Patch Deaths in Tropical Queensland Rainforests: association and impact of *Phytophthora cinnamomi* ***and other soil borne organisms***

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Preface

A preliminary report to the Cooperative Research Centre for Tropical Rainforest Ecology and Management (Rainforest CRC) highlighted a most urgent need to update our knowledge as it relates to the presence of soil pathogens of the genus *Phytophthora* in the Wet Tropics World Heritage Rainforests of North Queensland (Gadek 1997). That report was commissioned by the Rainforest CRC following requests and concern expressed to it by the ecotourism industry. Their principal concern at that time was the loss of present and potential future access to certain areas of World Heritage Rainforest which would occur with the proposed closure and quarantine of some areas and roads based in part on the previously recorded presence of *Phytophthora cinnamomi* in those areas. *P. cinnamomi* is recognised as a key threatening process to the conservation of native plants, and regional management agencies have applied the precautionary principle to management of areas under their control. Indeed, they are obliged to do so. However, it was clear there was a lack of up-to-date information concerning soil pathogens in these ecosystems. This need acted as a catalyst for a workshop held at the end of April 1998 at the Cairns campus of James Cook University, where interested groups – scientists, managers and local commercial ecotourism operators working in the World Heritage Rainforest area – came together to review the 'state of play' on *Phytophthora*.

A timely contribution by ecotourism operators Wait-A-While Environmental Wildlife Tours and Gondwana Travel Company, in the form of 4WD vehicles and drivers, allowed us to provide participants to the workshop with field experience of the rainforest environment. Bruce Brown, the scientist who undertook the original surveys in the early 1980's throughout the Wet Tropics rainforests, guided our visits to sites on Mt Lewis where *Phytophthora* had previously been detected, at a number of localities at altitudes between 920 – 1200m. The initial outbreaks of infestations and patch deaths were apparently correlated with logging and road construction, and infestations were possibly then spread secondarily by pigs.

Mt Lewis is situated in the rainforests of the Wet Tropics of Queensland World Heritage Area, the access road located approximately one hour drive north of Cairns. This 29 km access road climbs steadily, following the original forestry logging track, to around 1200 metres above sea level at its highest point (see Map). Mt Lewis comprises an outstanding area of botanical significance, sustaining a large area of high altitude relict rainforest. This granitic high peak refuge is one of the most accessible in the far north rainforests, and contains a disproportionately high number of endemic species. Both rare and evolutionary ancient taxa can be found from a number of families known to comprise species which are highly susceptible to adverse *Phytophthora* infection, such as Proteaceae, Lauraceae, Myrtaceae and Ericaceae / Epacridaceae. The field trip was accompanied by Mr Bob Jago, a local botanical expert, who provided a wealth of assistance with the botany of this region, and

a partial species list of the area courtesy of the local branch of the Society for Growing Australian Plants.

The workshop (and the associated field trip) was extremely valuable in facilitating interaction in a positive and educational manner amongst the participants. This report is the result of the workshop, and reflects entirely the generous contributions of the invited specialists and the enthusiasm of the participants.

Acknowledgments

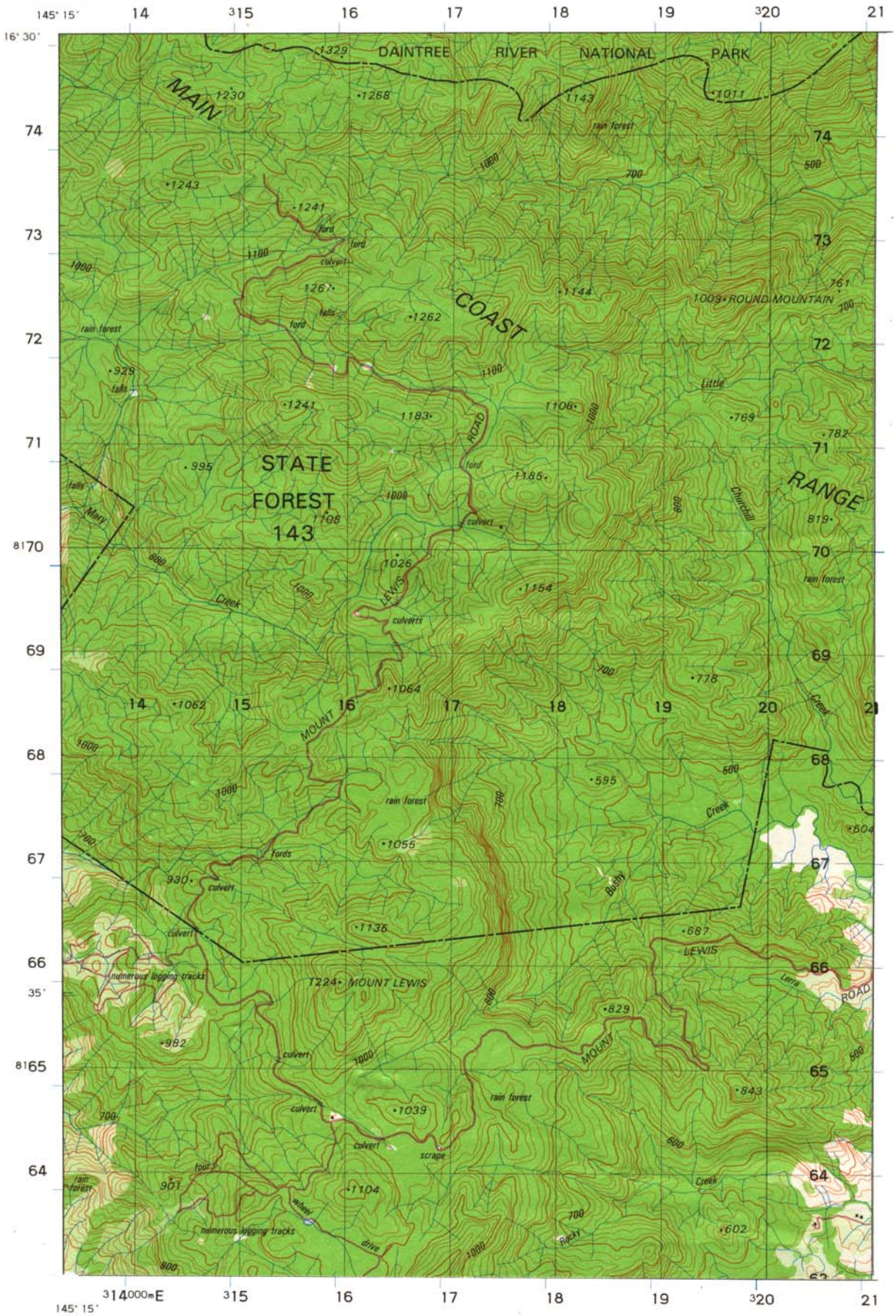
The cost of the workshop and the production of this technical report was underwritten by the Cooperative Research Centre for Tropical Rainforest Ecology and Management (Rainforest CRC), Queensland Department of the Environment (currently the Queensland Department of Environment and Heritage) and the Wet Tropics Management Authority (WTMA). I am grateful for the assistance of Nigel Stork (Director, Rainforest CRC), Lindsay Delzoppo (QDEH) and Tom Dacey (WTMA) for facilitating this arrangement. The time and energy of Nigel Stork contributed greatly to the success of the workshop. The CRC for Tropical Plant Pathology financially supported the participation of the Director, John Irwin. Several other organisations supported the participation of nominated personnel. The assistance of all involved is greatly appreciated.

Wait-A-While Environmental Wildlife Tours and Gondwana Travel Co., both members of the Alliance for Sustainable Tourism, provided a very valuable contribution to the success of this workshop by organising 4WD vehicles and drivers to transport participants into the field. The assistance of Bob Morrison and Rob Schelling is gratefully acknowledged.

I thank Bob Jago for his unselfish participation and contribution to the field trip; and the staff of the Rainforest CRC at Cairns headquarters for their assistance with both the field trip and the workshop.

I especially thank the workshop secretary Jann O'Keefe for her exemplary organisational abilities and efficient and cheerful energy, and without whom the workshop, field trip and production of this report would not have been as successful as they were.

Paul Gadek
EDITOR



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Map of Mount Lewis district, Far North Queensland

Source: Royal Aust. Survey Corp. *Rumula*. Series R733, Sheet 7964 1. Ed 1-AAS (SCALE 1:50 000)

Photographs taken during the workshop excursion to Mount Lewis

Top Photographs

Left: Bruce Brown revisits a diseased site from his earlier field work in the Mount Lewis area. The gap in the rainforest canopy is clearly visible.

Right: Some of the field trip attendees on the western escarpment of Mount Lewis. This area is one of the most accessible high altitude relict rainforest communities of the Wet Tropics.

Centre photographs

Left Rob Schelling (Gondwana Travel Co), Ken Pegg (QDPI)
David Guest (Melbourne University) sharing lunch at the end of the Mount Lewis road.

Upper right: (left to right) Bruce Wannan (environmental consultant with 'Environment North'), Bruce Brown (consulting pathologist), and Paul Gadek (Workshop Organiser) also over lunch.

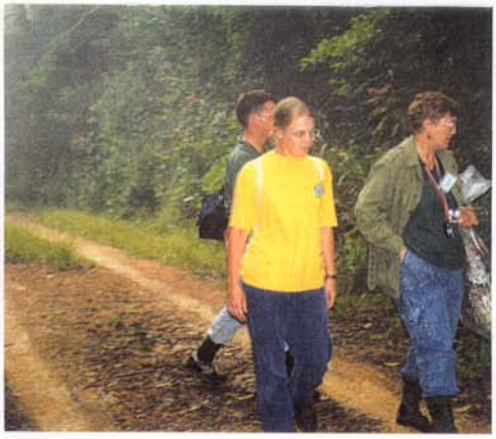
Lower right: Heather Walker (JCU student), Betsy Jackes (JCU Botanist) and Stuart Worboys (Rainforest CRC Masters student) on the Mount Lewis Road at approximately 1000 metres altitude. The access road cuts a gap through the canopy, increasing light levels and water runoff at road edges.

Bottom photographs
Examples of plants from the high altitude rainforest of Mount Lewis that are suspected of high susceptibility to adverse infection by *Phytophthora cinnamomi*. Both species illustrated are in the family Ericaceae.

Left: *Rhododendron lochiae*, Australia's only native Rhododendron, restricted to altitudes over 1000 m on some of the highest peaks in North Queensland. It commonly grows in exposed positions with rainfall of up to 4000 mm per year.(photo Mary Gandini)

Right: *Agapetes meiniana* – a rare high altitude vine, whose vivid pink-red tubular bell shaped flowers are often conspicuous on the forest floor.

Unless otherwise noted, all photographs by Di Daly.



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* John Irwin presented the paper in this volume.

1 INTRODUCTION AND OVERVIEW

PAUL GADEK

Worldwide the root and collar rot organism *Phytophthora cinnamomi* is known as one of the most destructive pathogens of woody plant hosts. In Australia, *P. cinnamomi* and other species of *Phytophthora* are responsible for economic losses amounting to tens of millions of dollars annually in forestry, horticultural and agricultural activities. In natural ecosystems it poses a serious threat to the conservation of native plant species: indeed, it is recognised by the Australian Federal Government as a key threatening process under the *Endangered Species Act 1992*. Few Australians would be unaware of the terrible destruction caused to our southern and western heaths and woodland communities in recent years, with descriptions in the media of a distinctly visible scar, marked by dead and dying understorey plants, slowly moving through these highly fragile ecosystems. As a consequence there has been considerable time and money spent on instituting management practices to ameliorate the impact of this pathogen in National Parks and Reserves in Western Australia, Victoria and Tasmania.

Occurrence of *Phytophthora* in north Queensland Rainforests

Species of *Phytophthora* are also known to occur across extensive areas of rainforest in northern Queensland. Sampling of rainforest sites by Queensland Forestry Service Pathologist Bruce Brown (Chapter 7) during the mid to late 70's has shown that the pathogen is widespread. He detected 10 species of *Phytophthora*, the most ubiquitous being *P. cinnamomi* including both the A_1 and A_2 mating types (and therefore the potential for sexual reproduction and recombination), although the A_1 strain was only detected in a few instances. Interestingly, most sites from which *P. cinnamomi* was identified displayed no obvious signs of dieback or patch death.

Brown's research, presented in this report, represents the only intensive study of *Phytophthora* pathogens in north-east Queensland rainforests. Field work terminated in 1981. The association of *P. cinnamomi* and other *Phytophthora* pathogens with patch deaths or dieback in the tropical Australian rainforests has therefore not been rigorously assessed or monitored for the last 17 years, during which time our understanding of the biology and ecology of this group of organisms has substantially increased. For example, despite earlier speculation of only a secondary role of *P. cinnamomi* in patch deaths and dieback, recent studies show it to be a primary invader, attacking only healthy plant tissue and causing a subsequent physiological disruption of vascular activity. In susceptible plant species, infection may quickly result in dieback of foliage and eventual death.

The management implications of the occurrence of *Phytophthora* in northern rainforests are succinctly outlined in this report by Steve Goosem and Nigel Tucker (Chapter 2), representing

the authorities charged with the management of the Wet Tropics of Queensland World Heritage Area. Of particular immediate concern is the recent increase in tree planting schemes and their activities in areas abutting World Heritage rainforests, and the possible spread of *Phytophthora* organisms in the region.

Concerns and questions from the ecotourism perspective are similarly outlined here by Guy Chester (Chapter 3). Some of their concerns, particularly with regard to up-to-date information, were answered during the workshop and in papers included in this report. It is still apparent, however, that the concerns of this industry are shared with, and contained within, the more extensive list of questions posed by Steve Goosem.

Biology and Ecology of *Phytophthora*

The biology and ecology of *Phytophthora* is extensively reviewed here by David Cahill (Chapter 4) and Adrienne Hardham (Chapter 5). Spore producing structures (sporangia) develop on hyphal tips, within which motile spores (thus termed zoospores) are formed and released. These motile spores are the primary infective agent, which are then capable of rapid dissemination and spread via free water. The mode of infection of *Phytophthora* is well established, involving the encysting of motile zoospores at the root surface, and their subsequent germination and invasion of root tissue. Zoospores show a positive chemotactic response to the region of root tip elongation, and have been shown to infect the roots of both resistant and susceptible plant species. Under laboratory conditions, all plant species so far studied are prone to infection, but not all will suffer the severe symptoms of dieback and death. In susceptible plant species and varieties, infection causes a progression of symptoms, starting with the cessation of root growth, discolouration of the infected region and tissue necrosis. In highly susceptible plant species, infection affects water uptake and translocation, and quickly causes dieback and eventual death.

Phytophthora can persist in the soil for long periods, both as a mycelium of hyphae or through the production of either chlamydospores – highly resistant, resting spores produced by the hyphae; or oospores – the product of fertilisation (between two different mating strains). Both these latter resting stages are highly resistant and very long lasting (many years) in soils.

It is incumbent on us now to refrain from calling *Phytophthora* species “fungi”. Both David Cahill and Adrienne Hardham stress their close structural, biochemical and genetic similarities to some algal and protozoan organisms. This recognises that we can no longer treat or manage these pathogens in the same ways normally used for fungal pathogens.

Triggers of infections

Sporangial production by the pathogen appears dependent on several environmental factors, primarily the presence of water, usually at soil field capacity or full saturation, and warm soil temperatures. Zoospores require free water for long distance dispersal, although they can be transported very long distances in soil attached to a dispersal agent.

Whilst rainfall and temperature are important determinative factors of the outbreak of this disease in the southern regions of Australia, we still do not know if similar factors are as important in the rainforest ecosystem. Nor are we any closer to answering the question of

whether the appearance of symptoms of *Phytophthora* disease in rainforests represents a flare-up of a pre-existing infection or the recent arrival of the organism into this environment. Bruce Brown suggests that a likely trigger in tropical rainforests could be rainfall, either at very high levels to stimulate the production of *P. cinnamomi* zoospores, or alternatively a period of unseasonally very low rainfall, thereby stressing trees with an already diseased root system and exacerbating the symptoms of infection.

Disturbance caused by road building and the road itself may increase runoff and raise soil moisture levels in areas adjacent to the road, simulating high rainfall conditions. A change in hydrological conditions adjacent to the road may also cause 'ponding' in the vicinity. Similarly, forestry logging is suggested to increase soil moisture levels through decreased transpiration of the remaining vegetation. Recently feral pigs have been implicated not only in the dispersal of zoospores from areas of epidemic outbreaks, but in triggering zoospore production via their habit of making wallows, which retain water in small depressions.

Virulence

An important distinction in discussing the disease effects of *Phytophthora cinnamomi* should be drawn between the organisms' pathogenicity and its virulence. The organism appears universally pathogenic, that is, it will cause disease. Virulence is the ability of the organism to cause disease, its degree of pathogenicity, and this ability may vary in different subsets of the species. Although variation in virulence has not been intensively investigated in *Phytophthora* species, results of a recent study provoke some interesting questions. Robin and Desprez Loustau (1998) report a range in the levels of virulence amongst different isolates of *P. cinnamomi* collected from different countries. This suggests the possibility that different isolates from a range of habitats in Australia may also show a range of virulence. Does this explain the different appearance of the disease in different habitats between, for example, heath ecosystems and rainforests, where in the latter broadscale deaths and ongoing epidemics are not apparent?

Infection in native vegetation in southern Australia appears concentrated into three phases: an aggressive phase lasting 1-3 years causing death of 50-75% of species; a period where resistant plant species recolonize the ecosystems combined with a fall in the soil concentration of detectable *Phytophthora* species; and subsequently the regeneration of some *Phytophthora* susceptible species. Are these phases indicative of a long term decline in the virulence of the pathogen in a particular habitat?

Clearly genetic diversity studies need to be undertaken to determine whether the pathogen is genetically similar in all regions of Australia.

Is *Phytophthora cinnamomi* native or introduced?

The presentations and discussion at the workshop highlighted the fact that there is no definitive evidence currently available to answer this question. We are still unclear as to whether *P. cinnamomi* is an invasive introduced pathogen, to which our sclerophyll flora and many important elements of our rainforest flora do not have immunity, or whether its pathogenic effect is just part of the natural process of the regeneration cycle. Did *P. cinnamomi* arrive in Australia through horticultural and agricultural imports, and escape into our native ecosystems through human activities?

The preliminary data on the occurrence of *P. cinnamomi* and other *Phytophthora* species detected by Bruce Brown in the rainforests of northern Queensland, as well as the presence of both mating types of the former, suggest that this genus may well be native to these areas. The absence of both mating strains of *P. cinnamomi* from the Eungella Tableland may suggest this organism has been introduced to that area at least. However, without any understanding of the role and maintenance of *Phytophthora* species in natural ecosystems, these observations are no more than speculation.

Molecular phylogenetics is one of the more potent techniques now available to allow us to answer some of these questions. Such techniques are currently being refined and developed for identification and detection of *Phytophthora* species in soil and plant tissues. These are outlined by **John Irwin** (Chapter 8) and are becoming more common in the literature (for example, Liew et al., 1998). As indicated above, genetic diversity studies need to be undertaken, comparing isolates from rainforest habitats to those found in other habitats and in commercial plantations. Information from these studies are vital in understanding the status of these species in Australia, and would provide a much clearer understanding of the historical spread of *P. cinnamomi* in Australia and the relationship of our species to those found in other countries.

Distribution of *Phytophthora* in the Wet Tropics Rainforests

Since the field studies of Bruce Brown terminated in 1981, there has been no systematic follow-up surveys or monitoring of *Phytophthora* species in these rainforests. There is a need to resample and reanalyse these areas to determine any long-term effects of previous outbreaks and to determine if the pathogen has spread into areas where it had previously been undetected.

Monitoring and detection of soil pathogens in rainforest soils can now be undertaken by sophisticated molecular technologies, with increasing sensitivity of detection, but there still remain problems of detecting very low levels of highly dispersed propagules. Some of these problems are outlined in the papers presented by John Irwin (Drenth et al.), Bruce Brown and David Cahill. An inexpensive field technique, such as the use of dipsticks (Hardham, pers. comm.), which could be handled by personnel with limited training, would be a great help in undertaking tasks of detection and monitoring in rainforest communities.

Which communities within the rainforest ecosystem are likely to be at risk? Studies in southern Australia, outlined by David Cahill and Bruce Brown, have shown a strong correlation between the disease (virulence) and aspects of the abiotic environment, including slope, depth to impeding layer, soil texture and soil bulk density. Combined with data on the extreme sensitivity of certain species within a number of plant families (see Table 3 in Brown, for example), it should be possible to indicate particular areas of high risk. David Cahill suggests the utilization of GIS technology, to produce risk assessments of localities and on which consequent management decisions can be based. Rainforest communities which are currently suspected to be highly susceptible include the montane communities on heavily leached infertile soils. These montane communities are often of great conservation importance due to their refugial nature and the presence of many species endemic to these areas. Many of these species also belong to families known to contain species highly susceptible to *P. cinnamomi*.

The apparent lack of extensive damage to tropical rainforest communities contrasts with other areas of woodland and heaths in southern Australia, and the southern temperate rainforests in Tasmania. Given the virulence of these pathogens in the suboptimal conditions of woodlands and heaths, the lack of devastation in the tropical rainforest in what would be expected to be optimal conditions is surprising unless there is something fundamentally different in their behaviour in this ecosystem. Of course it is still possible that the effects of small infestations are masked by the much more dynamic turnover in rainforests, and we will not be aware of these effects unless we undertake substantial monitoring.

Long-term studies in woodlands have shown an initial progressive reduction in susceptible hosts, with subsequent survival of resistant plant species. Eventually partial regeneration of some susceptible species occurs, and they may survive in infested quadrants even in the presence of the pathogen (Weste 1997). Certain species did not regenerate, possibly due to the lack of a seed bank in the soil. Some isolated small resurgences of disease, possibly due to an unseasonable warm wet summer triggering zoospore production and dissemination, suggests the possibility of recurring cycles of disease and recovery.

Management

Anecdotal evidence and casual observation doesn't suggest that there has been large scale death of trees in the last few decades in tropical Australian rainforests, at least not since the rapid increases in patches of dead forest recorded by Bruce Brown on the Eungella Tableland and in the Garrawalt regions of the Wet Tropics, where dead forest increased from 4.6% in 1976, to 11.9% in 1978, and finally to 19.3% in 1980. Anecdotal observations are not a good basis for management decisions. Certainly there have been sporadic reports to this author and to other scientists, from members of the public, field workers in authorities such as DPI Forestry, and aerial photography programs, of visible patch deaths, some in the rainforests and some in associated woodlands. There has been no investigation as to whether these patch deaths are caused by isolated flare-ups of virulence and activity of *P. cinnamomi*, or whether they are the result of other processes, such as lightning strikes. Unfortunately there is no program in any central authority that will receive, record and investigate public reports of patch deaths in the tropical northern rainforests. While there is an absence of any concerted detection and monitoring program, it is quite possible that isolated outbreaks go unnoticed, and the extent of patch deaths in rainforests is currently under-estimated. Nor is reliance on patch death incidence a reliable indicator of the presence of *P. cinnamomi* in ecosystems, as it can remain in infected roots and not provoke any symptomatic response in particular hosts; and survive in soil as resting spores over long periods of time.

Short term effects of infection and virulence on natural vegetation are quite clear, and these are often of most concern to management agencies and tourism operators. The most obvious effect in WA, SA and Tas has been a direct attack on the flora, often in communities containing endangered species. A change in management of areas perceived to be "at risk" is required, for the protection of susceptible rare or threatened plant species and communities.

Management techniques for the control of outbreaks of *Phytophthora*-mediated disease in agriculture and horticulture are outlined here in several reports, by Nigel Tucker (Chapter 2) David Guest (Chapter 6) and Ken Pegg Chapter 9).

A surprising result from current research into horticultural management and control practices is the observation that chicken manure, but not other animal manures, has some considerable suppressive effect on outbreaks of *Phytophthora* disease. David Guest presents preliminary evidence for the elimination of *Phytophthora* infestation of soils two months after the application of chicken manure. Its effect occurs presumably by improving soil drainage and nutrition and thereby stimulating soil biological activity. It is well known that *Phytophthora* species have a limited saprophytic ability, exhibiting poor growth and limited competitive ability in the presence of other soil microorganisms. But why chicken manure and not other animal manures?

It would be criminal to suggest dispersing chicken manure to suppress outbreaks of *Phytophthora* in native ecosystems, as many of our native plants are highly sensitive to even moderate levels of soil phosphorus, and soil fungal communities (mycorrhiza) are also sensitive to nutrient enrichment of soils. Management of outbreaks in rainforests would appear to continue to lie with practices that limit and contain the potential for dissemination of the infectious agent into surrounding communities. A possible secondary strategy may lie with the use of phosphonates. Phosphonate will reduce both stem infection and mortality of diseased plants, but will not eliminate the pathogen. A problem with phosphonate application is that concentrations as low as 3% have been shown to be slightly phytotoxic to several plant species known to be highly susceptible to *Phytophthora* infection (Peters and Weste 1997).

Some of the management practices in agriculture and horticulture have been translated to management of *P. cinnamomi* outbreaks in natural ecosystems, particularly in Tasmania and Western Australia. The clear lesson from *P. cinnamomi*-mediated disease in heath and woodland communities is that the most important factor in its dissemination appears intimately associated with human activity, either through movement of infected plant material or infested soil or gravel during roadworks. Given the high association of *P. cinnamomi* dissemination with human activities, it is hardly surprising that quarantine of infected areas has been a cornerstone of management practice. However, this does not, by itself, eliminate the organism from the ecosystem, nor necessarily stop further outbreaks occurring in the community.

Is *Phytophthora cinnamomi* a threat to the rainforests of north-east Queensland?

It is quite apparent that the disease caused by *P. cinnamomi* in native vegetation is very complex. Outbreaks of disease appear to be another effect of disturbance that put flora at risk, often with catastrophic outcomes. We are already aware of many of the sensitivities of the mycorrhizal community to habitat disturbance, particularly those associated with cultivation and nutrient enrichment (Read 1998). Given the known short-term devastation to vegetation that *P. cinnamomi* is capable of causing in some ecosystems, and the lack of our understanding of the presence or even the role of this organism in rainforests, the question is unanswerable at this time.

It is also important to take into account the other *Phytophthora* species detected in the rainforest. They have known impacts in horticulture, yet we know even less of their effects in native vegetation. Further, they have different life cycles to *P. cinnamomi*, and therefore different management strategies need to be considered should they also be identified as threat

to native vegetation. Some of the strategies employed in agriculture to combat other *Phytophthora* species are outlined by David Guest in this report.

Host-pathogen interactions and rainforest diversity

Given our lack of basic knowledge of *Phytophthora cinnamomi* in tropical rainforests, the role of this, and indeed other *Phytophthora* species and soil pathogens, in rainforest ecosystems remain uncertain. Floristically rich ecosystems are now viewed as more productive, showing greater stability and are more likely to provide alleviation of global problems posed by atmospheric CO_2 enrichment, than floristically simple ecosystems (Read 1998). Our increasing awareness of a range of threats to terrestrial vegetation means it is increasingly important that we understand the mechanisms that determine species composition in these communities.

Species richness is clearly the most distinctive feature of the tropical rainforest. Quite recently there has been speculation of an association between host-pathogen interactions and the maintenance of rainforest plant diversity (Wills et al., 1997; Givnish, T. pers. comm.). Working in the neotropical rainforests of Panama, Wills et al. (1997) suggest that floristic tree diversity may not only be maintained, but may also have been generated, by host-pathogen and host-parasitic interactions. Van der Heijden and co-workers (1998) have recently provided the first empirical study that supports the hypothesis that plant biodiversity and ecosystem productivity will increase with increasing numbers of fungal symbionts. Thrall and co-workers (1997) have modelled host-pathogen populations and shown that stable co-existence is possible even when the pathogen has a positive intrinsic growth rate. Is it possible that the diversity we see in complex ecosystems is not only maintained, but may also be in part generated, by host-pathogen interactions? Indeed the preservation of diversity (including the community's ability to evolve in the future) may require the retention of the full range of pathogens and other parasites in these ecosystems.

The workshop and renewed focus on this particular host-pathogen interaction is timely. The current discussions in the literature on the causes of rainforest diversity, and speculation of a possible association with host-pathogen interactions, serve only to indicate how little we know about our complex rainforest ecosystem, not only that part we see above the ground, but particularly that hidden on, and below, the forest floor.

2 CURRENT CONCERNS AND MANAGEMENT ISSUES OF *PHYTOPHTHORA CINNAMOMI* IN THE RAINFORESTS OF THE WET TROPICS

STEVE GOOSEM and NIGEL TUCKER

Introduction

Phytophthora cinnamomi is regarded as one of the most devastating pathogens in natural ecosystems yet recorded. In southern parts of Australia it has had a major impact on a wide range of plant species and communities and is altering ecosystems of Australia on a mammoth scale, sometimes in a subtle way, but also dramatically as is the case in parts of Western Australia.

P. cinnamomi is known to have a very wide host range and occurs in a wide range of environments where the correct conjunction of susceptible host plants and a suitable environment exist.

P. cinnamomi is a potentially devastating organism which has been listed as a key threatening process under the Commonwealth's *Endangered Species Act 1992* which has triggered the requirement for a National Threat Abatement Plan for the control of dieback caused by *P. cinnamomi.*

Conflicting Opinions

But is *P. cinnamomi* really a serious problem in the Wet Tropics? Do we really know the nature and extent of the threat in tropical rainforest?

