Forest Focus

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Cover photograph: Jarrah regeneration in the '100 year old' forest — Mundlimup — regenerated in 1875 following the logging of 1872.

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An electron microscope was used to take this highly magnified ▲ picture of *Phytophthora cinnamomi* mycelium invading the bark cells of a jarrah root.

Microscopic research of *Phytophthora cinnamomi* — compare this equipment with the grossness of the Rocksaw on page 11.

Severely diseased jarrah forest. Thousands of hectares of forest were killed by *Phytophthora cinnamomi* in the period 1940-1965.

A NEW PERSPECTIVE ON JARRAH DIEBACK

by
S.R. Shea, B.L. Shearer, J. Tippett and P.M. Deegan

Jarrah dieback has been a major factor affecting South West Australian forest management and land use practice for over thirty years. The disease caused the decline and death of thousands of hectares of jarrah forest between 1940-1965, but it was not until 1965, after years of research by many scientists, that the cause of the disease was identified by Dr. Frank Podger as *Phytophthora cinnamomi*.

An introduced, soil-borne fungus, *Phytophthora cinnamomi* is believed to have evolved in the tropical and subtropical regions of South East Asia. Even though it grows and multiplies best under tropical conditions, this fungus has proved to be one of the most widespread plant pathogens known to man. It attacks nearly one thousand different plant species and is a major problem in horticulture, agriculture and forestry throughout the world.

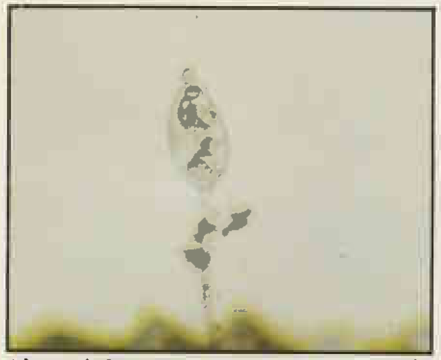
It is not surprising, therefore, given *Phytophthora cinnamomi's* record as a 'plant destroyer' and its demonstrated capacity to kill large areas of jarrah forest, that there was grave concern that in the long term it would destroy the whole forest. Recent research, however, has provided the basis for a more optimistic outlook.

Phytophthora cinnamomi in the Jarrah Forest Environment

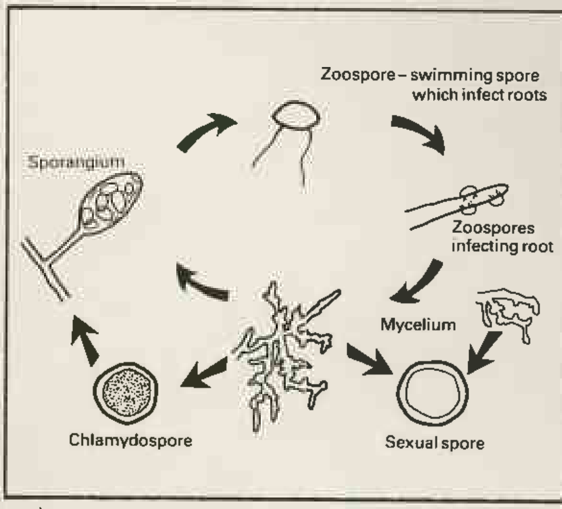
Following the identification of *Phytophthora cinnamomi*, a major research programme was commenced.

Phytophthora cinnamomi had been the subject of intensive investigation in many different countries, and much was known about its life cycle, but there was virtually no data on how the fungus reproduced and survived in West Australian soils. One of the first studies undertaken needed to determine how *Phytophthora cinnamomi* functioned in the jarrah forest environment.

Understandably, given its tropical origins, *Phytophthora cinnamomi* only thrives when soil conditions are warm and wet. Prolonged soil drying kills the fungal spores.



