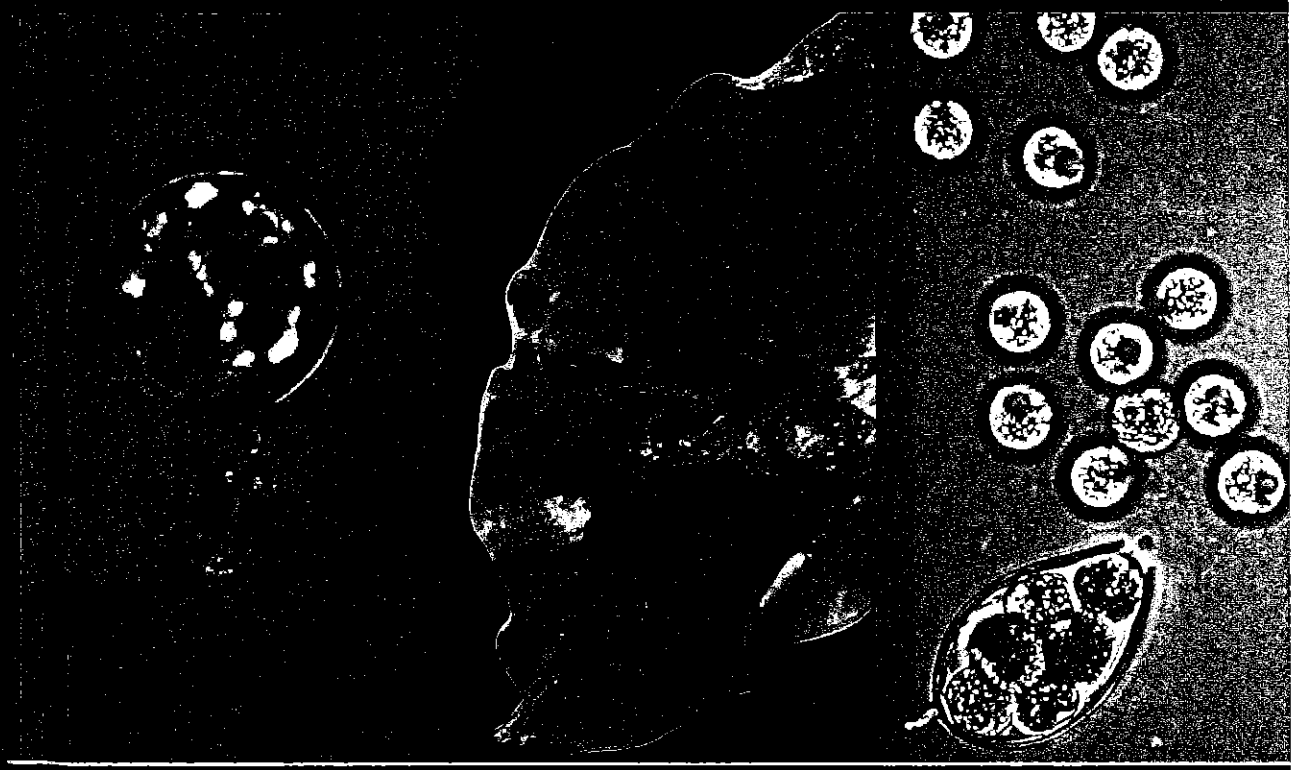

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22 The Occurrence and Impact of *Phytophthora* on the African Continent

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22.1 Introduction

Surprisingly little is known about *Phytophthora* on the African continent, and most of what is known is limited to South Africa. To date 23 species of *Phytophthora* have been reported, of which 20 are known from South Africa and only ten from the rest of Africa (Table 22.1). As elsewhere, *Phytophthora* attacks several cultivated plant species, particularly agronomic crop plants, and occurs in native ecosystems. Here we review the occurrence, importance and potential threats of *Phytophthora* to agriculture and natural ecosystems in Africa.

Table 22.1. *Phytophthora* species occurrence in Africa.