There is differing opinion regarding whether *P. cinnamomi* is indeed a management concern or an ecological threatening process as regards the rainforests of the Wet Tropics. Statements have been made and advice given that it is not an issue in rainforests, that there is no management concern, that we haven't done anything so far and that nothing seems to have happened, or statements such as: "I drive along that road several times a week and have never seen patches of dead trees – it's all highly exaggerated". The validity of concerns about *P. cinnamomi* are particularly challenged when restrictions to road access are canvassed.

Patch Deaths in Tropical Queensland Rainforests, P. Gadek (ed)
Report, Rainforest Cooperative Research Centre, Cairns, 1999

It has also been suggested that rainforest soils usually have very high rates of microbial activity and that organisms with effects antagonistic to *P. cinnamomi* should therefore also be highly abundant and act as a natural control. There has also been the suggestion that mycorrhiza associated with the roots of most rainforest plants confer resistance to *P. cinnamomi* infection.

On the other hand, the issue of *Phytophthora cinnamomi* was considered significant enough to be explicitly mentioned in several management documents (see details at the end of this paper). It is interesting to look at the wording in this chronosequence of management documents – the level of concern seems to have been progressively diluted over the years.

Basis of Management Concern

Basically all we know about *P. cinnamomi* in the Wet Tropics derives from the extensive surveys by Bruce Brown and colleagues, then with the Queensland Department of Forestry (now Qld Forest Service) over a seven year period between July 1975 and September 1982. They associated the presence of *P. cinnamomi* with the serious decline in the health of numerous tree species of the rainforests of both Eungella and the Wet Tropics. Several other *Phytophthora* species were also recorded during these surveys, but their significance is apparently unknown. These surveys were extensive with a total 3,019 soil samples analysed over a wide range of rainforest sites - *P. cinnamomi* was isolated from 33 of the sites examined, although the number of sites actually displaying dieback attributable to *P. cinnamomi* apparently totalled 53.

Brown's research has established the causal role of *P. cinnamomi* in disease of a wide range of rainforest species on disturbed sites. The longer-term influence which this pathogen might exert upon the development of rainforest is unclear. However, the local damage can apparently be severe and the ecological and evolutionary consequences of this disease either entering or being activated in certain areas of the Wet Tropics could be devastating.

The extraordinary biological values of the Wet Tropics region and the World Heritage Area in particular, have been thoroughly described elsewhere, so there is no need to go into detail here.

The Wet Tropics is Australia's most floristically rich area at both family and generic level. At least 1,160 species of higher plants representing 523 genera from 119 families are recorded from this region's rainforests. Forty three percent of the total regional species complement are endemic to the rainforests of the Wet Tropics. Ten of the seventeen angiosperm families recognised to be primitive are represented in the Wet Tropics. There are also monotypic genera restricted to this region. The level of generic endemicity in the Wet Tropics is second only to New Caledonia in the number of endemic genera conserved per unit area. Many Gondwanan families are very well represented in the Wet Tropics including several which have been shown from other areas to be particularly susceptible to *P. cinnamomi*. The Proteaceae is one of these with 13 of the world's 76 genera occurring in the Wet Tropics. Forty species are local endemics with 24 species listed on Queensland's Nature Conservation (Wildlife) Regulation as rare or threatened. Several of these are highly restricted. The family Lauraceae is also very diverse in the Wet Tropics with over 100 species, many with very restricted distributions and 20 officially recognised as rare or threatened. The region is also very diverse in rainforest Myrtaceae including several highly restricted, evolutionary relictual taxa which occur as refugial populations (eg, *Barongia, Mitrantia, Ristantia, Sphaerantia,* and

"Stockwellia") representing developmental stages in the evolution of more drought-adapted Myrtaceous genera such as *Eucalyptus*.

Management Concerns

There are certain areas which can be described as biological 'hotspots' (including very special botanical refuges) which due to their unusually high levels of restricted, locally endemic species are particularly important, vulnerable and irreplaceable. Any threatening process with the potential to cause the death of any of these unique and locally restricted evolutionary relicts is of major concern.

There are four main areas of concern with respect to the ecological implications of *P. cinnamomi*:

- the possible elimination of species from the flora of an area and the impoverishment of species diversity and abundance;

- the possibility of a radical reduction in the complexity of a community to a relatively fewer number of tolerant species could have profound effects on the biodiversity and evolutionary potential of significant areas;

- the possibility of more subtle long-term impacts on ecosystem processes with respect to rhizosphere ecology and impacts on other soil organisms; and

- the possibility of feral pig activity either introducing or activating the fungus to otherwise undisturbed, inaccessible areas.

The evidence to date suggests that the disease occurs in disturbed rainforest especially in proximity to road building and maintenance activities, and past logging operations. The major areas of on-ground management concern therefore involve roads, walking tracks and nursery hygiene associated with various tree planting and rehabilitation programs.

If *P. cinnamomi* is indeed part of a threatening process within the rainforests of the Wet Tropics then the management of all access will be critical in minimising its spread. Access management is a major focus of the Wet Tropics Plan and an integral component of its Zoning Scheme. The roads we are generally concerned with are unsealed roads and tracks originally constructed to service the logging industry and to a lesser extent, to service infrastructure such as powerlines. The siting, type, maintenance and use patterns of many of these roads was for a different purpose than is the case now. There are road maintenance hygiene protocols which have been developed in other parts of Australia to minimise the spread of *Phytophthora*, however their applicability to the Wet Tropics has not been assessed – a major difference being the very wet climate, the wet season occurring in the summer months and the likelihood of some rain in all months of the year.

Management of *P. cinnamomi* in most other areas generally focuses on minimising or preventing the establishment of new infection foci and containment of further spread of existing infections. Such a management approach presupposes that we know where the infections are located.

Plant Nursery and Tree Planting Concerns

Over the past 15 years the popularity, interest and participation in vegetation re-establishment in north Queensland has increased tremendously. Landcare groups are now spread throughout the Wet Tropics region and the community tree planting group T.R.E.A.T. Inc (Trees for Evelyn and Atherton Tablelands) has seen membership expand to almost 600 households (as at March 1998). A large number of these community nature conservation organisations and Landcare groups have formed specifically to undertake vegetation re-establishment works. The ethic of these groups varies from farm forestry to ecological restoration and generally reflects the guiding principles of the government agency and/or nursery from whom the group receives its practical and/or financial support.

Vegetation re-establishment projects vary according to the size of the proponent and project aim. Most revegetation in the Wet Tropics falls into two broad categories:

- ecological rehabilitation which is undertaken generally along drainage lines, and
- farm forestry in other topographical situations.

Specialist projects such as road decommissioning and rehabilitation of electricity tower footprints within the WHA are generally undertaken by government agencies only. There are many areas in the Wet Tropics requiring vegetation re-establishment and continued expansion of this activity is expected. Projects are undertaken across the whole Wet Tropics bioregion encompassing a very wide range of soil, rainfall and altitude variables.

In the region a number of government agencies produce seedling stock for their own projects and to facilitate many community based projects. There are now nurseries with associated tree planting crews based in most north Queensland shires, in addition to the nurseries operated by QDPI and QDEH at Walkamin and Lake Eacham respectively. Collectively these nurseries produce in excess of 500,000 trees annually for projects and, in the case of the QDPI, also for commercial sale. In addition to these nurseries, local authorities and private contractors also bid for production and supply of a range of species for various government agencies.

At present there are only three nurseries in the region which have Queensland Nursery Industry Association Accreditation (QNIA) supplying plants for rehabilitation and farm forestry initiatives. The government facilities at Walkamin and Lake Eacham and one commercial facility are accredited. All other plants are being sourced from facilities with varying levels of hygiene and product quality. The absence of any monitoring program at these facilities (or follow up with plant pathologists) presents significant problems in actually trying to quantify the potential for pathogens to be spread.

The greatest risk of pathogen spread can be attributed to the movement of infected plant stock and the associated risks of infected hand tools, vehicles and other machinery associated with preparation, planting and maintenance operations. Works are undertaken throughout the year though most planting operations are undertaken during the summer-autumn months, corresponding to seasonal rainfall peaks.

Many of these plants also show susceptibility to other *Phytophthora* species, the taxonomy, origins and ecology of which are largely unknown. These species of *Phytophthora* and their potential for spreaad into uninfected areas may be of equal importance to the distribution and damage potential of *P. cinnamomi.*

It is well accepted that *Phytophthora* species are established in nurseries in the Wet Tropics region. Concern over its possible spread via infected plant stock led to the QDEH Lake Eacham Regional Nursery upgrading its hygiene to QNIA standards in 1995. Adopting these standards reflects a precautionary approach, consistent with management in the absence of rigorous scientific evaluation. However, unless a standard set of protocols is adopted by all nursery facilities, especially those undertaking landscape rehabilitation and farm forestry, preventative actions taken by a small subset of the total industry will be ineffectual.

The adoption of recommendations outlined in the Nursery Industry Accreditation Scheme, Australia (NIASA) Best Practice Guidelines (1997) has many benefits. The Department of Environment nursery at Lake Eacham has seen a marked decrease in the number and severity of infections caused by a range of fungal pathogens since adoption of NIASA recommendations in 1995. Improvements to nursery drainage, water, container and media management are the key features associated with decreasing fungal infections. A variety of other benefits to stock management and product quality have also been noted. There are also obvious environmental benefits accruing from decreased use of fungicide to control outbreaks.

Regular monitoring for soil pathogens such as lupin baiting is undertaken at accredited facilities, and results as well as plant infections and their respective fungicidal treatments are recorded. In the event of recurring infection in individual species, the pathogen is identified and appropriate treatment schedules prepared to limit potential future losses. *P. cinnamomi* has never been recorded from the Lake Eacham Regional Nursery, however one other (unidentified) species has been isolated from the nursery on one occasion. This same species has also been isolated from a complex notophyll vine forest adjacent to the nursery where it exhibits no effect on the vegetation. Costs of adopting best practice guidelines depend on the size and production focus of the nursery.

Concluding Remarks

There is some controversy regarding the threat of *Phytophthora* in rainforests of the Wet Tropics, however, at present, the only studies that have been undertaken are those of the Qld Forest Service – these studies terminated in 1981. It is time that this whole issue was re-examined.

Access is recognised as being one of the most crucial factors in the spread of the fungus and it continues to be a critical and contentious issue when considering the management objectives for land set aside for conservation purposes.

The application of hygiene measures has been haphazard at best to totally non-existent apart from active measures on the part of three plant nurseries in the region.

It can be concluded that more research is needed into the effects of *Phytophthora* on rainforest ecosystems, and that management decisions must be based on sound knowledge from that research. To make informed management decisions, information is required to:

- assess if the threat is real or perceived.
- assess the threat *P. cinnamomi* poses to rainforest
- develop effective and practical management guidelines

- prepare a current disease distribution map at an appropriate scale
- identify threat mitigating management practices applicable to the Wet Tropics region
- identify potentially susceptible areas
- determine the extent of susceptibility of rainforest species to *P. cinnamomi*
- identify site characteristics consistently associated with the expression of this threat
- identify the key environmental parameters for disease development/activation so that management strategies and protocols can be developed aimed at reducing disease impact.

In addition to this list of management needs, there are a myriad of questions whose answers would also assist our understanding and management of the threat:

Questions

- Are *P. cinnamomi* outbreaks episodic events and if so what is the environmental trigger?
- Are there specific physical, chemical or biological conditions which favour or inhibit its development?
- Can *P. cinnamomi* colonise undisturbed rainforest and persist?
- Can *P. cinnamomi* be activated in undisturbed rainforest and cause dieback disease?
- Is there a certain disturbance threshold required for the expression of dieback symptoms?
- Is there a correlation between dieback and altitude in the Wet Tropics? (eg. are lowland forests safe?)
- Is there a correlation between climatic patterns and dieback?
- Is there a correlation between geological substrate, soil type or fertility and the expression of dieback? (eg. are fertile, well drained areas not at risk?)
- What is the interaction between disease activity, fluctuations in population levels of the fungus, return period of epidemics, frequency of disturbance events, and period of time following disturbance for the development of non-conducive habitat?
- What are the direct and indirect impacts on both flora and fauna?
- What are the short-term versus long-term impacts of the disease?
- Is the flora of parts of the Wet Tropics being subjected to a new and powerful force of selection?
- Do any susceptible plant species with restricted ranges face the possibility of extinction in the medium term?
- Are any susceptible plant species comprising small disjunct populations suffering genetic erosion through local extinction of populations?
- If *P. cinnamomi* has been established for a long period, will there still be obvious symptoms apparent at Bruce Brown's old sites? Will the majority of susceptible species have been killed and replaced by resistant or tolerant species (post-disease manifestation of resistant species)? What bearing will this have on the present day interpretation of these results?
- Are there more subtle effects of *Phytophthora* in rainforest such as acting as a post-emergent damping off pathogen thereby effecting regeneration patterns – an impact which is difficult to detect and impossible to map?
- What is the risk of an activity introducing or spreading *P. cinnamomi* dieback?
- How can society resolve the conflict between those that want access to susceptible ecosystems for recreational reasons and the need to control the spread of diseases?

Management Documents specifically referring to *Phytophthora cinnamomi*

Wet Tropics World Heritage Nomination document prepared by DASETT (December 1987, pp. 15)

> "Outbreaks of the soil fungus Phytophthora cinnamomi have caused considerable patch deaths of trees and shrubs and are a serious problem in some logged areas such as near Mt. Lewis and Garrawalt Falls."

Queensland Government's Document No.2 to the IUCN (May 1988, pp. 15a)

> "The root rotting fungus *Phytophthora. cinnamomi* is widespread throughout, but by no means ubiquitous to, the tropical rainforests north of Townsville. At Garrawalt it was associated with numerous dead patches in both virgin and logged rainforest. In some of the largest patches observed at Garrawalt, approximately 30 trees greater than 5 cm dbh had died. At Mt. Lewis the fungus was associated with dead patches in logged and road-affected virgin rainforest. Elsewhere it was recorded from dead patches in virgin rainforest."

Preliminary Draft – Management Plan for Queensland Crown Lands in the Wet Tropics (Government of Queensland, October 1989, pp. 177)

> "The only disease known to pose a significant threat to natural rainforest stands is the root-rotting fungus *Phytophthora cinnamomi*."

Wet Tropics Plan Strategic Directions (Wet Tropics Management Authority, 1992, pp. 98)

> "In addition to introduced plants, the fungal disease *Phytophthora cinnamomi* (known as "Dieback") occurs in the Kirrama and Carbine Tableland Areas."

Draft Wet Tropics Plan (Wet Tropics Management Authority, October 1995, pp. 74)

> "The fungus *Phytophthora cinnamomi* which causes "Dieback" disease in native vegetation is know to occur in many places within the area."

Protection Through Partnerships (Wet Tropics Management Authority, August 1997, pp. 56, 70-72)

> "The fungus *Phytophthora cinnamomi* which causes "Dieback" disease in native vegetation is know to occur in many places within the area.
>
> The extent of *Phytophthora cinnamomi* infection in the Area and the effectiveness of control techniques need to be reviewed."

3 *PHYTOPHTHORA CINNAMOMI* – TOURISM INDUSTRY CONSIDERATIONS

GUY CHESTER

Abstract

The Alliance for Sustainable Tourism has, in past submissions on the Wet Tropics Plan, raised concerns that the extent and ecology of *Phytophthora cinnamomi* in the Wet Tropics is poorly understood. This paper briefly sets out the critical research areas, from the tourism perspective, to address this issue.

Background

The Alliance for Sustainable Tourism was formed in 1995, creating a single representative body for the tourism industry to address issues relating to natural areas in far north Queensland, the Inbound Tourism Association of Australia (North Queensland Branch), the Pacific Asia Travel Association (North Australia Chapter), Far North Queensland Tour Operators Association and the Ecotourism Association of Australia. During 1994 and 1995, the members of the Alliance had spent many hundreds of hours inspecting the Wet Tropics Area and discussing management issues with land managers towards the development of the Wet Tropics Ecotourism Strategy.

The Draft Wet Tropics Plan (WTMA, 1995) stated that: "The fungus *Phytophthora cinnamomi* which causes "Dieback" disease in native vegetation is known to occur in many places within the Area." The draft plan had roads classified to be closed for use by visitors to the Wet Tropics World Heritage Area (including tour operators). Some of these roads have unique presentation opportunities and their closure could have resulted in financial hardship to individual permitted tour operators. At the time, the tourist industry in the Wet Tropics was unaware of the issue, nor the implication that road use for presentation purposes had the potential to cause impacts such as dieback.
Upon the publication of the draft Wet Tropics Plan, the Alliance sought further information on *Phytophthora* from the Wet Tropics Management Authority and relevant experts. The Alliance compiled a detailed submission on various aspects of the Draft Wet Tropics Plan. In relation to *Phytophthora*, it concluded:

> " There is no doubt that *Phytophthora cinnamomi* causes dieback in areas of Australia. There is no doubt that *Phytophthora cinnamomi* has been found throughout the Wet Tropics in undisturbed virgin rainforest, near roads and in logged areas. *Phytophthora cinnamomi* occurs throughout horticultural areas in the Wet Tropics region. It has been reported that dead patches of rainforest in various areas of the Wet

Patch Deaths in Tropical Queensland Rainforests, P. Gadek (ed)
Report, Rainforest Cooperative Research Centre, Cairns, 1999

> Tropics can be attributed to *Phytophthora cinnamomi*. There would appear to be no scientific evidence to reject this.
>
> However, there has been no ongoing research since the studies undertaken prior to 1988.
>
> It would appear that *Phytophthora cinnamomi* causes a degree of patch death in rainforest in the Wet Tropics. That it has been within the Wet Tropics for at least ten years and only patch deaths have been recorded would suggest that broadscale dieback of forest as has been seen elsewhere in Australia is unlikely to occur. However, the local impacts on rainforest communities, species and ecological processes has not been studied. Further, the impacts on surrounding sclerophyll communities is unknown.
>
> With regard to Mount Lewis, it would appear that it has been 'singled out' for quarantine on the basis of the 1988 report rather than more recent studies. Sites where *Phytophthora* has been found would appear to be included in the section of the Mount Lewis road which is to remain open.
>
> The closure of the upper section of the Mount Lewis road will not stop it's spread along the road. It is understood pigs disburse *Phytophthora* and there is a significant feral pig population along the entire Mount Lewis corridor.
>
> As *Phytophthora* is understood to be common on agricultural land throughout the Wet Tropics, its continued spread throughout the region is not expected to be in any way arrested by the closure of the Mount Lewis Road."

Current Distribution

The most recent work on *Phytophthora* in the Wet Tropics was undertaken by Brown between 1975 and 1981. The work was at a time of significant disturbance in the forest with logging being undertaken in the vicinity of all sites where patch deaths occurred.

Whilst Brown (1976) concluded that patch deaths occurred in virgin forest, this appears to be on the presumption that the spread of *Phytophthora* could only occur through downslope surface waterflow from contaminated sites. Hence sites laterally away from disturbance were typed as "virgin". However, Kliejunas and Ko (1976) found that *Phytophthora cinnamomi* was spread by humans (boots), pigs and vehicles in tropical forest on the Island of Hawaii. It is of course merely conjecture, but it could be that *Phytophthora* could have been introduced by these vectors to the "virgin" areas at the time of the initial disturbance in logging areas.

It would seem that we know little of the current distribution of *Phytophthora* in the Wet Tropics. To the tourism industry, this would appear to be a fundamental question which needs to be addressed. As an urgent issue (before other major research projects are resourced) an opportunistic (rather than systematic) survey of likely areas would tell us whether *Phytophthora* is still active in the Wet Tropics, and whether it has spread.

Ongoing Patch Deaths

The 1976 to 1981 work by Brown identified patch deaths attributable to *Phytophthora*. However, there has been little work undertaken since then to identify patch deaths in rainforest in the Wet Tropics, and their cause. It would appear critical that we identify areas experiencing current patch death and establish the cause. Anecdotal evidence suggests that there are no major ongoing "dieback" processes. The mere fact that patch deaths have not grown in extent and number in contaminated areas over the last twenty years raises questions as to whether this is an ongoing threatening process in the Wet Tropics.

Again, it is merely conjecture, could patch deaths only occur as a result of the spread of *Phytophthora* from radically disturbed areas (such as road construction and logging)?

Native or Not?

From the literature the Alliance has reviewed (much of it quite dated), it would appear that there is conjecture on whether *Phytophthora* is native or not. Shepherd (1975) suggests that *P. cinnamomi* is an ancient immigrant to Australia which entered northern Australia along with the Indo-Malayan elements of the flora. However, Brown, following analysis of species which are affected by *Phytophthora* in the Wet Tropics concluded that there is doubt as to whether or not it is native to Wet Tropics rainforest.

It would appear that this is a fundamental question. Is *P. cinnamomi* a native, in fine balance with the forest, which only causes dieback at times of drought or after radical forest disturbance when plants are stressed? Or is *P. cinnamomi* an introduced pathogen with the potential to cause significant impacts on the integrity of the Wet Tropics?

Impacts on the Integrity of the Wet Tropics

There have been numerous comments by the Wet Tropics Management Authority and others on the potential threat *P. cinnamomi* poses to the unique World Heritage values of the Wet Tropics. The actual impacts are poorly understood. The threat to communities or populations of rare and threatened species appear unknown.

"Control"

The control of *Phytophthora* in other areas of Australia would appear to be based mostly on quarantine. Indeed the closure of some roads in the Wet Tropics was proposed owing to the need to keep vehicles and ongoing roadworks away from areas.

If *P. cinnamomi* does occur in the Wet Tropics, is not native and is causing patch death (or other impacts), mechanisms which can control its spread need to be identified. However, the tourism industry has concerns with a "closure" approach to such control and would rather work with researchers to find successful hygiene techniques which stop any spread.

Conclusions and Recommendations

The Alliance for Sustainable Tourism is concerned that *P. cinnamomi* has been used as a management issue requiring the management response of closure of roads. This would cause financial hardship for individual tour operators and would result in the loss of significant presentation opportunities. Given this, the Alliance concludes that there is a need to research the fundamental questions in relation to *P. cinnamomi* and if necessary, work with researchers to develop appropriate control and/or hygiene methods to avoid its spread.

Given the dated nature of research and the significantly changed land use (a conservation regime rather than logging) the Alliance recommends that the following questions are resolved:

- Where does *P. cinnamomi* occur in the Wet Tropics?
- Is *P. cinnamomi* causing patch death?
- What (if any) other circumstances contribute to patch deaths?

- Is *P. cinnamomi* a native of the Wet Tropics forest, or is it a recently introduced pathogen?
- What are the threatening processes (and other environmental impacts) *P. cinnamomi* is the direct or indirect cause of in the Wet Tropics?
- What control mechanisms are required for sustainable vehicle use, bush walking and road maintenance practices?

4 GENERAL BIOLOGY AND ECOLOGY OF *PHYTOPHTHORA* WITH SPECIAL REFERENCE TO *PHYTOPHTHORA CINNAMOMI*

DAVID CAHILL

Characteristics of the Oomycetes

The Class Oomycetes to which *Phytophthora* belongs was traditionally included with the true fungi in the Kingdom Fungi because of their 'fungal-like' characteristics. Their close structural, biochemical and genetic affinities to the golden brown-algae (Division Chrysophyta), however, has meant a reassessment of their taxonomic placement and they are now considered with the algae and protozoa to be members of the Kingdom Protista. This recognition of the Oomycetes as a separate group of organisms distinct from the fungi has implications for the way in which we deal with them. *Phytophthora* is not a fungus and thus cannot be treated or managed using the same strategies that are normally used for fungal pathogens.

Characteristics of the genus *Phytophthora*

All described species are pathogens that attack various plant parts including leaves, flowers, stems, buds, fruits, crowns and roots. Members of the genus are responsible for wide scale economic losses in horticulture and in the ornamental, pastoral and forestry industries. In natural vegetation communities several species, especially *P. cinnamomi*, are responsible for reductions in biodiversity, dramatic floristic changes and the threat of species extinction.

Life cycle

Asexual reproduction is by the development of sporangia and/or chlamydospores, depending on the species. Sporangia are produced on sporangiophores and are variable in size and shape are usually subspherical, ovoid or pyriform and hyaline to light brown. Sporangia may germinate directly by one to several germ tubes or indirectly by undergoing zoosporogenesis to produce motile zoospores. Sporangia may be papillate, containing a mucilaginous area that allows emission of the zoospores, or non-papillate (as in *P.cinnamomi*). Biflagellate zoospores, single cells that lack a cell wall, emerge from the sporangium under appropriate conditions and may swim from several minutes to several hours until they reach a host surface where they lose their flagella, round-up and form a cell wall. Chlamydospores are spherical to ovoid, non-papillate, hyaline to deep brown thin to thick-walled terminal or intercalary structures capable of germination to form hyphae or sporangia.

Patch Deaths in Tropical Queensland Rainforests, P.Gadek (ed)
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Phytophthora species can either be homothallic (selfing) or heterothallic (outbreeding). Homothallic species are capable of forming the sexual oospore readily whereas heterothallic species such as *P. cinnamomi* require the specific interaction of two different mating types (designated as A_1 and A_2). In Australia the A_2 mating type of *P. cinnamomi* is more commonly found than the A_1 but the latter has been found in Queensland, New South Wales, Tasmania, Western Australia and the Australian Capital Territory. There is considerable variation in both genotype and virulence within Australian populations of *P. cinnamomi* but the A_2 mating type is generally considered to be the more virulent.

Sexual reproduction is by antheridial and oogonia interaction resulting in the formation of an oospore. The antheridium is usually produced as a multinucleate swollen hyphal tip cut off by a septum. It attaches firmly to the oogonium wall during early developmental stages - the antheridia may be paragynous (attached to one side of the oogonium) or as in *P. cinnamomi*, amphyginous (tightly surrounding the stalk of the oogonium). The oogonium is characteristically spherical to pyriform, smooth, hyaline to light brown and delimited from hypha by a septum. After fertilisation a single smooth, spherical hyaline to light brown oospore fills the oogonium interior. The oospore may germinate to produce hyphae or sporangia but is also capable of long-term survival (years) in the soil.

The mycelium of *Phytophthora* is hyaline, branched, coenocytic, and may become septate with age. Individual hyphae are variable in diameter, sometimes swollen, nodose or tuberculate. Certain species including *P. cinnamomi* have regularly or irregularly swollen hyphae or hyphal swellings that may be single, bunched, spherical, intercalary or terminal. *Phytophthora cinnamomi* typically has hyphal swellings and hyphae that are distinctively coralloid.

Dissemination

Of great importance for an understanding of the ability of *Phytophthora* to cause disease is the way in which the asexual and sexual structures are disseminated. Depending on the species they may be dispersed by one or several means such as the movement of sporangia by wind and rain, of zoospores by surface water and run-off and as hyphae, chlamydospores and oospores in infected plants and plant debris, seed pods and cuttings. Most commonly *Phytophthora* is dispersed in infested soil on implements, vehicles, shoes and clothing but also by animals through ingestion of infected plant parts or by transport of infested soil. The influence of animals has been demonstrated at some sites in the wet tropics where pig wallows are associated with patch death in vegetation (Pavlov *et al.* 1992). It is well known that spread of P. *cinnamomi* is greatly aided by movement of infested soil during human activity such as road making.

Diseases caused by *Phytophthora*

Of the fifty or so morphological species of *Phytophthora* described world wide twenty-two are currently recorded as causing plant disease in Australia (Cahill 1993, Irwin *et al*. 1995). In both economic and conservation terms these species are causing considerable damage and loss to our plant based industries and native vegetation. *P. cinnamomi* is the species of main concern but others including *P. nicotianae, P. megasperma, P. cryptogea* and *P. palmivora* have reasonably wide host ranges and therefore considerable impact.

How important a disease is in natural vegetation can be measured by a number of criteria (Podger *et al*. 1996). The primary criteria are 1) the direct and indirect effects on plant communities and their dependent biota, 2) the extent of areas affected, 3) the rate at which infestation increases, 4) the extent of epidemic spread of disease. Using these criteria disease caused by *P. cinnamomi* in Australia must be seen as the most damaging and significant disease of plant communities ever recorded.

P. cinnamomi is the cause of disease in a diverse range of environments throughout Australia and is the cause of disease in all states and territories. It has a particularly high impact in the heathlands and dry sclerophyll forests of southern and southwestern Australia (Weste and Marks 1987, Shearer 1994) but also in the cool temperate rainforests of Tasmania (Podger and Brown 1989). There are a very large number of plant families that are affected but species within the Epacridaceae, Fabaceae, Proteacea, Dilleniaceae, Lauraceae and the Myrtaceae are especially vulnerable to disease. Much of what we know about the biology and ecology of *Phytophthora* especially *P. cinnamomi* comes from the huge amount of research that has been conducted in Victoria and in Western Australia. From this work it is clear that the way in which *P. cinnamomi* interacts with native vegetation varies considerably between different environments. Therefore applying what we know about the biology and ecology of *P. cinnamomi* in the south of Australia to situations in the tropical north must be done with caution.

