

Jarrah Dieback:
The Dynamics and Management of
Phytophthora cinnamomi **in the**
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South-western Australia

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B.L. Shearer¹ and J.T. Tippett²

1. Department of Conservation and Land Management
Research Centre, Dwellingup. W.A. 6213

2. Department of Conservation and Land Management
Research Centre, Hayman Rd Como W.A. 6152

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Front cover photo: Jarrah forest destroyed by *Phytophthora cinnamomi*
in an infected high impact area near Dwellingup.

Back cover photo: Beginning of a new day in healthy jarrah forest near Dwellingup.

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Preface

Patches of dying jarrah trees observed in the Darling Range in 1922 were the first observation of what was to be generally known as jarrah dieback. Ironically, in the same year, a Dutch plant pathologist published the first description of the fungus *Phytophthora cinnamomi*. However, over 40 years elapsed before the association between jarrah dieback and *P. cinnamomi* was discovered. By this time the fungus had destroyed thousands of hectares of shrubland, woodland and jarrah forest throughout south-western Australia.

Recognition of the association between *P. cinnamomi* infection and jarrah dieback led to an upsurge of research on the fungus in Australia. It also had a far-reaching influence on forest management and the public through the need to understand the biology of *P. cinnamomi* and to control spread and intensification of the fungus in soil.

Much information has been obtained on the biology of *P. cinnamomi* in Australia and overseas. However, most of the information has been published in technical papers or reviews or exists as unpublished reports or files. Limited attempt has been made to provide a readily available and comprehensive synthesis of the various interactions between *P. cinnamomi* and the jarrah forest ecosystem.

The aim of this bulletin is not to provide an extensive review of the literature on *P. cinnamomi* or the jarrah forest, but rather to integrate information relevant to the management of the jarrah forest in the presence of *P. cinnamomi*. The bulletin focuses primarily on research carried out by the Department of Conservation and Land Management (incorporating the Western Australian Forests Department) since the 1960s, but reference is made to research done outside the Department where relevant. Additional funding for the research was provided by a Foundation for Jarrah Dieback research.

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Summary

Jarrah dieback caused by *Phytophthora cinnamomi* is a major factor affecting the ecology and management of the jarrah (*Eucalyptus marginata*) forest. The disease is an exceptional example of an introduced pathogen with a wide host range causing great damage to a diverse but mainly susceptible plant community. This review integrates the information relevant to the management of the jarrah forest in the presence of disease.

Although *P. cinnamomi* is the *Phytophthora* species most frequently isolated from areas of dying vegetation, *P. citricola*, *P. cryptogea*, *P. megasperma* var. *sojae*, *P. nicotianae* and unnamed *Phytophthora* species have been recovered from the jarrah forest. All of these *Phytophthora* species have a wide host range and a dependency on moisture to complete their life cycles. *Phytophthora cinnamomi* is distributed throughout south-western Australia, but affected areas of forest are most frequent on the western edge of the Darling Scarp and decrease in number with distance east. There is also a north/south gradient with southern forest less affected than northern forest. The regional pattern of affected areas has not occurred by accident but resulted from the interactions between topography, climate, soil, drainage, vegetation, and intensity of human activity creating niches favourable for the pathogen.

The jarrah forest remains on the western edge of the ancient Great Plateau of Western Australia on soils unsuited to agriculture. The climate is typically mediterranean with cool wet winters and hot dry summers. The soils reflect earlier periods of peneplanation, laterization and uplift. The gently undulating remnant plateau uplands are mantled with relict laterite. Red earthy deep loams have developed on the slopes of dissected river valleys on the uplifted western edge of the plateau. Duplex soils with a range of textures and depths predominate on gentle slopes near the eastern edge of the forest. Structure, morphology, hydrological properties, temperature, and fertility are the most important soil factors influencing the life cycle of *P. cinnamomi* in the jarrah forest. Fire is a natural part of the jarrah forest environment. Understorey composition affected by fire intensity and frequency can greatly affect the behaviour of *P. cinnamomi*.

The forest is characteristically dry sclerophyll with a uniform overstorey dominated by jarrah, but with a diverse shrub layer having a high level of endemism and speciation. The understorey occurs as a complex mosaic wherein the vegetation integrates and hence serves as an indicator of environmental conditions. The variation in understorey vegetation is a multidimensional continuum which has been classified into site-vegetation types, each having a characteristic group of indicator species. The vegetation

has adapted and specialized over a long geological period in response to isolation by barriers to migration, nutrient poor soils, recurrent climatic stress and a mosaic of landforms. This has occurred particularly within the families Proteaceae, Epacridaceae, Dilleniaceae and Myrtaceae, whose species are main constituents of the forest. Members of these families have adapted to poor soils and drought by specialization of root systems that are vulnerable to infection by *P. cinnamomi*.

There is no doubt that the composition of vulnerable communities dramatically alter once infected by *P. cinnamomi*. Jarrah is the only eucalypt species of the jarrah forest killed by *P. cinnamomi*. Jarrah can resist invasion by the fungus on free draining sites and when cool, dry conditions disfavour rapid fungal growth. Many species of the families Proteaceae, Epacridaceae, Dilleniaceae, Xanthorrhoeaceae and Papilionaceae that make up a large component of the forest understorey and shrub layer are commonly killed, resulting in irreversible decline in the diversity of vegetation in infected areas. Some understorey species, mainly grasses and sedges, are resistant. These and a few other species such as marri (*E. calophylla*) colonize old dieback sites. The appearance of infested sites varies according to the time elapsed since the fungus was first introduced. Although *P. cinnamomi* has been present in parts of the jarrah forest for at least 50 years, its introduction to some areas has been relatively recent. The intensity of disease varies on different sites from no to low through to high impact as floristic composition varies with site types. Partly for this reason, the site-vegetation classifications of the jarrah forest have been useful in describing disease impact. For sites with other than high impact, one can never be sure how long the sites have been infected and if disease has been fully expressed in terms of damage. Impact may worsen depending on climate, site and disturbance.

Prediction of the likely outcome of disease is difficult because disease is the cumulative effect of various interactions between pathogen, host and environment that mostly go unobserved. The asexual sporangium-zoospore cycle of *P. cinnamomi* has been emphasized as it produces large numbers of infectious spores and is probably the main form of reproduction of the pathogen in upland jarrah forest soils. Infection results from sporulation, dispersal, survival and build-up of population levels in the soil in space and time. Sporulation mainly involves stimulation and production of sporangia and release of zoospores. *Phytophthora cinnamomi* has very specific requirements for sporangium production; no spores will be produced unless some inherent soil property stimulates the formation of sporangia. The precise nature of the stimulatory factor(s) in soil is unknown but it can be

influenced by soil type and the composition of the soil microflora. In stimulatory soils, sporangium production is favoured by warm, moist and aerobic conditions. Release of motile zoospores from sporangia is favoured by wet soil conditions and fluctuating temperatures, modified by soil type and season. Once released, motile zoospores swim over short distances in water or are passively dispersed over larger distances in infected moist soil or flowing water. Lateral near-surface seepage of water is one of the main mechanisms of passive dispersal of inoculum at depth in upland jarrah forest soils where coarse textures or aggregate structure occur over a perching layer. This significant finding linked disease development in upland areas with specific site factors that affected behaviour of the fungus at depth in the soil and the infection of jarrah. As the jarrah forest is a mosaic of site-vegetation types it is also a mosaic of sites with different drainage characteristics that can influence dispersal of *P. cinnamomi*. Relatively free draining sites favouring vertical percolation of water are interspersed between sites with near-surface seepage of water, with gradations between the two extremes. The fungus can also be dispersed in infected roots either actively by growth through root systems or passively in infected roots transported in soil. Once dispersed fungal propagules must survive to produce new inoculum and infect host tissue. Temperature, moisture, floristic composition of the understorey, antagonistic microflora and soil type affect survival of *P. cinnamomi* in the jarrah forest.

The various components and interactions previously described are the building blocks from which *P. cinnamomi* develops in space and time. In free draining surface soil greatest number of sporangia form in autumn and spring when warm moist conditions favour sporulation. Generally sporulation is inhibited by dry summers and cool winters. Propagules surviving dry summers in plant material act as sources of inoculum in autumn. Wet conditions in winter favour survival of this inoculum which may increase with the return of favourable conditions for sporulation in spring. Inoculum levels decrease rapidly as the surface soil dries out in late spring. Viable inoculum occurs in infected, water-gaining lowland areas and in the soil at depth throughout the year, reflecting extended periods of moist conditions favourable for survival and maximum coincidence of warm, moist conditions favourable for sporulation. The seasonal pattern of inoculum increase varies from year to year depending on the timing of opening and closing rains, soil type and changes in canopy cover.