Species	Host	Country
Agriculture		
Phytophthora cactorum	*Citrus* spp., *Malus domestica*, *Vitis vinifera*	South Africa
	Malus domestica	Tunisia
Phytophthora capsici	*Capsicum* spp., *Cumus melo*, *Curcurbita* spp., *Solanum lycopersicum*	South Africa
	Capsicum sp.	Nigeria
Phytophthora cinnamomi	*Annanas comosus*, *Macadamia* spp., *Persea americana*, *Pyrus communis*, *Vitis* spp.	South Africa
	Persea americana	Various countries
	Macadamia spp.	Kenya
Phytophthora citricola	*Citrus* spp.	South Africa
Phytophthora citrophthora	*Citrus* spp.	South Africa
	Citrus spp.	Liberia
Phytophthora cryptogea	*Citrus* spp., *Vitis vinifera*	South Africa
Phytophthora drechsleri	*Brassica oleracea*, *Medicago sativa*	South Africa
Phytophthora infestans	Solanaceous crops	Various countries
Phytophthora medicaginis	*Medicago sativa*	South Africa
Phytophthora megakarya	*Theobroma cacao*	Various countries
Phytophthora megasperma	*Vitis vinifera*	South Africa

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Species	Host	Country
Phytophthora multivora	*Medicago sativa*	South Africa
Phytophthora nicotianae	*Chamaecytisus palmensis*, *Citrus* spp., *Musa* sp., *Nicotiana tabacum*, *Rheum rhaponticum*, *Solanum lycopersicum*, *Vitis vinifera*	South Africa
	Nicotiana tabacum, *Solanum betacae*	Ghana
	Passiflora edulis	Kenya
	Agave spp., *Citrus* sp., *Hibuscus cannabinus*	Tanzania
	Capsicum annuum, *Malus domestica*	Tunisia
	Nicotiana tabacum	Zimbabwe
Phytophthora niederhauserii	*Vitis* spp.	South Africa
Phytophthora palmivora	*Agave* spp., *Cocos nucifera*, *Hevea brasiliensis*, *Musa* sp., *Persea americana*, *Theobroma cacao*	Various countries
Phytophthora porri	*Allium cepa*	South Africa
Phytophthora syringae	*Citrus* sp.	South Africa
	Citrus sp.	Libya
Forestry		
Phytophthora alticola	*Eucalyptus* spp.	South Africa
Phytophthora boehmeriae	*Acacia mearnsii*, *Eucalyptus* spp.	South Africa
P. cinnamomi	*Eucalyptus* spp., *Pinus* spp.	South Africa
Phytophthora frigida	*Eucalyptus* spp.	South Africa
Phytophthora meadii	*Acacia mearnsii*	South Africa
P. nicotianae	*Acacia mearnsii*, *Eucalyptus* spp.	South Africa
Ornamental/exotic		
P. cactorum	*Antirrhinum majus*, *Centaurium moschata*, *Dianthus caryophyllus*, *Verbena* sp.	South Africa
P. cinnamomi	*Araucaria angustifolia*, *Banksia* spp., *Casuarina cunninghamiana*, *Cedrus deodara*, *Centaurium* sp., *Chamaecyparis lawsoniana*, *Cryptomeria japonica*, *Rhododendron* sp., *Telopea speciosissima*, *Thuja* sp.	South Africa
P. cryptogea	*Godetia* sp.	South Africa
P. infestans	*Petunia* × *hybrida*	South Africa
P. nicotianae	*Delphinium* sp., *Gypsophila paniculata*, *Trichocaulon* sp.	South Africa
P. palmivora	*Mimusops elengi*	Ghana
Native plants and habitats		
Phytophthora capensis	*Curtisia dentata*, *Olea capensis*, rivers	South Africa
P. cinnamomi	*Bruniaceae*, *Ericaceae* and *Proteacae*, *Agasthoma* spp., *Cliffortia* spp., *Curtisia dentata*, *Nymania capensis*, *Ocotea bullata*, *Priestleya* sp., *Widdringtonia* spp., rivers	South Africa
P. citricola	Rivers	South Africa
P. cryptogea	*Agathosma* spp., *Osteospermum* sp., rivers	South Africa
P. drechsleri	*Agathosma* spp., rivers	South Africa
Phytophthora heveae	Unknown	Cameroon
P. infestans	*Aspalia africa*, *Solanecio biafrae*, *Solanum* spp.	Cameroon, Kenya
P. megakarya	*Dracaena mannii*, *Funtumia elastica*, *Irvingia* spp, *Ricinodendron heudelotii*, *Sterculia tragacantha*	Cameroon, Ghana
P. multivora	*Agathosma* spp., *Ocotea bullata*	South Africa
P. nicotianae	*Agathosma* spp., *Cotyledon* sp.	South Africa
Phytophthora taxon 'emzansi'	*Agathosma* spp.	South Africa