Symptomatology of disease

Phytophthora species have a limited saprophytic ability, that is they exhibit poor growth and have low competitive ability in the presence of other soil microorganisms. They are primary rather than secondary invaders that attack only healthy, intact plant tissues or freshly made wounds and do not invade tissue previously invaded by other microorganisms. They may attack the roots and collar region of woody trees months to years before foliar symptoms are observed and therefore the disease may not even be suspected unless proper and detailed isolation assays are conducted. It is important to note that in extensive surveys conducted in the Wet Tropics *P. cinnamomi* was isolated frequently from apparently healthy vegetation (Gadek 1997). It is imperative that the absence of disease in vegetation where *P. cinnamomi* is present be confirmed. There are several possibilities that need to be tested further: *P. cinnamomi* may be endemic to the Wet Tropics, the vegetation may consist primarily of resistant species and environmental conditions may be unfavourable for disease development.

Interactions of *Phytophthora* species with their plant hosts range from those that involve host-specific, gene-for-gene interactions to those in which there are interactions with a broad host range. Symptoms of disease vary widely depending on the species of *Phytophthora*, the host and prevailing environmental conditions. In host-specific interactions incompatible responses are characterised by the rapid, hypersensitive death of host cells and the containment of pathogen growth. Pathogen containment or limitation of growth is also a feature of the more common polygenic resistance. In susceptible hosts rotting and necrotic lesion formation in roots is a common symptom but in addition there may also be lesion formation and destruction of above ground parts including fruit. Zoospores are attracted chemotactically to the root surface and adhere preferentially to the unsuberised tissues of the zone of elongation close to the root tip.

Zoospores may also encyst at the junctions of tap and lateral roots, or around subterranean stomata. Where surface water accumulates there is often stem or hypocotyl invasion with subsequent lesion development and stem girdling (Irwin *et al*. 1995, O'Gara *et al*. 1996).

There is a considerable body of information that demonstrates clear and substantial differences between the susceptible and resistant reactions of various plants to *Phytophthora*. For *P. cinnamomi* the physiological, biochemical and anatomical responses of plants to infection are reasonably well documented. For example we know that in resistant reactions there are anatomical changes that include deposition of lignin in host cell walls and production of callose that impedes pathogen growth (Cahill *et al.* 1989). We also know that in resistant hosts there is activation of secondary metabolic pathways that lead to the production of specific phenolics (including lignin) (Cahill *et al.* 1993). In susceptible plants cell walls and membranes are broken down and hormone synthesis and transport is affected. There is a decrease in root hydraulic conductivity and xylem vessels may become occluded leading to reduced water and mineral uptake (Dawson and Weste 1984).

Usually the first indication that *P. cinnamomi* is present and causing disease in native vegetation is the browning and chlorosis (yellowing) of foliage followed soon after by the death of species from susceptible plant families. Highly susceptible species such as *Xanthorrhoea australis* and *Isopogon certatophyllus* in Victorian dry sclerophyll forests and *Banksia grandis* in the jarrah forest of Western Australia are usually the first species to die. On sites that are favourable to disease development a line of dead and dying understorey species delineates a disease margin or infection front at the boundary of infested and non-infested sites. On less favourable sites such as those that are free draining there may be a mosaic of diseased plants with apparently healthy plants with no clear demarcation between infested and non-infested areas. Disease is more severe on shallow poorly drained soils with low densities of antagonistic soil microorganisms. In contrast disease is suppressed on nutrient rich, highly organic soils with high levels of soil microorganisms. Flat to undulating topography may promote disease and there are strong correlations between disease, slope, depth to impeding layer and hydrologically important features such as soil texture and bulk density (Marks and Smith 1991). *P. cinnamomi* can be isolated from most soil types over a wide pH range.

It is apparent however that the disease caused by *P. cinnamomi* in native vegetation is much more complex than just outlined. There are at least three major disease syndromes that can be described and attributed to infection by *P. cinnamomi* (Podger *et al.* 1996). In southern Australia the diseases can be classified as: 1) disease of high impact on many susceptible species irrespective of site characteristics and is readily observable, 2) disease that causes mass collapse at sites where there is complete mortality in overstorey and understorey vegetation and is site responsive, 3) disease where forest is replaced by resistant/tolerant species but the pathogen is still present and able to cause disease sporadically depending on rainfall events. In this final disease type the pathogen acts almost as if it is endemic. Long-term studies in Victoria (over 30 years) have shown that there is progressive reduction in susceptible hosts, survival of resistant and partly resistant species and eventually partial regeneration of some susceptible species (Weste and Ashton 1994).

Conditions conducive to disease

Phytophthora species have life cycles, reproductive structures and propagules that enable them to reproduce and be disseminated, and remain viable, under a diverse range of environmental conditions. While hyphae of *P. cinnamomi* are known to be agents of disease through close root contact from plant to plant it is the motile zoospore that is the main dispersive propagule. Chlamydospores, with their thick walls and lipid reserves are the principal long-term survival structures. Whether within host plant tissue or free in the soil, under the right conditions they will germinate, produce sporangia and hyphae and the next generation. The ability to isolate *P. cinnamomi* from soil and plant parts is dependent essentially on environmental factors. It is commonly found that *P. cinnamomi* is not easily isolated from soil during the dry summer months in southern Australia or during long rain-free periods. Optimal soil moisture content for sporangial production is at field capacity or saturation and free flowing surface or subsurface water is required for long distance dispersal of zoospores of *P. cinnamomi*. Zoospores released from sporangia on infected roots are capable of downslope and lateral movements in water at considerable depths (Shearer and Tippett 1989). In low-lying areas waterlogging of root systems may predispose plants to infection (Davison 1994). The minimum temperature for growth of *P. cinnamomi* is 5- 6° C, optimum (for both hyphal growth and sporangial production) between 24 and 28° C and maximum 32 to 34° C (Erwin and Ribeiro, 1996). Temperatures outside the optimal range are likely to be inhibitory to sporangial and zoospore production. Rainfall and temperature are not likely to be as important as determinative factors of disease in tropical rainforests as they are in the southern regions of Australia.

Medium to long term consequences of the disease caused by P. cinnamomi

Detailed studies in Victoria have shown that disease caused by *P. cinnamomi* has permanent and severe effects on the structure and floristics of a range of plant communities (Weste 1994). Similarly severe and permanent impacts have been recorded in Tasmania (Podger and Brown 1989) and in Western Australia (Shearer and Dillon 1996, Wills 1993). Until the full distribution and extent of damage caused by *P. cinnamomi* in tropical vegetation communities is assessed it is difficult to predict what the long-term outcomes may be. It is, however, already established that several rare plant species are under threat at Mt Lewis (Gadek 1997). In Western Australia a number of species that are endemic are threatened with extinction. In all these areas there is the potential for significant loss of biodiversity through changes in community structure favouring resistant species and in the extinction of local populations of numerous species and the subsequent loss of genetic diversity (Keighery et al. 1994 There is likely to be the extinction of many rare and geographically restricted susceptible species and the loss of animals that rely on intact vegetation as habitat (Newell and Wilson 1993). There will be severe genetic depletion of wide spread susceptible taxa and a loss of conservation values will have consequences for the public use of land and for tourism.

Tackling the complexity of disease caused by *P. cinnamomi*

While we clearly have a mammoth task in attempting to control *P. cinnamomi* in native vegetation there are avenues of approach that will provide important information for future management. It is imperative that we know the distribution of *P. cinnamomi* in threatened vegetation communities and also the distribution of elements that are as yet not infested. We need to know also the factors that combined, determine the disease risk to particular

communities and those species within threatened communities that are at most risk. Current strategies that include Geographical Information System (GIS) analysis such as has been developed in Western Australia (R. Wills *pers. comm*.) and in Victoria (Wilson *et al.* 1997) seem to be valuable approaches that utilise existing ecological, floristic, geographical and vegetation community data. Revegetation strategies for already degraded and damaged sites need to incorporate a multi-component approach that includes knowledge of the basic biology and ecology of the pathogen, GIS and perhaps selective use of systemic fungicides and natural plant resistance.

5 CELL BIOLOGY OF *PHYTOPHTHORA CINNAMOMI*

ADRIENNE HARDHAM

Life cycle of *Phytophthora cinnamomi*

Phytophthora cinnamomi belongs to the Oomycetes, a class of organisms quite distinct from any other. Throughout most of their life-cycle, Oomycetes grow as fungus-like hyphae in soil, water or an infected host. The hyphae are long, thread-like structures, about 5-10 μm in diameter. As well as looking like fungi, the Oomycetes have an absorptive mode of nutrient acquisition, however, they are not true fungi. A range of structural, biochemical and molecular characteristics indicate that the Oomycetes are more closely related to the Chrysophyte algae, than they are to the true fungi. One of their main distinguishing features is the production of biflagellate asexual spores called zoospores, a feature which is extremely important in terms of their rapid dissemination and spread of disease.

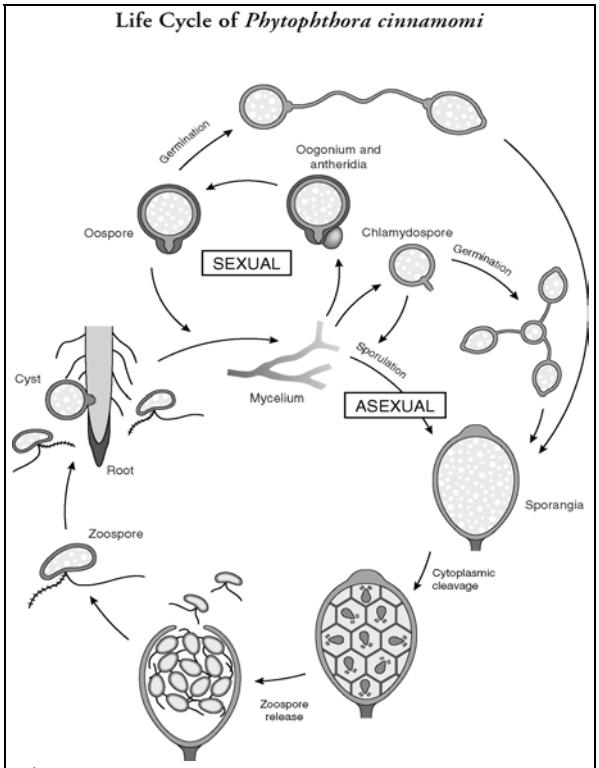


Fig. 1

Figure 1 shows a diagrammatic summary of the life cycle of species of *Phytophthora*. Under certain conditions, including reduction in the levels of available nutrients, vegetative hyphae enter the asexual sporulation phase. In this process, multinucleate sporangia form at the hyphal apices.

Sporangia (Fig. 2 left) are about 20-50 μm in diameter and, when mature, are separated from the cytoplasm of the subtending hypha by a basal septum. Sporangia may re- main in this state for several days and then given an appropriate signal, such as a drop in temperature, they rapidly subdivide to form uninucleate zoo spores (Fig. 2 centre) which are released through an apical pore in the sporangium (Fig. 2 right).

Zoospores are motile, moving at speeds of 100-200 μm/sec. They may swim for hours or even days without the need for exogenous nutrients. They are chemo- tactically attracted to the roots of potential host plants. They swim up to the root, and encyst at the root surface. The process of encystment involves loss of motility through the detachment of the two flagella, secretion of material including an adhesive which glues the spores to the root surface, and, after about 5 minutes, the formation of a cellulosic cell wall. Cysts of *P. cinnamomi* germinate about 20-30 minutes after encystment (Fig. 3).

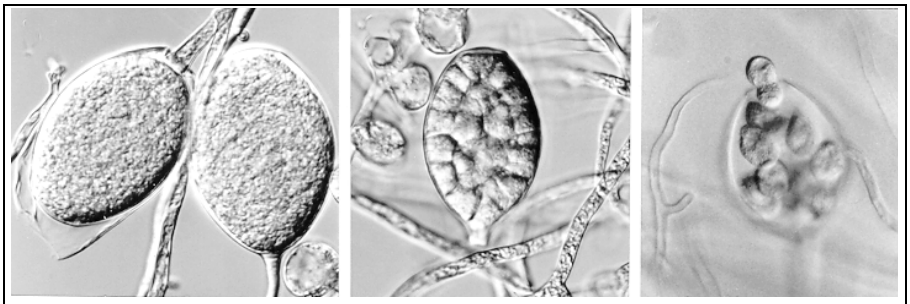


Fig. 2 Mature (left) and cleaving (centre) sporangia, and zoospore release (right) in *P. cinnamomi*.

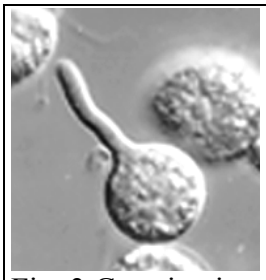


Fig. 3 Germinating cyst of *P. cinnamomi*

The germ tubes can grow for about an hour in the absence of exogenous nutrients. In the vicinity of a root, they grow chemotropically towards the root, penetrating the root surface between the epidermal cells. Two to three days after the onset of infection, the pathogen can sporulate again, forming sporangia on the surface of the root and releasing more zoospores into the medium surrounding the root. In this way, the inoculum can be rapidly amplified.

Vegetative hyphae can also form another type of asexual spore, called chlamydospores. These are approximately spherical, multinucleate cells that serve as resistant, resting spores that can survive adverse conditions for up to several years. When favourable conditions return, the chlamydospores germinate, producing hyphae or sporangia.

The sexual phase of the life cycle of *P. cinnamomi* occurs much less frequently than the asexual cycle. *P. cinnamomi* is normally heterothallic and has A_1 and A_2 mating types. Oogonia and antheridia, the only cells of *Phytophthora* that are haploid, may develop when the two mating types come together, but selfing can be induced by the presence of several stimuli, for example, compounds exuded by avocado roots. Fertilisation results in the formation of oospores, highly resistant cells which can remain viable for long periods of time. In laboratory conditions, it is difficult to get oospores of *P. cinnamomi* to germinate.

Zoospore and cyst structure and function

Phytophthora zoospores are wall-less cells and thus their outer surface is that of the plasma membrane. They are ovoid in shape, with a longitudinal groove along what is known as the ventral surface (Fig. 4). The two flagella emerge from the centre of the groove. The circular depression visible at the anterior of the zoospore in Figure 4 is a water expulsion vacuole.

Because zoospores do not have a cell wall, they cannot build up turgor pressure, and thus water continually enters the cell across the plasma membrane. In order to maintain cell volume and osmoregulation the zoospores use the water expulsion vacuole to pump water out of the cell, cycling every 6 seconds or so.

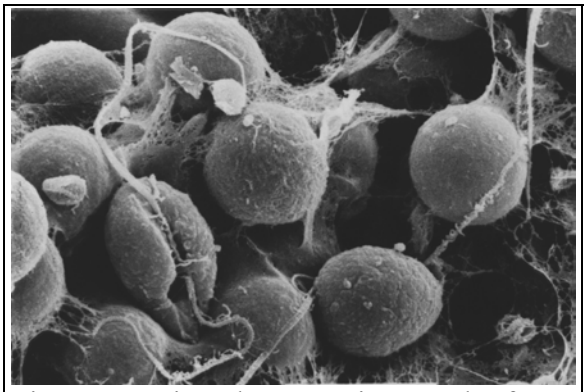


Fig. 4 Scanning electron micrograph of *P. cinnamomi* zoospore and cysts on a root surface

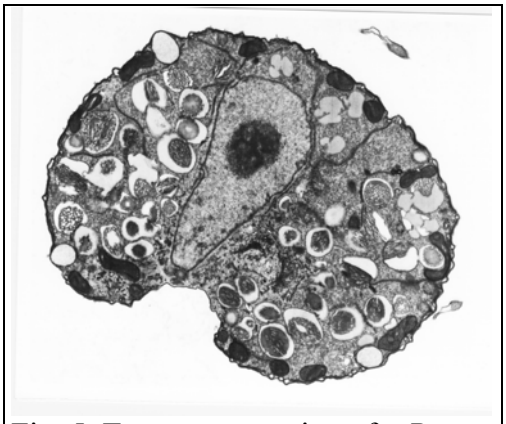


Fig. 5 Transverse section of a *P. cinnamomi* zoospore

Internally, the zoospore cytoplasm is highly structured and displays a very precise architecture (Fig. 5). The nucleus is prominent and pear-shaped, coming to a point at the two basal bodies from which the flagella are formed. ;The cytoplasm is packed with vesicles of different types. The central cytoplasm is filled with so-called fingerprint vesicles which contain mycolaminarins, a form of β 1,3 glucan thought to function in carbohydrate storage. The peripheral cytoplasm contains three different types of vesicles. Some are about 800 nm in diameter and are called large peripheral vesicles; others are about 400 nm in diameter and are of two types called dorsal and ventral vesicles because they occur on the dorsal and ventral surfaces respectively. Mitochondria also occur in the peripheral cytoplasm.

Zoospores swim through the action of the two flagella. The anterior flagellum, which projects forwards, is primarily responsible for forward movement. A sinusiodal wave is generated at the base of the flagellum, where it emerges from the cell, and propagates to its tip. This wave propagation would be expected to propel the zoospores backwards, however, the anterior flagellum is covered by two rows of tubular hairs called mastigonemes which project out at right angles to the flagellar surface. The hairs can be seen using an electron microscope or by labelling them with an antibody that is specific for the protein from which the wall of the tubular hair is built (Fig. 6). As the anterior flagellum beats, the mastigonemes are swept backwards through the medium,

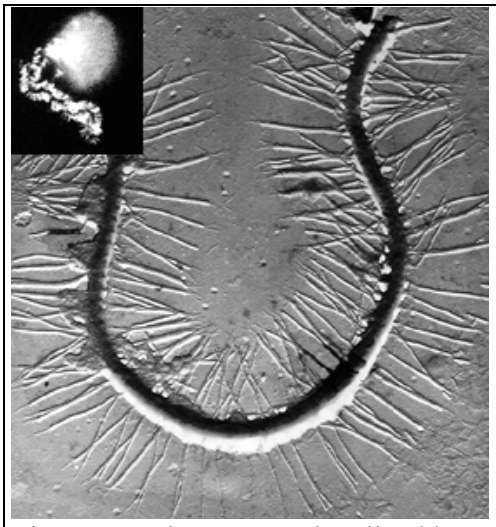


Fig. 6 Mastigonemes visualised by electron microscopy and immunolabelling (inset).

thus propelling the cell forwards. The posterior flagellum does not appear to actively participate in forward movement, but is used rather like a rudder to turn the cell as it swims.

A number of dramatic changes occur when the zoospores encyst. The flagella are detached and thus the cysts are not motile. The cysts are spherical in shape (Fig. 7) and are surrounded by a cell wall that rapidly becomes strong enough to allow turgor pressure to build up in cysts. This means that the water expulsion vacuole is no longer needed and disappears from the cells. During encystment, changes also occur in the composition and organisation of the spore cytoplasm. The nucleus and associated basal bodies move away from the plasma membrane, and the contents of the dorsal and ventral vesicles are secreted onto the cyst surface. The large peripheral vesicles are not secreted but move away from the cell cortex and become randomly distributed throughout the cyst cytoplasm.

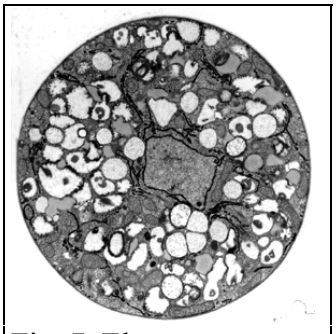


Fig. 7 Electron micrograph of a *P. cinnamomi* cyst

Within the first two minutes after the zoospores begin to encyst, they secrete adhesive material that sticks them to the adjacent substratum, such as a root of a potential host plant. The adhesive can be visualised by immunolabelling with an antibody specific for the adhesive protein (Fig. 8). Labelling of zoospores with this antibody reveals that the adhesive is stored within the ventral vesicles that lie on either side of the groove (Fig. 8 inset). This means that the zoospores must adopt a particular orientation with respect to the root before they enycst, i.e. they must orient their ventral surface towards the root so that the adhesive material in the ventral vesicles is released onto the root surface.

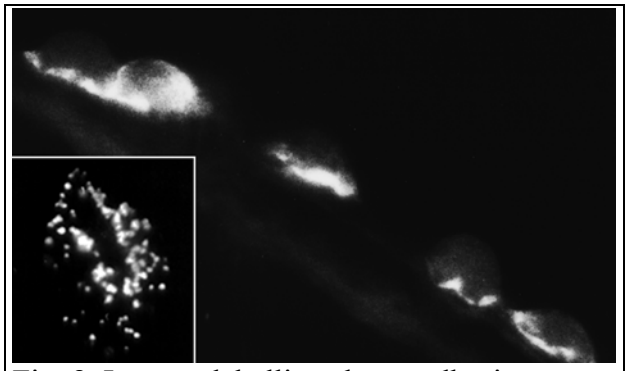


Fig. 8 Immunolabelling shows adhesive material between cysts and the root and in zoospore ventral vesicles (inset)

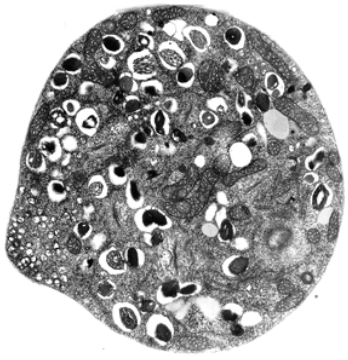


Fig. 9 Electron micrograph of a germinating cyst of *P. cinnamomi*

Cysts germinate from a point on the ventral surface. The tip of the emerging germ tube is marked by an accumulation of small apical vesicles (Fig. 9). Germination of *P. cinnamomi* cysts can occur in water and the germ tube can grow for about an hour or more in the absence of any external nutrients before extension ceases. During this time, the large peripheral vesicles that had become randomly distributed within the cysts, are degraded. The large peripheral vesicles contain high molecular weight glycoproteins and it is thus likely that they serve as stores of protein for use during the early stages of germling growth, before the pathogen has been able to tap into the nutrient supplies within the plant.

Zoospore formation

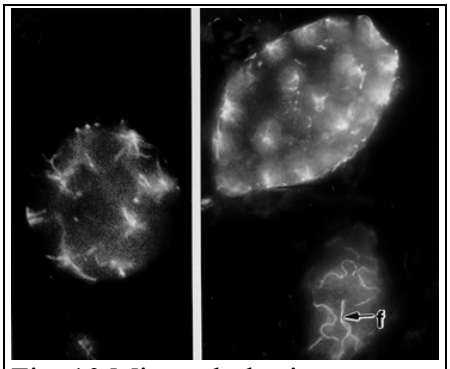


Fig. 10 Microtubules in mature (left) and cleaving (right) sporangia

Structural and immunocytochemical studies have shown that many zoospore components are not present in vegetative hyphae and are synthesised after the induction of sporulation. The large peripheral, ventral and dorsal vesicles appear in hyphae about 5-6 hours after sporulation is induced, as do packets of mastigonemes destined for the anterior flagellum. These organelles are randomly distributed within the cytoplasm of the hyphae, and in developing and mature sporangia. During zoospore formation, the sporangial cytoplasm becomes subdivided by sheets of membranes that extend between the nuclei and which will become the plasma membrane of the zoospores. Spatial regulation of the cleavage planes is controlled by cytoskeletal elements within the cytoplasm - microtubules (Fig. 10) and microfilaments. The microtubules radiate from the apex of each nucleus, and adjacent arrays interact and guide the developing cleavage planes. Microtubules are also responsible for the correct allocation of organelles to each zoospore during cleavage. During the subdivision process, the peripheral vesicles and mitochondria are transported into the cytoplasm below the zoospore plasma membrane which is forming. This transport is very precisely controlled because the large peripheral and dorsal vesicles are transported to the dorsal surface while the ventral vesicles are moved to the ventral surface. Microtubules are needed for this sorting to be achieved. During cleavage, the flagella form from the basal bodies associated with the apex of each nucleus and the water expulsion vacuoles also develop within the anterior cytoplasm of each zoospore.

Zoospores and the infection strategy of *P. cinnamomi*

The infection strategy of *P. cinnamomi* centres on the production of vast numbers of motile zoospores which can actively swim to the surface of a potential host plant or which, either as zoospores or cysts, can be transported long distances in moving water or in moist soil. In the presence of abundant nutrient supplies, *P. cinnamomi* will grow as vegetative hyphae but the organism seems always to be poised to sporulate, producing sporangia within 6-7 hours after a decrease in available nutrients. Zoospores contain ample supplies of nutrients - proteins, carbohydrates and lipids- to support long periods of motility, and several hours of germling growth after encystment. Recent immunocytochemical and molecular studies are beginning to yield information on the control of gene expresssion and protein synthesis that takes place during zoosporogenesis. Cell biological studies are also helping elucidate the nature and role of the precise architecture of the zoospore cytoplasm. There seems little doubt that the more detailed understanding of the molecular and cellular requirements of sporulation and zoospore function that is emerging will provide an invaluable basis for the development of novel means of controlling this destructive pathogen.

6 NATURE AND EFFECT OF *PHYTOPHTHORA* IN HORTICULTURE

DAVID GUEST

Significance of *Phytophthora* in horticulture

Oomycetes have a special place in the development of the science of Plant Pathology. The potato late blight epidemic of 1854-57 and the outbreaks of the grapevine downy mildew stimulated investigations into the aetiology of these diseases, and the identification of *Phytophthora infestans* and *Plasmopara viticola* as the causal pathogens of these two diseases preceded Pasteur's refutation of abiogenesis. These catastrophes also resulted in the development of copper-based fungicides, still in use today. Despite 150 years of research, *Phytophthora* diseases still cause significant losses to agriculture, horticulture and natural ecosystems.

Horticulture involves the cultivation of orchards of genetically similar, frequently clonal, planting material, usually in monoculture. Given favourable environmental conditions, these conditions increase the risk of epiphytotics–such as late blight of potato during the 1850s and grapevine mildew in the 1860s in Europe, and more recently, southern corn leaf blight in the early 1970s in the United States and witches' broom of cocoa in South America in the 1990s. However, genetically uniform monocultures are not essential for epiphytotics–dieback in dry sclerophyll forests of southern Australia affects genetically diverse communities.

Table 1 indicates the range of symptoms caused by *Phytophthora* in horticulturally-important plants. For many crops diseases caused by *Phytophthora* are the major limitation to improved productivity, and in some cases inadequate control measures make horticulture unviable. The scale of losses can be immense–estimates of the yield losses to the cocoa industry because of *P. palmivora* diseases range from 10-30% (1996 production was 2.8 million tonnes@$1,500/t)–costing growers $500-$1,500US million annually. Similarly, annual losses to the durian industry due to the same pathogen cost an estimated $600US million, and to the avocado industry *P. cinnamomi* causes estimated annual losses of $30US million in the US alone. Losses to natural ecosystems are impossible to quantify.

In horticulture *Phytophthora* species are responsible for major diseases in temperate, subtropical and tropical horticulture (Table 1). All parts of host plants are attacked–roots, stems, leaves, flowers and fruits, and many plants are susceptible to more than one species. Within the genus are examples of most modes of pathogenesis, and interesting trends are apparent with respect to host specificity, modes of parasitism and pathogen ecology (Table 2). *Phytophthora* species occur in most environments, including estuarine and marine environments. There is host specialisation within some species–for example cocoa isolates of

Patch Deaths in Tropical Queensland Rainforests, P. Gadek (ed)
Report, Rainforest Cooperative Research Centre, Cairns, 1999

P. palmivora are not aggressive on coconut, durian or paw paw. This complicates disease management in mixed cropping systems. The significance of host specialisation in undisturbed communities is not clear–there appears to be little or no host specialisation in *P. cinnamomi* from dry sclerophyll forests, but what happens to polyphagous species like *P. cinnamomi* after a few years in avocado orchards? There is evidence that *P. nicotianae* occurs naturally on a range of solanaceous hosts in north Queensland, but some isolates have become adapted to tobacco after several decades of tobacco monoculture on the Atherton Tableland.

Table 1. Some horticulturally important species of *Phytophthora*

Species	**Host**	**Disease**
P. boehmeriae	citrus	brown rot
P. botryosa	cocoa, rubber	leaf fall, pod rot
P. cactorum	***>200 spp. including apple, pear, maple, walnut, strawberry, gensing***	***root & collar rots, fruit rots, cankers, blights and wilts***
P. cambivora	~30 spp. including chestnut, apple, avocado, almond, rhododendron	root and collar rots
P. capsici	~50 spp. including cocoa, macadamia, avocado, vanilla	root rots, damping off, fruit rots
P. cinnamomi	***>1,000 spp. including avocado, pineapple, chestnut, rhododenron, eucalypts, pines, Prunus*, oak, kiwi, Proteaceae, Ericaceae**	***root & collar rots***
P. citricola	~100 spp. including kiwi, azalea, rhododendron, citrus, Proteaceae, rubber, apple, guava, peach, grape	canker, root & collar rot, blight
P. citrophthora	>100 spp. including citrus, cocoa, rubber and a wide range of tropical and temperate fruits	crown rot, gummosis, root rot, fruit rot, blight, damping off
P. cryptogea/ P. drechsleri	>150 spp. from 40 families, including banksias, grevilleas, bottlebrushes, ornamentals and trees	foot, root, crown and stem rots
P. heveae	Rubber, coconut, cocoa, avocado	pod rot and canker
P. megasperma	>50 spp. including fruit and vegetable crops, banksias, *Dryandra*, cocoa	root, crown and stem rots
P. nicotianae/ P. parasitica	***>400 spp. including tobacco, tomato, pineapple, citrus, banksias, pawpaw, orchids, palms, grevilleas, hibiscus, passionfruit, carnation, cotton***	***collar and stem rots, leaf blights, fruit rots***
P. palmivora	***>200 spp. including cocoa, palms, durian, rubber, macadamia, mango, pawpaw, breadfruit, orchids, citrus***	***fruit rots, leaf blights, canker, bud and root rots***
P. syringae	~30 spp. including citrus, apple, lilac	collar and fruit rot, canker, blight and dieback

Table 2. Evolutionary trends within the genus *Phytophthora*

	Host range	**Parasitism**	**Ecology**
P. cinnamomi	wide	necrotroph	root pathogen
	ॐ	ॐ	ॐ
P. citrophthora	ॐ	ॐ	ॐ
P. nicotianae	ॐ	ॐ	ॐ
P. palmivora	ॐ	ॐ	ॐ
P. infestans	narrow	biotroph	aerial pathogen

The basis of pathogenicity of *Phytophthora* spp. is complex. Symptoms are caused by the effects of parasitism and resulting necrosis, but more subtle effects result from disturbances to hormonal balance, the release of elicitins, enzymes and perhaps toxins.