The interaction between pathogen and host starts with infection. Zoospores probably initiate most infections. They encyst and germinate to produce germ tubes which penetrate roots. Hyphae proliferate within roots macerating all un lignified and un-suberized tissues; causing the roots to rot. *Banksia grandis* is readily infected by *P. cinnamomi*

because of its thin bark and the proliferation of rootlets associated with the specialized proteoid roots of *Banksias*. How *P. cinnamomi* infects the root system of jarrah is not known, but the vertical tap roots, on which jarrah depends to maintain internal water balance during dry periods, is prone to infection.

The patterns of fungal invasion and damage in infected root systems vary. Once infected *B. grandis* root systems become extensively colonised and die. Invasion and damage in jarrah root systems are more variable. Although jarrah can resist extension of the fungus, site and season can strongly influence the interaction. Temperature, moisture, mineral nutrition and the physiological status of host tissues influences the host-pathogen interaction. Evidence from experimentation and forest observations suggests that there is genotypic variation in resistance of jarrah to *P. cinnamomi*. Fortunately for tree breeders, intra-specific variation within *P. cinnamomi* is low.

Circumstantial evidence suggests that *Phytophthora* species other than *P. cinnamomi* have also been introduced into Western Australia. Although much is known about *P. cinnamomi*, relatively little is known about most of the other species in the jarrah forest. *Phytophthora citricola* probably has the greatest potential to exacerbate the problem of dieback caused by *P. cinnamomi*.

The excavation of infected root systems of jarrah has provided valuable information on the amounts of damage to fine and large root systems at a number of sites. Jarrah can suffer root infection and loss for a number of years before final symptoms are expressed and death occurs. Long term responses of trees to root loss include reduction in leaf area. However, the severity of damage sustained by jarrah following infection will depend on many factors including genotype, abundance of inoculum in the soil and chance of infection, site type and climate. The effects of different levels of infection on the growth of jarrah requires clarification.

Spectacular rapid death of trees is probably brought about by climatic conditions which synchronize symptom expression following high levels of fungal activity in the soil. Monitoring deaths of jarrah over the last two decades has shown that the relatively few deaths observed in some years did not mean that the fungus was not infecting and invading roots of trees in infected areas.

Disease management can be divided into the following four main areas: hazard rating (recognition of vulnerable sites), assessment of risk, hygienic procedures, and manipulation of conditions to disfavour the pathogen and enhance host resistance. Hazard is determined by the influence of climatic, site and management factors on disease expression. Risk is the probability of spread and infection determined by disease proximity and the type of

operation planned for an area. Hazard systems have been developed to rate uninfected areas. There is now a much better appreciation that the jarrah forest is composed of a mosaic of hazard types ranging from low hazard fertile red earths to high hazard infertile sandy gravels. Once an area has been mapped for disease hazard, the risk of introduction and spread of *P. cinnamomi* can be assessed from maps of distribution of disease and the type of operation planned for an area. Risk and hazard can then be combined to determine the consequences of an operation.

Significant progress has been made in using quarantine and hygiene procedures to minimize new infections by preventing or delaying entry of the pathogen. These methods need to be integrated with management practices aimed at reducing the rate of disease development such as manipulation of composition of the understorey, stimulation of antagonistic microflora, manipulation of drainage, chemical control, use of resistant species, and enhancement of host resistance.

Changes in microclimate, disease management, the risk of infection, assessment of damage from infection and regional differences must be areas of research priority. Although relationships between climate, site, and vegetation on water status and movement within a site, pathogen development and host susceptibility have been studied, precise information is lacking. It will be difficult to predict the effects climatic change will have on disease expression in the future, especially since most of the research has been conducted during a decade of below average rainfall. Greater emphasis needs to be placed on applying information through simple mathematics to help test assumptions and give indications of probable rates of change in disease development under a range of conditions.

Hazard and risk system development will be an ongoing process and modifications made as a result of experience. The hazard rating systems can predict the likely disease outcome only for undisturbed areas. An

understanding of major factors affecting hazard will help in updating hazard rating systems when management strategies are changed or are applied repeatedly over time. Relationships between environmental factors, sporulation, survival, dispersal, infection, and host susceptibility must be determined to improve the precision of risk rating systems and estimates of how quickly hazard will be expressed.

Further evaluation of chemicals and other methods of control must be a high research priority so that managers are provided with as many options as possible to reduce the spread and development of *P. cinnamomi*. Further work is needed into cost effective methods of reducing the density of *B. grandis* without causing unacceptable damage to jarrah and conservation values.

The assessment of damage and the monitoring of disease development over time will provide a sound basis for management decisions. It must be realized that an understanding of the phenology, growth, and physiology of jarrah forest vegetation is essential for sustaining a healthy forest in the future, despite the pressures and many types of disturbances to the ecosystem. There is a need for assessment of the effects of *P. cinnamomi* on intermediate impact sites where jarrah survives. In particular, greatest priority must be given to the detrimental effects of disease on conservation values, especially understorey species that are suffering the greatest ecological impacts of the disease.

Most of the information relating environment to disease development has come from research in the high rainfall zone of the northern jarrah forest. Emphasis must be given to studies on host susceptibility and pathogen dynamics in intermediate-low rainfall jarrah forest and southern jarrah forest, woodlands and shrubland-heaths. These findings will be essential for minimising the spread and intensification of *P. cinnamomi* and other *Phytophthora* species in these areas.

Introduction

The multiple uses of the jarrah forest, association of *Phytophthora cinnamomi* with jarrah dieback and the life cycle of the fungus are outlined. Mention is made of *Phytophthora* species other than *P. cinnamomi* that occur in the jarrah forest. The regional pattern of affected areas is described and illustrates how climate, vegetation, soil, topography, drainage and intensity of human activity interact to create niches which the pathogen can occupy.

THE JARRAH FOREST

The jarrah (*Eucalyptus marginata* Donn. ex Smith) forest extends over most of the south-western corner of Western Australia (Fig. 1), occupying an area of about 64 000 km² (Abbott and Loneragan 1986). It is unusual for a single eucalypt species to dominate such a large area. The forest ecosystem and its diverse flora and fauna have important conservation values. The profusion of wildflowers combined with forest, rivers, minor waterways, hills and monadnocks of the Darling Scarp have created an environment ideal for recreational pursuits. Most of the metropolitan water

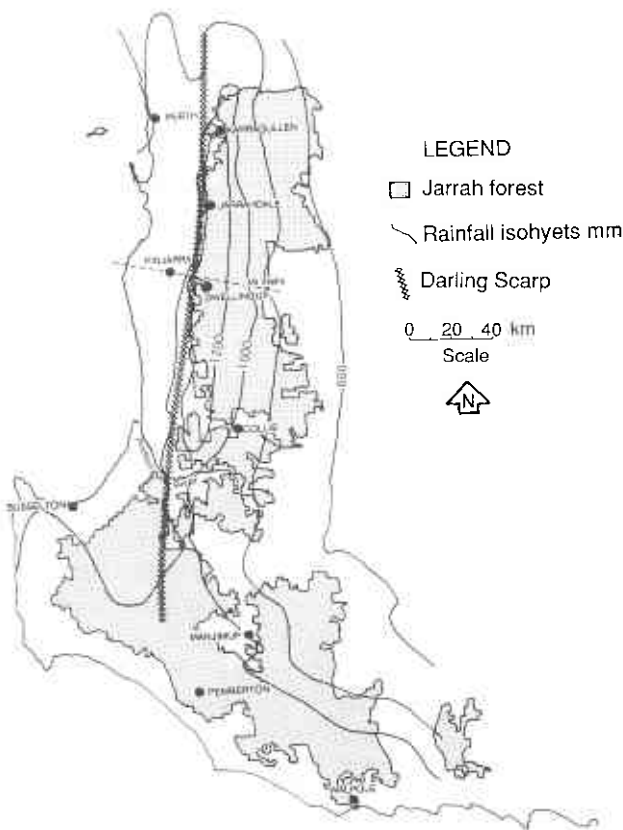


Figure 1

Distribution of the jarrah (*Eucalyptus marginata*) forest estate managed by the Department of Conservation and Land Management, the western edge of the Darling Scarp, annual rainfall isohyets in south-western Australia and position of a transect through Pinjarra and Mt. Wells (Fig. 6).

supply of Perth originates in jarrah-forested catchments. Jarrah timber has been an important renewable resource for the State since the establishment of timber mills in the forest in the mid 1800s (Calder 1980). Bauxite has been mined from the jarrah forest since 1963.

INTRODUCTION OF *PHYTOPHTHORA CINNAMOMI*

The jarrah forest was irreversibly changed with the introduction of the fungus *Phytophthora cinnamomi* Rands, probably near the turn of the century. At about the same time that Rands (1922) first discovered and described *P. cinnamomi* in Sumatra, unexplained deaths of jarrah and understorey species were observed near Karragullen, 35 km south-east of Perth (Fig. 1). These were the first records of what came to be known as 'jarrah dieback'. By 1928 additional small patches of dead and dying forest occurred 80 km south of Karragullen (Hopkins 1973). In the 1930s the timber industry changed from rail to road transport (Forests Department of Western Australia 1969) and the Main Roads Department and Shires conducted a massive postwar road building program. With the associated increase in road construction throughout the forest, the areas of dead and dying forest continued to increase in number and size and by 1948 the extent of affected areas was great enough to cause concern (Hopkins 1973).