22.2 *Phytophthora* in Agriculture

Africans depend heavily on agriculture, and plant diseases and insect pests are crucially important to the livelihood of many people. Seventeen *Phytophthora* spp. are known to cause diseases of agricultural crops but research has focused primarily on *Phytophthora infestans*, *Phytophthora megakarya*, *Phytophthora palmivora* and *Phytophthora cinnamomi*. For other species (e.g. *Phytophthora cryptogea*, *Phytophthora drechsleri*, *Phytophthora medicaginis*, *Phytophthora megasperma*, *Phytophthora porri* and *Phytophthora syringae*) there are often only first reports of the pathogen. Follow-up studies are rare and exceptions include *Phytophthora capsici*, *P. cinnamomi* and *P. infestans* where genetic diversity has been characterized in South African populations.

In most cases *Phytophthora* is found on the same plant hosts as on other continents. Although yet to be tested experimentally, the non-native crop plants cultivated in Africa are probably affected by non-native *Phytophthora* spp., for instance: (i) *P. cactorum* is recovered from *Malus domestica* (apple) from America, the UK and Switzerland; (ii) *Phytophthora citrophthora* from *Citrus* spp. from Egypt, Israel, Spain and various Mediterranean islands; and (iii) *P. porri* from *Allium cepa* (onion) from Japan and the Netherlands. The only exception is *P. megakarya*, one of the species involved in cacao black pod disease, which occurs exclusively in Central to Western Africa (Guest, 2007).

There are a few cases where new plant associations have been reported. One example is the proposed (but not formally described) *Phytophthora niederhauserii*. This species causes disease on several ornamental plants in Europe including *Banksia* spp., *Calistemon citrinus*, *Cistus* spp., *Laurus nobilis* and *Pistacia lentiscus* (Cacciola *et al.*, 2009; Scanu *et al.*, 2011), and almond (*Prunus dulcis*) decline in Spain (Pérez-Sierra *et al.*, 2010). *P. niederhauserii* was also reported in Western Australia from a *Banksia* sp. as well as from soil associated with nursery plants imported from the Northern Territory of Australia (Davison *et al.*, 2006). Recently it was isolated from the crowns of healthy grapevines from South Africa, which is the first report of *P. niederhauserii* on this host (Spies *et al.*, 2011).

While *Phytophthora* is associated with many crop diseases in Africa, only a few have a significant impact. These include blight caused by *P. infestans* on potato and tomato, black pod of cacao caused by *P. megakarya* and *P. palmivora*, and a range of important hosts that are attacked by *P. cinnamomi*. Each of these major disease systems is discussed individually and an attempt is made to highlight their importance in Africa.

22.2.1 Late blight of potato and tomato caused by *P. infestans*

Africa produces 12–18 million t/year of potato and 13–16 million t/year of tomato. Most of Africa's potato production is consumed locally; however, a small amount is exported. African countries, on average, import slightly more (470,970 t) potatoes than they export (386,240 t). On the other hand, African countries export almost ten times more tomatoes than they import (216,251 t versus 24,926 t, respectively) (FAO, 2011). These crops are economically very important in Africa.