Most species of *Phytophthora* are poor saprophytic competitors. Experiments in our group have shown that *P. palmivora* can no longer be isolated from infected cocoa tissue after eight months in the litter layer on the soil surface, but may survive for longer periods as a more or less dormant epiphyte living on cracks in the bark. However, *P. cinnamomi* can survive in the soil and infected debris up to six years.

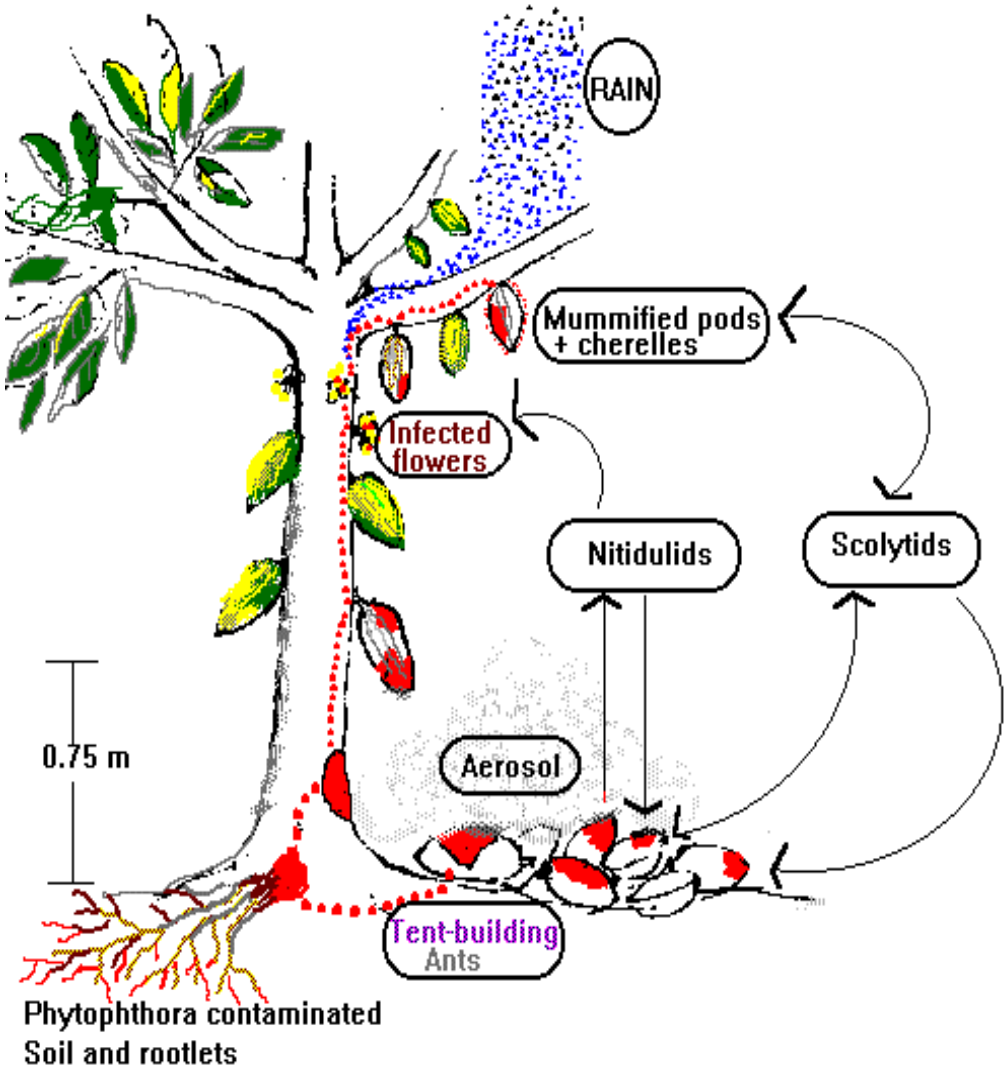
Although the life cycles of *Phytophthora* species are similar, their disease cycles on different hosts are diverse. *P. cinnamomi* is essentially a soil-borne pathogen that survives in infected roots as mycelium or chlamydospores. Upon the return of favourable environmental conditions (soil temperatures above 12^{o}, temporary flooding) sporangia release zoospores that swim through the soil water or are carried by surface floodwaters to new hosts. The most important factor in disease dissemination is human activity, either through the movement of infected plant material or the movement of infested soil or gravel, typically during roadworks. Disease sometimes progresses in a front through susceptible plant communities, although plant deaths are often patchy. Long-term observations indicate that susceptible species sometimes recolonise diseased-affected sites. Further studies are underway to determine if this results from disease escape, or whether there is a long-term decline in the population or virulence of the pathogen following the death of susceptible species, or whether there is a change in the resistance of host species due to pathogen-directed selection. These studies may lead to the development of management practices that promote recovery, and prevent a recurrence, of an epiphytotic, but require a long-term investment of funds and research effort. We are fortunate that the severity of dieback in the jarrah forests of West Australia and the dry sclerophyll in Victoria prompted relatively intense and sustained research into dieback over the past thirty years.

In contrast to *P. cinnamomi*, *P. palmivora* affects all parts of host plants, and is naturally disseminated as both zoospores and sporangia. A number of new dimensions are apparent in the disease cycle of *P. palmivora* on cocoa in Papua New Guinea (Figure 1). The dissemination of sporangia facilitates the movement of the pathogen between the soil and the canopy, enabling the pathogen to infect aerial as well as below-ground parts of the host. Flying nitidulid and scolytid beetles carry viable sporangia from their breeding sites in infected pod cases lying on the soil surface to flowercushions and pods. They rapidly colonise *Phytophthora*-infected pods, and their frass is rich in viable progaules. Tent-building ants build their tunnels using soil contaminated with the pathogen.

Pod rot commonly begins at the point of contact between the pod and an ant tent. *P. palmivora* survives not only in infected root tissue in the soil, but also in infected pod mummies, stem cankers and flower cushions and as an epiphyte living in cracks in the surface of the bark. Consequently, upon the commencement of the wet season primary inoculum emerges from several sources in the soil and in the canopy.

A complete appreciation of the disease cycle of the host/pathogen system under study is essential to the development of management strategies, but once again requires a sustained research effort.

Figure 1 Disease cycle of Phytophthora palmivora on cocoa in Papua New Guinea (Konan, Dennis and Guest, unpublished)



Disease management in horticulture

Horticulturalists have several weapons for managing *Phytophthora* at their disposal, however to be effective, viable and sustainable the key is to use these weapons strategically. An appreciation that an epiphytotic caused by *Phytophthora* requires a source of primary inoculum, susceptible host plants, warm temperatures, high humidity and temporary flooding invites an integrated disease management approach.This may involve:

- quarantine exclusion, where possible
- planting of resistant planting material or rootstocks, where available
- manipulation of the orchard environment to favour the host over the pathogen. For example, it is possible to improve soil drainage to minimise temporary flooding; to improve soil fertility to stimulate plant growth; to reduce levels of primary inoculum by adding organic matter to stimulate antagonists, predators, hyperparasites and competitors in the soil; to reduce secondary inoculum in the orchard canopy by increasing tree

spacing, regular pruning and harvesting
- orchard hygiene to reduce pathogen spread
- fungicide applications.

Successful examples of disease management in horticulture include the integrated management of *Phytophthora cinnamomi* on avocado in Australia using resistant, disease-free rootstocks, mulching and phosphonate trunk injections. An integrated management strategy for *P. palmivora* on cocoa in PNG has been developed, based on a thorough understanding of the disease cycle.

In the absence of disease-resistant planting material, disease management involves the use of mulches and ground cover to restrict the movement of flying beetles from inoculum reservoirs on infected pod cases lying on the soil surface, as well as increasing the activity of soil microbes, including antagonists; regular pruning to increase ventilation and reduce canopy humidity, thus reducing sporulation; regular harvesting to remove infected pods and secondary inoculum, and annual injections of phosphonate. In experiments in a range of environments in PNG, the incidence of pod yield losses due to *Phytophthora* has been decreased from around 30% to less than 5%. A cost-benefit analysis of annual phosphonate trunk injections as part of an integrated management strategy for *P. palmivora* diseases of cocoa in Papua New Guinea over 1990-91 showed a net benefit of $US586/ha, compared to the use of regular metalaxyl and copper oxychloride sprays, which resulted in a net loss of $US208/ha. Coincidentally, the adoption of trunk injections of phosphonate in place of regular fungicide sprays has reduced environmental pollution.

We have also found that plant deaths due to *P. cinnamomi* root rot are significantly reduced in soils amended with composted chicken manure (Table 3). While soil drainage and plant vigour is improved following amendment with manure composts, we found that disease control was primarily due to the stimulation of antagonistic endospore-forming bacteria and actinomycetes in amended soils (Table 4).

Table 3. Effect of incorporating composted animal manures into *Phytophthora cinnamomi*-infested potting mix on the survival of *Lupinus albus* seedlings. Manures (15% v/v) were incorporated in to potting mix and pre-composted for five weeks before inoculating with *P. cinnamomi*. Three day-old lupin seedlings were planted **two weeks** later, grown for two weeks, removed. Soil in the pots was maintained at field capacity, then replanted with three day-old lupin seedlings for a further eight weeks (i.e. **ten weeks** after inoculation with *P. cinnamomi*). The data indicates percent survival of thirty seedlings for each treatment. Stars (*) indicate that mean percentage survival is significantly greater than unamended control, as determined by logistic regression analysis of percent survival against composted manure amendments ($\alpha<0.05$). (Source: Aryantha & Guest, unpublished)

Compost	**Percent survival of lupin seedlings**		
	2 weeks	10 weeks	mean
No manure	28	57	**42.5**
Chicken manure	45	97	**71.0***
Cow manure	32	82	**57.0***
Horse manure	13	58	**35.5**
Sheep manure	28	52	**40.0**

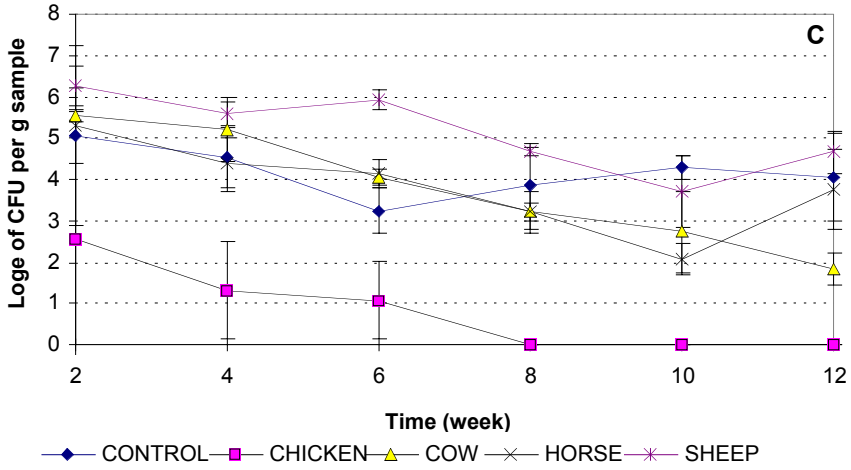
Our hypothesis is that composted manures (chicken, cow, sheep or horse) improve soil drainage and nutrition, and stimulate soil biological activity in general (thus the saprophytic competition faced by the pathogen), but that the suppression of *P. cinnamomi* is due to direct antagonism that is specifically stimulated by chicken manure, but not sheep, cattle or horse manure, compost.

Table 4. Logistic regression analysis of the correlation between the chemical and biological characteristics of composted chicken, cow, sheep and horse manure amended soils and the incidence of root rot of lupin seedlings caused by *P. cinnamomi*. (Source: Aryantha & Guest, unpublished)

Parameter	p value	Significant effect on disease incidence (a=0.05)
pH	0.265	No
Organic matter	0.000	Yes
Total microbial activity	0.000	Yes
Actinomycetes	0.000	Yes
Endospore-forming bacteria	0.000	Yes
Fluorescent pseudomonads	0.201	No
Total fungi	0.261	No

Whereas *P. cinnamomi* could be recovered from unamended soils after 12 months, it was not detected in chicken manure-composted soils after 2 months (Figure 2). Mixed formulations of antagonists isolated from composts have a similar activity in pot and field trials, and the durability of their antagonism is enhanced when added together with compost, as this presumably provides a substrate for their saprophytic growth. Phosphonate, applied as soil drenches or foliar sprays, do not suppress populations of *Phytophthora cinnamomi* in the soil, and reduce disease through their effects on the ability of the pathogen to infect and colonise host tissues.

Figure 2. Recovery of *P. cinnamomi* from soil amended with composted chicken, cow, horse and sheep manure. Soils were amended five weeks before inoculation with autoclaved wheat grains colonised by *P. cinnamomi*. The initial population in each treatment (0 weeks) was approximately $\log_e$ 6.0 CFU/g. Populations of *P. cinnamomi* were estimated by soil dilution plating onto PCH medium. (Source: Aryantha & Guest, unpublished)



One problem with the use of composts in the control of *Phytophthora* diseases in horticultural crops is that many plants, especially members of the family Proteaceae, are sensitive to high levels of soil phosphorus. We are investigating the use of reduced levels of compost in combination with phosphonate applications in two phosphorus-sensitive species of *Banksia*.

Challenges for *Phytophthora* researchers

Diseases caused by *Phytophthora* will continue to cause serious losses in horticulture, and to the natural environment. New confrontations or disturbances to existing delicately-balanced ecosystems pose the greatest threats. I conclude that the priorities for future research should include studies that aim to:

- Improve our understanding of the biological basis of host range determination and disease resistance
- Describe the biogeography of *Phytophthora* and use this information to estimate risk
- Understand and predict the population dynamics of *Phytophthora* in plant communities
- Understand disease dynamics in affected communities
- Design strategies to promote the regeneration of affected communities
- Design strategies to protect endangered communities
- Predict the effect of climate change on *Phytophthora* diseases.

7 OCCURRENCE AND IMPACT OF *PHYTOPHTHORA CINNAMOMI* AND OTHER *PHYTOPHTHORA* SPECIES IN RAINFORESTS OF THE WET TROPICS WORLD HERITAGE AREA, AND OF THE MAKAY REGION, QLD

BRUCE BROWN

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Abstract

The fungus *Phytophthora cinnamomi*, which was almost certainly present in Queensland before 1887, was detected in mid July and August 1975 from soil samples collected under dead rainforest at Dalrymple Heights on the Eungella Tableland (west of Mackay) and at Garrawalt (northwest of Ingham). Subsequent studies showed that, at those two localities, *P. cinnamomi* was associated with serious disease in both logged and virgin tropical rainforest. A soil-sampling survey showed *P. cinnamomi* to be widespread, but not ubiquitous, through tropical rainforests of Queensland between 16º 2' S and 21º 15' S latitudes. Although small areas of rainforest patch death were located elsewhere during the survey, it was only at Garrawalt and Dalrymple Heights that serious and extensive disease was found. The problem was particularly severe at Dalrymple Heights where about 20 percent of virgin rainforest in a part of the Eungella National Park was dead by 1980. In rainforest areas where the effect of logging and the influence of feral pigs (*Sus scrofa*) could be separated, there was evidence that both played a role in the dissemination of *P. cinnamomi*.

Patch Deaths in Tropical Queensland Rainforests, P. Gadek (ed)
Report, Rainforest Cooperative Research Centre, Cairns, 1999

During the survey nearly 13,500 isolates of *Phytophthora* were detected, nearly 86 percent being *P. cinnamomi*. The mating types were determined for nearly 40 percent of the *P. cinnamomi* isolates, and there were only 16 of the A_1 type compared to 4,413 of the A_2 type. Those A_1 type isolates were from virgin rainforest at only four sites, two on Mount Windsor, and the others in the Kuranda and Bartle Frere areas. Among the other *Phytophthora* taxa, all of which were in considerably lower numbers than *P. cinnamomi*, the most frequent was *P. heveae*. This species was also found to be widespread through the tropical rainforests of Queensland.

There were almost 200 tree species, often in low numbers, identified in a number of rainforest plots established to study the impact of the disease. Within the species present in reasonable numbers, losses were high in *Polyosma alangiacea* (Escalloniaceae), *Melicope fareana* (Rutaceae), *Carnarvonia araliifolia* (Proteaceae), *Alphitonia petriei* (Rhamnaceae), *Acronychia vestita* (Rutaceae), *Cinnamomum oliveri* (Lauraceae), and *Cryptocarya cinnamomifolia* (Lauraceae). A number of tropical rainforest species from Queensland were added to the list of confirmed hosts of *P. cinnamomi* by isolations from field and/or inoculated root samples.

Studies based on the Eungella Tableland showed that soil temperatures under rainforest are favourable for *P. cinnamomi* from September to May inclusive. During that 9-month period, soil moisture would undoubtedly become a critical limiting factor. The area has a 6-month summer rainfall distribution and during the 'wet' season rainfall in excess of 15 to 20 mm per week is common. The field studies showed that those weekly rainfall figures were sufficient to raise soil moisture to, or maintain it at, a level very favourable to *P. cinnamomi*. During the summer 'wet' season, and at other periods of heavy rainfall, soil moisture and temperature levels were frequently suitable for *P. cinnamomi*, sometimes for extended periods. Death of virgin rainforest resulted in increases in both soil moisture and soil temperature. However, whilst logging also caused increases in soil temperature, it resulted in some drying of the soil.

Although it was not possible to prove unequivocally that *P. cinnamomi* was the cause of the rainforest deaths, there is good reason to believe that this is so. It is possible that *P. cinnamomi* was introduced to the Dalrymple Heights area during the 1950's or early 1960's on vehicles and/or machinery. There is little doubt, whatever it origin, that it was substantially spread throughout that area by feral pigs.

The rainforest deaths associated with *P. cinnamomi* are in conflict with claims that the rainforest flora of Queensland is resistant to the fungus. Also, the very low proportion of A_1 type isolates of *P. cinnamomi* from the tropical rainforests of Queensland conflicts with the claim that the ratio of A_1 to A_2 isolates in tropical Queensland approaches unity. There was no evidence that disturbance *per se* initiated disease in the Dalrymple Heights area, particularly in the early days of road construction and logging in the area. The information that is available on *P. cinnamomi* in the tropical rainforests of Queensland does not support the hypothesis that the fungus is native to the area.

Introduction

The first confirmed record of the fungus *Phytophthora cinnamomi* Rands from Queensland was as *Phytophthora* sp.[1] from 'top rot' disease of pineapple (*Ananas comosus* (L.) Merr.)

[1] Subsequently identified as *Phytophthora cinnamomi* by the Commonwealth Mycological Institute, Kew (Simmonds 1966).

(Simmonds 1929). *Phytophthora cinnamomi* was subsequently identified as also being the cause of the 'root rot wilt' of pineapple (Simmonds 1966). Simmonds noted that the pineapple wilt disease had been observed as early as 1887 (Tryon 1904), as an undetermined fungal disease dependent on wet soil conditions. Tryon himself commented that the wilt disease had probably occurred in the pineapple growing areas of southeastern Queensland some fifteen years earlier than 1887, ie, about 1872. A root rot and decline disease of avocado (*Persea americana* Mill.) was first observed in Queensland during 1949, with the causal fungus, *P. cinnamomi*, being isolated in 1952 (Simmonds 1966). Between 1957 and 1960, *P. cinnamomi* was isolated in Queensland from diseases of a range of plant species, including *Carica papaya* L (papaw), *Lupinus digitatus* Forsk. (West Australian blue lupin), *Passiflora edulis* Sims (passion fruit), *Callitrus rhomboidea* R. Br. Ex A. & L.C. Rich. (cypress), and the exotic conifers, *Pinus elliottii* Engelm., (slash pine) *P. radiata* D. Don (radiata pine) and *P. taeda* L. (loblolly pine) (Simmonds 1966). The first record of *P. cinnamomi* from native vegetation in Queensland was from the coastal heathlands, ie, 'wallum', of the southeast (Pegg and Alcorn 1972). *Phytophthora cinnamomi* was also reported from native vegetation in north Queensland at Bingil Bay, Kennedy, the Millstream (Ravenshoe), and Tumoulin (Pratt and Heather 1973).

During July 1975, *P. cinnamomi* was detected from soil samples taken from under dead patches of rainforest at Dalrymple Heights on the Eungella Tableland, west of Mackay, and in August 1975 it was detected from under dead rainforest patches in the Garrawalt area, north-west of Ingham (Brown 1976). Initial investigations at both Dalrymple Heights and Garrawalt showed that *P. cinnamomi* was usually present in soil from under the dead patches of rainforest. At Dalrymple Heights a number of dead patches in virgin rainforest appeared to be of recent origin, were in no way affected by logging or vehicle movement, and did not receive any drainage water from logged or roaded areas. At Garrawalt some dead patches were found during extension of logging roads into virtually virgin rainforest, and although some of these patches were adjacent to the new roads, some were clearly ahead of the road construction. During discussions it was revealed that at Dalrymple Heights deaths had been observed at other sites prior to logging and the fungus was subsequently detected under dead forest at those sites. It was also found under dead deaths in logged rainforest at Garrawalt.

There were some obvious differences in the location and appearance of the dead patches of rainforest between Dalrymple Heights and Garrawalt. At Dalrymple Heights the patches were essentially located on the ridge tops (Figures 1 and 2) where the soil was shallow over heavy clay subsoil. Feral pigs heavily infested the area and created wallows on those ridge tops. The dead patches at Dalrymple Heights consisted of discrete areas with a central zone, largely devoid of living vegetation except for some small regeneration. This was surrounded by an intermediate zone containing a mixture of living, dying and dead understorey with a few moribund or dead trees but with much of the canopy still alive. The dead patches at Garrawalt fell into two types, apparently dependent on the mode of their initiation. One type consisted of long narrow strips extending down gullies and apparently originating from road construction along the ridge top. The other patches occurred part way down a slope and were not necessarily associated with drainage lines. The margins of both types of patches were not necessarily clearly defined and in some areas a number of patches occurred in close proximity and were not always clearly separated. Early observations suggested that feral pig activity, such as soil rooting and the creation of wallows, occurred at such positions on the side slopes between the uphill buttresses of large *Flindersia* trees. In some of the Garrawalt patches there were central bare areas, with most of the under- and over-story dead, surrounded by an

intermediate zone of dead, dying and healthy forest, similar to the Dalrymple Heights patches. However, there were some instances there was no central zone of almost complete mortality; possibly these were of comparatively recent origin.

In September 1975 and May 1976 aerial inspections of the rainforests to the north and south of Eungella Township[2] revealed the occurrence of dead patches at Dalrymple Heights in both State Forest and over a wide area of the Eungella National Park. Deaths were also seen at several localities in the southern portion of the Eungella National Park at Crediton and in State Forest 679 Crediton and Mia Mia. Samples collected at Crediton following the second flight lead to the detection of *P. cinnamomi* from under a dead patch, from under scattered dead trees and from under apparently healthy rainforest.

There is no information on the historical occurrence of dead patches in the Garrawalt area. However, when one area was assessed for logging in mid 1973, there were many deaths (E.A. Martin pers comm). Some thin crowned and possibly dead trees were observed in some parts of the Garrawalt area on aerial photographs taken in 1968 and 1970, but no patches were discernible.

By mid 1976 the Queensland Forestry Department had established a field program to investigate the rainforest patch death problem. These studies covered a number of different elements as will be discussed below. For a number of years, the Department of Forestry had two full-time field staff involved in the studies[3], and as well, these studies formed a major part of the work program of one Professional and up to three Technical staff of the Department's Forest Pathology Laboratory in Brisbane. Additionally, many other Forestry staff, both in the field, and in Brisbane, were involved to some extent in various aspects of the work. Although most of the field elements were terminated in 1981, soil samples and some data were collected in 1982.

[2] To somewhat confuse the locality issue, the Dalrymple Heights Post Office is located in the Eungella Township on the Eungella Tableland.
[3] They were based at Eungella.

Figure 1. Photograph taken from the air that shows the ridge-top rainforest tree deaths in part of the Eungella National Park in May 1976. This area was included in the sequence of colour aerial photographs that showed probably no deaths in 1970 and an increase in rainforest deaths from 4.6 percent in 1976 to 11.9 percent in 1978 and 19.3 percent in 1980.

Figure 2. Aerial view of a single patch at Dalrymple Heights in September 1975 showing details of crown dieback and death. This patch was discovered when a logging road was constructed (space to the top right) before the isolation of *P. cinnamomi*. The patch was definitely not present in 1973.

THE QUEENSLAND DEPARTMENT OF FORESTRY INVESTIGATIONS

The research program conducted by the Queensland Department of Forestry can be divided into a number of different elements, some of which are discussed below. Crucial to the initial establishment of the program, and an important on-going feature, was the survey of tropical rainforest soils for the presence of *P. cinnamomi* and, secondarily, other *Phytophthora* species. While many of the sites sampled were in localities of specific interest such as the Eungella Tableland areas and Garrawalt, there was a concerted effort to sample a wide geographic range of rainforests of tropical Queensland, both logged and virgin. In order to assess the impact on the rainforest vegetation a number of permanent observation plots were established on the Eungella Tableland, and at Garrawalt and elsewhere. At two locations on the Eungella Tableland studies were made of soil temperature, rainfall and soil moisture to assist in understanding the environmental influences at work. Following initial aerial reconnaissance and examination of previous aerial photography, colour-film aerial photography was conducted on several occasions over the Dalrymple Heights area.

The major study areas

From the start of these studies, it became apparent that the main occurrence of rainforest patch deaths was at Dalrymple Heights (northern part of the Eungella Tableland) and at Garrawalt along the southwestern rim of the Herbert River Gorge. Consequently those areas, and also the Crediton area at the southern end of the Eungella Tableland, became the main foci of much of the soil sampling and were the locations for the other studies conducted between 1976 and 1981.

Whilst there was no temperature information for Dalrymple Heights, Crediton or Garrawalt, these localities are all within the Queensland wet tropics, but temperatures would be modified due to the comparatively high altitudes. Garrawalt is more tropical and at a lower elevation than Dalrymple Heights (soil samples were collected between 560 and 660 m at Garrawalt, and between 680 and 1,080 m at Dalrymple Heights). Thus temperatures within the rainforest and in the soil at Garrawalt would undoubtedly be higher than at Dalrymple Heights. Crediton, to the south of Dalrymple Heights, is at similar elevations (soil sampling was between 840 and 920 m), so the temperatures would be similar to those at Dalrymple Heights. The three areas have a pronounced summer ‘wet’ season with the 59-year average annual rainfall for Dalrymple Heights Post Office at Eungella Township (see footnote 4 on page 3) being 2,221 mm. While Dalrymple Heights, to the north east of the Eungella Township, possibly receives over 2,500 mm per annum, Crediton, to the south east of the township, probably receives less rain, perhaps still in excess of 2,000 mm per annum. While there is no specific rainfall data for the Garrawalt area, it lies between the 914 and 1,270-mm isohyets in the climate map of Anon. (1970) and it is possible that rainfall at Garrawalt would exceed 1,270 mm per year.

The major geological formation underlying the rainforests of the Eungella Tableland is the Urannah complex of granite, diorite, and granodiorite, with an area of tertiary olivine basalt at Crediton (Jensen 1965). Soils that have developed on much of the area are red acid leached structured earths (pb2 and pb3 of Isbell and Murtha 1970). These soils are dark crumbly clay loams grading through a pale subsurface A_2 horizon into deeply structured acid red clays. At Crediton red acid structured earths (pa7 of Isbell and Murtha 1970), or krasnozems, are associated with the basalt area. Most of Garrawalt, and of the nearby Mount Fox area, is on

the Glen Gordon volcanics, massive rhyolites to dactites (de Keyser *et al*. 1965). Dominant soils in the area are red polzolics and xanthozems (GM3.14 and GM3.75 of Northcote 1965) (G.G. Murtha personal communication).

Much of the rainforest of Garrawalt and Mount Fox area is Type 8 simple notophyll vine forest (SNVF) of Tracey and Webb (1975) as are the rainforests on the red acid leached structured earths of the Eungella Tableland (J.G. Tracey personal communication). At Garrawalt the Type 8 forest is a complex community of at least 190 tree species[4] with the dominant families being Rutaceae, Lauraceae and Myrtaceae. The Eungella Tableland rainforests are dominated by the families Lauraceae and Myrtaceae, with Cunoniaceae, Elaeocarpaceae, Moraceae, and Sterculiaceae also important numerically (Anon. 1972).