Although research had been part of forestry since 1919, the establishment of a research station at Dwellingup in 1948 marks the foundation of organized formal forest research in Western Australia (Forests Department of Western Australia 1969). Initially the Commonwealth and State jointly funded the research effort at Dwellingup, but later the Commonwealth moved support for forestry research to the Forest Research Institute at Kelmscott. Podger (1968) describes in detail the investigations of Hamilton, Harding, Hatch, Wallace and Waring on the cause of the unexplained deaths in the jarrah forest during the period from the late 1940s to the mid-1950s.

It was not until the mid-1960s that Podger, working initially from Dwellingup and then from Kelmscott, firmly established the association between the death of jarrah and infection by *P. cinnamomi* (Podger *et al.* 1965;

Podger 1968, 1972). *Phytophthora cinnamomi* was isolated from 55 species of indigenous plants in infected forest but not from healthy forest. Typical dieback symptoms developed in healthy forest infected with pure cultures of *P. cinnamomi* or with soil from beneath nearby diseased forest. Healthy forest inoculated with soil from unaffected forest remained healthy (Podger 1972).

Podger's breakthrough provided the catalyst for extensive work in State and Commonwealth departments and Universities throughout Australia (Fig. 2) on the distribution of *P. cinnamomi* and environmental factors affecting the host-pathogen interaction. The work was further stimulated by funding from a Foundation for Jarrah Dieback Research. The aluminium and timber industries contributed to the Foundation which was chaired by the Conservator of Forests with representatives from industry, universities and government departments. The foundation funded new and existing research during the period 1979 to 1987.

BRIEF DESCRIPTION OF THE FUNGUS AND THE DISEASE IT CAUSES

Phytophthora cinnamomi is a soil-borne fungus belonging to the evolutionary primitive group called the Oomycetes or 'water moulds'. The fungus is pathogenic, requiring plant tissue as a food source. As the name 'water mould'

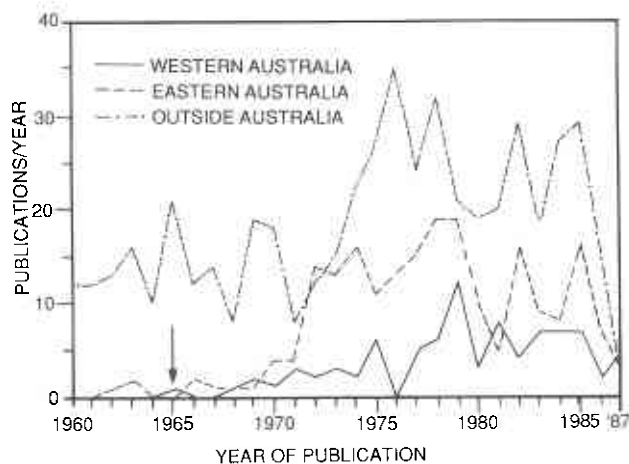


Figure 2

The increase in the number of publications per year on *Phytophthora cinnamomi* from Western and Eastern Australia, compared with areas other than Australia during the period 1960-1987. The arrow indicates the publication by Podger *et al.* (1965) of the association between *P. cinnamomi* and jarrah dieback. (Numbers of publications per year since 1960 are those abstracted in the Review of Plant Pathology.)

suggests, the life cycle of *P. cinnamomi* depends on moist conditions which favour survival, sporulation and dispersal. When conditions are warm and moist, microscopic spore sacks called sporangia and thick walled chlamydo spores are produced vegetatively from mycelial strands that form the body of the fungus in the soil or host tissue (Fig. 3).

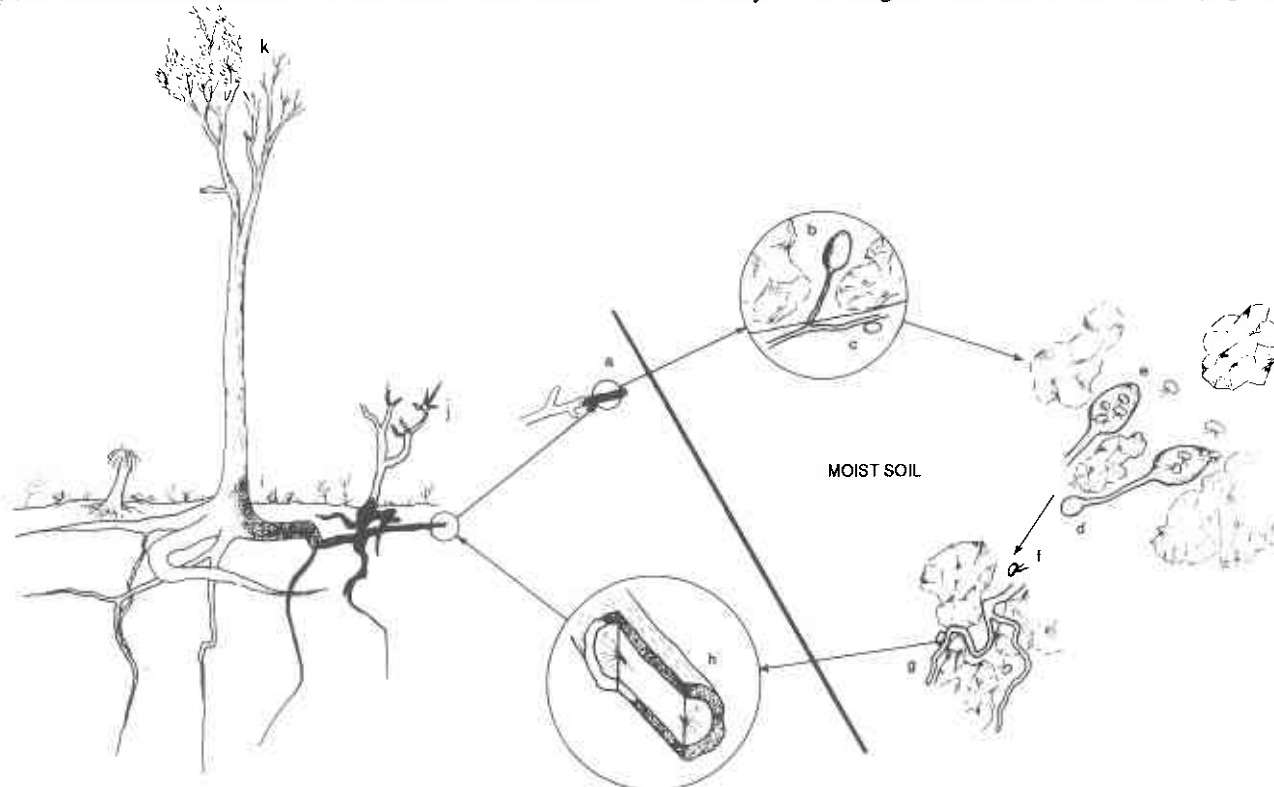


Figure 3

Life cycle of *Phytophthora cinnamomi* in the jarrah forest. Microscopic mycelium overwintering in infected roots (a) form chlamydo spores (c) or sporangia (b) when the soil is warm and moist. Chlamydo spores may germinate directly to form sporangia (d). Sporangia release motile zoospores in water (e) which are actively or passively dispersed through the soil to uninfected roots (f, g). Following infection the fungus invades root bark (h) to form lesions which are actively or passively dispersed through the soil to uninfected roots (f, g). Infection of roots and collar results in death of the host (j) or crown decline (k). (not to scale).

The sporangia release motile zoospores in free water to infect host roots. Mycelium of different mating types may grow together inducing the production of thick walled sexual spores called oospores. The mating types are called A₁ or A₂ with the A₂ mating type being the most common in the jarrah forest.

Once dispersed the spores of the fungus may infect a wide range of resistant and susceptible hosts. In 1980 at least 1000 species had been recorded as known hosts of which nearly half of these records were from research in Australia (Zentmyer 1980). The pathogen only flourishes in susceptible tissue, so that a great variety of susceptible hosts provides a readily available food base for repetition of the life cycle.

The large number of plant species susceptible to *P. cinnamomi* infection distinguishes the epidemic in the jarrah forest from epidemics in most other forest ecosystems. Checks and balances enhanced by diversity within forest ecosystems often limit the damage caused by indigenous pathogens to native communities. Instances where the jarrah forest is buffered against *P. cinnamomi* infection will be outlined throughout the review, but in general the impact of *P. cinnamomi* in the jarrah forest is an exceptional example of an introduced pathogen with a wide host range causing great damage to a diverse but mainly susceptible plant community.