Although late blight caused by *P. infestans* is one of the most important diseases (both socially and economically), the impact is difficult to quantify. Yield losses result in loss of sustenance and/or loss of income for farmers, and chemical control agents are a necessity. However, chemicals are costly and decrease profit. In Africa late blight can result in total crop losses of potato and tomato if no chemical control measures are taken, although disease severity varies considerably. This variation can be attributed to variable weather conditions and to the degree of resistance in the cultivars being planted (Mukalazi *et al.*, 2001; Olanya *et al.*, 2001).

The centre of origin of *P. infestans* is believed to be Central Mexico. The initial dissemination of *P. infestans* occurred in the 1840s, when the A1 mating type and a few genotypes spread to the USA on potatoes. The subsequent spread to Europe and the rest of the world was made by a single clonal lineage of the A1 mating type and has led to the presence of the A1 mating type in every potato- and tomato-growing country in Africa. Thereafter, additional migrations of *P. infestans* introduced the A2 mating type and new genotypes into the USA and the rest of the world on several occasions. The A2 mating type of *P. infestans* was first reported from Africa from infected potato tubers originating from Egypt. However, a later study did not yield the A2 mating type from Egyptian *P. infestans* isolates. The A2 mating type and new genotypes have also recently been observed in Morocco, where the A1 mating type is also present. Other than Egypt and Morocco, there have been no other reports of the A2 mating type or new genotypes in Africa. If the A2 type is introduced to Africa and outcrossing with the A1 genotypes already present is possible, then the resulting genetically diverse populations may be able to evolve more rapidly, allowing them to develop fungicide resistance or to overcome host defences of resistant varieties of potato in a shorter time compared with an asexually reproducing population. In addition, the oospores may allow the pathogen to survive for longer periods outside of host tissue, compared with asexual populations.

P. infestans can also infect other plant species and causes late blight of huckleberry (*Solanum scabrum*), which is native to Africa, in Cameroon, where its leaves and shoots are widely used as a vegetable for subsistence and commercial production. *P. infestans* has also been reported from other solanaceous and asteraceous plants from Cameroon and Kenya (Table 22.1) (Fontem *et al.*, 2004). These alternative hosts complicate control measures as they can act as an overwintering cache and a continuous source of inoculum.

22.2.2 Black pod disease caused by *P. palmivora* and *P. megakarya*

Africa is the world's largest cacao grower, producing on average 70% of the world's crop, of which 38% is produced by Côte d'Ivoire and 19% by Ghana (ICCO, 2007). When this is contrasted with the production of the Americas (12%), Asia and Oceania (17%), it is clear that cacao production is one of Africa's most significant agricultural industries. Pod rot is the most important symptom of *Phytophthora* infection of cacao because it results in direct loss of crop yield. Infection can occur on mature or immature pods (cherelles) and is readily visible as spreading brown to black lesions (see Drenth and Guest, Chapter 20, this volume) (Guest, 2007). Initially the infection does not affect the cacao beans, but as the disease progresses the beans are infected, which renders them unusable. *Phytophthora* spp. can infect other parts of cacao trees besides the pods, such as the main stems, leaves, flower cushions and roots. The importance of these types of infection has been underestimated as they influence cacao tree health and thus indirectly decrease cacao yield (Appiah *et al.*, 2004). Diseased pods and other infections such as stem cankers contribute to the spread, establishment and severity of further infections as they are a source of secondary inoculum (Bowers *et al.*, 2001).

In cacao-producing regions of the world several *Phytophthora* spp., including *P. capsici*, *P. citrophthora*, *Phytophthora hevea*, *P. megasperma* and *Phytophthora nicotianae*, cause cacao black pod disease. However, in Africa only two species cause disease of cacao. Initially *P. palmivora* was implicated as the sole cause of black pod, but later a second species, *P. megakarya*, was also shown to be involved (Brasier and Griffin, 1979). *P. palmivora* occurs globally, whereas *P. megakarya* is restricted to parts of Central and Western Africa. Initially *P. megakarya* was known only to occur in Nigeria and Cameroon, but later its range was expanded to Gabon, Ghana, Equatorial Guinea, Côte d'Ivoire and Togo (Guest,

2007). Both mating types of *P. megakarya* and *P. palmivora* are present in Africa. Most isolates of *P. megakarya* encountered on cacao are A1, but both mating types are found in Equatorial Guinea, Cameroon, Ghana and Nigeria (Appiah *et al.*, 2003). In contrast, *P. palmivora* is mostly A2 in Africa, with both mating types found only in Ghana and Togo (Appiah *et al.*, 2003). The dominance of one mating type limits the opportunity for sexual reproduction within populations of the pathogen.