The earliest 'European' activity in the Garrawalt area was the explorer/settler G.A. Dalrymple in an unsuccessful attempt to find a route to the coast from the Valley of Lagoons in 1863 (Jones 1961). The following year Dalrymple was successful in finding a route in the other direction from Cardwell to the Valley of Lagoons. Dalrymple's track became a wagon route, apparently the first 'road' in north Queensland, and this was used for many years to transport supplies from the port of Cardwell to the pastoral lands of the upper Burdekin (Jones 1961). Dalrymple's track passes through the Garrawalt forests, a legacy reflected in the name of the 'Pack Track' Logging Area in the State Forest. Much of the Mount Fox area, to the southeast of Garrawalt was logged prior to 1971. However, logging of the Garrawalt area did not commence until 1970, following the progressive construction of the road past the Wallaman Falls from 1968/69 onwards.

It is likely that the first Europeans to visit the Eungella Tableland were in a party who climbed Mount Dalrymple from the Pioneer Valley in May 1878 (Kerr 1980). Gold was discovered at Eungella in 1888 and the road from the Pioneer Valley was completed in 1908 (Kerr 1980). Dairying commenced on the Tableland in the early 1930's (Everett 1971) with much of the Crediton area being cleared prior to 1947[5]. The road to the north of the Tableland, towards Dalrymple Heights was apparently constructed *circa* 1937, with the southern part of that area being cleared prior to 1947. However, a large part of the dairying land in the Dalrymple Heights area was not cleared until the period between 1947 and 1962. At the time of these studies about 2,000 ha of the Dalrymple Heights rainforest was in State Forest 62, much of which had been logged from about 1960 to 1976.

Soil survey program

Soil samples collected in the field were air freighted to Brisbane where a laboratory baiting procedure, using germinating New Zealand blue lupin (*Lupinus angustifolius* L.) seeds[6], was used to detect *Phytophthora* species. A total of 3,108 samples from 1,897 sites in tropical rainforest areas were processed (Table 1). The separation into regions was based on the existing Forestry management units, and whilst the Mackay region comprised a discrete area, consisting of a number of separate rainforest blocks, the Atherton and Ingham regions joined together in the Tully Gorge area.

[4] Data from Tracey (1982), CSIRO (G.C. Stocker personal communication), and these studies.
[5] Based on 1947 aerial photography.
[6] Flooded soil samples were baited twice (2 or 3 day periods for a total of 4 to 5 days) with germinating NZ blue lupins; on removal from the samples the lupin radicles were excised, surface sterilised and plated on prune pimaricin agar.

This work produced 13,464 *Phytophthora* isolates, nearly 86 percent of them being *P. cinnamomi* (Table 1). Most of the other *Phytophthora* taxa were isolated in numbers of less than 1.5 percent of the total isolates, except for *P. heveae* Thompson which was detected at just over 9 percent of the total isolates (Table 1). About half of the sites sampled were at the three key localities (Crediton, Dalrymple Heights and Garrawalt) and these accounted for over three-quarters of the sites where *P. cinnamomi* was detected and for almost 85 percent of the isolates of this fungus. The mating type was determined for about 40 percent of the *P. cinnamomi* isolates, and only 16 were the A_1 type with 4,413 being the A_2 type. The A_1 type isolates came from virgin rainforest from four discrete areas at Bartle Frere (A_1:A_2 at 6:0 from 1 collection), Kuranda (A_1:A_2 at 5:43 from 1 collection) and Mount Windsor (A_1:A_2 at 2:63 from 1 collection and 3:4 from another collection).

During the survey, *P. cinnamomi* was found in soil under rainforest at a number of localities in tropical Queensland. The sample localities, and those where *P. cinnamomi* was detected under rainforests of the Wet Tropics World Heritage Area are shown in Figures 3 and 4. The localities where *P. cinnamomi* was detected include Cowley Beach (*P. cinnamomi* was detected from 5 of 20 sites sampled), Daintree (15/62 sites), Dinden (7/13), Garrawalt (96/161 sites), Herberton (4/27 sites), Kirrama (9/35 sites), Kuranda (23/29 sites), Mount Fox (13/40 sites), Mount Lewis (8/8 sites), Mount Spec (3/3 sites), Mount Windsor (9/65 sites), and Walter Hill (4/37 sites). As well as Crediton (134/434 sites) and Dalrymple Heights (264/407 sites) in the Mackay region, *P. cinnamomi* was a detected from under rainforest at Cathu (14/138 sites) to the north west of Mackay and from Conway (1/42 sites) north east of Proserpine.

Data collected in the field at the time of sampling included forest health status, forest history, influence of roads, elevation and other site information. This data allowed the results to be analysed according to site factors such as locality, elevation, forest health, management history and feral pig activity (Table 2).

There was a significant difference in rate of detection of *P. cinnamomi* between Dalrymple Heights and Crediton, but not between Dalrymple Heights and Garrawalt. At both Dalrymple Heights and Garrawalt detection of *P. cinnamomi* was dependent on forest health, with higher detection rates under areas of dead forest than under apparently healthy[7] forest. However at Crediton, where most of the sites were 'healthy' forest (325 of 438 sites), detection was not statistically dependent on forest health. *Phytophthora cinnamomi* was detected from nine of 20 sites from under rainforest dead patches and from 95 of 325 sites in healthy forest at Crediton. It is possibly of significance that, of the three major areas sampled, it was only at Crediton that there was a significant effect of management history on detection of *P. cinnamomi*, with higher detection from logged than virgin forest.

Soil sampling results for the study areas at Dalrymple Heights and Crediton give important information on how *P. cinnamomi* was probably spread through the tropical rainforests of Queensland. At Dalrymple Heights nearly 70 percent of 705 samples were from 407 discrete sites in virgin rainforest where there was no direct effect of roads or logging but where feral pigs were prevalent, as they were at Garrawalt. At Crediton, however, there was no evidence of feral pig activity from the start of sampling in 1976 until the end of 1979, but in January 1980 the first feral pig activity in the area was noted.

[7] The term 'healthy' should be taken to mean showing no obvious symptoms; it is possible for a fungus, including *P. cinnamomi*, to be active on the roots of some hosts without causing visible effects to the crown.

Table 1. Summary of the results of a soil sampling program for *Phytophthora* species in soils of Queensland tropical rainforests between 1975 and 1982.

	Region	Isolation results			Mating types	
		Samples	Sites	Isolates	A_1	A_2
Sampling Totals	Atherton	966	548	1,992		
	Ingham	437	266	2,161		
	Mackay	1,705	1,083	9,311		
	Total	3,108	1,897	13,464		
P. cinnamomi	Atherton	160	114	1,377	16	794
	Ingham	214	119	1,915	0	622
	Mackay	620	413	8,255	0	2,997
	Total	994	646	11,547	16	4,413
P. boehmeriae	Atherton	12	7	36		
	Ingham	0	0	0		
	Mackay	14	14	16		
	Total	26	21	52		
P. citricola	Atherton	7	6	26		
	Ingham	3	3	3		
	Mackay	76	67	155		
	Total	86	76	184		
P. cryptogea	Atherton	1	1	2	2	0
	Ingham	2	2	19	19	0
	Mackay	1	1	1	1	0
	Total	4	4	22	22	0
P. drechsleri	Atherton	1	1	1	0	0
	Ingham	0	0	0	0	0
	Mackay	6	6	13	0	1
	Total	7	7	14	0	1
P. heveae	Atherton	140	98	528		
	Ingham	61	58	188		
	Mackay	198	168	511		
	Total	399	324	1,227		
P. katsurae	Atherton	6	6	17		
	Ingham	1	1	1		
	Mackay	60	54	150		
	Total	67	61	168		
P. meadii	Atherton	3	3	3	1	0
	Ingham	1	1	8	0	0
	Mackay	19	19	29	5	0
	Total	23	23	40	6	0
P. nicotianae var. nicotianae	Atherton	0	0	0	0	0
	Ingham	0	0	0	0	0
	Mackay	3	3	5	0	3
	Total	3	3	5	0	3
P. nicotianae var. parasitica	Atherton	0	0	0	0	0
	Ingham	0	0	0	0	0
	Mackay	6	6	27	3	2
	Total	6	6	27	3	2
P. palmivora	Atherton	2	2	2	2	0
	Ingham	5	2	27	7	0
	Mackay	27	27	149	37	56
	Total	34	31	178	46	56

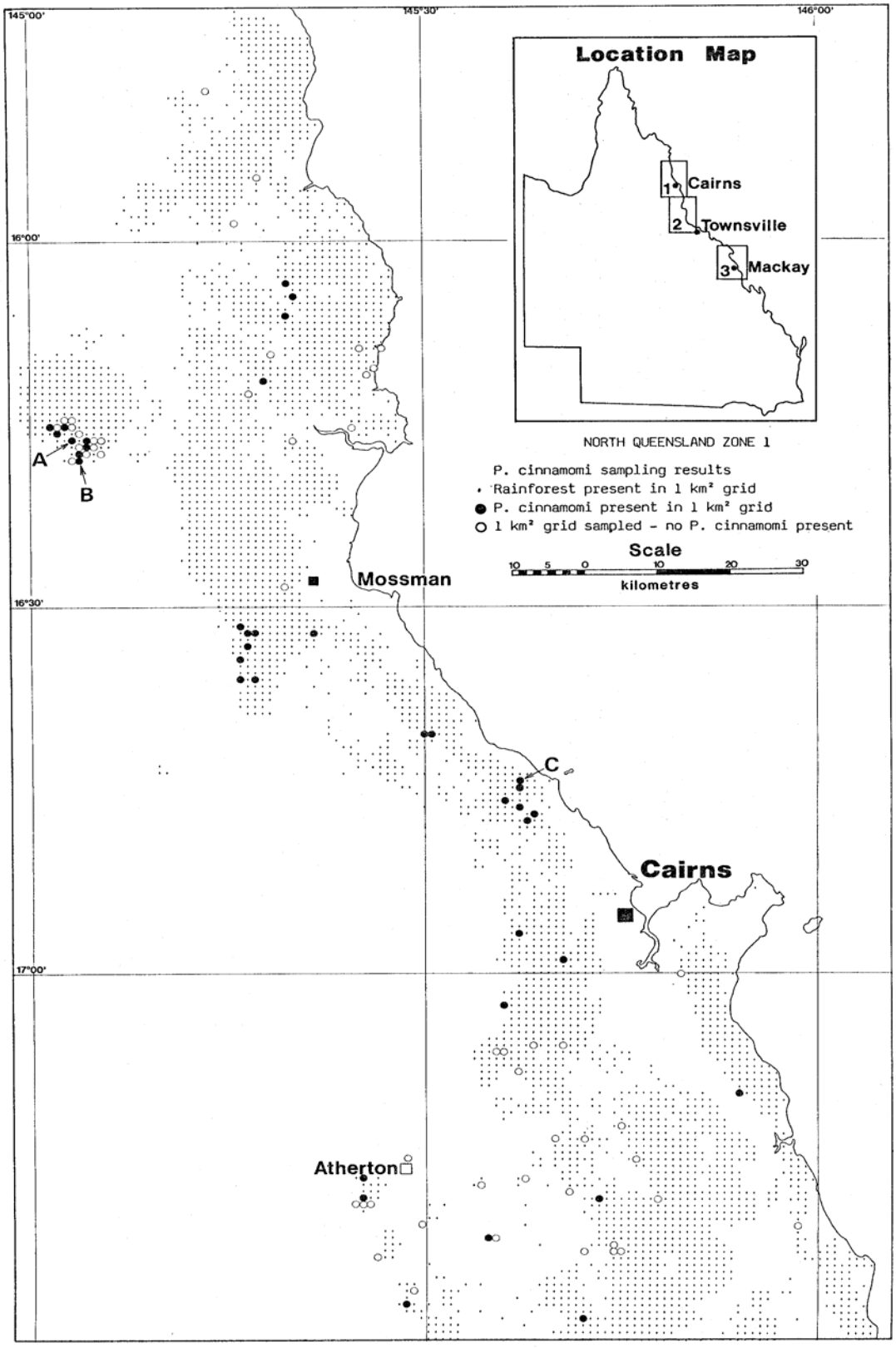

Figure 3. Zone 1 of the North Queensland area included in the survey of tropical rainforest soils of Queensland for *Phytophthora* species. This figure shows rainforest in the area, sample locations and those where *P. cinnamomi* was detected. Also shown are three of the four locations (A and B on Mount Windsor and C at Kuranda) where the A_1 mating type of *P. cinnamomi* was detected.

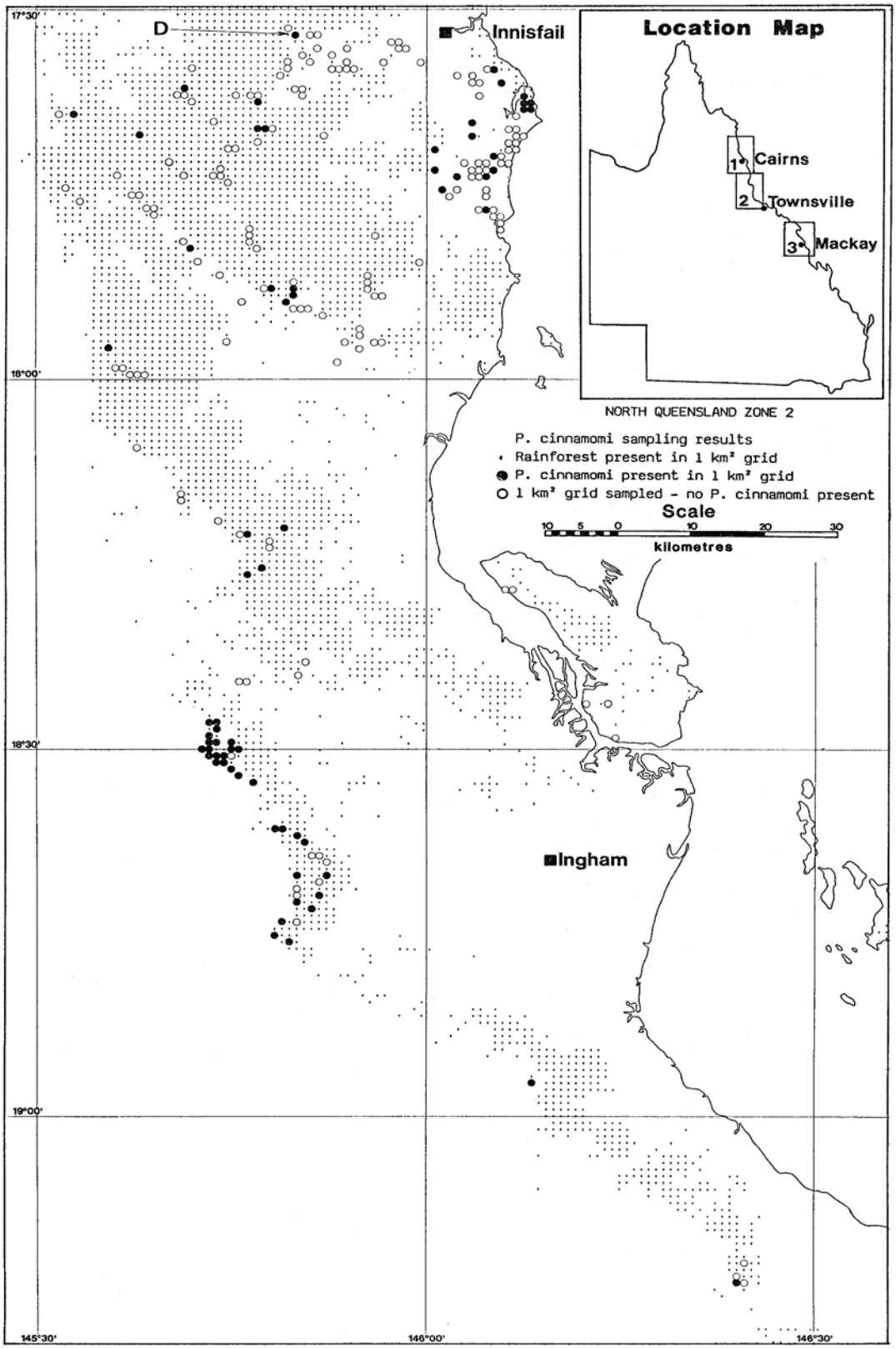

Figure 4. Zone 2 of the North Queensland area included in the survey of tropical rainforest soils of Queensland for *Phytophthora* species. This figure shows rainforest in the area, sample locations and those where *P. cinnamomi* was detected. Also shown is one of the four locations (D in the Bartle Frere area) where the A_1 mating type of *P. cinnamomi* was detected.

At Crediton, where 751 samples were collected from 438 sites, *P. cinnamomi* was isolated more frequently from logged (47.6 percent of sites) than from virgin forest (26.3 percent of sites). Most of the *P. cinnamomi* sites at Crediton were in the northern part (35.8 percent of samples and 57.3 percent of sites). The only positive sites in the southern part (about 5.5

Table 2. Detection of *Phytophthora cinnamomi* during survey of tropical rainforest soils of Queensland[1].

Forest Category	Samples		Sites	
	Total	*P. cinnamomi*	Total	*P. cinnamomi*
Total survey	3,019	990	1,817	645
Locality				
Crediton	751	174	438	138
Dalrymple Heights	701	425	403	263
Balance for Central Qld	220	18	216	15
Garrawalt	292	182	130	92
Balance for North Qld	1,055	188	630	137
Elevation (m)				
0-399	466	49	336	48
400-799	735	284	509	177
800+	1,818	658	972	420
Forest health				
Definite patch	531	255	135	85
Diffuse patch	258	108	112	64
Scattered deaths	467	170	347	150
Single death	92	27	64	24
Healthy	1,671	431	1,159	322
Management history				
Virgin	1,318	534	777	323
Virgin/road	415	91	227	68
Logged	395	101	300	88
Logged/road	617	176	404	130
Planted	195	78	54	25
Planted/road	79	11	55	11
Pig activity				
Old signs	456	192	347	144
Fresh signs	523	233	308	135
No signs	1,457	328	845	260
Not recorded	583	238	317	106

[1.] This table does not include all the data that was included in Table 1.

percent of samples and sites) were located about the centre of the study area, in locations associated with logging, or in one case, a vehicle track. In one section at Crediton, where there were no tracks and where clearing of adjacent dairying land from the west did not extend to the top of the Clarke Range, *P. cinnamomi* was not detected in virgin rainforest.

It was suggested by sampling in Hawaii (Kliejunas and Ko 1976), that feral pigs can actively spread *P. cinnamomi* in infested soil. Hence, at Dalrymple Heights where they were prevalent they could have been a major means of spread of the fungus. However, at Crediton where feral pigs were ‘late arrivals’ the effect of machinery, primarily through logging, appears to

stand out. It is undoubtedly important that Crediton, prior to the discovery of *P. cinnamomi* in rainforests of the area, was used for dry-weather logging on the Eungella Tableland, with machinery being frequently moved from Dalrymple Heights to Crediton and then returned to Dalrymple Heights (L. McVeigh personal communication). In view of the high level of *P. cinnamomi* rainforest soils at Dalrymple Heights there can be no doubt that it would have been transported to Crediton on the logging equipment and vehicles.

About one fifth of the sites in the survey yielded one or more of the *Phytophthora* taxa, other than *P. cinnamomi*, as are listed in Table 1. It was not uncommon for several *Phytophthora* taxa to be detected from an individual site or even from an individual soil sample. All 12 *Phytophthora* taxa except *P. cryptogea* Pethbry. & Laff. were found in the Crediton area and all except *P. cryptogea* and *P. nicotianae* Breda de Haan var. *nicotianae* were found at Dalrymple Heights. However, other than *P. cinnamomi*, only *P. citricola* Sawada*, P. heveae* and *P. cryptogea* were found at Garrawalt.

Phytophthora heveae was widespread through the tropical rainforests of Queensland and was detected from about 17 percent of the survey sites (Table 1). The recorded distribution for *P. heveae* is shown in Figures 5 and 6 for the Wet Tropics World Heritage Area. While not shown in the figures, *P. heveae* was the only *Phytophthora* species detected from a single soil sample from the McIlwraith Range area (13° 46' S latitude), north east of Coen on Cape York Peninsular. In general, *P. heveae* was more frequent at elevations above 400 m, in soil under dead patches of rainforest, and from areas free of feral pig activity. However, the detection rates for *P. heveae* were comparatively low compared to detections of *P. cinnamomi* from the same situations.

Of the other *Phytophthora* taxa, *P. citricola* and *P. katsurae* W.H. Ko & H.S. Chang were more frequent in the Mackay region than further north (Table 1) and both were more common under virgin than logged forest. *Phytophthora palmivora* (Butler) Butler was also more common in the Mackay region, and while over the whole survey the mating types were in almost equal proportions, for most sites only one of the two types was found. *Phytophthora boehmeriae* Sawada was only found at 21 sites, two thirds of these being in central Queensland and a species identified as near *P. meadii* was found in only 23 sites, most of these in central Queensland.While both *P. cryptogea* and a species near *P. drechsleri* Tucker were found in both north and central Queensland, the two varieties of *P. nicotianae* were only detected in the Mackay region.

Isolations of *Phytophthora cinnamomi* from identified trees

Although lupin bating was used for most of the *Phytophthora* survey, there were some direct isolations for *P. cinnamomi* from roots of identified species collected in diseased areas. These, and isolations from inoculated plants, produced a number of new host records for *P. cinnamomi* (Table 3). The record from *Archontophoenix cunninghamiana* (Wendl.) Wendl. & Drude was apparently the first record in the world on any species of palm. None of the species in Table 3 had previously been reported as hosts of *P. cinnamomi*. The only other Queensland rainforest species included in earlier host lists for *P. cinnamomi* are *Macadamia integrifolia* Maid. & Betche, *M. tetraphylla* L.A.S. Johnson, and *Lophostemon confertus* (R. Br) Wilson & Waterhouse (Zentmyer 1980).

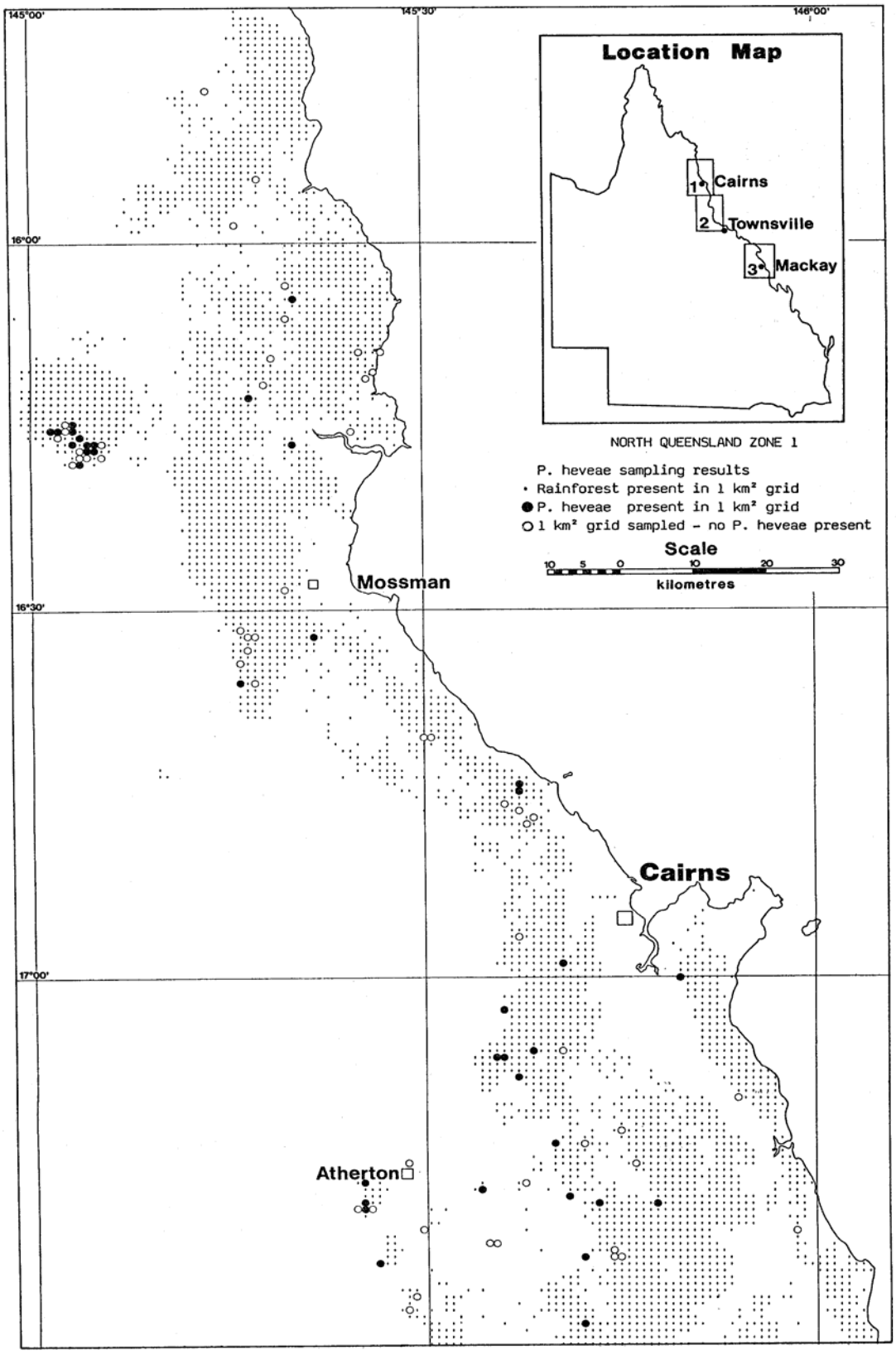

Figure 5. Zone 1 of the North Queensland area included in this survey of tropical rainforest soils of Queensland for *Phytophthora* species. This figure shows rainforest in the area, sample locations and the locations where *P. hevea* was detected.

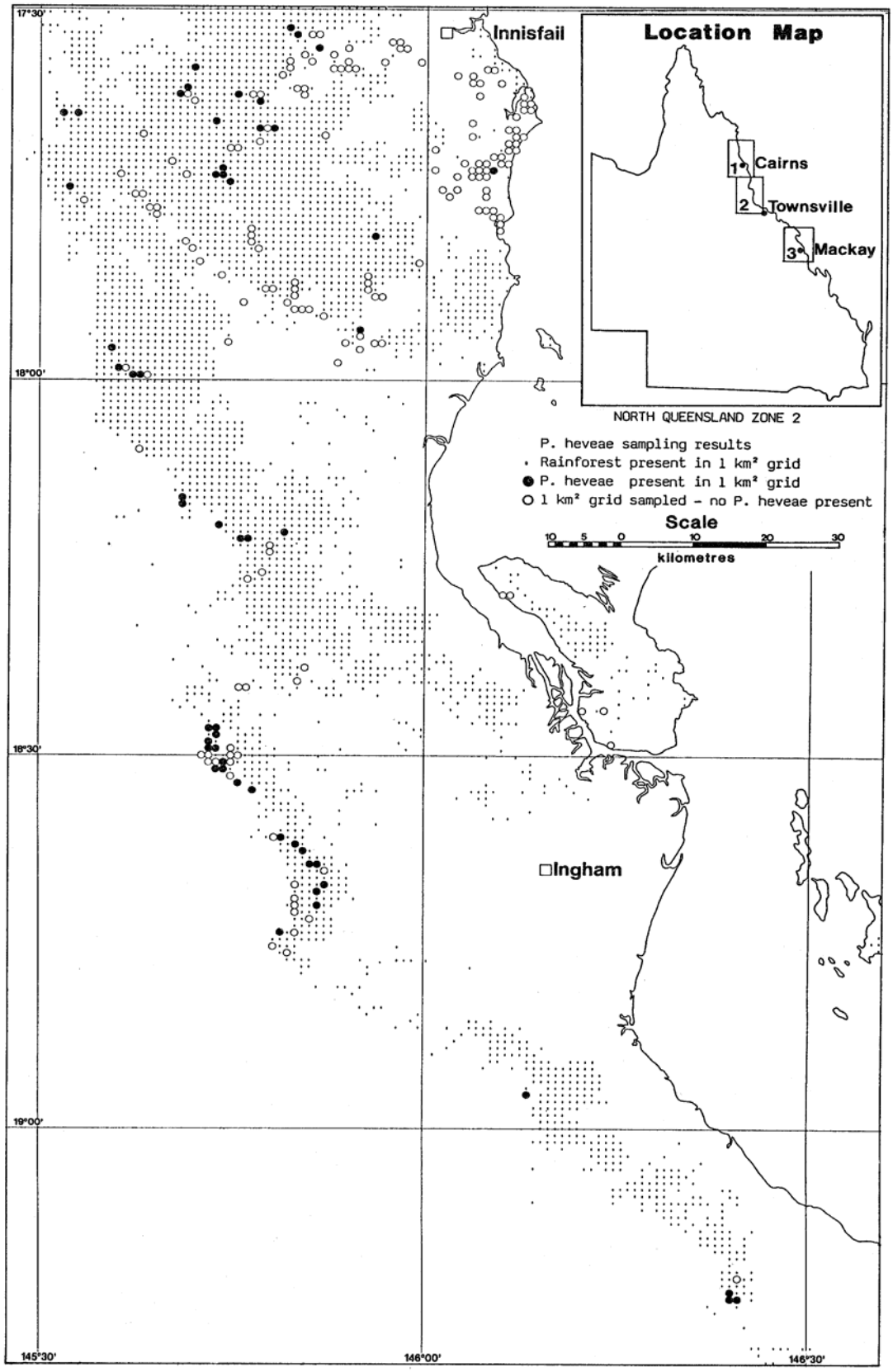

Figure 6. Zone 2 of the North Queensland area included in the survey of tropical rainforest soils of Queensland for *Phytophthora* species. This figure shows rainforest in the area, sample locations and the locations where *P. heveae* was detected.