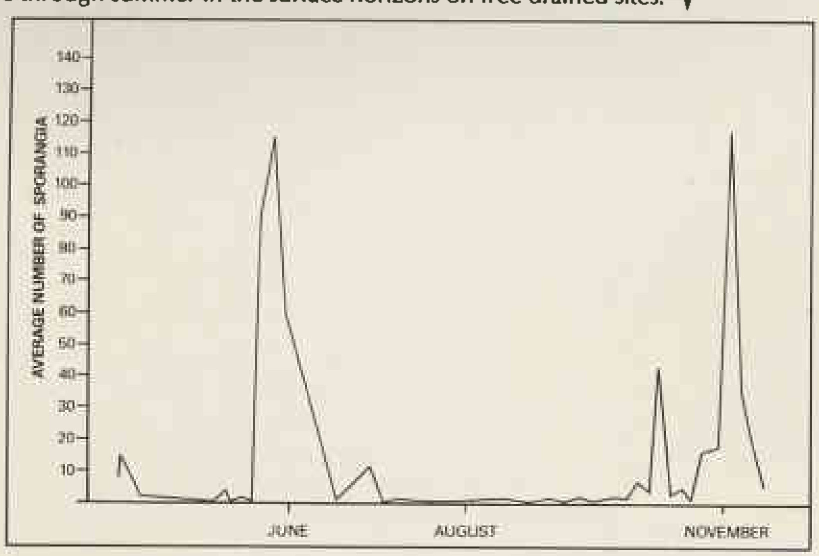
Phytophthora cinnamomi mycelium. ▲



▲ Life cycle of *Phytophthora cinnamomi.*

◄ Sporangia of *Phytophthora cinnamomi* releasing mobile zoospores. Saturated soil conditions are required for zoospore release and transmission.

Phytophthora cinnamomi is readily detected in soil throughout the year in the moisture gaining valley sites. The fungus is frequently difficult to recover from the surface soil horizons and does not survive through summer in the surface horizons on free drained sites. ▼



In the valley floors of the jarrah forest the soil remains moist for most of the year, creating a favourable soil environment for the fungus. These areas form only a relatively small proportion of the jarrah forest landscape, and many of the shrub and understorey species growing in these valleys are resistant to *Phytophthora cinnamomi.*

The majority of the jarrah forest grows on upland slopes and ridges, where the surface soil layers are well drained. Detailed measurements of soil moisture and temperature over several years showed that the soil environment on these sites is only marginally suitable for *Phytophthora cinnamomi.* On the ridges and slopes it was found that the fungus could only produce mobile spores during brief periods in autumn and spring, when the soil is warm and wet. During the summer months, soil conditions are so dry the fungus is almost eradicated. Rapid movement of the fungus, apart from its transport in infected soil, is restricted to areas where the soil has been disturbed and an overland flow of water occurs.

Detection of *Phytophthora* species in soil has always been difficult. In recent years, however, a variety of reliable techniques have been developed, and thousands of soil samples taken from infected sites have now been analysed for *Phytophthora cinnamomi.* While it was possible to readily detect *Phytophthora cinnamomi* in the infected valley floor sites, the recovery rates from surface soil layers on slopes and ridges were usually low. Even on severely diseased sites, less than 10 samples in every 100 analysed yielded *Phytophthora cinnamomi.*

The surprising conclusion from these studies was that despite the fact that the fungus caused mass destruction of the forest on some upland sites, all measurements of the soil environment and the activity of the fungus in the surface layers on these sites indicated that they should not be subject to severe disease. Two of the most perplexing questions which confronted jarrah dieback research workers were : how did *Phytophthora cinnamomi* operate in a soil environment which was only marginally favourable; and how could it cause so much damage at apparently low soil population levels?