Although the two *Phytophthora* spp. occurring on cacao in Africa cause the same disease, they have slightly different disease cycles and attributes. *P. megakarya* is much more virulent than *P. palmivora* and consequently results in higher yield losses of up to 100% compared with the 20–30% yield loss caused by *P. palmivora*. *P. megakarya* has a propensity for earlier and more profuse release of zoospores than *P. palmivora* allowing it to spread faster (Brasier *et al.*, 1981). *P. palmivora* is better at surviving in mummified pods and *P. megakarya* is unable to endure the dry season in shrivelled pods. They also differ in their ability to cause cankers. *P. megakarya* has a higher incidence of tree girdling cankers, whereas *P. palmivora* causes cankers higher up on the stems (Appiah *et al.*, 2004).

Cacao is a major cash crop in the African countries, with many smallholder farmers reliant on cacao as an important source of income. Black pod disease is a serious constraint of cacao production due to the high yield losses, especially when caused by *P. megakarya*. *Phytophthora*-infested cacao plantations incur additional expenses as chemical control agents are necessary to reduce yield loss. The high cost associated with fungicides and their application decreases the farmer's profit per unit of cacao sold. Simply planting more cacao is not an option because of the limited land available for production (see Drenth and Guest, Chapter 20, this volume).

P. megakarya and *P. palmivora* occur on several tree species other than cacao. In Ghana *P. megakarya* infects *Funtumia elastica*, *Sterculia tragacantha*, *Dracaena mannii* and *Ricinodendron heudelotii* (Table 22.1). These native trees are often retained in cacao plantations to provide shade. In Cameroon *P. megakarya* was also reported from the fallen fruit of a native *Irvingia* sp. occurring in a native forest habitat. Although *P. palmivora* has a very broad host range and occurs globally, in Africa it has only been reported from a small number of hosts other than cacao. These include *Hevea brasiliensis* and a *Mimusops* sp. in Ghana, *Musa* sp. in Nigeria, and *Cocos nucifera* in Tanzania (Table 22.1). All the above-mentioned trees, with the exception of the *Mimusops* sp., are commonly intercropped together with cacao trees. The effect that these alternative hosts have on the disease incidence is not clear, but they could act as reservoirs for *P. megakarya* and *P. palmivora* (Opoku *et al.*, 2002).

22.2.3 Avocado root root caused by *P. cinnamomi*

Avocado (*Persea americana*) trees are widely planted in Africa and the fruit are consumed locally and exported. Annually Africa produces ≈14% of the world's avocados, with Kenya, South Africa, Democratic Republic of the Congo, Ethiopia and Cameroon having the largest production (FAO, 2011). The most important disease of avocado in Africa is root rot and dieback caused by *P. cinnamomi*. The first African reports misidentified *P. cinnamomi* as *Phytophthora cambivora* in South Africa (Wager, 1941). Root rot is particularly severe in South Africa due to the high soil temperatures and excessive moisture it receives via summer rainfall. In South Africa losses due to *P. cinnamomi* are estimated at 10% of the annual gross value of avocados (Bekker, 2007). Although estimates of the impact are scarce, root rot is widespread and is known to be a serious disease of avocados in other African countries including Cameroon, Ethiopia and Kenya.

P. cinnamomi is heterothallic, with the A2 mating type the more common globally.

Both mating types occur in South Africa in agricultural and native environments but the overall distribution is not known for most areas. The A1 mating type is restricted to the South Western Cape while the A2 mating type occurs in both the South Western Cape as well as the Mpumalanga province of South Africa (Linde *et al.*, 1997). In Kenya both mating types are also present on *Macadamia* spp. (Mbaka *et al.*, 2010).