Table 3. Queensland rainforest species from which *Phytophthora cinnamomi* was isolated from natural infections or by artificial inoculations. All species on the list are new host records.

Species	Natural infections[1]	Artificial infections[2]	Present in study plots[2]
GYMNOSPERMAE – CONIFERAE			
Podocarpaceae			
Pruminopitys amara		X	X
MONOCOTYLEDONEAE			
Agavaceae			
Cordyline murchisoniae[3]	E		
Palmae			
Archontophoenix cunninghamiana[4]	E		
DICOTYLEDONEAE			
Lauraceae			
Beilschmiedia sp. aff. *B. obtusifolia*	G		X
Cinnamomum oliveri	E		X
Cryptocarya corrugata[3]	E	X	X
Cryptocarya glaucescens[3]	E		X
Leguminosae			
Castanospermum australe[3]		X	X
Meliaceae			
Synoum glandulosum[3]		X	X
Myristicaceae			
Myristica insipida		X	X
Myrtaceae			
Acmena resa[3]		X	X
Syzygium erythrodoxa[3]		X	X
Syzygium wesa[3]		X	X
Ochnaceae			
Brackenridgea nitida ssp. *australiana*[4]	G		X
Proteaceae			
Buckinghamia celsissima[3]		X	X
Carnarvonia sp.[3]	G		X
Darlingia darlingiana[3]	G		X
Rutaceae			
Acronychia oblongifolia[3]	E		X
Flindersia brayleyana[3]		X	X
Sterculiaceae			
Argyrodendron actinophyllum[3]		X	X
Sapindaceae			
Jagera pseudorhus[3]		X	X
Symplocaceae			
Symplocos stawellii[4]	G		X

1. Isolations from Eungella Tableland (E) or Garrawalt (G).
2. Positive entries marked X.
3. A new genus record.
4. A new genus and a new family record.

Tree decline and deaths

Defoliation began at the smallest branchlets on the outer surface of the crown (Figure 2). After these had died, leaves deeper in the crown then died with the fine branches remaining bare. Re-shooting occurred mainly on the larger branches and stems, with many of these

shoots surviving for 1 to 2 years before themselves dying. Depending on the tree species, further re-shooting could occur, but eventually trees became fully defoliated.

Rate of decline of the cambium of the lower stem varied with species, but mostly it was dead within 6 months of full defoliation.

Permanent plot studies

The impact of patch death on the various rainforest tree species was studied in 25 observation plots and in two line transects, mostly located at Crediton, Dalrymple Heights and Garrawalt. Deaths recorded in individual plots ranged from a single tree to 51 trees while most plots and the two line transects showed continuing deaths of rainforest trees over the study period. Almost 90 percent of the trees located in the observation plots and line transects were identified, most to species level. Unfortunately, however, about one third of the dead stems could not be identified because of their advanced deterioration. At the time of the final measures over 12 percent of the study trees were dead.

Individual species that showed heavy to average mortality were from the families Escalloniaceae (*Polyosma alangiacea* F. Muell. 46.3 percent), Rutaceae (*Melicope fareana* Engl. 40.0 percent, *Acronychia vestita* F. Muell. 22.2 percent, *A. acronychioides* (F. Muell.) Hartley 18.8 percent, and *Brombya platynema* F. Muell. 11.5 percent), Proteaceae (*Carnarvonia araliifolia* F. Muell. 35.7 percent), Rhamnaceae (*Alphitonia petriei* Braid & White 23.1 percent), Lauraceae (*Cinnamomum oliveri* F. Bailey 21.8 percent), *Cryptocarya cinnamomifolia* Benth. 20.2 percent, *C. corrugata* C. White & Francis 16.0 percent, *C. glaucescens* R. Br. 12.7 percent), Sphenostemonaceae (*Sphenostemon lobosporus* (F. Muell.) L.S. Smith 17.1 percent), Araliaceae (*Polyscias australiana* (F. Muell.) Philipson 11.4 percent), and Meliaceae (*Synoum muelleri* C. DC. 10.2 percent).

The list of trees that showed above average mortality in tropical rainforest sites infested by *P. cinnamomi* in Queensland contains four laurels, three species of Rutaceae, but only one species of Proteaceae, a family noted for a high proportion of highly susceptible hosts in southern *P. cinnamomi* infested areas. There were no species of Myrtaceae in the rainforest species in the average to severely affected range.

Aerial photography

In late 1976, the Queensland Forestry Department commissioned aerial photography of about 600 km^2 of the Eungella Tableland. Standard survey format (9 inch) colour negative film was used at a scale of 1:10,000. Part of the area, selected because of the high intensity of patch death in virgin rainforest, was re-photographed in the same format in 1978 and it was again photographed using Forestry Department small-format equipment (35-mm film with prints enlarged to 1:10,000) in July 1980.

Interpretation of the aerial photography by cartographic staff of the Forestry Department was based on the presence of crown defoliation (tree death) and/or brown canopies. This information for the most severely affected area of rainforest at Dalrymple Heights was transferred to a composite map that included the three sequences of air photos. The area under discussion had also been included in one earlier (1970) run of colour aerial photography, at a scale of 1:18,000. Because of the smaller scale, interpretation of crown

condition was difficult. However, within the area of interest there were four roadside areas of death, one definitely associated with clearing at some time between 1962 and 1970. All four, because of their position could have resulted from clearing and/or fire. Otherwise there were only scattered dead stags and some individual trees that may have been dead.

The sequence of aerial photographs from 1976 to 1980 showed increase in area of dead forest by increase in both the number of, and the size of, affected patches. All areas present in 1976 increased during the 20 months to the 1978 photography, and while some patches increased in size from 1978 to 1980, others showed no increase. Area calculations over the most severely affected 641 ha at Dalrymple Heights indicated that, while there were probably no deaths in 1970, by 1976 4.6 percent of the forest was dead. This increased to 11.9 percent in 1978 and further to 19.3 percent (125 ha in total) in 1980.

The Dalrymple Heights area covered by these studies was by far the most severely affected area of rainforest seen from aerial observation, aerial photography and ground inspections anywhere in the tropical rainforests of Queensland. It is part of a plateau that extends up to 3 km to the east of the road from Eungella Township to the Mount Dalrymple-Mount William area. This road more or less follows the top of the range that forms the watershed between the Cattle Creek catchment of the Pioneer River to the east and the Broken River catchment to the west. As with much of the tropical rainforests of Queensland, it is probable that there had been mining exploration[8] and possibly some isolated logging activity[9] within this area which became part of the Eungella National Park in 1941. Otherwise it was largely, if not completely, unaffected by mechanised equipment. The area consists of flat, poorly drained ridge tops with deep, V-shaped valleys with eastern drainage from the road going directly into the valleys (see Figure 1).

Soil environment studies

Detailed studies of *P. cinnamomi* itself, and its role in inciting disease of a number of plant species, have shown that a number of factors influence the fungus and the diseases that it causes. The following is a summary of the factors known to influence disease development, largely from Zentmyer (1980).

- soil temperature – the range 15° to 30° C favours disease
- soil pH – disease is favoured by pH values in the range 4.5 to 7.5
- soil aeration – *P. cinnamomi* requires oxygen, but in the soil situation it is difficult to separate the effects of aeration and soil moisture
- soil moisture – this is a critical factor:
  - –*P. cinnamomi* requires free water for formation of sporangia, and for release and motility of zoospores
  - –Since zoospores are the primary infective agent of *P. cinnamomi*, free soil water is required for infection of host roots
  - –Often diseases caused by *P. cinnamomi* are associated with drainage lines and other areas where water accumulates
  - –Matric water potentials in the range of 0 to -0.1 bar (ie. very wet soils) lead to severe disease (Sterne *et al* (1977); Gisi *et al.* (1980))

[8] Mount Dalrymple was apparently first climbed in 1878 from the Pioneer Valley, and gold was discovered at Eungella in 1888 (Kerr 1980).

[9] Although Francis (1928) who visited the Eungella Tableland in 1922 observed that felling and removal of the cedar (*Toona australis* (F. Muell.) Harms) had begun; the road past the area was apparently only constructed about 1937 with the dairying area across the road to the west of the site being cleared after 1953/1954.

–From experimental and theoretical considerations the soil water potentials must lie within the range of 0 to -0.12 bar for either passive or autonomous (including chemotaxis to host roots) zoospore movement within soil[10]

- interactions in soil – frequently several soil environmental factors interact to influence development of disease caused by *P. cinnamomi*

- soil nutrient status – there is evidence that a number of soil chemical factors have a role in development of *P. cinnamomi* induced diseases (Broadbent and Baker 1975); the factors that have been listed include:
  –amount of nitrogen (N_2)
  –form of N_2 – *P. cinnamomi* is sensitive to nitrate N_2
  –calcium (Ca) – disease is reduced by high levels
  –complete fertilisers – sensitivity of some *Eucalyptus* species was increased by fertilising

- absence of suppressive soil microflora – high organic matter, high nitrogen, and high levels of exchangeable cations, especially calcium and magnesium, are associated with soil microflora known to suppress *P. cinnamomi* in certain soils. This effect is now used to advantage in the cultivation of avocados (*Persea americana* Mill.), a South American rainforest species important in horticulture in Queensland (Pegg *et al*. 1982; Stirling *et al*. 1992).

One notable feature of the rainforest patch deaths in the Dalrymple Heights area was that its major occurrence was on the broad, apparently poorly drained, ridge tops of the area. At first impression this is in contrast with the usual occurrence of disease caused by *P. cinnamomi* in water-gaining sites. However, it seemed probable that the high rainfall of the area would create long periods of high soil moisture, even on the tops of the broad ridges. In the field this was more or less confirmed by the retention of water in ridge-top depressions for several weeks after rain.

Complementary studies were established to investigate soil temperature and moisture under rainforest at Dalrymple Heights and Crediton. At Dalrymple Heights the studies were conducted at and near a ridge top under a healthy area and under a nearby area of deaths, both in virgin rainforest. The Crediton studies were centred on steep slopes in virgin rainforest and in canopied and also open sites[11] within a logged forest area. Soil moistures were determined by permanently installed tensiometers (Soilmoisture Jet Fill Model No. 2725) at 50 mm and 150 mm depths. Temperatures were recorded in a vertical, stone-free, soil core pre-installed at each site, using stainless steel sheathed thermocouple probes at 50 mm and 150 mm depths with a Matronics 515K Meter. As far as possible, recordings were taken at weekly intervals between November 1978 and August 1981 and for a further period over the next summer from November 1981 to May 1982. Rainfall was recorded in a rain gauge located in cleared land close to each study site.

At both Dalrymple Heights (Figure 7) and Crediton the soil temperatures under healthy virgin rainforest reached 20° to 21° during summer and fell to between 12° and 13° in winter.

[10] see Appendix 1.
[11] In the absence of additional clearing in the area, during the study there was natural regeneration that converted these ‘bare’ areas to ‘canopied’ logged rainforest.

However, average soil temperatures under diseased virgin rainforest were one to several degrees higher than under healthy virgin rainforest. The difference in temperatures between diseased and healthy rainforest increased over the study period, reflecting the increased defoliation in the area with time. At Crediton, soil temperatures under canopied logged rainforest were generally 0.6° to 1.5° C higher than under nearby virgin rainforest. Although average soil temperatures under uncovered areas were essentially the same as under canopied logged rainforest, there was much more variability in temperature with depth (ie. 50 mm compared to 150 mm) under the open areas.

Rainfall recorded at the Dalrymple Heights study area during three years average over 3,000 mm, and this exceeded the recordings at the Dalrymple Heights Post Office to the southwest of 2,653 mm. On the other hand, the average annual recordings at the Crediton study site of over 2,400 mm were slightly lower than the records at the Dalrymple Heights Post Office to the northwest. Both study areas had a pronounced summer wet season, with weekly rainfall totals of between 50 mm and 100 mm being usual during that time.

During the summer wet season, and at other times of heavy rainfall, the soils under healthy virgin rainforest were usually very wet, ie, 0 to -0.10 bar[12], at both Dalrymple Heights and Crediton. On occasions soils remained very wet for many weeks. The lower slope positions stayed wetter following rain, presumably as result of lateral drainage from uphill. The upper slope positions showed a greater degree of wetting from rain and drying in the absence of rain than did the down-slope positions while the surface soils at 50 mm depth responded more readily to rainfall than the deeper (150 mm) soils.

Under diseased rainforest the soils were consistently wetter than under the nearby healthy rainforest, an effect that was small when both areas were wet, but which increased as the soils dried out. In the diseased rainforest, the lower slope positions were usually wet or at least moist, while ridge-top soil dried out much more rapidly.

As with the soils under virgin rainforest, during the summer wet season and at other times of heavy rain, the soils under both canopied and open areas of rainforest at Crediton were very wet (soil water potentials of 0 to -0.10 bar). There was a similar effect from slope in logged forest as was observed under healthy virgin rainforest. In the absence of rain, the logged rainforest soils tended to be drier than those of healthy virgin rainforest, with the open areas being the driest.

When the relationship between weekly rainfall and consequent soil moisture was examined the data showed that weekly rainfall of between 15 to 20 mm at both locations was sufficient to maintain the soil moisture levels in, or raise them to, the 0 to -0.12 bar range (Figure 8).

Using soil temperature and soil moisture data it is possible to postulate that *P. cinnamomi* would be active under healthy rainforests of the Eungella Tableland between September and May inclusive, providing weekly rainfall exceeds 15 to 20 mm. With average monthly rainfall of more than 200 mm from December to April, these conditions would occur regularly, and, in fact, were recorded on numerous occasions during the studies.

Canopy removal through tree death or logging leads to increase in soil temperature, thus increasing the periods when conditions would favour *P. cinnamomi*. Death of the canopy

[12] 0 to –0.1 bars is the same as 0 to –10 centibars on the scale used in Figure 7.

trees also results in increase in soil moisture, further extending the duration of periods when conditions would favour *P. cinnamomi*.

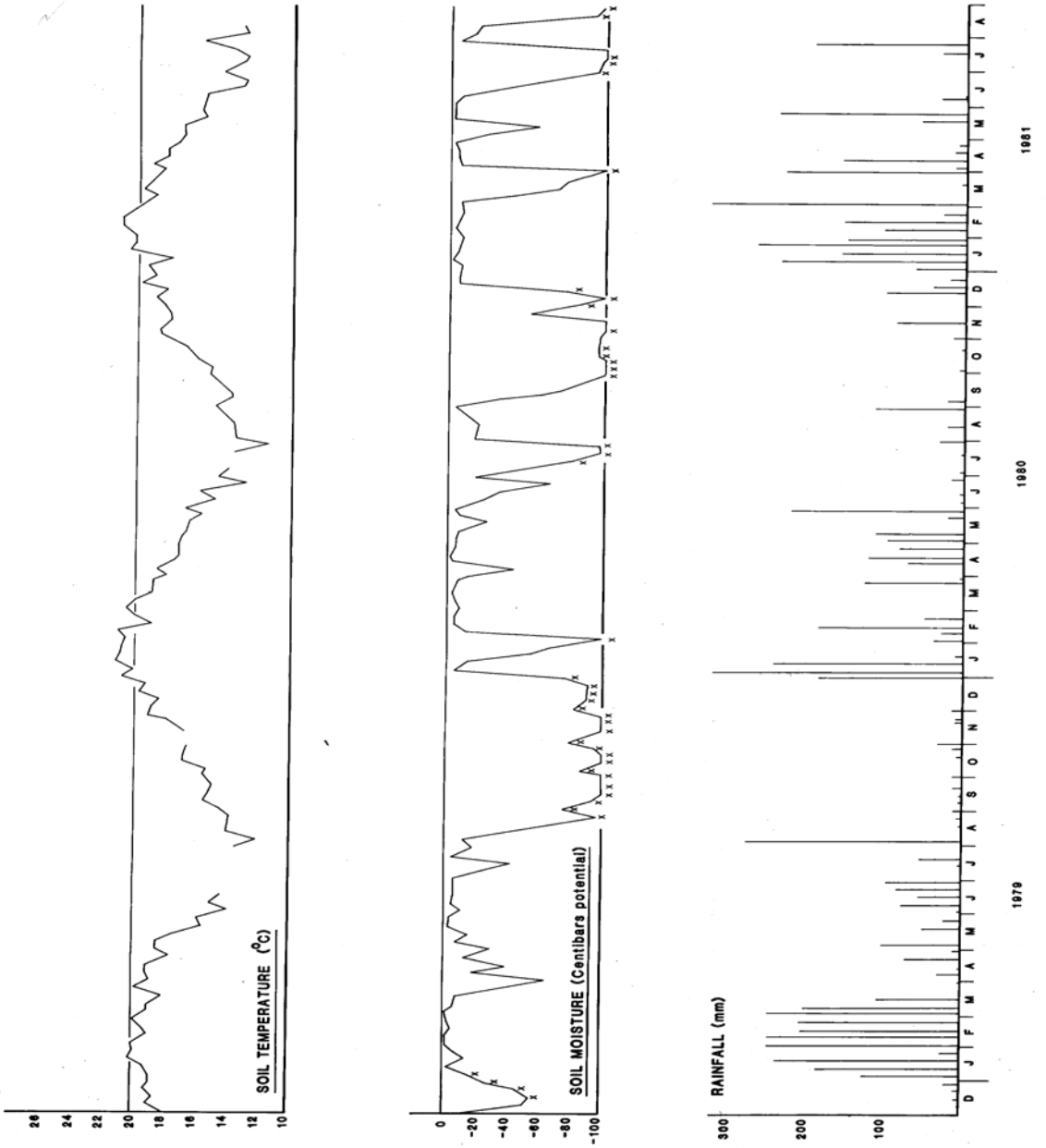

Figure 7. Summary of environmental data recorded under healthy virgin rainforest at Dalrymple Heights and rainfall recorded in a nearby cleared paddock. Data was collected more or less weekly and the soil temperature and moisture data are the means of measurements taken at 50 mm and 150 mm depth at each of four positions along a transect. The transect started at the top of the ridge and ran directly down the side of the ridge. The soil moisture was measured with porous cup-type tensiometers which 'failed' (ie. became air-filled) when the soil water potential fell below about –0.8 bars (-80 centibars). The tensiometers did not recover until manually reactivated with water from an in-built reservoir. An 'X' against a soil moisture average indicates that one or more of the eight tensiometers had 'failed' between measures. Such 'failures' were allocated a nominal value of –1.0 bars (–100 centibars) for calculation purposes, as that figure was below the level at which *Phytophthora cinnamomi* would be active.

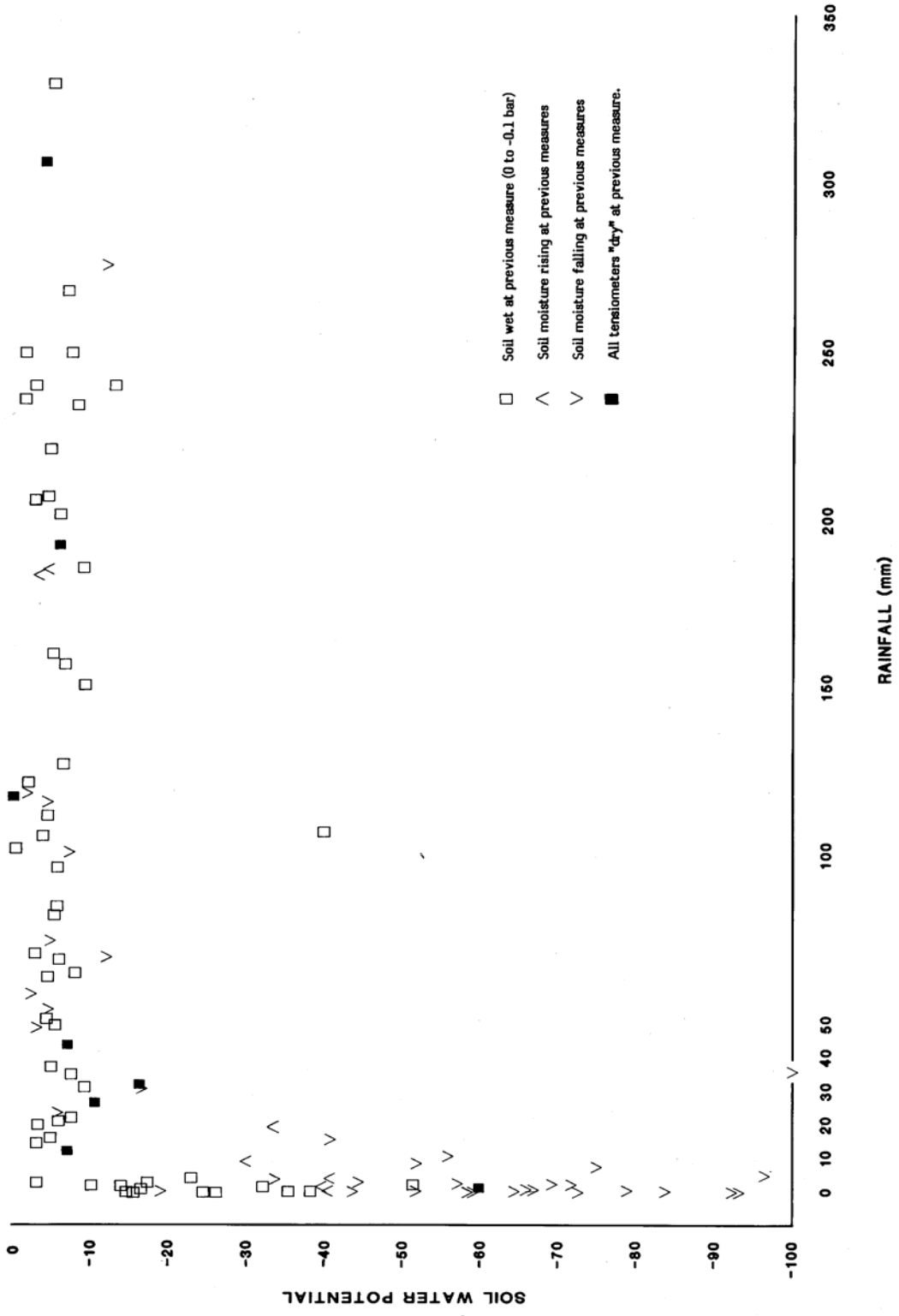

Figure 8. Relationship between rainfall, mostly for 7 but occasionally for up to 10 days, and resultant soil moisture levels under healthy virgin rainforest. Summary of environmental data recorded under healthy virgin rainforest at Dalrymple Heights and rainfall recorded in a nearby cleared paddock. The soil moisture data are the means of measurements taken at 50 mm and 150 mm depth at each of four positions along a transect. The transect started at the top of the ridge and ran directly down the side of the ridge. The soil moisture was measured with porous cup-type tensiometers which 'failed' (ie. became air-filled) when the soil water potential fell below about –0.8 bars (-80 centibars). The tensiometers did not recover until manually reactivated with water from an in-built reservoir.

Phytophthora cinnamomi and other *Phytophthora* species in tropical rainforests

Historical information for the Dalrymple Heights area, including aerial photography, indicates almost no disease in the area prior to the early 1970's with rapid escalation during the subsequent decade. Disturbance associated with road construction and logging in the Dalrymple Heights area over the previous 30 years had not resulted in significant disease development. Although records of feral pig activity in the area are scant, they had been pests in the area for some years prior to 1975 (H.A. Kerswell and P.J. Stanton personal communications). It seems unlikely that *P. cinnamomi* was a natural inhabitant of the rainforests of Eungella Tableland, rather that it was accidentally introduced to the Tableland at some stage during the late 1950's or early 1960's. One possible source is the pineapple cultivation in the Mackay region, as some of the machinery used in logging of the Tableland rainforests was apparently also used for cultivation on the coastal area. Although observations at Garrawalt suggest that the fungus may have been activated or spread by logging and road activities, there were dead patches in virgin rainforest that could not have originated from such activities.

It was not possible to prove that *P. cinnamomi* was the cause of the rainforest deaths at Dalrymple Heights and Garrawalt. Despite this, there is good reason to believe that this is so, and the results of the Queensland Forestry Department's research program were consistent with such a hypothesis. Of particular importance are the following;

- the almost constant association of *P. cinnamomi* with diseased forest,
- the lesser association with 'healthy' forest,
- the spread of *P. cinnamomi* as shown by sequential soil sampling studies, in these studies many of the 'healthy' areas of rainforest remained free of *P. cinnamomi* over several years,
- the spread of both rainforest tree deaths with time, and
- the successful root isolations from field samples and from glasshouse inoculation studies.

The soil-sampling program showed that *P. cinnamomi* was widespread, but by no means universal, in tropical rainforest soils of Queensland. At Dalrymple Heights and Garrawalt, detection of *P. cinnamomi* was dependent on forest health, with lowest detection from under apparently healthy rainforest. There were relatively few isolates of the A_1 mating type (16 of 4,429 isolates tested) and these were from four discrete sites, all in the Wet Tropics World Heritage Area.

There were over 800 rainforest sites sampled in the Wet Tropics World Heritage Area (Table 4) and *P. cinnamomi* was detected from 28.6 percent of these. *Phytophthora cinnamomi* was detected in soil from under 88.2 percent of dead patches sampled at Garrawalt and in soil from under another 23 dead patches (24.2 percent) sampled elsewhere in the Wet Tropics rainforests. Sampling from under scattered or single dead trees from Garrawalt rainforests yielded 70.8 percent detections as compared with 24.3 percent from the remainder of the Wet Tropics rainforests. However, while the detection results from under apparently healthy rainforest were similar to those from under both dead patches and from areas with a few deaths throughout most of the Wet tropics area, the level from under apparently healthy rainforest at Garrawalt was 57.1 percent. This was much lower than from the other situations in that area. During the survey there were 215 sites sampled in virgin forest unaffected by

roads throughout the whole wet tropics area, with 81 of these at Garrawalt. For the non-Garrawalt virgin rainforest sites there was a 15.7 percent detection rate, a level similar to the detections from under comparable logged rainforest.

Table 4. Detection of *Phytophthora cinnamomi* from rainforest soils of the Wet Tropics World Heritage area of Queensland showing totals and data arranged by forest health or by forest history status[1].

	Samples		Sites		Isolates of
	Total	*P. cinnamomi*	Total	*P. cinnamomi*	*P. cinnamomi*
TOTALS					
Garrawalt	250	182	131	92	1,674
Other Parts of the Wet Tropics	1,153	192	683	141	1,618
Total for the Wet Tropics	1,403	374	814	233	3,292
FOREST HEALTH					
Dead Patch					
Garrawalt	146	117	34	30	1,105
Other Parts of the Wet Tropics	425	67	95	23	666
Total for the Wet Tropics	571	184	129	53	1,771
Scattered or single deaths					
Garrawalt	51	34	48	34	247
Other Parts of the Wet Tropics	201	31	111	27	229
Total for the Wet Tropics	252	65	159	61	476
Healthy					
Garrawalt	53	31	49	28	322
Other Parts of the Wet Tropics	470	88	424	86	692
Total for the Wet Tropics	523	119	473	114	1,014
FOREST HISTORY					
Logged Forest					
Garrawalt	51	29	43	26	164
Other Parts of the Wet Tropics	215	32	146	24	198
Total for the Wet Tropics	266	61	189	50	362
Logged Forest With Road Effect					
Garrawalt	8	4	7	4	39
Other Parts of the Wet Tropics	358	72	260	58	694
Total for the Wet Tropics	366	76	267	62	733
Virgin Forest					
Garrawalt	191	149	81	62	1,471
Other Parts of the Wet Tropics	354	41	134	21	350
Total for the Wet Tropics	545	190	215	83	1,821
Virgin Forest With Road Effect					
Garrawalt	0	0	0	0	0
Other Parts of the Wet Tropics	54	13	14	5	134
Total for the Wet Tropics	54	13	14	5	134

[1.] This table does not include all the data included in Table 1.

While a number of *Phytophthora* taxa other than *P. cinnamomi* were detected from tropical rainforest soils, the total number of isolates of those was considerably lower than the number of isolates of *P. cinnamomi*. It may have been expected that the high detection of *P. cinnamomi* would have 'swamped' the other taxa. However, the results from Dalrymple Heights, where 65 percent of sites yielded that fungus, and where all taxa with the exception of *P. nicotianae* Breda de Haan var. *parasitica* (Dastur) G.M. Waterh. were detected, indicate that 'swamping' may not have occurred. The records for *P. katsurae* and *P. meadii* were

apparently the first for those species from Australia and those of *P. citricola*, *P. cryptogea*, and *P. heveae* the first from Queensland. In addition to the new Australian records of *P. katsurae* and *P. meadii*, a number of the taxa were reported for the first time from native vegetation in Australia (*P. boehmeriae*, *P. heveae*, and *P. palmivora*) or from Queensland (*P. citricola*, *P. cryptogea*, and *P. nicotianae* var. *parasitica*).