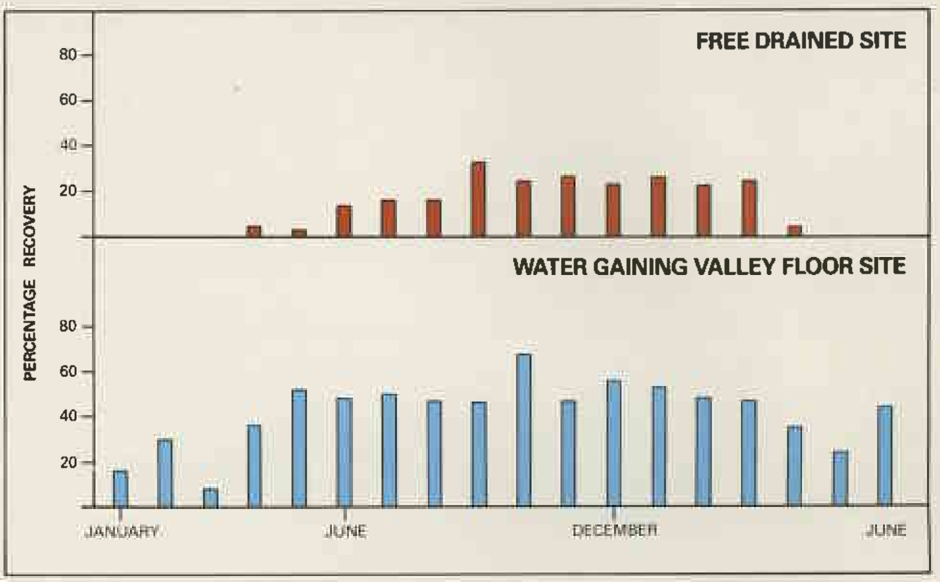
The Role of the Banksia Understorey

Investigation of the highly susceptible *Banksia grandis* understorey helped to explain why *Phytophthora cinnamomi* is able to survive and spread in jarrah forest soils. This species is usually the first to die, after the fungus is introduced into healthy forest.

Banksia grandis tissue is so favourable to the fungus, that the rate of mycelial growth through banksia roots (up to 1.5cm per day) is as rapid as any observed on the most advanced laboratory produced media. This rapid growth, combined with the fact that banksia trees have extensive vertical and horizontal roots, means the fungus can spread through the forest without having to move into the soil. Banksia tissue thus provides a buffer from the often hostile soil environment and allows the fungus to persist in infected areas, even after most of the vegetation has been killed. In one study, for example, it was found that the fungus could survive for more than two years in dead *Banksia grandis* roots.

Although the Banksia understorey has proved to be a major contributor to the spread and intensification of the disease, this factor alone could not entirely explain the mass collapse of jarrah trees and the death of other species in severely diseased areas.

Banksia grandis is usually the first species to die in recently infected healthy forest. The perimeter of a diseased area is often marked by a wall of dead banksia. ▲



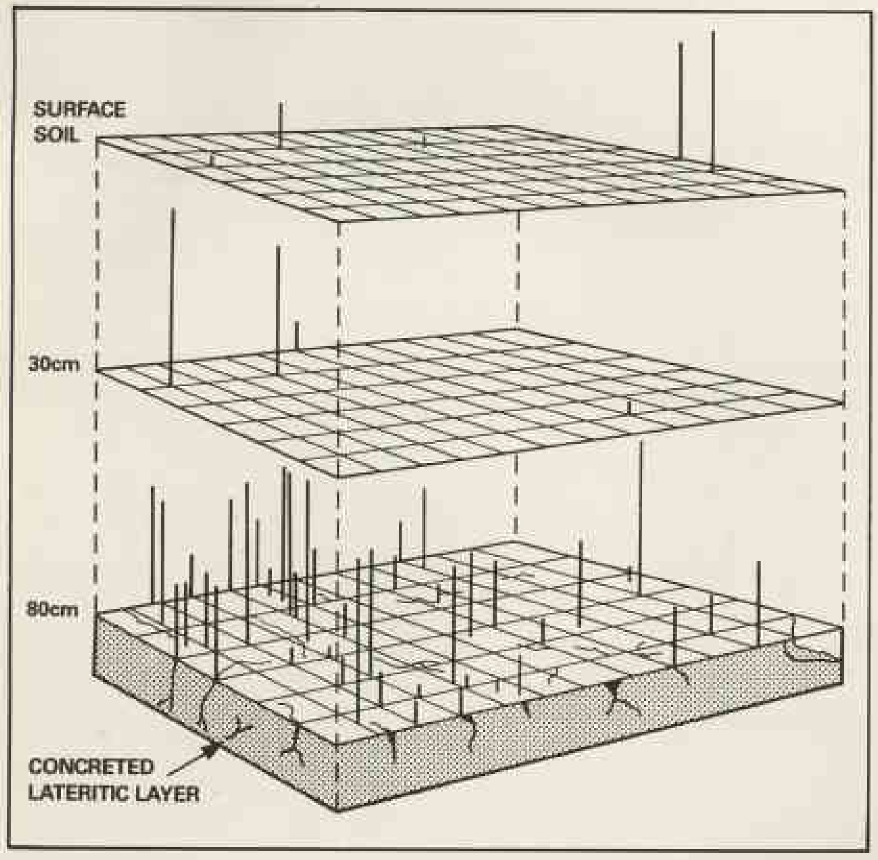
In the surface horizons of the soil on slopes and ridges in the forest the environment is only marginally suitable for spore production. Spores can only be produced during relatively brief periods in autumn and spring when the soil is warm and wet.