In contrast to other forest diseases, human activity has played a major role in the long and short distance spread *P. cinnamomi* in infected soil. Although human activity has been involved in the long distance spread of a number of diseases, most forest diseases are primarily dispersed by natural agencies such as wind, insects and rain.

OTHER PHYTOPHTHORA SPECIES

Although *P. cinnamomi* is the *Phytophthora* species most frequently isolated from areas of dying vegetation, *P. citricola*, *P. cryptogea*, *P. megasperma* var. *sojiae*, *P. nicotianae* and unnamed *Phytophthora* species have been recovered from the jarrah forest (Shearer *et al.* 1987a, 1988). The life cycle of these *Phytophthora* species can differ from that of *P. cinnamomi*. For example, *P. citricola* and *P. megasperma* var. *sojiae* do not need different mating types in order to produce sexual spores. *Phytophthora cryptogea* can produce sporangia under drier conditions than *P. cinnamomi*. *Phytophthora cinnamomi* grows and sporulates better at warmer temperatures than other *Phytophthora* species. However, all of these *Phytophthora* species have a wide host range and a dependency on moisture to complete their life cycles. Greatest emphasis in this review will be given to the life cycle of *P. cinnamomi*, although differences in pathogenicity between *Phytophthora* species are compared in Chapter 5.

GENERAL DISTRIBUTION PATTERNS

Since the first observation of jarrah deaths in the early 1920s, *P. cinnamomi* has infected a wide range of plant communities in south-western Australia, ranging from coastal shrub-heath to tall forest. By 1977 an estimated 280 000 ha of Crown land was infected, increasing at the rate of 20 000 ha/year (Shea 1978). However, as will be illustrated in Chapters 3 to 6, the rate of increase from year to year has not been constant and not all plant communities are equally affected.

Regionally, affected areas are most frequent on the western edge of the Darling Scarp and decrease in number with distance east (Fig. 4). There is also a north/south gradient with the southern forest less affected than the northern forest. As a reflection of these regional differences, most of the research on *P. cinnamomi* has been done in the western part of the northern jarrah forest rather than in the eastern and southern forest. Conditions are most favourable for pathogen development in lowland water gaining areas such as depressions, gully heads and the bottom of shallow valleys. The dendritic pattern of affected areas in Figure 5

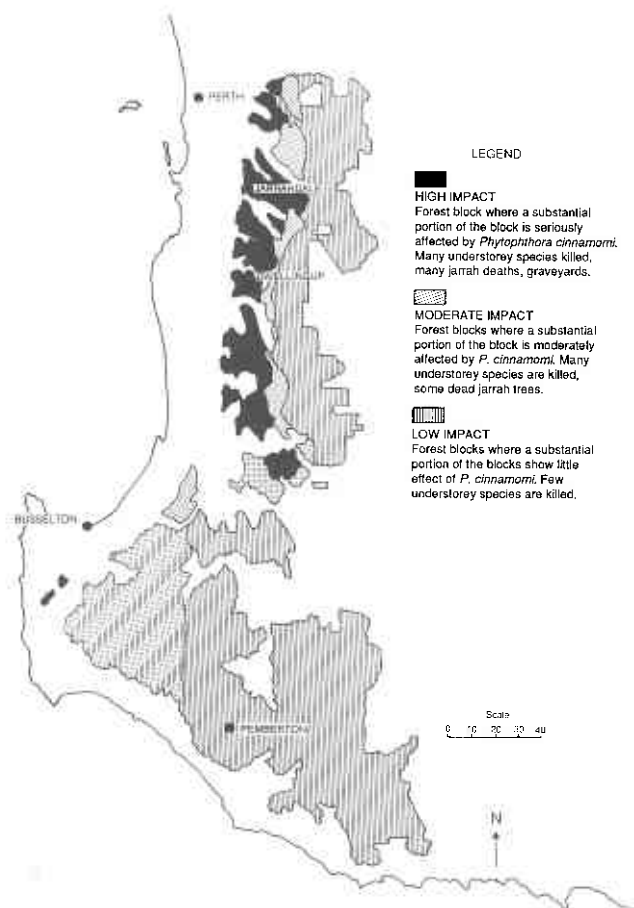


Figure 4

Impact of *Phytophthora cinnamomi* in south-western Australia (Department of Conservation and Land Management Mapping Section).

illustrates the interaction of the fungus with the streams in shallow valleys draining upland areas. The least impact is in red loams associated with the more deeply dissected river valleys.

The regional pattern of affected areas has not occurred by accident, but is the result of the interaction of the pathogen with climate, vegetation, soil, topography, drainage, time since infection and intensity of human activity. It reflects how factors of the environment interact to create niches which *P. cinnamomi* can or

cannot occupy. In order to fully appreciate how research has improved an understanding of some of these interactions and patterns, it is instructive to examine the environment and ecology of the jarrah forest.

In the following chapters the Preston River (Fig. 1) is used as a convenient divide between northern and southern jarrah forest. The southern jarrah forest understorey has many species not normally found north of the Preston River, in response to differences in landform, geomorphology and climate between the two areas.

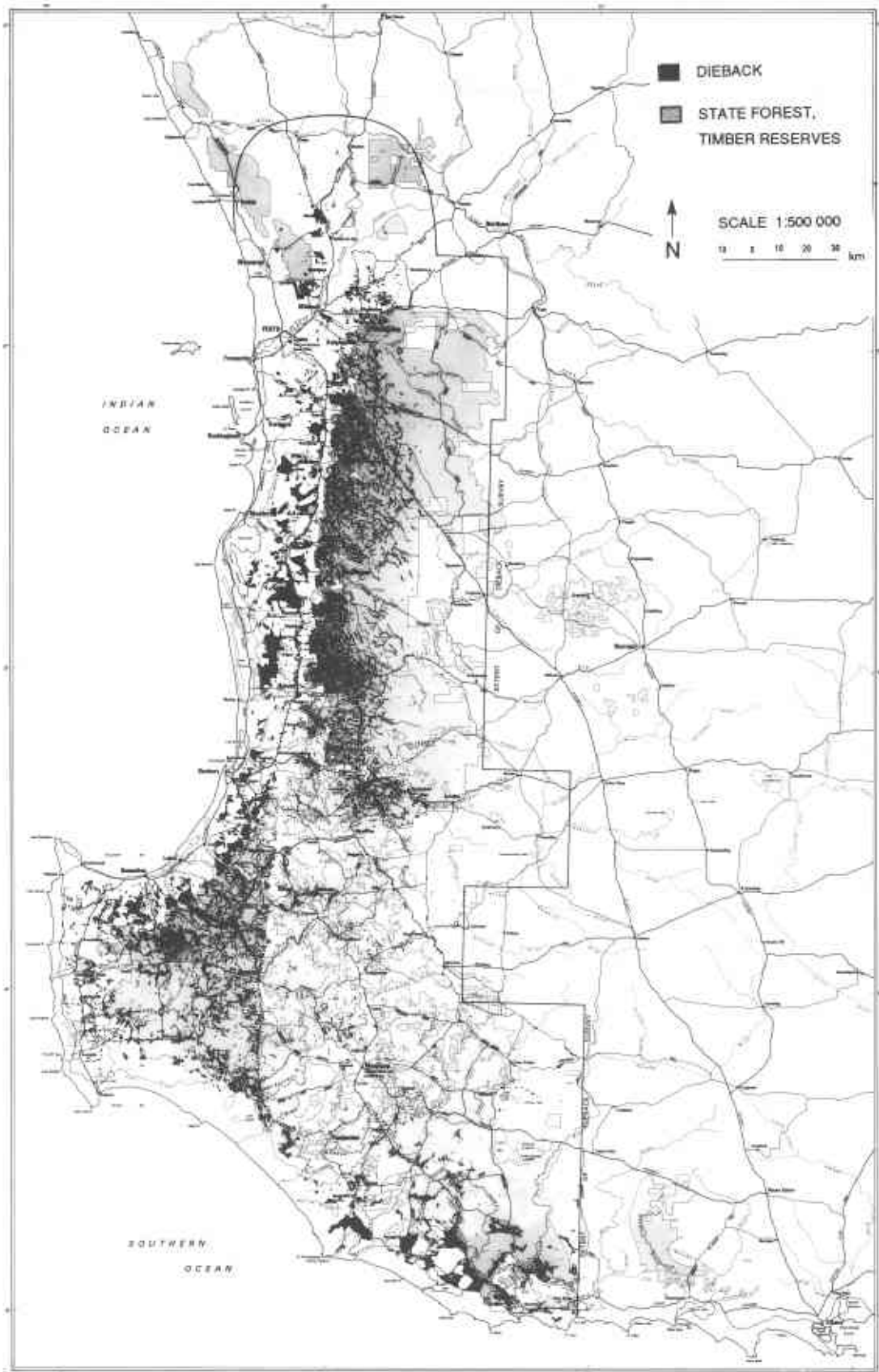


Figure 5

Areas affected by *Phytophthora cinnamomi* in south-western Australia (Department of Conservation and Land Management Mapping Section).