Although *P. cinnamomi* is best known from avocado, it causes disease on several other important crops that receive much less attention. In the Western Cape of South Africa it caused crown and root rot of grapevines during the 1970s (van der Merwe *et al.*, 1972). Although other *Phytophthora* species were involved, *P. cinnamomi* was the most virulent (Table 22.1). More recently *Phytophthora* has become much less common on grapevines in South Africa, probably due to widespread use of chemical control measures. *P. cinnamomi* also occurs on *Macadamia* spp. in South Africa and Kenya, as well as on pineapple in South Africa and Ghana, but little research has been done on these important hosts. *P. cinnamomi* has also been recovered from various other countries, including the Republic of Congo, Democratic Republic of Congo, Republic of Guinea, Côte d'Ivoire, Morocco, Uganda, Zambia and Zimbabwe (Zentmyer *et al.*, 1976) but the hosts were not mentioned.

22.2.4 *Phytophthora* spp. in plantation forestry

In Africa forests are a valuable natural resource and important source of timber and non-timber forest products. Of Africa's total forest area only 2.3% consists of planted forests and 38% of these plantations contain non-native tree species. Thirty per cent of Africa's forest area is primarily for production of timber and non-timber forest products. The majority of timber harvested in Africa, be it from natural or planted forests, is used as fuel wood and only about 10% for industrial purposes. Countries with planted forests produce a significantly larger proportion of industrial wood. Plantations of non-native trees are uncommon and irregularly distributed, but where they do occur, countries rely almost exclusively on them for industrial wood (FAO, 2010). Of these the most prominent plantation species are *Pinus*, *Eucalyptus*, *Acacia* and *Cupressus*.

Black wattle (*Acacia mearnsii*) plantations make up approximately 8% of the total forestry land usage in South Africa, and the trees are mainly used for tannin production and pulpwood. In the 1960s a serious disease, known as black butt disease (Fig. 22.1B and C), appeared in South African plantations. The disease is characterized by blackened bases of the tree trunks, copious gum exudation as well as mottled lesions occurring on the stems of young trees (Zeiljemaker, 1971). Initially, *P. nicotianae* was shown to be the cause of this disease, but two additional species, *Phytophthora boehmeriae* and *Phytophthora meadii*, were later shown to be associated with the same symptoms (Roux and Wingfield, 1997). Black butt disease is also present in Kenya and Tanzania, but the *Phytophthora* sp. involved has not been identified (Roux *et al.*, 2005).

Pines and eucalypts provide the backbone of the South African forestry industry and make up about 50% of the total forestry land area planted. Several *Phytophthora* species attack these trees (Table 22.1). In plantations *P. cinnamomi* causes root and collar rot of both pines and eucalypts (Fig. 22.1A). In forestry nurseries *P. cinnamomi* causes damping off of pine and eucalypt seedlings and has resulted in nursery quarantine and the destruction of countless seedlings. Until 20 years ago *P. cinnamomi* was the only species known to cause disease in pine and eucalypt plantations. Thereafter two species, *P. boehmeriae* and *P. nicotianae*, were identified on several *Eucalyptus* species (Linde *et al.*, 1994). *P. nicotianae*, in particular, became so prevalent that it was more consistently recovered from dying eucalypts than *P. cinnamomi*. More recently two new species, *Phytophthora alticola* and

Fig. 22.1. Plantation trees affected by Phytophthora diseases. **(A)** Dead, defoliated *Eucalyptus* spp. caused by *Phytophthora cinnamomi* infection. **(B, C)** Basal stem canker of *Acacia mearnsii* suffering from black butt disease with exposed stem lesion **(B)** and bleeding stem cankers **(C)** (photographs courtesy of Jolanda Roux).

Phytophthora frigida, were found to cause root and collar rot of cold-tolerant eucalypts in the Kwazulu-Natal province (Maseko *et al.*, 2007).