Left: Horizontal root of *Banksia grandis*. *Phytophthora cinnamomi* can extend through Banksia tissue at rates up to 1.5cm per day. ➤
Right: *Phytophthora cinnamomi* has been recovered from the vertical roots of *Banksia grandis* at depths exceeding 1.5 metres. ➤

Sampling soil for *Phytophthora cinnamomi* in severely diseased sites. ▲

Concreted lateritic layer which underlies soil on sites where mass decline and collapse of forest occurs. Water pools on the surface of the layer providing ideal conditions for spore production. Spores are spread in water moving laterally over the surface of the layer. ▲

Phytophthora cinnamomi occurs at high density in soil at the surface of the lateritic layer. Spores are concentrated in the root channels. (Vertical bars show relative concentration of *Phytophthora cinnamomi* spores at each sample point). ▼



Unseasonal Rainfall

Other tests, made to reconcile the conflict between field observations of the disease and the analysis of the pathogen-environment, sought to recreate heavy unseasonal rainfall. Although this heavy irrigation during warm weather favoured the fungus, fungal activity and mobility in the surface soil layers was, again, not sufficient to explain the severity of the disease observed.

Detection of *Phytophthora cinnamomi* at Depth

Another early assumption was that *Phytophthora cinnamomi* primarily occurred in the surface soil, where soil temperatures and oxygen levels were highest, and where a large food base of fine feeder roots existed. Although the soil on some sites had been sampled at depth, the fungus was not detected.

It had also been assumed that the lateritic soils of the uplands were very porous and that vertical water flow would not be impeded. However, during root excavations of trees undergoing rapid decline, it was found that all the sites were characterized by the presence of a concreted layer of laterite, at depths between 10 and 100cm. Water was observed to pond on this layer, and it was decided to test movement by sampling surface soil and the deeper soil adjacent to the concreted lateritic layer. There was a dramatic difference in the recovery rates, with the deeper soil showing high concentrations of the fungus — between 60-90%. Subsequently it was proved that, on these specific upland sites, water in the root channels of the concreted lateritic layer provides ideal conditions for spore production. Water flowing across the layer spreads the zoospores and accounts for the rapid disease extensions which have been observed.

The discovery that *Phytophthora cinnamomi* could reproduce and survive at depth in the soil had never been reported previously, and was a major advance in our understanding of how this remarkable pathogen can cause mass destruction of vegetation.

How did *Phytophthora cinnamomi* kill Jarrah Trees?

Although *Phytophthora cinnamomi* has been known to attack the lower stems of some plants, it had been generally assumed that for most tree species the fungus could only kill the fine feeder root system. It had also been assumed that repeated attacks on the fine roots would cause trees to slowly decline; but this did not explain the rapid collapse of jarrah trees.

Over a number of years, attempts were made by a number of research workers to determine if *Phytophthora* could invade the trunk and large roots of jarrah trees. It was not until 1979, however, that *Phytophthora cinnamomi* was detected in the large roots and lower trunks of a number of recently killed jarrah.

Phytophthora cinnamomi lesion (see darkened tissue) formed in the stem of a small jarrah tree. It had previously been assumed that the fungus could only attack the fine feeder roots of jarrah trees. ▲

Rapid collapse of large trees could not be explained by fine feeder root attrition. ►

Jarrah — A Resistant Species?

This discovery posed another question. If *Phytophthora cinnamomi* could invade jarrah roots and trunks why didn't jarrah trees always die in large numbers like the banksia understorey? Detailed aerial colour photography had shown that, in large areas of forest where the banksia understorey had been killed by *Phytophthora cinnamomi*, the jarrah death rate was less than one tree per hectare per annum.

Overseas research had shown that some tree species became highly susceptible to *Phytophthora* species for only short periods of the year. It was thought that a possible explanation of jarrah's patchy response was some environmental factor which affected the ability of jarrah to withstand infection and invasion by *Phytophthora cinnamomi*.