The Jarrah Forest Environment

The environment of the jarrah forest is a complex of microclimates characterised by the weathering of an ancient landscape over a long period of time. The various facets of the environment are interrelated, but have been categorized into geology and geomorphology, climate, the soils and their architecture and morphology, the hydrological cycle, soil temperature, fertility, and fire to aid description.

GEOLOGY AND GEOMORPHOLOGY

The jarrah forest is delineated on the western edge by the Darling Scarp (Fig. 1). The Scarp is a significant topographic feature of south-western Australia (Figs 1, 6). It was formed by displacement along the Darling fault line due to a marginal upwarping (Mulcahy *et al.* 1972) of the Great Plateau of Western Australia. The ancient plateau

is composed mainly of granitic rocks intruded by dolerite dykes and mantled with laterite. It rises to 250-400 m in the highest plateau remnants and culminates in isolated granitic hills or monadnocks up to 580 m in height (Fig. 6). Uplift of the plateau caused rejuvenated drainage and downwasting by streams, resulting in the normal sequence of valley shape being reversed. The valleys of the major rivers are deeply incised (V shaped) near the Scarp,

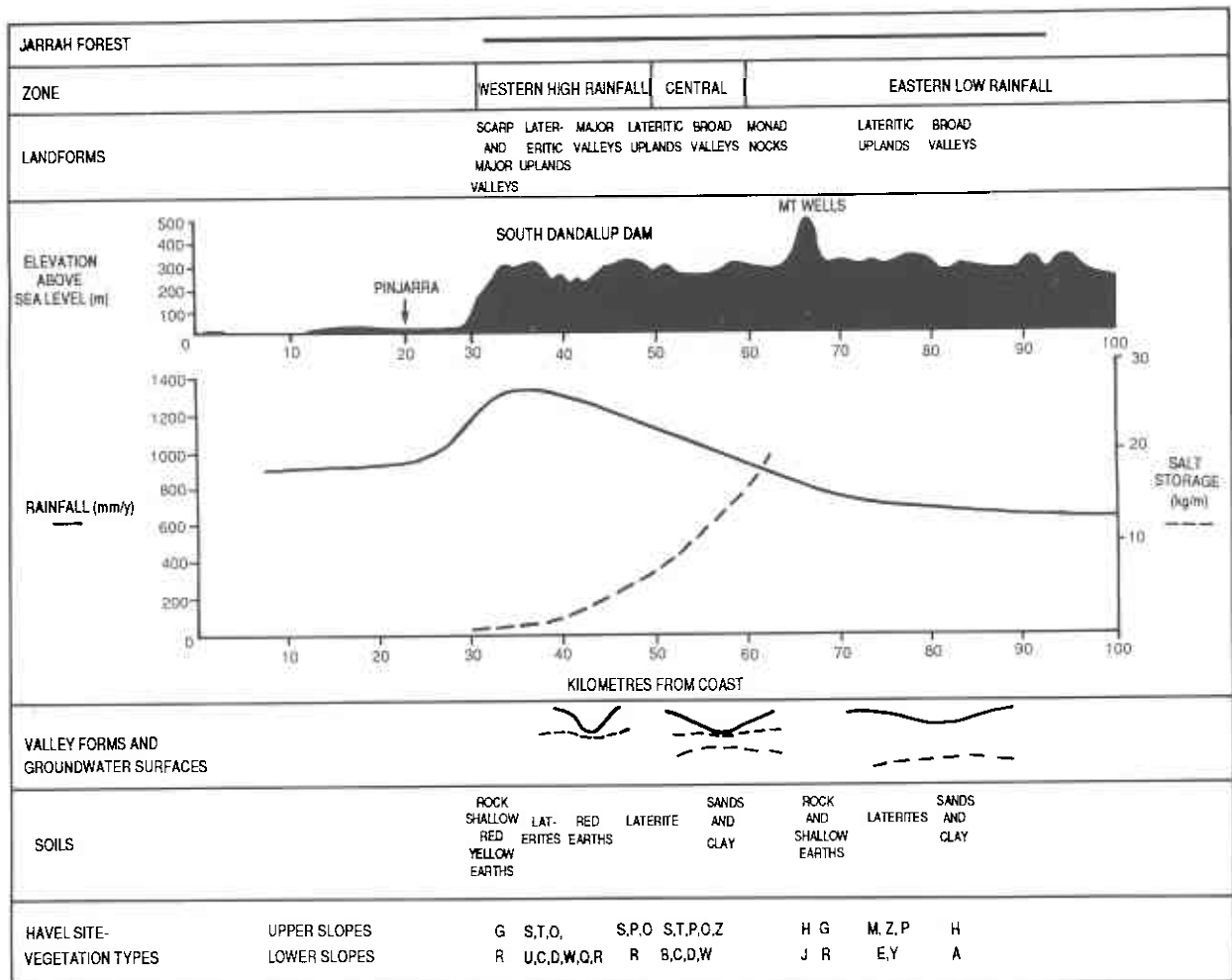


Figure 6

Variation in topography, rainfall, salt storage, valley form, soils and Havel site-vegetation types on a west-east transect across the jarrah forest. The transect passes through Pinjarra in the west and Mt. Wells in the east (Fig. 1). Havel site-vegetation types are described in Chapter 3. [Adapted from Shea and Herbert (1977) with additional information from Heddle *et al.* (1980)]

becoming gentle flat valleys near the head waters further east (Fig. 6). Thus the eastern edge of the forest is topographically less distinct and has much gentler relief than the western edge.

CLIMATE

The climate of the south-west is typically mediterranean with cool wet winters and hot dry summers. The seasonal pattern of rainfall and temperature strongly influences temporal changes in activity of *P. cinnamomi* in south-western Australia (ch. 5).

Most of the winter rainfall occurs when cold fronts meet the land mass during the period from May to October. Summers are dry because high pressure systems deflect rain-bearing frontal systems south of the land mass. Less than 5 per cent of annual rain falls in summer illustrating the marked seasonal distribution of rainfall. Evaporation is high in summer to the extent that the potential evaporation for Perth is more than the total annual rainfall. The summer drought limits plant growth (Havel 1975a) and plants have evolved specific adaptations to cope with the dry season (ch. 3). Interactions between heat troughs and moist tropical air can result in substantial summer rainfall in some years with significant effects on pathogen survival and disease expression (ch. 5).

Annual rainfall is greatest near the western edge of the Darling Scarp and decreases with distance east of the

Scarp (Figs 1, 6). Rainfall distribution is partly responsible for the decreasing incidence of *P. cinnamomi* with distance east of the Darling Scarp. As a management aid, the west-east rainfall gradient has been divided into high, intermediate, and low rainfall zones (mean rainfall > 1100 mm; ≤ 1100 to > 900 mm; and ≤ 900 to > 700 mm per annum respectively; Fig. 6). Rainfall also decreases from south to north because the frontal systems cross the southern coast more frequently than northern areas. Although annual rainfall on the high western edge of the central portion of the Darling Scarp can be as great as areas further south (Fig. 1), the wet season is shorter, ranging from 90 days in the northern areas to 120 days in the south.

Variation in rainfall between years may be large as illustrated in the annual rainfall and the 9-year moving mean for Dwellingup since 1935 (Fig. 7). The 1975-1987 period of continuous below average rainfall is the longest such period during the 53 years of records. The implications that this has for research and management are discussed in Chapter 8.

Average summer temperatures range from 18°C in the south to 27°C in the north falling gradually to 7 to 15°C respectively in July, the coldest winter month. Changes in soil temperature are described in the following section. Chapter 5 describes the effects of cool wet winters and hot dry summers on the development of *P. cinnamomi* in the soil profile and host tissue.