Phytophthora palmivora is not uncommon in horticulture in Queensland (Forsberg 1985; Simmonds 1966). The apparent absence of *P. nicotianae* var. *nicotianae* from the north Queensland area is unexpected because of its occurrence in the Mareeba tobacco area (O'Brien and Davis 1981) and in mangroves of the Normanby River, Princess Charlotte Bay (Weste *et al*. 1982). While there may not be any of the known hosts for these *Phytophthora* taxa in the tropical rainforests of Queensland, they could occur on other members of the plant families that include known hosts. For example, *P. heveae* is known to cause disease of *Heveae* (Euphorbiaceae), *Mangifera* (Anacardiaceae), *Persea* (Lauraceae), *Psidium* (Myrtaceae), and *Theobroma* (Sterculiaceae) (Stamps 1978), and although none of these genera occur in Queensland rainforests, all the families are represented (Francis 1970, Hyland 1983 and Queensland Department of Forestry records).

Soil analyses

As discussed by Broadbent and Baker (1975), the soils in southern where *P. cinnamomi* causes severe disease in native vegetation are generally infertile. These areas include the jarrah (*Eucalyptus marginata* Donn. ex Smith) forests and a number of heathland and forest communities in Western Australia, areas such as the Brisbane and Grampian Ranges, Wilson's Promontory, and the Gippsland forests of Victoria and heathlands, dry sclerophyll forests and disturbed rainforests of Tasmania (Kennedy and Weste 1986; Marks *et al*. 1975; Peters and Weste 1997; Podger and Brown 1989; Podger *et al*. 1990; Shearer 1990; Shearer and Tippett 1989; Weste 1986; Weste and Ashton 1994; Weste and Kennedy 1997; Wills 1992). On the other hand, by contrast to those areas which are regarded as conducive to disease, there are areas in subtropical eastern Australia where suppressive soils have been identified under avocado plantations on basaltic soil sites, which previously carried sub-tropical rainforest (Broadbent and Baker 1975).

A number of differences can be seen in soil analyses between the basaltic and non-basaltic soils of the tropical rainforests of Queensland (Table 5). Analyses of a number of samples of Garrawalt and Dalrymple Heights soils indicated that those soils were at the acidic end of the range for non-basaltic soils. Both total and available phosphorus and also calcium are also comparatively low for non-basalt soils (Table 5, and data that is not shown for Dalrymple Heights). Carbon levels of the Garrawalt and Dalrymple Heights soils were high by comparison with the published data for non-basalt soils, and were somewhat comparable to the data for basalt soils. While the data in Table 5 shows that the upper range of total nitrogen in the Garrawalt soils exceeded that for basalt soils, the range of total nitrogen for 17 of the 20 samples analysed was from 2,320 to 6,500 ppm.

Broadbent and Baker (1975) indicated that sub-tropical basalt soils which are suppressive to *P. cinnamomi* have a high content of organic matter, sometimes with a deep humus layer, high exchangeable calcium, a pH of 5.5 to 7.0, high levels of both ammonium and nitrate nitrogen, and high biological activity. They reported these characteristics from under rainforests or from adjoining avocado plantations which had received regular cover cropping, calcium applications, and applications of poultry manure and fertilisers. The data in Table 5 for the Garrawalt soils, and also data for Dalrymple Heights soils, show that soils where rainforest patch deaths have occurred are more acid and have lower exchangeable calcium levels than do the suppressive soils of south eastern Queensland.

Table 5. Soil analyses of Garrawalt soils, and for comparison, a summary of soil analyses[1] from basaltic and non-basaltic tropical rainforest soils of Queensland. Some characteristics reported for sub-tropical rainforest soils suppressive to *P. cinnamomi* under avocados are also included**.**

Property	Garrawalt analyses	Range of published data		Characteristics of suppressive soils
		Non-basalts	Basalts	
pH	4.1 – 5.1	4.4 – 6.5	5.0 – 6.9	5.5 – 6.5
Conductivity	0.018 – 0.060	0.050 – 0.146	0.045	0.07 – 0.26
% silt and clay	35 – 43	29 – 75	57 – 88	
Boron (available)	1.0 – 1.6			
Phosphorus (total) ppm	123 – 323	30 – 700	1,220 – 4,500	
Phosphorus (acid) ppm	6 – 11	3 – 25	5 – 146	4.9
Carbon[3] %	3.1 – 6.5	1.7 – 4.2	4.2 – 8.7	
Nitrogen (total) ppm	2,320 – 13,100	1,100 – 3,430	3,450 – 7,900	6,170 – 6,730
Nitrogen (ammonium) ppm	13 – 202			10 – 91
Nitrogen (nitrate) ppm	0 - 23			10 – 38
Na meq %	0.05 – 0.37	0.04 – 0.21	0.14 – 0.35	0.2 – 0.8
K meq %	0.31 – 0.56	0.06 – 0.56	0.19 – 1.71	0.46 – 1.47
Ca meq %	1.03 – 2.11	0.20 – 13.88	2.37 – 28.14	21.2 - 22.9
Mg meq %	1.15 – 1.78	0.34 – 4.19	0.80 – 5.07	5.1 – 6.0
Sulphur ppm	8 – 1,428	0.020 – 0.056	0.054 – 0.104	

[1.] Soil analysis data summarised from Teakle (1950), Gilman (1976), Isbell *et al*. (1976), and Murtha (1986).
[2.] Avocado plantation soils at Mount Tamborine south of Brisbane (Broadbent and Baker 1975).
[2.] Walkley-Black.

Response of tree families and species

Plant families such as Lauraceae, Myrtaceae, and Proteaceae contain species highly susceptible to *P. cinnamomi*, with many Australian host species in the latter two families. There a number of species of Lauraceae in the list of confirmed hosts (Table 3) and in the presumed hosts as shown by high mortalities in the field plots as discussed earlier (*Cinnamomum oliveri*, *Cryptocarya cinnamomifolia*, *C. corrugata*, and *C. glaucescens*). However, there were several other Lauraceae which did not show any deaths, or for which the proportion of trees that died was low (ie, *Cryptocarya angulata* C.T. White, *C. mackinnoniana* F. Muell. and *Endiandra* sp. aff. *E. muelleri* Meissn.). The Lauraceae was the most numerous tree family in the observation plots and mortalities in the family averaged almost 12 percent. However, for the second most numerous family (Myrtaceae), there was only about 4.5 percent loss. *Syzygium wesa* Hyland was the only myrtaceous species, present

in substantial numbers, to have a mortality figure close to the study average (9 of 91 trees). While there was only a total of 140 trees in the Proteaceae, mortality for that family was over 9 percent. While the proteaceous species *Carnarvonia araliifolia* and *Bleasdalea bleasdalei* (F. Muell.) A.C. Scott both showed high mortality, another, *Cardwellia sublimis* F. Muell. only had 2 deaths out of 55 individuals.

The possible role of feral pigs in spread of *P. cinnamomi*

At Dalrymple Heights, where most of the samples were from under virgin rainforest, heaviest detection was associated with areas of recent feral pig activity. These results do not indicate if feral pigs are vectors of the fungus, or if they are attracted to naturally wetter areas that favour the fungus or to areas where tree death has altered the soil moisture conditions. However, the report by Kliejunas and Ko (1976) from Hawaii established that feral pigs do have the potential to spread *P. cinnamomi* in native forest. At Garrawalt there were signs of extensive soil disturbance from past feral pig activity across the slopes where scattered dead rainforest patches occurred. Crediton was the only major study area that was essentially free of feral pigs, and there, heavier detection was recorded for logged than for virgin rainforest and there was an increase in detection if either forest type was affected by roading. Thus, it appears that in areas free of feral pigs, activities such as logging and roading probably spread the fungus, but this effect was not obvious in areas where feral pigs are present, possibly because they are such efficient vectors of the fungus. I believe that there is little doubt that feral pigs are an important, but definitely not the only, factor in the spread of *P. cinnamomi* within tropical rainforest areas of Queensland.

Much of the disease in the Dalrymple Heights area appears to originate from sites on or near the ridge tops, sites that are subject to severe feral pig disturbance, even in otherwise undisturbed virgin rainforest. Possibly it could be argued that such disturbance would be sufficient to initiate disease due to a pre-existent fungus such as *P. cinnamomi*. Over the duration of the soil-sampling program 1,897 sites were sampled on one or more occasions. Data recorded during sampling reveals that pig activity was recorded at 34 percent of the sites sampled during the full survey (Table 6). However, for Dalrymple Heights the recorded pig activity was much higher at over 61 percent. It is probable that many of the 'Not recorded' sites were free of obvious signs of feral pigs, making those percentages representative of the level of pig activity in the areas that were sampled. During a 3-year period during which nearly 74 percent of the samples were collected, there were only 6 months (all non-consecutive) when there were no samples, effectively eliminating a seasonal bias in the sampling.

Pavlov *et al*. (1992) reported that 80 percent of 209 transects showed evidence of feral pig activity in 1988, concluding that feral pigs occurred throughout the rainforests in the Cooktown-Townsville region. In more recent studies Laurance and Harrington (1997) studied feral pig activity over a range of forest habitats in the Wet Tropics area, late in the dry season (October to December) in 1994 and 1995. They showed that a little over one eighth of the rainforest sites had evidence of feral pig activity. This figure was only about half of the recorded pig activity shown for the balance of the *Phytophthora* survey sites in Table 6. In another part of their study Laurance and Harrington found that just over 21 percent of 402 plots in sclerophyll forests in the Wallaman Falls area had feral pig damage (this latter study did not include rainforests). The Wallaman Falls area presumably adjoins the rainforests of Garrawalt where 35 percent of the sites were observed to have evidence of pig activity (Table

6). In one of their studies Laurance and Harrington (1997) found higher activity (about 50 percent of plots) in Type 1[13] wet sclerophyll forest fringing Wet Tropics rainforests. In the other study, while the sites showing feral pig activity in Type 1 forest was only 25 percent, feral pig activity was present in over 43 percent of the Type 4[14] sites. Based on data from another study on the activity of feral pigs in forests of the Wet Tropics World Heritage Area, Mitchell and Mayer (1997) observed that feral pig diggings occupied just over 4 percent of 144,500 m^2 in 237 transects 100 to 3,000 m long and 5 m wide. Diggings by feral pigs were recorded at 67 percent of the 237 transects. In those studies there were comparisons between highland rainforest at both Paluma and Kirrama and there was no difference in the total area of pig diggings (2.0 to 2.4 percent of area) between the two forest types at either locality.

Even if *P. cinnamomi* does not pose a direct threat to these open wet sclerophyll forest types, such sites may act as a 'staging area' from which the fungus can be subsequently spread into rainforest areas by the feral pigs.

Is *Phytophthora cinnamomi* native or introduced?

Some Australian authors (Pratt and Heather 1973; Shepherd 1975) considered that *P. cinnamomi* was native to, and apparently widespread in eastern Australia, while others (Marks *et al*. 1972; Newhook and Podger 1972; Weste and Marks 1974) disagreed with this view. The factors, which have been used to support the hypothesis that *P. cinnamomi* indigenous[15] to eastern Australia, are;

- the 'reported' widespread occurrence in native forests in eastern Australia,
- its recovery from an apparently remote area in New South Wales,
- the co-occurrence of A_1 and A_2 mating types,
- the 'resistance' of flora in parts of eastern Australia, in particular the rainforest flora of Queensland,
- a suggested role of *P. cinnamomi* in the determination of vegetation distribution,
- the lack of evidence of known soil transport into an affected area,
- the suggestion that disease is initiated by disturbance, and
- the presence of highly suppressive soils in Queensland.

It is possible to consider the occurrence, and presumed impact, of *P. cinnamomi* in tropical rainforests of Queensland to test the indigenous hypothesis.

Certainly the fungus is widespread through the tropical rainforests of North Queensland, and occurs in some 'remote' locations. However, as only relative small quantities of infested soil can transmit the fungus[16], and as feral pigs can undoubtedly transmit the fungus, the occurrence of *P. cinnamomi* in 'remote' virgin forest areas, away from logging or roading, is not surprising.

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[13] Wet sclerophyll forest dominated massive rose gums (*Eucalyptus grandis* W. Hill ex Maiden) with mainly grasses and sedges in the understory (Harrington and Sanderson 1994).

[14] Wet sclerophyll forest, somewhat drier than Type 1, dominated by several tall tree species (*Eucalyptus resinifera* Smith, *Corymbia intermedia* (R. Baker) K. D. Hill & L. A. S. Johnson, *Syncarpia glomulifera* (Smith) Niedenzu) with a grassy understory (Harrington and Sanderson 1994).

[15] Indigenous – originating in and characterising a particular region or country; native (*The Macquarie Dictionary New Budget Edition*, 1990).

[16] The association of *P. cinnamomi* with both walking trails and animal tracks in Tasmania and in Western Australia leave little doubt that soil carried on the boots of hikers, or on animals (ie, kangaroos, wombats and even birds), is able to transmit the fungus (Barker 1994; Podger *et al*. 1990; Podger *et al*. 1996; Wills 1992).

There was not any evidence of disease in virgin rainforest of the Dalrymple Heights area in 1970 aerial photographs. This, coupled with reports from local sources that there were only a few areas of deaths prior to 1970, would indicate either some 'trigger' event that caused a flare-up of a pre-existing problem or the comparatively recent arrival of the cause of the disorder. In a truly undisturbed area, a likely 'trigger' for P. cinnamomi would be rainfall, either very high through a direct effect on P. cinnamomi, or very low by stressing trees with a diseased root system. The effect of rainfall would be enhanced if a wet period were followed by dry conditions as reported for *Pinus elliottii* Engelm. in southeastern Queensland (Oxenham and Winks 1963).

Rainfall records for Dalrymple Heights indicate six wet months (December to May inclusive with both average and median rainfall values for the month greater than 100 mm) and six dry months. The 'wet' season December 1973 to May 1974 had the most rainfall recorded at Dalrymple Heights over the 45-year recording period to that time with a total of 3,757 mm compared with the 59-year median value of 1,676 mm (Figure 9). This total has only been exceeded once, in 1990/1991 when 4,395 mm was recorded. The 1973/1974 'wet' season was followed by a much below average 'dry' season (249 mm compared to the 59-year median of 392 mm). However, there were earlier occasions at Dalrymple Heights when very wet periods were followed by very dry periods. For example, December 1945 to May 1946 (2,191 mm) was followed by the driest 'dry' season ever recorded (83 mm). During the 'wet' season of 1967 to 1968 the rainfall totalled 2,115 mm followed by a 'dry' season of 186 mm.

There is no evidence to suggest that either of those wet/dry periods induced rainforest deaths similar to those that followed, or were at least associated with, the 1973/1974 seasons. During the four consecutive 6-month periods from December 1975 to November 1977 the rainfall totals at Dalrymple Heights were 3,425 mm, 483 mm, 2,114 mm and 194 mm. These wet and dry sequences may have played a role in the continuing spread of disease as was recorded by the aerial photography program.

It is interesting to speculate what was the effect of the more recent wet periods of 1988/1989 and 1990/1991. They were followed by a very dry 5-year period that included the lowest rainfall 'wet' season on record for Dalrymple Heights. This was 1991 when with only 604 mm of rain was recorded (Figure 9).

Shepherd (1975) reported that the A_1 and A_2 mating types of *P. cinnamomi* occurred in roughly equal proportions in Australia north of 20° S latitude (ie. north of Bowen) with the proportion of A_1 isolates declining towards southern Australia.

This is certainly not true for the rainforests of tropical Queensland where the recorded ratio of A_1 to A_2 mating types was 16 to 4,413. Even if the presence of the A_1 mating type in parts of North Queensland does suggest that *P. cinnamomi* is native, the apparent absence of the A_1 mating type from the whole of the Eungella Tableland would suggest that it was introduced to that area at least.

There was the claim that the Indo-Malayan component of the Australian flora is 'on the whole highly resistant to *P. cinnamomi*' (Shepherd 1975). This was based on absence of disease in

rainforest and wet sclerophyll areas, and was not substantiated. The evidence from Dalrymple Heights and Garrawalt must cause the rejection of this claim.

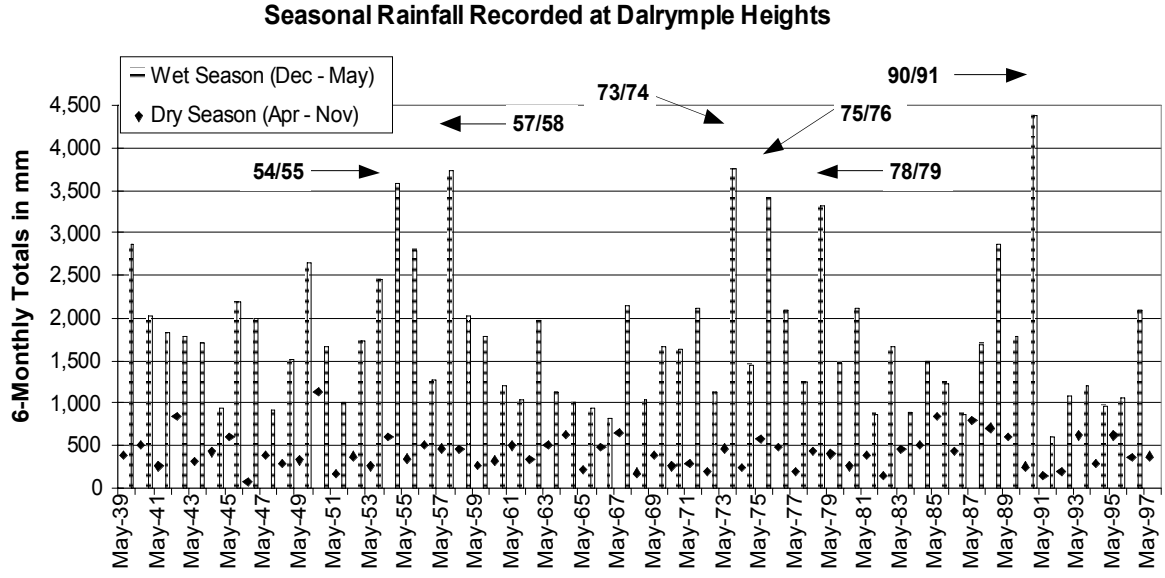

Figure 9. Seasonal rainfall records for the Dalrymple Heights Post Office for the years from 1939 to 1997. The six month 'wet' season was defined from months with both average and median rainfall of over 100 mm.

Disturbance has been suggested as being responsible for disease (Pratt *et al*. 1973), this influence apparently operating through raised soil moisture levels as result of increased run off following roading and decreased transpiration following logging. Disturbance *per se* does not appear to be a possibility on the Eungella Tableland because road construction to and through the Dalrymple Heights area about 1937 and clearing and logging of rainforests at Dalrymple Heights (starting before 1947) did not have an effect until, perhaps, the 1970 to 1973 period.

Reports from long-term residents, the lack of obvious disease in 1970 aerial photos, the presence of healthy forest in 1973 in areas where deaths were first found in 1975, and the obvious spread of visible disease during the study period, all suggest significant spread of *P. cinnamomi* through the Dalrymple Heights area, possibly from the mid 1960's. The fungus could have been introduced to Dalrymple Heights on logging machinery that had been previously used in farming areas on the coast. Alternatively, if *P. cinnamomi* was originally present on the Eungella Tableland, it may have been spread through logging and clearing. However it was originally introduced and/or spread, it is probable that after initial establishment at a few locations feral pigs played a major role in further spread throughout the rainforest.

Conservation implications

Apart from the direct effect on timber production in the jarrah (*Eucalyptus marginata*) forests of southwestern Australia there are costs associated with managing the forest in the presence of *P. cinnamomi*. For example, the estimated expenditure on 'dieback' by Government and

industry in Western Australia for 1989 was $3.37 million dollars, comprising $0.41 million for mapping and detection, $1.69 million for disease prevention, and $1.27 million for research (Shearer 1990). The closure of, or restricted access to, areas considered to be at risk within the jarrah forest clearly affects a wide range of forest users in addition to those directly involved in management of the forest itself. The jarrah dieback disease also has a significant effect on the mining industry of the area.

It is clearly recognised in Western Australia, and elsewhere in southern Australia, that there are considerable conservation and ecological implications associated with the presence of *P. cinnamomi* and/or other species of *Phytophthora* in native vegetation. Davison and Shearer (1989) commented that it was on conservation values, in contrast to timber and water production, that *Phytophthora* species have had the greatest impact. The most obvious effect has been the direct attack on the flora of affected areas, often in communities containing endangered species in Tasmania (Barker 1994; Barker and Wardlaw 1995), in Victoria (Peters and Weste 1997; Weste and Ashton 1994; Weste and Kennedy 1997) and in Western Australia (Lamont *et al*. 1995; Shearer 1990; Shearer and Dillon 1996a; Shearer and Dillon 1996b; Wills 1992). Thus there need to be changes to the management of areas perceived to be 'at risk' or specifically for the protection of rare threatened plant species that are susceptible to, and potentially threatened by, *P. cinnamomi* (Barker 1994; Barker *et al*. 1996; Podger *et al*. 1996; Shearer and Dillon 1996a).

In recognition of the threat to native vegetation, *P. cinnamomi* has been listed as a key threatening process under the Commonwealth *Endangered Species Protection Act 1992*. As a consequence of that listing, the Australian Nature Conservation Agency, now Environment Australia, contracted the Western Australian Department of Conservation and Land Management to prepare a draft National Threat Abatement Plan for *Phytophthora*. Meetings were held throughout Australia last year to assist in the formulation of the draft Threat Abatement Plan, release of which is imminent.

The distribution of *P. cinnamomi* throughout the wet tropics area was shown in Figures 3 and 4, and summaries of samples and sites at Garrawalt and throughout the remainder of the wet tropics rainforests which were positive for *P. cinnamomi* were given in Table 2. A more detailed summary of the isolation results based on rainforest history is presented in Table 7. *Phytophthora cinnamomi* was detected from between 16 and 36 percent of sampled sites in all the rainforest history categories, except for planted sites. The largest numbers of sites were in the logged and virgin rainforest categories ± the effect of roads or tracks. In both cases *P. cinnamomi* was detected from a higher percentage of sites that had been affected by roads or tracks, with this effect being particularly pronounced for the virgin rainforests (Table 7).

During the soil survey program, *P. cinnamomi* was detected from under healthy and/or diseased rainforests at elevations ranging from near sea level to heights of over 1,000 m. It was found in lowland rainforest at Cowley Beach (10 to 40 m elevation in Type 2A[17] rainforest) and near Bartle Frere (at about 40 m elevation in Type 1A[18] rainforest).

Table 7. Detection of *Phytophthora cinnamomi* from rainforest soils of the Wet Tropics World Heritage area of Queensland showing data arranged by forest history[1].

	Samples		**Sites**		**Isolates of**
	Total	***P. cinnamomi***	**Total**	***P. cinnamomi***	***P. cinnamomi***
Logged Forest					
Garrawalt	51	29	43	26	164
Other Parts of the Wet Tropics	215	32	146	24	198
Total for the Wet Tropics	266	61	189	50	362
Logged Forest With Road Effect					
Garrawalt	8	4	7	4	39
Other Parts of the Wet Tropics	358	72	260	58	694
Total for the Wet Tropics	366	76	267	62	733
Planted Forest					
Garrawalt	0	0	0	0	0
Other Parts of the Wet Tropics	9	6	9	6	74
Total for the Wet Tropics	9	6	9	6	74
Planted Forest With Road Effect					
Garrawalt	0	0	0	0	0
Other Parts of the Wet Tropics	10	6	6	5	31
Total for the Wet Tropics	10	6	6	5	31
Virgin Forest					
Garrawalt	191	149	81	62	1,471
Other Parts of the Wet Tropics	354	41	134	21	350
Total for the Wet Tropics	545	190	215	83	1,821
Virgin Forest With Road Effect					
Garrawalt	0	0	0	0	0
Other Parts of the Wet Tropics	54	13	14	5	134
Total for the Wet Tropics	54	13	14	5	134

[1.] This table does not include data that was not properly classified at the time of sampling.

Phytophthora cinnamomi was also found at elevations above 1,000 m at Mount Lewis, Mount Windsor and the Ravenshoe area in Type 9[19] rainforest and in the Herberton area in Type 5A[20] rainforest. *Phytophthora cinnamomi* was isolated from under 30 dead patches in the Garrawalt area at elevations between 560 and 620 m elevation in Type 8 rainforest (Table 8). The rainforests of the Dalrymple Heights area are a similar forest classification (J.G. Tracey personal communication). All but one of the 53 dead patches associated with *P. cinnamomi* in the Wet Tropics Region occurred at elevations ranging from 400 to 1,200 m, the exception being one patch at 40 m in Type 1A rainforest in the Bartle Frere area (Table 8). The other localities where *P. cinnamomi* was found in dead rainforest patches in the Wet Tropics Area were Dinden, Kirrama, Kuranda, Mount Lewis, Mount Spec and Mount Windsor (Table 8).

[17] Rainforest types from Tracey and Webb (1975) and Tracey (1982);
2A = mesophyll vine forest (MVF) of very wet and wet lowlands and foothills.
[18] 1A = complex mesophyll vine forest (CMVF) of very wet and wet lowlands and foothills.
[19] 9 = simple microphyll vine-fern forest (MFF) of cloudy wet highlands.
[20] 5A = complex notophyll vine forest (CNVF) of very wet and wet lowlands and foothills.

Table 8. Location and some characteristics of the rainforest areas in the Wet Tropics Region where *P. cinnamomi* was detected under dead patches of rainforest.

Locality	Forest Type[1]	Elevation (m)	P. cinnamomi		
			Samples	**Patches**	**Isolates**
Bartle Frere	1A	40	2	1	6
	2A	560	1	1	6
Dinden	2A	400	1	1	2
Garrawalt	8	560	2	2	13
	8	580	2	1	51
	8	600	70	14	613
	8	620	18	8	202
	8	640	17	4	125
	8	660	1	1	22
Kirrama	2A	600	4	3	19
	8/9	800	1	1	14
Kuranda	2A	560	9	2	96
Mount Lewis	9	920	3	1	19
	9	960	17	5	226
	9	1000	1	1	4
	9	1200	6	1	95
Mount Spec		900	3	1	20
Mount Windsor	8	960	6	1	65
	9	1000	6	2	51
	9	1040	3	1	7
	9	1080	1	1	12
Total for Wet Tropics			**174**	**53**	**1,668**

[1.] Classification of Tracey and Webb (1975) and Tracey (1982).
1A = complex mesophyll vine forest (CMVF) of very wet and wet lowlands and foothills.
2A = Mesophyll vine forest (MVF) of very wet and wet lowlands and foothills.
8 = simple notophyll vine forest (SNVF) of cloudy wet and moist highlands and uplands.
9 = simple microphyll vine-fern forest (MFF) of cloudy wet highlands.

The data presented in Table 7 and in Figures 3 and 4 clearly indicates that there was a widespread distribution of *P. cinnamomi* throughout the Wet tropics World Heritage Area at least 16 years ago. Dead patches occurred principally, but not exclusively, at elevations above 550 m in Types 8 (SNVF) and 9 (MFF) rainforests. The continuing widespread activity of feral pigs throughout the region (Laurance and Harrington 1997; Mitchell and Mayer 1997) undoubtedly resulted in further spread of *P. cinnamomi*, even without consideration of additional spread due to human activities in the rainforests and adjoining areas. The present situation with regard to the distribution and impact of *P. cinnamomi* in rainforests of the Wet tropics World Heritage Area is obviously unknown.

In a recent report from Victoria, the long-term effect of disease in open forests, woodlands and heathlands was discussed (Weste 1997). Those studies, spanning 20 to 30 years, showed three phases in the development of dieback in native vegetation. The first, aggressive, phase lasted one to three years and was characterised by high populations of *P. cinnamomi* and the death of 50 to 75 percent of the species. The density and distribution of *P. cinnamomi* were at a maximum at the disease front. In environments conducive to the pathogen, large mature trees died suddenly with all leaves intact, whereas in less conducive conditions branch dieback occurred first and trees died about three years later. During the second phase, which lasted about 10 years, diseased sites were rapidly colonised by resistant species and the pathogen populations fell. During this phase, regenerating susceptible species rapidly became

infected and died. The third, or declining phase of disease, began after a period of more than 10 years. This was characterised by a larger decline in pathogen populations and in their distribution and there was regeneration and survival of susceptible species. However, there was a resurgence of disease in some sites after the conducive summer of 1995/96. Weste concluded by suggesting that the re-appearance, in the presence of *P. cinnamomi*, of susceptible plant species previously annihilated by this pathogen may initiate a new disease cycle provided conditions are conducive. She emphasised the need for long-term monitoring of population density and distribution of the pathogen and the re-appearance of susceptible plant species in a range of communities to determine the long-term impact of the pathogen, particularly in relation to endangered species.