22.3 *Phytophthora* spp. in Native Environments

There has been very little research on *Phytophthora* in native environments in Africa. This is evident when comparing the number of *Phytophthora* species from crops to those occurring on indigenous plants or in native environments (Table 22.1). Even among *Phytophthora* spp. identified from indigenous plants, many have been isolated from plants cultivated as food crops, medicines, cosmetics or for the flower trade.

Recently, there has been an increased international focus on *Phytophthora* associated with native ecosystems because a number of very serious Phytophthora diseases have emerged in native woody ecosystems. But, surveys for these organisms in native African environments have yet to be made. The Cape Floristic Region (CFR), and especially the sclerophyllous shrubland known as fynbos in South Africa, has received more attention relating to *Phytophthora* spp. than any other native habitat in Africa. This was initially motivated by the dramatic death of the iconic silver trees (*Leucodendron argenteum*) (Fig. 22.2) and other *Proteaceae* in this megadiverse flora. Multiple *Phytophthora* species are now known to occur in CFR rivers and their catchments including *Phytophthora capensis*, *P. cinnamomi*, *Phytophthora citricola*, *P. cryptogea* and *Phytophthora dreschleri* (Von Broembsen, 1984). Multiple *Phytophthora* species are involved in disease of buchu (*Agathosma* spp.), including a yet-to-be described taxon in the *P. citricola* complex informally referred to as *Phytophthora* 'emzansi'. Additionally, *P. capensis* was described as a new species after re-examining isolates from buchu previously classified as *P. citricola* (Bezuidenhout *et al.*, 2010). Apart from *P. capensis* and the newly discovered *Phytophthora* 'emzansi', the other species have a cosmopolitan distribution and diverse host range.

P. cinnamomi is the most commonly encountered *Phytophthora* in the CFR. It is associated with root rot and decline of several native species in the *Bruniaceae*, *Ericaceae* and *Proteaceae* families in the fynbos. *P. cinnamomi* is also a serious problem for the cut flower industry, where it causes root rot of cultivated members of the *Proteaceae*. Additionally, *P. cinnamomi* is associated with the decline of stinkwood (*Ocotea bullata*) trees in native forests of the Eastern Cape of South Africa (Table 22.1).

22.4 Conclusions

Phytophthora has a major socio-economic impact on the countries and people of Africa. The most important are losses in agriculture to pathogens such as *P. infestans*, which severely affects potato and tomato yields. Black pod disease of cacao is responsible for substantial losses of cacao, of which Africa is the largest producer. Black pod disease directly impacts resource-poor farmers who are dependent on cacao as a source of income (see Drenth and Guest, Chapter 20, this volume). Avocado production is also severely affected by *P. cinnamomi* and can result in extreme economic losses.

Although forestry is an important industry, little is known about the impact of *Phytophthora* on native or non-native trees. Several of the most commonly planted trees, including non-native acacias, eucalypts and pines, are affected by various *Phytophthora* species. *P. cinnamomi* is a significant threat to commercial forestry and also surrounding native ecosystems. In addition to *P. cinnamomi*, *P. nicotianae* has emerged as a serious pathogen disease of eucalypts and pines and other *Phytophthora* species also appear to be involved. Vigilance is required for the early detection of possible new *Phytophthora* species or known pathogenic species from elsewhere in the world.