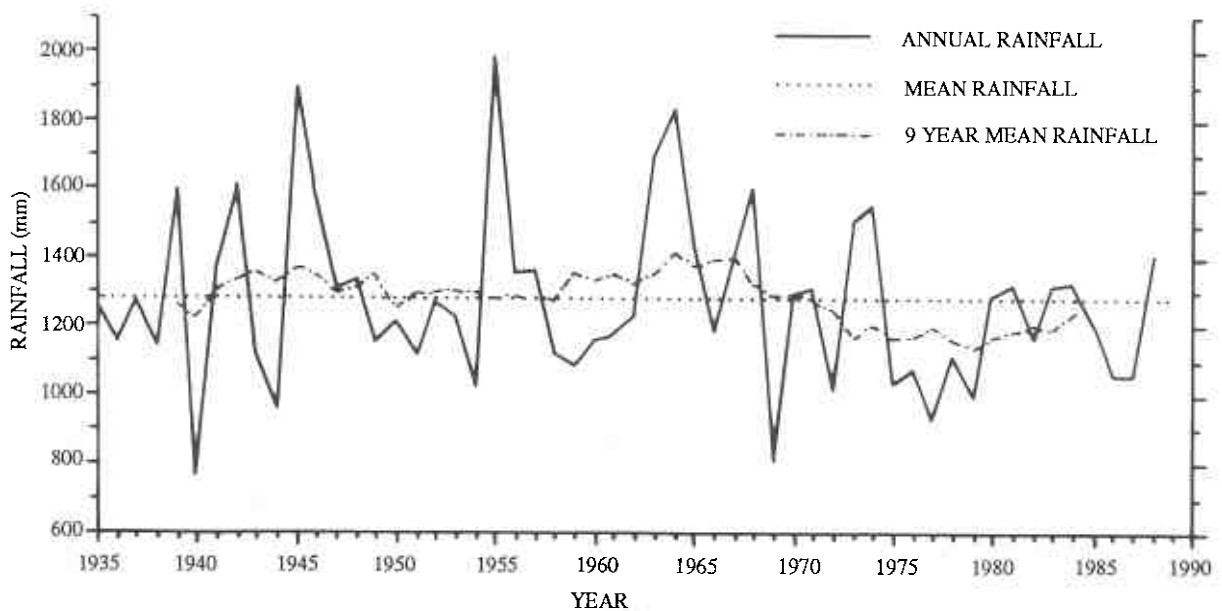


Figure 7

Annual and nine-year moving mean rainfall for Dwellingup during the period between 1935-1988.

SOILS

The evolution of the soils of the jarrah forest has been controlled by topographic position and geology, modified by climate (McArthur and Clifton 1975). In turn, the soil characteristics described in this section have strongly influenced the ecophysiology of jarrah and the behaviour of *P. cinnamomi* (chs 3 to 5). The soils reflect earlier periods of peneplanation, lateritization and uplift.

The architecture of the soil, morphology, hydrologic properties, temperature, and fertility are the most important soil factors that influence the life cycle of *P. cinnamomi* in the jarrah forest. The factors are interrelated, but are described under the main headings as follows.

ARCHITECTURE OF THE SOIL

The soil is composed of particles with a network of air and water filled pores between them. The size and distribution of the interconnecting network of pores, called the pore space, is important for plant growth, the hydrologic cycle (described in a following section) and sporulation and dispersal of *P. cinnamomi* within the soil profile (ch. 5). The fundamental properties of a soil depend on the geometry of the pore space, movement of water within the pores on

the properties of the bounding surfaces, and on the mechanisms that supply nutrients to the water in the pores and also to the solid surfaces.

The pore space depends not only on the kinds and sizes of individual particles (soil texture) but also on how these are arranged and bonded together (soil structure). The properties of some jarrah forest soils are given in Table 1. Later sections and chapters describe relationships between texture, water holding capacity and development and dispersal of *P. cinnamomi*.

Clayey and loamy soils with a well developed structure are relatively porous because the particles bond together to form aggregates. Soils with weak structural development, such as the sandy gravels, can also be relatively porous as the pore space is partly determined by the way the inert sand and gravel fractions are packed together. Gravel content varies between soil type (Table 1), being up to 99 per cent in some lateritic soils (McArthur and Clifton 1975). It may also increase with depth; in a Havel site-vegetation type S (ch. 3), gravel content varied from 24 per cent in the top 5 cm of soil to 84 per cent at 80-100 cm depth (Hingston *et al.* 1981). Pore size is also determined by the development of macropores by roots and invertebrates. Little is known of the pore size distribution in jarrah forest soils.

Table 1

Properties of soils of the jarrah forest sampled from selected Havel site-vegetation types (after Havel 1975a). The Havel site-vegetation types are described in Chapter 3.

Soil	Position	Havel Site Type	Gravel %	Silt & clay %	% N x 100	P ppm	K me% x 100	ex Ca me x 10
Dark brown sandy silt-loam over red-brown clay loam	Slopes of major valleys	Q	18	18	14	114	82	47
Yellow-brown sandy loams to loams	Lower slopes and valley floors	W	14	12	14	36	58	35
Orange to brown gravel with sandy loam to loam matrix	Upper slopes and ridges in high rainfall zone	T	44	25	14	89	60	73
Yellow to orange lateritic gravel with loamy sand matrix	Mid & upper slopes, & ridges in high-intermediate rainfall zone	S	51	10	25	25	35	29
Lateritic gravel with sand or loamy sand matrix	Mid & lower slopes in high-intermediate rainfall zone	P	55	8	6	35	30	35

SOIL MORPHOLOGY

The gently undulating remnant plateau uplands are mantled with relict laterite whose surface horizons contain gravelly sandy soils overlying pavements of duricrust. The laterite profile consists of about 0.5-1 m of gravelly sandy loam topsoil overlying a concretionary zone of ferruginous and aluminous horizons of ironstone gravels in a yellow-brown sandy loam matrix up to 5 m thick. Beneath this, deep kaolinitic clay extends up to 30 m to bedrock (Fig. 8). Bauxite mining occurs in those profiles where the alumina content is sufficiently high. Areas with the greatest development of a friable bauxite layer most suitable for mining mainly occur in good quality forest (Abbott and Loneragan 1986) in mid slope positions.

Massive ironstone duricrust pavements are common just below the surface of lateritic soils near ridge tops and occasionally on slopes (Fig. 9). The pavements may be extensive (Fig. 9a) or broken into discrete slabs (Fig. 9b). Following weathering of the mantle and movement and sorting of the detritus, finer gravels have been cemented into a duricrust that becomes discontinuous with distance downslope. The duricrust is most extensive and thickest towards the western edge of the northern part of the forest and is reduced to scattered residuals further east (Fig. 10) and south. Thinner development of the ferruginous duricrust layer in the east than the west may account for the greater stripping of the laterite landscape with distance east (McArthur *et al.* 1977).

Red earthy deep loams (Fig. 11) have developed on the slopes of the dissected river valleys and in association with dolerite dykes in the west where stripping of the mantle has exposed the substrate. Shallow valleys occurring in lateritic uplands have gravelly slopes and yellow brown sandy loams associated with the flat swampy floors. Near the eastern edge of the forest, duplex soils with a range of textures and depths predominate (McArthur and Clifton 1975; McArthur *et al.* 1977; Fig. 6).

THE HYDROLOGIC CYCLE

Spatial and temporal variation in the elements of the hydrologic cycle determines the availability of water in the jarrah forest (Fig. 12). The water cycle affects not only the distribution and growth of plant species, but also the life cycle of *P. cinnamomi*. As described in later chapters, the water status of soil and host tissue are important factors determining survival and dispersal of the pathogen and disease expression.

Precipitation, mainly as rain, reaches the forest by frontal systems. The soil gains water directly from rain falling between canopies. Indirect gain comes from water dropping from intercepting foliage (throughfall) or flow along trunks (Fig. 12).

Jarrah forest soils are characteristically very permeable when moist, encouraging rapid infiltration of water through the soil surface. Little overland flow occurs in forested