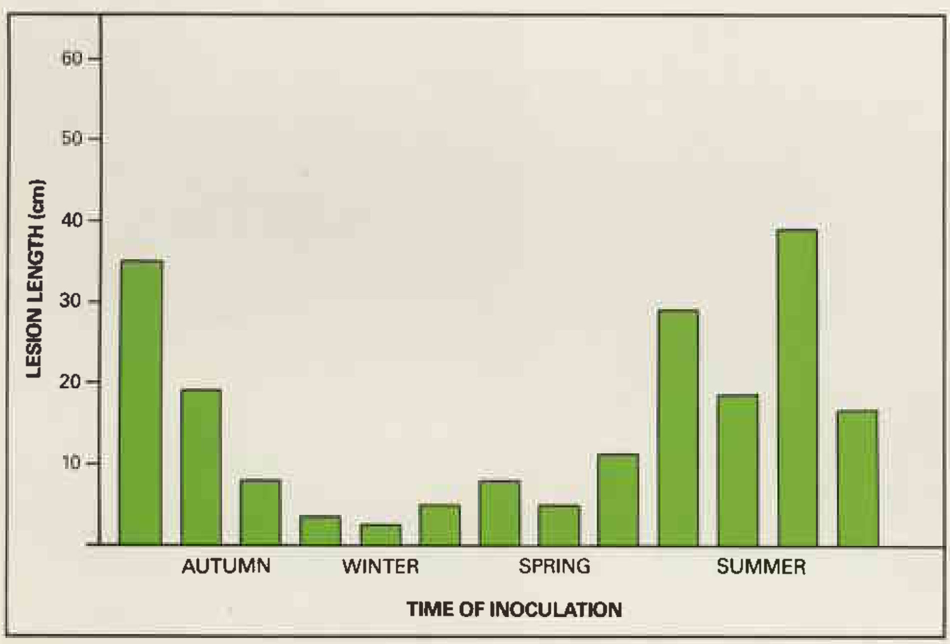
A number of ideas were formulated and tested in field trials.

Aerial photograph of patch death of jarrah trees caused by *Phytophthora cinnamomi*. ▼

Left: Inoculating a jarrah stem with *Phytophthora cinnamomi* mycelium.

Top Right: *Phytophthora* lesion contained by host resistance mechanisms.

Bottom Right: Barrier formed by jarrah root to prevent Phytophthora mycelial extension. Jarrah appears to have a number of mechanisms which, under normal conditions, makes it relatively resistant to *Phytophthora cinnamomi.*



The rate at which *Phytophthora cinnamomi* can invade jarrah tissues varies with season.

In one trial, some 3000 root and stem inoculations were carried out, over a period of 18 months, and the progress of the fungus was monitored by microscopic examination of the tree's tissue. The conclusion from this study was that jarrah trees have a range of defence mechanisms which curtail the spread of the fungus, even when it is introduced directly into a wound. Seasonal variation in susceptibility was observed, but it was proved that the trees have the capacity to form a barrier to the invading fungus.

Again, it didn't add up. If jarrah was tolerant to *Phytophthora cinnamomi,* how could the fungus cause the rapid collapse of some trees? The missing factor had to be a variable which would account for the fact that in some situations, in some years, mass death of jarrah occurred, while in other areas the fungus was present and jarrah root systems were exposed to it, but the trees did not die.

Identification of Highly Susceptible Sites

Although the layer of lateritic soils that occurs over most of the jarrah forest is of uniform surface appearance, the forest grows in a mosaic of different soil structures. It was recognized in early studies that trees on some upland sites were much more prone to *Phytophthora cinnamomi* than those on other sites. The upland sites were frequently characterized by the presence of black gravels on the soil surface. Although this site variation in the impact of *Phytophthora cinnamomi* had been observed, previous attempts to determine the biological reasons for these differences had failed, and there was no objective method of identifying the sites.

During the summer of 1981 and 1982 several sites were located where the process of rapid collapse of forest was occurring. This was the first time since the early period of mass decline and death (1945-1965) that this phenomenon had been observed in action.

Initial attempts to detect *Phytophthora cinnamomi* in the surface roots of the dying trees failed. On one site, extensive excavation and sampling of the horizontal root systems of more than 20 dying trees also failed to identify any pathogen. In a final attempt to locate the fungus the vertical root systems were exposed.

At the points where the vertical roots passed through channels formed in the layer of concreted laterite, one metre below the soil surface, the roots were found to be lesioned. *Phytophthora cinnamomi* was recovered from the lesions.

Following this discovery, over 50 trees were excavated on a number of severely diseased sites. On every site the concreted layer of laterite was present and the vertical roots of the jarrah trees were infected by *Phytophthora cinnamomi*.