There has also been recognition that the occurrence of native vegetation deaths due to *P. cinnamomi* has impacts much wider than the effect on the flora itself. For example, studies in Victoria have shown that there were significantly lower populations of *Antechinus stuartii* in dieback-affected sites (Newell and Wilson 1993). As discussed by Wills (1992) and Shearer *et al*. (1991) the changes in availability of resources and in habitat, due to the alteration of community structure and composition, may affect associated groups of animals (eg. pollinators and grazers) and soil biota. In a study on the abundance of ground-dwelling invertebrates in a Victorian forest affected by *P. cinnamomi*, Newell (1997) found that significant differences on the basis of infection were uncommon. However, where differences were identified, elevated abundances were more commonly observed in sites infested by *P. cinnamomi*. Studies in the jarrah forest have shown that dieback affected areas of forest provided less suitable reptile habitats than did healthy forest (Nichols and Bamford (1985) and also that dieback sites supported few bird species and have low bird densities and diversity (Nichols and Watkins 1984).

The studies that were carried out by the Queensland Forestry Department certainly did not consider impacts of the disease, other than the direct effect on the rainforest tree component. While those studies were of limited duration in time, they may provide a basis for longer-term consideration of the ecological impact of this disease in the tropical rainforests of Queensland. There would seem to be significant value in attempting to re-visit and re-assess these old Queensland Forestry Department *Phytophthora* observation plots, especially those in the Garrawalt and Dalrymple Heights area.

Another plot of interest is one maintained by CSIRO Division of Forest Research at Garrawalt in Burgoo Logging Area. This plot was started in healthy rainforest in 1975 (K.D. Sanderson. personal communication); and while *P. cinnamomi* was first detected in the plot during 1976, the first deaths of understory and tree species were not recorded until 1977. Further deaths were noted at the biennial assessments in 1979, 1981, and 1983. In all, a total of nearly 31 percent of trees in the plot died between 1977 and 1981 (G.C. Stocker and K.D. Sanderson personal communications). Following cyclone damage to the plot in 1986, the original patch had extended further by 1987 when another patch was observed. At the most recent assessment of this plot in 1991, there were no more deaths and there was evidence of recovery. The plot is due for re-assessment later this year (K.D. Sanderson personal communication). Another of the CSIRO sample plots was established in healthy rainforest at Mount Lewis in 1973 (K.D. Sanderson personal communication). This plot, assessed biennially from 1973 to 1991, was found to have a 30-m diameter dead patch intruding into one side in 1987. This patch extended between 1987 and 1989 and had spread further by 1991. However, there was nothing observed at the next, and most recent, measure in 1996.

The disease situation at Dalrymple Heights has been relatively inactive over the past 8 or 9 years with affected areas being recolonised (S.G. Pearson personal communication). While there have been some dead patches noted from aerial and ground inspection, these have mostly been associated with shallow skeletal soils over granite and were presumably in response to the drought years of recent times (S.G. Pearson personal communication and see also Figure 9). There have been small pockets of deaths of *Syzygium* at the heads of creeks on the Tableland area, and deaths of *Calophyllum australianum* F. Muell. along the edge of walking tracks in the Finch Hatton Gorge area[21]. In the absence of isolations for *Phytophthora* species, the cause of these deaths is uncertain.

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APPENDIX 1.

Theoretical Considerations Of The Soil-Pore Size Necessary For Passive And Active Movement Of *Phytophthora Cinnamomi* Zoospores.

Newhook *et al*. (1981) summarised studies on the movement of *P. cinnamomi* zoospores in 'ideal' soils based on glass beads, coarse sand and sand/soil mixtures. They concluded that motility was scarcely affected by static confinement in, or passive movement through, the various media. However, passive movement was dependent on the presence of a continuous system of pores with neck diameters about 25 to 30μm, a size somewhat larger than the zoospore body itself (15 X 6 μm) and about the length of the zoospore with flagella extended (30 μm). They showed that zoospores were able to move autonomously in particulate systems, with or without chemotropism, but that such movement was greatly dependent on the proportion of pores with necks as large as, or larger than, the wavelengths of the swimming pathway. *Phytophthora cinnamomi* zoospores traverse a helical swimming pathway that has an amplitude of 40 to 50μm and a wavelength of 170 to 190μm (Allen and Newhook 1973).

In an attempt to relate the data of Newhook and co-workers to matric soil water potential, the equation of Griffin (1972, p. 78) can be used. The effective soil pore radius ('*r*' in cm), ie. the

[21] *Phytophthora cinnamomi* was not isolated from 7 sites in the Gorge area sampled in December 1977.

pore-neck radius retaining water in drying soils and the widest pore radius filled with water in wetting soils shows the following relationship to matric water potential ('*h*' in cm H_2O).

$$h = -\frac{0.15}{r}$$

The relationship between soil water potential and effective soil pore diameter is expressed in Appendix Table 1. This clearly shows that the soil pores of diameters large enough to allow movement of zoospores of *P. cinnamomi* are only filled with water at soil water potentials of between -0.12 and -0.02 bar, ie. in very wet soil. Based on these figures, and on the data of Newhook and co-workers, the minimum soil water potential for passive zoospore movement in drying soils would only be from 0 to about -0.12 bar matric potential (ie. 24 μm pore neck diameter) and active zoospore movement would only occur down to about -0.015 bar matric potential (ie. 190 μm pore neck diameter). However, in wetting soils the effective pore diameter values relate to maximum pore diameters, rather than pore neck diameters, and hence matric potential values closer to 0 (ie. saturated soil) would be required for both passive and active zoospore movement.

Appendix Table 1. Relationship between the matric soil water potential and the effective soil-pore diameter that is filled with water.

Matric soil water potential (bar)	Soil pore diameter (μm)
-0.0100	294.20
-0.0155	190.00
-0.0230	128.00
-0.1000	29.42
-0.1226	24.00
-0.2000	14.71
-0.3000	9.81
-0.5000	5.88
-1.0000	2.94

Despite the limitations involved in converting the data of Newhook and co-workers to matric potential, it is obvious that for zoospore movement, either passive or autonomous (including chemotaxis to susceptible host roots), soil water potentials must be within the very wet range of 0 to -0.12 bar. When soils are at field capacity, soil water potentials range from -0.1 to -0.5 bar, ie. soil pores filled with water would range from about 29 down to 5 μm in diameter.

8 DETECTION AND IDENTIFICATION OF *PHYTOPHTHORA CINNAMOMI*

DRENTH, A., WAGELS, G., SMITH, B.N., MACLEAN, D.J. and IRWIN, John

The *Phytophthora* problem

Phytophthora incited diseases cause severe devastation to a great variety of tree, ornamental, crop plant species, and native ecosystems. Although the severity of disease can vary greatly from year to year, depending on differences in climatic conditions (e.g. temperature, waterlogging) and cultivation practices, good diagnostic procedures are essential for proper identification of the causal agent and identify potential problems prior to widespread outbreaks of disease and quarantine purposes. Management options to control *Phytophthora* are rather limited in many situations. Resistance or tolerance is often used in field crops but this is not always a valid option in forestry, nursery, fruit crops, or native vegetation. The use of chemicals is limited to drenching the soil with metalaxyl or injection of phosphonates which has proven to be successful to combat *Phytophthora* root rot in horticultural crops such as avocado and pineapple. Phosphonates and metalaxyl do not have a curative effect. Therefore, unless these compounds are continuously re-applied the *Phytophthora* root rot reoccurs very quickly. In the nursery industry, which is increasingly moving towards container grown plants, disease free planting material and disease free soil are the sole means of producing plants free of *Phytophthora*. In native vegetation, the cause of dieback needs to be first unequivocally proven in each case and when *Phytophthora* is suspected to be the culprit correct identification of the *Phytophthora* species is important. Management of diseases in native ecosystems is rather limited with prevention to limit further spread of these soilborne pathogens the main strategies.

The genus *Phytophthora* contains many different species which differ in their ability to damage different hostplants. For example, host specific and homothallic species such as *P. sojae* can be easily identified by distinctive symptomatology in infected soybean roots and stems. By contrast, many *Phytophthora* species with wider host ranges and which cause generalized rotting can only be identified by first isolating the pathogen in pure culture, by conducting host preference tests, or by baiting and the conduct of laboratory tests to induce spore formation; all of which are tedious procedures not amenable to mass screening of samples. In addition, a limited number of morphological characters are available for the identification of many *Phytophthora* species, and confusion and mis-identification can easily occur.

Diagnostics of *Phytophthora*

Soil samples are routinely submitted to diagnostic laboratories for testing for the presence of *Phytophthora* spp. Diseased plant samples are also submitted to diagnostic laboratories for disease identification and *Phytophthora* is often the causal organism, both from nursery and field

Patch Deaths in Tropical Queensland Rainforests, P. Gadek (ed)
Report, Rainforest Cooperative Research Centre, Cairns, 1999

situations. The conventional diagnostic tests currently available for the diagnosis of *Phytophthora* in plants and the detection of *Phytophthora* in soil rely on baiting, isolation of the fungus and growing it in pure culture prior to morphological identification. This is a time consuming process.

In order to improve the efficiency and accuracy of the detection of *Phytophthora* alternative methods such as enzyme immuno-assays have been developed (Hardham *et al.*,1986), (Gabor *et al.*,1993), (Deverrgne *et al.*, 1994) as well as a dipstick immuno assay for specific detection of *P. cinnamomi*. (Cahill and Hardham,1994). None of these methods has proven to be universally useful, for a variety of reasons, for large scale detection of *Phytophthora* in plant material and soil. Three important reasons as to why these tests are not widely used include: *i)* the lack of specificity leading to cross reactivity with other pathogens; *ii)* failure to detect limited infections due to lack of sensitivity; and *iii)* the cost and time needed to conduct some of these tests.

Developments in DNA based diagnostics

Recent developments in molecular genetics have opened up new avenues for the detection and identification of pathogens, in particular the development of the Polymerase Chain Reaction (PCR) has revolutionised diagnostics of micro-organisms. PCR allows small amounts of DNA to be amplified effectively and very specifically more than a million fold in a couple of hours. The nature of the PCR process is such that levels of specificity, manipulated through the design of oligonucleotide primers, and sensitivity, manipulated through the choice of reaction conditions, can be reached which are significantly better than any test previously available. PCR tests are now widely used in the diagnostics of viral pathogens in mammals and plants. The second significant development concerns the ease at which DNA sequence information can be obtained. Software specifically designed for analysing and manipulating large amounts of DNA sequence data has made it possible to reveal evolutionary relationships between different species and in the design of highly specific oligonucleotide primers. Another development of importance is the availability of neutral genetic markers, such as RFLPs and RAPDs, useful to rapidly detect different genotypes and access levels of genetic diversity within and between populations of pathogens.

Objective

The objective of our research was to design a diagnostic test for a number of species of *Phytophthora* which are important pathogens in Australia. The latest developments in biotechnology and molecular genetics have been used to develop quick and reliable tests which are highly specific and very sensitive and amenable for routine screening of plant material and soil for the presence of *Phytophthora* pathogens.

Strategy for development of DNA based diagnostics for *Phytophthora*

Our strategy involved the use of the Polymerase Chain Reaction (PCR) which allows small amounts of DNA of any organism to be specifically amplified over a million fold in a couple of hours. The power of the PCR reaction was combined with the use of the ribosomal DNA (rDNA) repeat as a target for diagnostic purposes for the following reasons: *i)* it shows little variation among isolates within a single species allowing for design of widely applicable tests; *ii)* it shows considerable variation between species allowing design of highly specific tests; and *iii)* the rDNA repeat occurs in 100-200 copies per haploid genome making it an ideal target for highly sensitive tests.

Phytophthora culture collection

In order to design species and genus specific DNA based diagnostic tests, sequence information from the ribosomal RNA (rDNA) repeat needs to be obtained from representative isolates of each species. Therefore a culture collection containing authentic cultures of each species as well as a large number of isolates from the targeted species collected in Australia is a vital part to the successful development of any diagnostic test. Before and during the conduct of this project the CRC for Tropical Plant Pathology has built up a large *Phytophthora* collection consisting of 1843 isolates of 29 different *Phytophthora* species.

Genetic diversity in *Phytophthora* populations

In order to detect all isolates of a given species it is important to have access to many different isolates and information concerning the amount of genetic diversity present in the pathogen population. Some *Phytophthora* species such *as P. palmivora, P. cryptogea* and *P. drechsleri* were known to be genetically diverse and the species boundaries are not straightforward and have been much discussed in the literature. Unclarity concerning what a species comprises of, poses problems to the development of diagnostic tests. Therefore, it is imperative to assess levels of genetic diversity in the targeted *Phytophthora* species to address these issues. Only biologically relevant and evolutionary correct classifications will allow the development of appropriate DNA based diagnostic tests.

Our genetic diversity studies on different *Phytophthora* species in Australia indicate that levels of genetic diversity are high for most heterothallic *Phytophthora* species. High levels of genotypic diversity have been observed *in P. palmivora, P. cryptogea, P. drechsleri*, and *P. nicotianae* and *P. parasitica.* This is in contrast to the homothallic species such as *P. megasperma*, *P. sojae* and *P. cactorum* which showed low levels of genetic diversity within Australia. Overseas isolates, included in our study, are important so the diagnostic tools ultimately developed will also recognise these isolates, thus allowing the diagnostic tools to be used for import and quarantine procedures to protect the Australian primary industries from new introductions of such pathogens.

Ribosomal DNA sequence information

We have obtained rDNA sequence information from ITS1 and ITS2 regions of 65 isolates representing 26 different *Phytophthora* species and 12 isolates representing 8 different *Pythium* species. This sequence information enabled us to design PCR primers specific for the genus Phytophthora as a whole and 5 of the important species (Table 1).

Table 1 Specific primer pairs designed for the targeted *Phytophthora* species and the genus *Phytophthora.*

Species	Forward Primer	Reverse Primer
Genus	A/2	I/2
P. cinnamomi	Pcinn02	Pcinn03
P. palmivora	Ppalm03	Ppalm02
P. nicotianae/parasitica	Pnic03	PnicR1
P. drechsleri/cryptogea	Pcd05	Pcd04
P. cactorum	Pcact03	Pcact02

UQ#	Species	PCR test
UQ734	***P. cinnamomi***	
UQ1529	*P. capsici*	
UQ1551	*P. erythroseptica*	
UQ227	*P. drechsleri*	
UQ839	*P. citrophthora*	
UQ747	*P. nicotianea*	
UQ754	*P. cryptogea*	
UQ1294	*P. palmivora*	
UQ458	*P. medicaginis* (chickpea)	
UQ125	*P. medicaginis* (lucerne)	
105B4050	*P. trifolii*	
PVIFO	*P. vignae*	
UQ136	*P. vignae*	
UQ1200	*P. sojae*	
UQ852	*P. parasitica*	
UQ205	*P. macrochlamydospora*	
Neg. control		
UQ734	***P. cinnamomi***	
UQ734	***P. cinnamomi***	
CBS374.42	*P. iranica*	
UQ1322	*P. syringae*	
CBS55467	*P. gonapodyides*	
UQ1318	*P. cactorum*	
UQ	*P. megasperma* (Douglas fir)	
PMS12	*P. megasperma* (Spain)	
UQ1388	*P. megasperma*	
UQ1390	*P. megasperma*	
UQ1395	*P. megasperma*	
UQ	*P. megasperma* (Almond)	
UQ	*P. megasperma* (Lilac)	
UQ	*P. megasperma* (Walnut)	
UQ1497	*Pythium ultimum*	
UQ1424	*Pythium arrhenomanes*	
UQ1454	*Pythium graminicola*	
UQ1476	*Pythium irregulare*	
Neg. control		
UQ734	***P. cinnamomi***	

Figure 1 Photograph of an ethidium bromide-stained agarose gel showing the specific Amplification of PCR products in only the *P cinnamomi* samples and in one of the Other *Phytophthora* nor *Pythium* species using the *P. cinnamomi* specific primer pair Pcinn02-Pcinn03.

Pc#	UQ#	Date	Location	State	Host	PCR test
Pc3	UQ633					
Pc5	UQ642				Rice Flower	
Pc9	UQ734	1981	Jarrahdale	WA	Allocasuarina fraseriana	
Pc10	UQ735	1980	Jarrahdale	WA	Pinus radiata	
Pc11	UQ736	1990	Eneabba	WA	Adenanthos spp	
Pc13	UQ738	1992	Jarrahdale	WA	Banskia grandis	
Pc14	UQ739	1992	Narrogin	WA	Banskia spp	
Pc16	UQ741	1992	Busselton	WA	Pinus radiata	
Pc17	UQ742	1992	Dwellingup	WA	Xanthorrhoea preissii	
Pc18	UQ743	1994	Yule Brook		Myrtaceae	
Pc20	UQ772		Nambour	Q	Avocado	
Pc21	UQ787		Ourimbah	NSW	Eucalyptus globoidea	
Pc22	UQ788		Norton Summit	SA	Castenae sativa	
Pc23	UQ789		Kiolao	NSW	Eucalyptus gummifera	
Pc24	UQ790		Wynabeel	Q	Pinus radiata	
Pc25	UQ791		Grampains	VIC	Banskia marginata	
Pc26	UQ792		Beerburrum	Q	Pinus elliotti	
Pc27	UQ793		Barton	ACT	Casuarina	
Pc30	UQ817		Coles Bay	TAS	Aotus ericoides	
Pc31	UQ818		Cooloola	Q	Dillwynia floribunda	
Pc32	UQ822		Kioloa	NSW	Soil	
Pc33	UQ823		Browns Palins	TAS	Monotoca glauca	
Pc34	UQ824		Ourimbah	NSW	Soil	
Pc35	UQ825		Ourimbah	NSW	Soil	
Pc36	UQ826		Canberra	ACT	Eucalyptus spp	
Pc37	UQ827		Cooloola	Q	Allocasuarina littoralis	
Pc38	UQ828		Murwillumbah	NSW		
Pc39	UQ837		Ourimbah	NSW	Soil	
Pc40	UQ871	1985	Adelaide Hills	SA	Chestnut	
Pc42	UQ873		Adelaide Hills	SA	Soil	

Figure 2 Photograph of an ethidium bromide-stained agarose gel used to detect PCR amplification of DNA from 30 different Australian isolates of *P. cinnamomi* using the primer pair Pcinn02-Pcinn03.

The specificity of the *P. cinnamomi* primer pairs is exemplified in Figure 1. *P. cinnamomi* did not cross react with any of the 23 different *Phytophthora* species nor the four *Pythium* species tested. This primer pair correctly identified all 30 Australian (Fig. 2) isolates *of P. cinnamomi* tested. Along similar lines primer pairs highly specific for the other targeted *Phytophthora* species have been developed. The genus primer correctly detects all *Phytophthora* species.

Sensitivity

The primer pair specific to *P. cinnamomi* has been tested further for sensitivity. In preliminary experiments up to 2 pg *of P. cinnamomi* DNA could be detected. In theory, this equals the amount of DNA in two single nuclei of a *Phytophthora* species. Hence, the sensitivity of these PCR based tests looks promising for detecting minute levels of infection in plant tissue and soil samples.

Rapid identification of the *Phytophthora* species

In order to quickly determine what species of *Phytophthora* is involved we have developed a molecular key based on a restriction digest of the PCR product obtained with our genus primer. When an unknown plant or soil sample comes in to the laboratory we first detect the presence of *Phytophthora* in the sample by subjecting it to our primers specific to the genus *Phytophthora*. The resulting PCR product is then subjected to a restriction digest of which the product is specific to each species as exemplified in Figure 3.

Figure 3 Photograph of an ethidium bromide-stained agarose gel containing PCR products Digested with a restriction enzyme for identification of Phytophthora species

Conclusions

- The CRC for Tropical Plant Pathology has developed PCR-based diagnostic tests with high levels of specificity and sensitivity, allowing specific detection of *Phytophthor*a at very low inoculum levels.

- The availability of rapid diagnostic tests for *Phytophthora* will change the way in which the diagnostics are used in the nursery and horticultural industries. The availability of cheap tests which can be routinely applied will lead to improvements of nursery hygiene, the routine testing of planting material and soil forms an integral part of accreditation schemes. The tests do not prevent disease but they are important in detecting pathogens before they become troublesome.

- Rapid and correct identification of *Phytophthora* species will help resolve problems in plants from which *Phytophthora* is hard to isolate and in root diseases on plants from which *Phytophthora* has not been reported before.

- When routine diagnostics are implemented, more samples can be routinely screened. This will lead to better disease management strategies and diseased plants can be identified more quickly before spread of *Phytophthora* can take place.

- The CRC for Tropical Plant Pathology is currently preparing a manual and organising a hands-on workshop to make this technology available to diagnostic laboratories.

9 *PHYTOPHTHORA CINNAMOMI* IN TROPICAL RAINFOREST – MANAGEMENT OF OUTBREAKS

KEN PEGG

BACKGROUND INFORMATION

(a) First report of *Phytophthora cinnamomi* in Queensland

Tryon (1905) first recognised root and heart (top) rot of pineapple at Nundah in Queensland in 1887. Pineapple growers in that district had observed the disease some 15 years earlier. Tryon recognised the importance of heavy rainfall in disease development and observed the "the history of the disease supports the conclusion that the baneful effects of unsuitable soil can alone be exerted when special meteorological conditions obtain". He observed the importance of improving soil drainage to minimise losses from the disease and suggested planting "along the summit of an elevation caused by throwing the furrows in ploughing". Tryon concluded that the disease was caused by "a special fungus which lives at the expense of and so destroys the roots". However, it was not until 1929 that J.H. Simmonds isolated a *Phytophthora* sp. from heart leaves collected from pineapple plants with heart rot at Bracken Ridge. This isolate was identified as *Phytophthora cinnamomi* Rands by S.F. Ashby of the Commonwealth Mycological Institute (IMI 1590). Pineapples were first planted by Lutheran Missionaries in Queensland in 1838. They imported plants of the cultivar Queen from India. In 1880 the original plants of Smooth Cayenne, now the major cultivar grown, were imported from Kew Gardens, London, the original stock having come from French Guiana.

(b) First report of avocado root rot

Avocado root rot was first recognised in Queensland by J.H. Simmonds in 1949, who reported isolated instances of mature avocado trees dying in the Nambour area. Simmonds did not isolate the causal organism, *Phytophthora cinnamomi*, until 1952. Avocado trees were sold from the Kamerunga State Nursery as early as 1914.

These reports indicate that *P. cinnamomi* has been present and caused disease in horticultural crops in Queensland for at least120 years. The pathogen is extremely widely distributed in coastal regions.

(c) First recording in native vegetation

In Queensland, despite a long history of serious losses in horticulture there has been little damage to natural vegetation. Sclerophyll, 'wallum' and rainforest communities often adjoin

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Report, Rainforest Cooperative Research Centre, Cairns, 1999

infested horticultural areas. Pegg and Alcorn (1972) found that *P. cinnamomi* was widely distributed in the coastal lowlands ('wallum') of south-east Queensland without causing serious losses to the indigenous flora. The fungus seems to be in ecological balance with the wallum environment and plant losses only occur at localised sites. The low incidence of disease in native vegetation in sub-tropical Australia led Shepherd (1975) to suggest that *P. cinnamomi* was indigenous to that region and that the flora had developed resistance to the fungus during evolution. This was countered by Podger (1975) who argues the case for introduction since first European man, and suggests that the low incidence of disease in northern forests is due to environmental control. The question of whether *P. cinnamomi* is introduced or indigenous needs to be resolved using the latest developments in biotechnology and molecular genetics. 'Wallum' areas yield both A_1 and A_2 mating types whereas only the A_2 mating type is recovered from horticultural crops (Pegg, 1974). One hundred and seventy-two isolates from south-east Queensland were tested, 154 were the A_2 mating type and 18 were A_1 mating type. This may indicate that P. cinnamomi has a high level of genetic diversity in 'Wallum' communities.

(d) *Phytophthora* in rainforests

P. cinnamomi has been found to be associated with tree loss in tropical rainforests in central and northern Queensland (Brown, 1976). Deaths were associated with pig wallows which, because of heavy clay subsoil close to the surface, retained water even when the soil under apparently healthy rainforest was relatively dry. Both A_1 and A_2 mating types are found in rainforest communities.

(e) *Phytophthora* in mangroves

Phytophthora spp. (have been transferred to *Halophytophthora*) were found associated with the death of mangroves (*Avicennia marina* (Forsk.) Vierh.) in several localities in coastal Queensland (Pegg *et al*., 1980). It was found that these fungi only affected stressed mangrove trees (waterlogging, pollution etc), their basic role in the mangrove community being to convert nutrient poor mangrove leaf litter to a protein-rich food for fish and crustaceans.

MANAGEMENT OF OUTBREAKS IN HORTICULTURE

Integrated disease management is the major goal for sustainable production systems in horticulture. Complementary management practices used to reduce disease to economically acceptable levels may be described within four broad categories:

(a) Cultural control

This involves:

1. Site selection – trees should only be established in soils that have good internal and surface drainage;

2. Planting on ridges to increase the drainage;

3. The use of disease-free nursery trees – trees are propagated under strict hygiene procedures, on raised benches (45 cm above the ground) in steam sterilised or fumigated potting medium, with pathogen-free seed and irrigated with *Phytophthora*-free water, or

water decontaminated with chlorine (the most commonly used procedure is to treat the water and store for at least 20 minutes at which time the chlorine residual should be at least 2mg/L). The use of systematic fungicides (metalaxyl and phosphonates) to temporarily suppress populations of *P. cinnamomi* and reduce root damage in nursery stock is not recommended. Neither metalaxyl or phosphonate will kill 100% of the *Phytophthora*;

4. Using a balanced nutritional program to aid replacement of damaged roots eg. in avocado particular attention should be paid to phosphorus, calcium and boron nutrition as these elements are particularly important for healthy root growth;

5. Application of soil calcium – calcium stabilises membrane permeability and prevents leaking of carbohydrate and/or amino acids which attract zoospores to roots; it induces premature encystment and high soil levels reduce sporangial production and sporangial size.

(b) Chemical control

The use of acylanilide and phosphonate systematic fungicides have had a dramatic influence on the control of *Phytophthora* diseases in horticulture.

Metalaxyl
The acylanilide fungicide metalaxyl (Rodomil®) is highly water soluble, has good mobility in soils and is taken up readily by the roots and translocates upwards in the plant in the transpiration stream. It is formulated as a wettable powder, granular material or as an EC product which facilitates application via the irrigation system. Because of its long half life in soils (15-30 days) and its high mobility, activity in soil is excellent. When used repeatedly in some soils it biodegrades rapidly because of a build-up of fungal and bacterial flora.

Phosphonate
Phosphonate can be applied as soil drenches, foliar sprays, trunk paints or trunk injections and are considered to control *Phytophthora* spp. by a combination of direct fungitoxic activity and enhancement of host defence mechanisms. Trunk injection is preferred as very little contamination of the environment occurs. An understanding of tree phrenology is essential so that injections can be timed to provide maximum protection of the roots. The phosphonate anion is strongly inhibitory to sporulation, but only has a weak effect on mycelial growth. When phosphite is present in high concentrations it disrupts the fungal cell wall thus inducing a more rapid host defence response (Guest and Grant, 1991). Phosphonate is an inexpensive fungicide with low mammalian toxicity (less toxic to humans than table salt). Phosphonate remains essentially inert in plants, and persists in treated tissues until diluted or lost as the plant grows and senesces.

(c) Biological control

This includes the use of regulated mulches to reinforce the natural leaf litter mulch under trees. High fibre straw mulches (wheat, oats, barley) or composted chunky *Pinus radiata* bark are recommended. Composted chicken manure is often added to these mulches. This creates a suppressive environment for *P. cinnamomi*. Mechanisms involved include:

1. Increased populations of microbial flora that are antagonistic to pathogen activity;

2. Production of inhibitory volatile compounds such as ammonia and nitrite and toxins such as saponins and organic acids;

3. Encystment of zoospores by organic matter;

4. Increased host resistance;

5. Improved aeration and drainage in the mulch and soil;

6. Improvement in root growth and reduced plant stress.

Although individual antagonistic micro-organisms have been isolated from naturally suppressive soils, the addition of a single antagonist to conducive soils is unlikely to succeed. It is far better to stimulate the activity of resident antagonists.

(d) Resistant root stocks

Resistance may be expressed by the rapid regeneration of roots or inhibition of the progress of infection.

MANAGEMENT IN RAINFORESTS

With the exceptions of the possible use of phosphonate (ultra-low volume application from aircraft), management strategies must be based on hygiene ie. Target the vectored spread of the pathogen and to constrain as far as is possible the establishment of new areas of infestation.

Hygiene
Effective hygiene will depend on:
1. Accurate maps of the location of disease;

2. A knowledge of the distribution of *Phytophthora cinnamomi* in the rainforest;

3. Disease hazard rating of sites – presently it is assumed that only small localised areas, where sub-surface features lead to impeded drainage, favour disease in the rainforest. It is assumed that most rainforest sites are not at risk ie. not conducive to *Phytophthora cinnamomi* activity;

4. Monitoring of the disease in known sites;

5. A better understanding of host/pathogen/environment interactions;

6. Improvement in root growth and reduced plant stress.

Phosphonate
Komerek et al (1994) found that 10% potassium phosphonate was highly effective against *P. cinnamomi* in native plant communities in Western Australia for up to two years, when

applied as aerial sprays of 60L/ha. Phosphonate does not prevent root infection, nor does it eradicate *P. cinnamomi* from the soil. Phosphonate remains essentially inert in palms, and persists in treated tissue until diluted or lost as the plant grows and senesces.

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