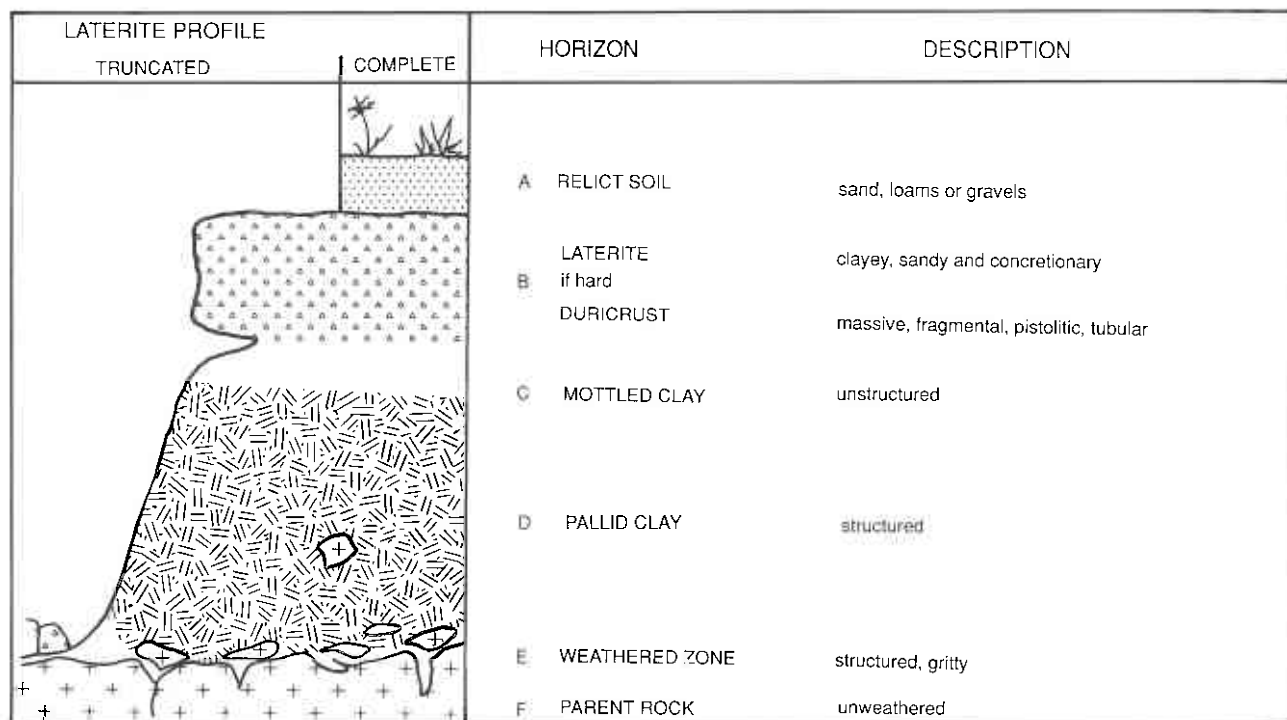


Figure 8
Morphological zones of a laterite profile (not to scale).

areas as the infiltration capacity of jarrah forest soils is rarely exceeded, even during heavy downpours in winter (Bettenay *et al.* 1980). However, the soils resist wetting when dry (McArthur and Clifton 1975) and overland flow may occur during heavy summer rain.

Water is redistributed both vertically and laterally in the profile during and following infiltration. The coarse-

textured laterites that have a high water storage capacity absorb a large proportion of the rainfall in winter. Absorbed water is held as films within the soil pores by surface tension. Soil water availability, determined largely by the surface tension forces holding the films of water, is measured in terms of energy as soil matric potential. Soil water status is an important determinant of survival and sporulation of *P. cinnamomi* (ch. 5).

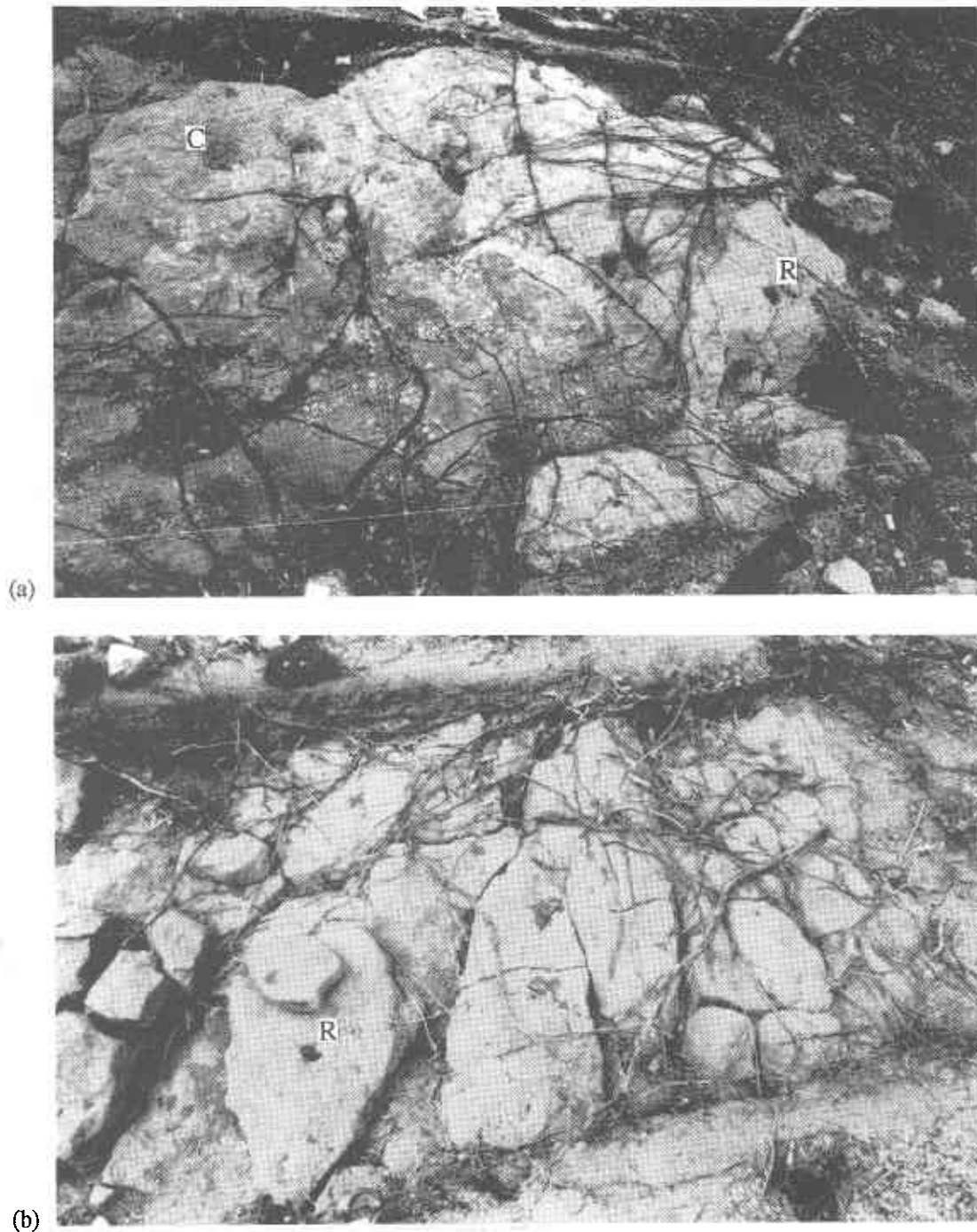


Figure 9

Upland laterite near Dwellingup with the gravelly sand topsoil removed to expose the duricrust layer. The duricrust layer may outcrop or occur up to 1 m below the soil surface. (a) Duricrust occurs as a continuous layer with cementation (C). Note the circular depressions where roots pass through the layer (R). (b) Duricrust layer occurs as discrete slabs. Roots can penetrate the layer through cracks or root channels (R).

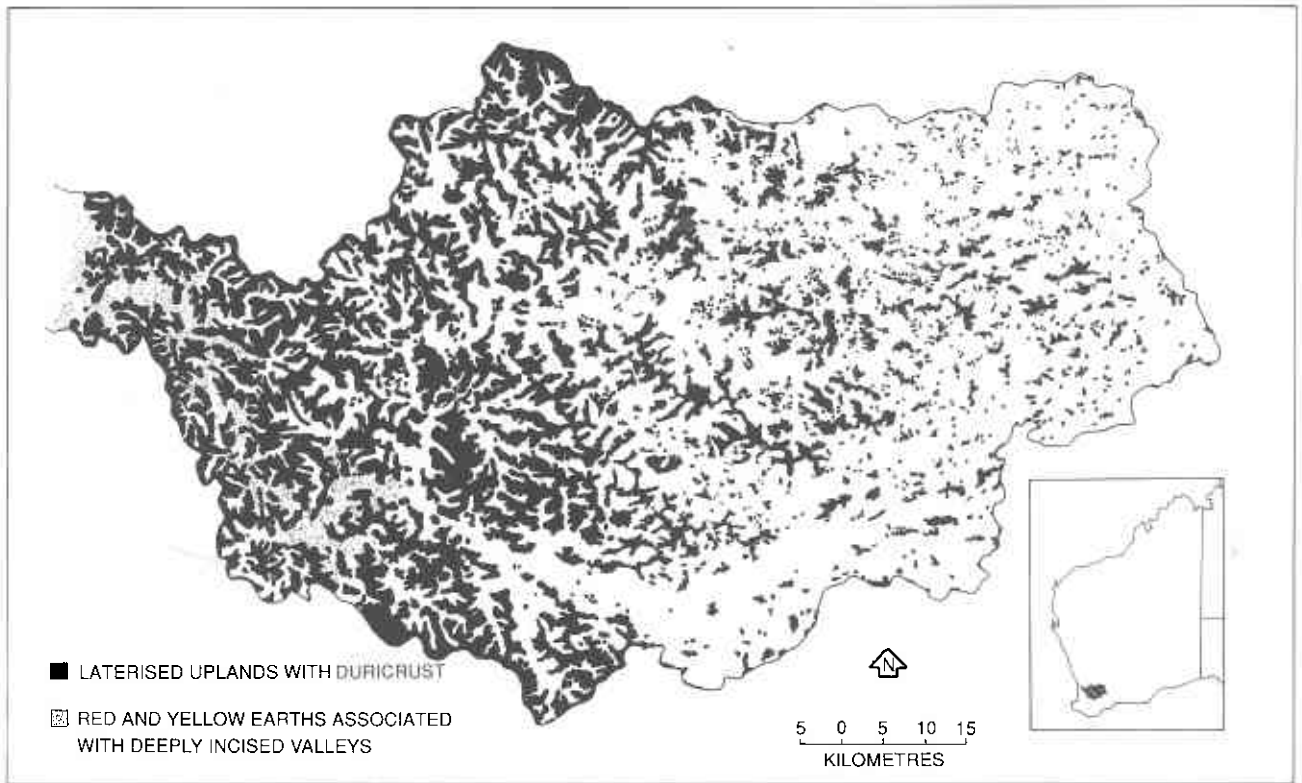


Figure 10

Distribution of laterite underlain by duricrust and the dissected river valleys in the Murray River catchment of the northern jarrah forest (McArthur *et al.* 1977).