Prognosis

Disease results from often complex interactions between host, pathogen and the environment. It is only by understanding the processes which drive these interactions that it is possible to predict how a disease will develop. Methods of control, then, reflect the level of knowledge about these processes.

The major problem which has been confronting jarrah forest managers was the prospect that the conditions, which caused the death of thousands of hectares of forest between 1945-1965, would recur. For, although the death rate of jarrah trees has declined markedly in the past fifteen years, the infected area has expanded. It was thought that if the process which caused mass collapse was triggered by unusual climatic events, such as heavy summer rainfall, the severity of damage in large areas of infected forest would increase sharply.

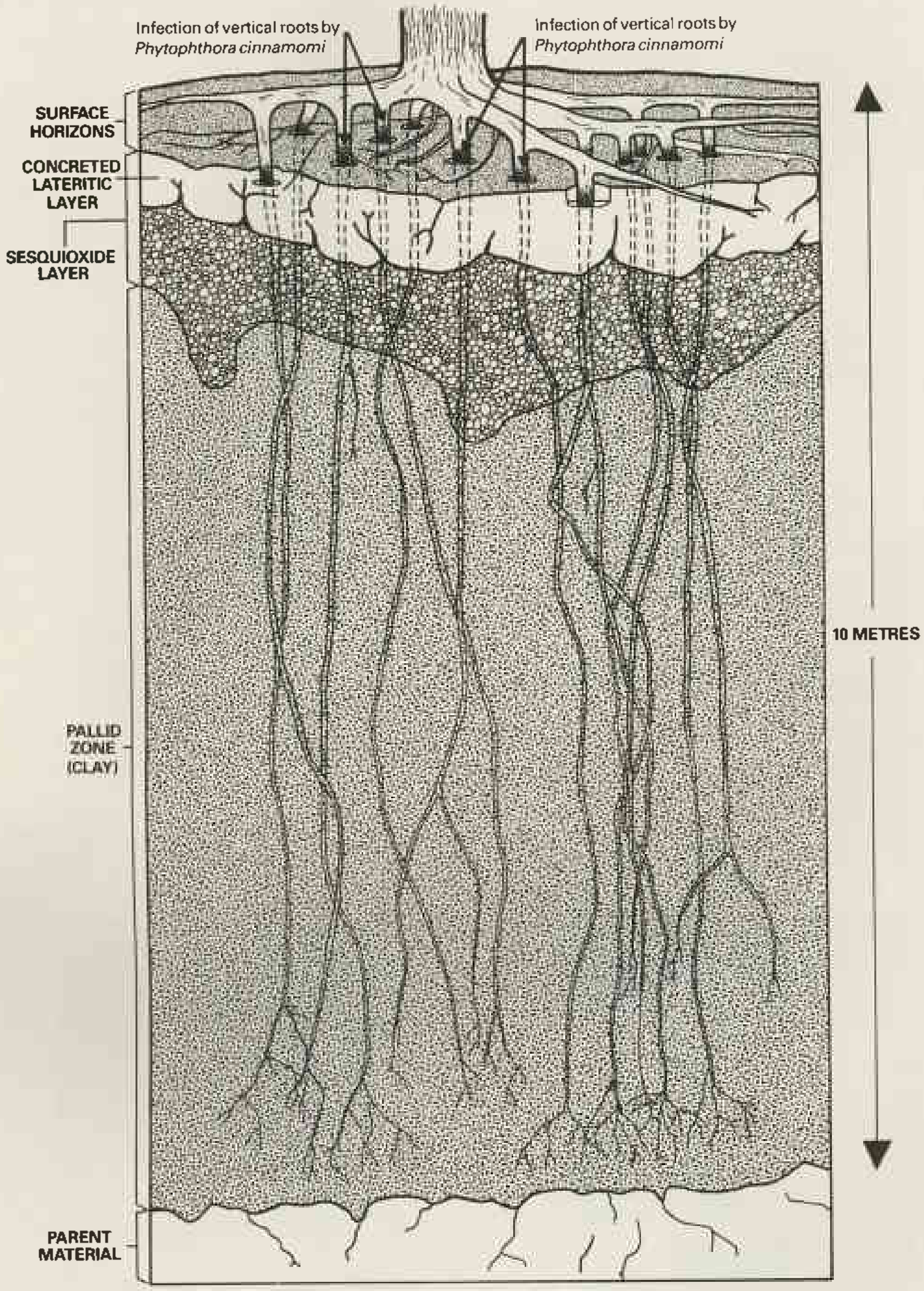
▲ Forests Department fire tankers, supplied with water from large tankers provided by Alcoa, were used for the hydraulic excavation of root systems.