Compared with the research on agronomic crops, *Phytophthora* in native

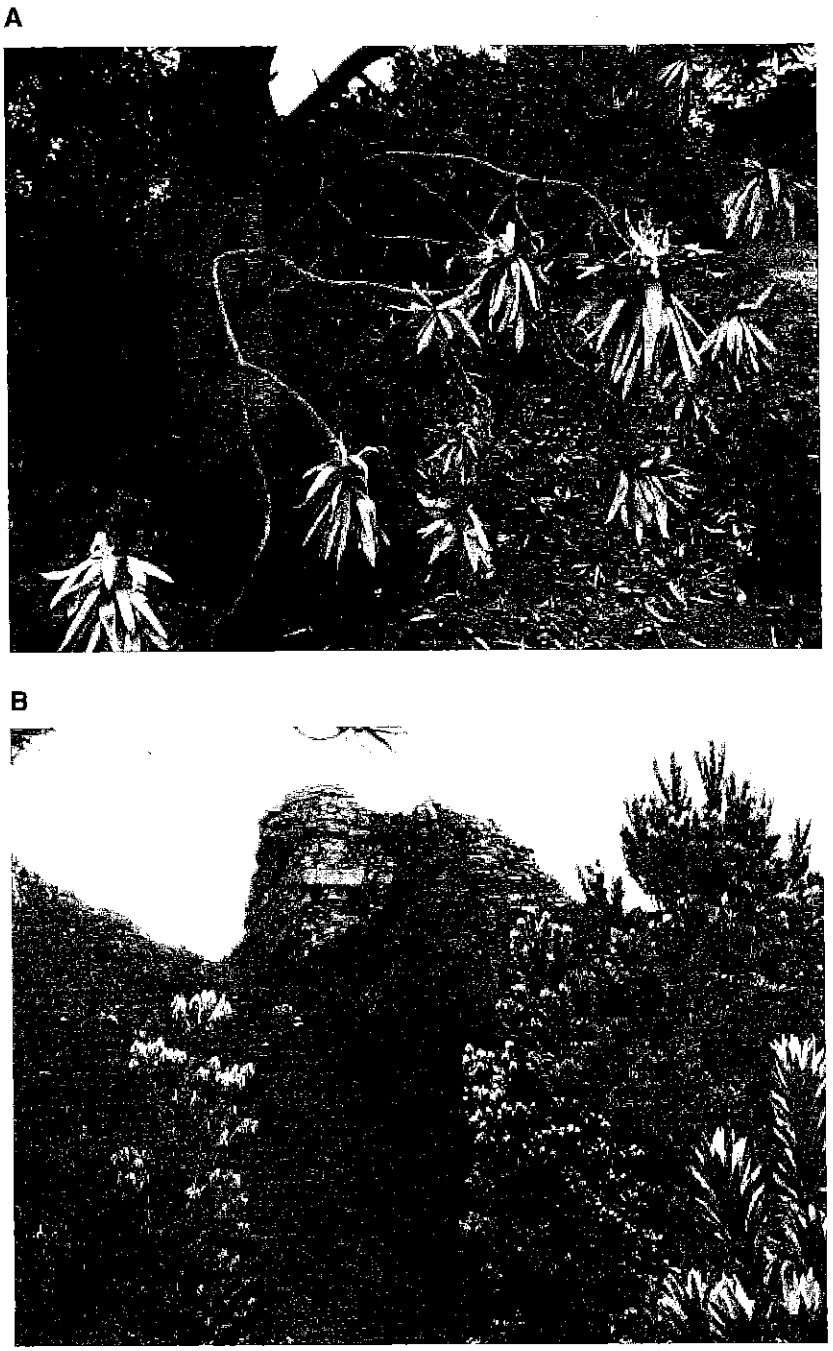

Fig. 22.2. Dieback of *Leucodendron argenteum* (*Proteaceae*) caused by *Phytophthora cinnamomi*. **(A)** Cracking of the bark, covering affected areas of the tree stem and early signs of wilting visible from the leaves. **(B)** A severely wilted tree (left) with grey discoloured leaves.

habitats has received limited attention. Although this bias is understandable, there is much room for further investigation. Africa has several regions of plant mega-diversity and endemism and probably harbours several new *Phytophthora* species. Thus far the majority of *Phytophthora* species on native and indigenous plant hosts have been found in the CFR of South Africa. In just the last decade the number of described *Phytophthora* species has more than doubled, but only three of these new species descriptions originated from Africa. This lack of species discovery is due to: (i) the limited number of studies investigating species diversity; (ii) a focus on economically important species; and (iii) a lack of funding and trained researchers in the field. There is consequently a great need for comprehensive studies on *Phytophthora* species diversity, especially in native habitats in Africa. This is especially important because novel *Phytophthora* species may be a threat to important non-native or native plants elsewhere in the world.

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