▲ All of the vertical roots of this tree were killed by *Phytophthora cinnamomi* at the point where they passed through the concreted lateritic layer.

▲ Vertical roots of jarrah trees (painted silver) extend to the water table which may be more than 30 metres below the soil surface.

The discoveries that *Phytophthora cinnamomi* could invade woody tissue, that the fungus can occur at high density at depth in the soil of specific site types, and that the tree's vertical root system is vulnerable, gave a new perspective on how *Phytophthora cinnamomi* operated in upland sites of the jarrah forest environment.

Only now is it possible to answer some of the fundamental questions and to formulate the beginnings of a rational model for the disease.



Diagrammatic representation of jarrah root system. Jarrah's ability to tap groundwater at depth permits it to use water at a high rate during summer months. But on specific sites *Phytophthora cinnamomi* is able to infect and kill the vertical roots causing the trees to die from drought.

Jarrah trees appear normally to be resistant to the fungus. The fine root system is infected and some invasion of major horizontal roots can take place but, over large areas of forest, where *Phytophthora cinnamomi* has killed the banksia understorey, the rate of spread of the disease and the death rate of jarrah trees is relatively low.

The ability of *Phytophthora cinnamomi* to cause rapid destruction of some jarrah forest is the consequence of a bizarre combination of factors.

Jarrah trees have evolved to cope with long dry summers by developing an extensive root system to tap groundwater supplies. This allows the trees to continue to use large amounts of water over the summer, but has left them vulnerable to root attack by *Phytophthora cinnamomi.*

On *specific site types,* where there is a layer of concreted laterite present, vertical movement of water is impeded and lateral flow occurs. These are ideal conditions for spore production and movement just below the surface. Vertical roots of jarrah and banksia pass through depressions in the concreted layer. The presence of infected banksia roots and the fact that the root channels are formed in depressions which accumulate water, cause zoospores to be concentrated around jarrah's vertical roots. The fungus first infects jarrah's fine roots, which often profilerate in the root channels, then invades and kills the major vertical roots. Whereas fungal invasion of a horizontal root (unless it takes place near the trunk) appears to have little impact on the tree's capacity to obtain water, the fungus has only to invade a small distance into a vertical root to cut off the water supply. Once the tree's vertical roots are destroyed, its unsated demand for water results in desiccation and death.

While climatic conditions, particularly unseasonal rainfall, play an important role in determining disease intensity, *it*

▲ This giant 'Rocsaw', provided by ALCOA, was used to cut sections through the soil profile on severely diseased sites in an attempt to identify the characteristics of the laterite layer.

◄ Jarrah vertical root passing through concreted lateritic layer. *Phytophthora cinnamomi* zoospores are concentrated in these root channels where they infect the vertical roots.

appears that the processes which cause mass death of jarrah and rapid spread of the fungus operate only on specific site types. There is little prospect of controlling the disease on these sites.

It is not known how much forest which has not been affected by *Phytophthora cinnamomi* is growing on these highly susceptible sites, but there are large areas of forest growing on soils that do not have the properties which permit rapid disease development. The forest growing on these free draining sites has the greatest potential for management and protection from *Phytophthora cinnamomi*. Scientists are optimistic that on these sites long term control of jarrah dieback disease can be achieved.

Current management practices now include reducing the density of the banksia understorey, the maintenance of the free draining characteristics by minimizing soil disturbance, the employment of stringent hygiene techniques, and the promotion of resistant understorey species such as legumes.

Where do we go from here?

Control of serious forest diseases has rarely been achieved. Although the prognosis for the jarrah forest is now much more optimistic, key questions remain to be answered. What proportion of the forest is growing on highly susceptible sites for which there is little prospect for control? How can these sites be identified in the forest? Are there factors, other than vertical root destruction, which will cause jarrah death? What are the factors which affect the ability of jarrah to withstand infection and invasion by *Phytophthora cinnamomi?* Can the *Banksia grandis* understorey be controlled? How much soil disturbance or increase in rainfall is required to make normally resistant forest susceptible? What are long-term effects on forest quality of *Phytophthora cinnamomi* infection in sites which are not subject to mass collapse? These questions are currently being researched and will be the subject of future reports.

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