Figure 11

Profile of a deep red loam found on mid and lower slopes of dissected valleys in the high rainfall zone at the western edge of the Darling Scarp (cf. Fig. 9).

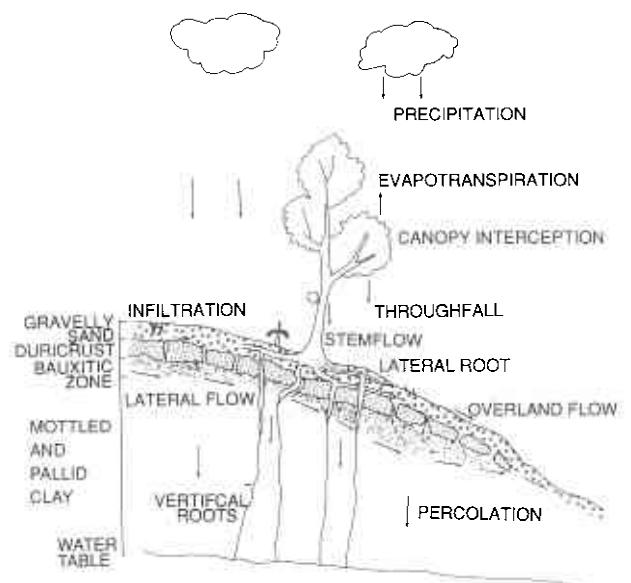


Figure 12

Schematic diagram showing potential pathways of water in the hydrologic cycle of the jarrah forest (not to scale).

Figure 13 shows the relationship between soil matric potential and water content for some jarrah forest soils. The physical characteristics of sieved gravelly sandy loam soil from the surface 10 cm of upland areas were sufficiently similar to give similar water contents at the same matric potentials. In contrast, there were large differences in water contents at the same matric potential between lateritic soil from upland areas and yellow fine sandy loam from a lowland area (Fig. 13). At a matric potential of -40 kPa, the water content of surface lateritic soils from upland areas was about 10 per cent compared with about 45 per cent for the yellow earth from the lowland area. Figure 26 shows changes of soil matric potentials with season in a lowland and an upland area.

Water moves in the large pore spaces of the soil, either downwards towards the water table or up towards the soil surface where it is evaporated. Water readily percolates through the surface horizons of coarse-textured gravelly sand typical of upland areas. The gravelly sands have a high saturated hydraulic conductivity of about 2 m/day, in contrast to the underlying duricrust and the sandy clay layers which have a low hydraulic conductivity of about 10^{-3} m/day (Sharma *et al.* 1987). Duricrust and clay layers can impede the vertical percolation of water resulting in near-surface transient perching with lateral flow and seepage of water below the soil surface in some upland areas (Fig. 12; Kinal 1986). Chapters 5, 7 and 8 describe and assess the importance of subsurface perching and lateral flow of water to the life cycle of *P. cinnamomi* in the jarrah forest.

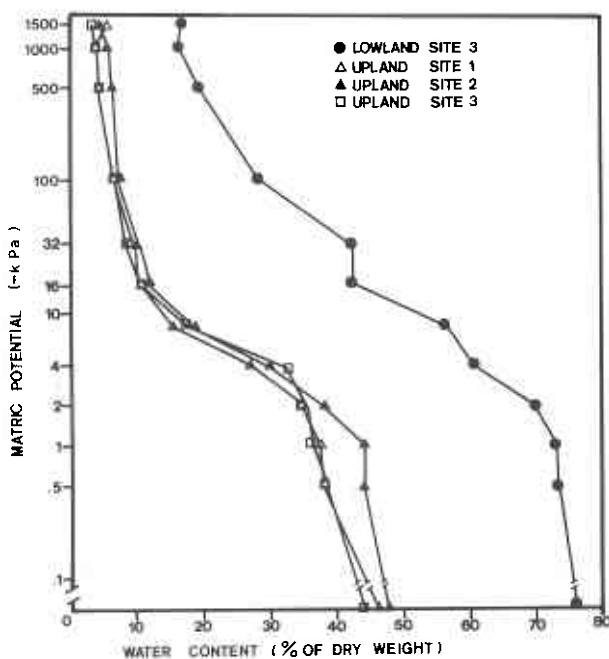


Figure 13

Relationship between matric potential and water content for sieved surface gravelly sandy loam from three upland areas and a sieved surface fine sandy loam from a lowland area in the jarrah forest (Shearer and Shea 1987).

The amount of near-surface perching and lateral flow of water varies between areas depending on topographic position, soil type and the occurrence of pathways for vertical percolation of water. Water seepage from upslope keeps the gravel over clay soil profiles occurring in the zone transitional between upland laterites and the headwaters of streams in shallow upland valleys moist well into summer. Conditions are consequentially favourable for survival of *P. cinnamomi* in these areas through most of the year (ch. 5).

Root channels (Dell *et al.* 1983) and cracks in the duricrust layer (Bettenay *et al.* 1980) are preferred flow pathways which encourage rapid vertical percolation of water. Flow along preferred paths is an important but unquantified component of the jarrah forest hydrologic cycle (Loh *et al.* 1984). Vertical percolation through the subsoil is probably related to root distribution. The high biomass associated with the high fertility of the red earths probably enhances vertical percolation of water because of the large number of root channels. Subsoil parent material also influences the occurrence of root channels as they are permanent features of profiles derived from granite but generally absent from profiles derived from dolerite (Dell *et al.* 1983).

Groundwater recharge is an important component of the jarrah forest hydrologic cycle and is affected by many factors such as topography, climate and vegetation. However, only those relevant to the life cycle of *P. cinnamomi* are considered here. Permanent groundwater directly affects the activity of *P. cinnamomi* in near-surface soil horizons where discharges to the surface occur within first and second order streams where bedrock frequently outcrops and soils are shallow (Fig. 6). Permanent groundwater in upland and eastern areas of the forest mainly occurs 15-30 m below the soil surface (Fig. 6) and in these areas does not affect the life cycle of *P. cinnamomi* in upper horizons as much as near-surface lateral seepage of water. However, the vertical tap root system of jarrah which taps the large water stores held deep in the soil (ch. 3) is vulnerable to infection by *P. cinnamomi* (ch. 5). Plant species distribution (ch. 3) is also affected by the depth to groundwater.

Relatively little recharge of groundwaters occurs in forested areas, even in the high rainfall zone. This is partly due to efficient extraction of water from the profile by vegetation to maintain photosynthesis and plant water status (ch. 3). Borg *et al.* (1987) estimate that water transpired by the jarrah forest vegetation accounts for 60-70 per cent of the total rainfall in the high rainfall zone and 80-90 per cent in the low rainfall zone. The high *in situ* consumption of rainfall has caused accumulation within the soil profile of salt carried inland mainly by rain. Salt accumulation in the soil is low in the high rainfall zone forest because of high rates of leaching. Salt accumulation increases with decreasing rainfall and stream yields, and

hence leaching in the intermediate and low rainfall zones further east (Fig. 6).

Reduction in vegetation density affects the hydrologic cycle by reducing transpiration and interception. Decreases in transpiration and interception decrease the amount of water extracted from the profile and increase water gained by infiltration respectively. Soil moisture storage was significantly greater throughout most of the year in a jarrah forest stand thinned from 37 to 17 m²/ha compared with unthinned forest (Stoneman 1988). Reducing stand density affected soil moisture storage at 5 m depth more than storage at 2 m depth. Groundwater in a midslope position rose four metres in the four years following a two-thirds reduction in the basal area of an intermediate rainfall zone first order catchment (Stoneman 1988).

The amount and duration of changes in vegetation density determine the magnitude of change in hydrological response. When logging is followed by rapid regeneration and regrowth, changes in hydrological conditions return to pre-logging values in about 10 years (Borg *et al.* 1987). Removal of vegetation and topsoil by bauxite mining and revegetation of the mined areas affects the hydrological balance in a complex and variable way. The effects of a range of mining and revegetation practices on the hydrological balance has yet to be fully evaluated (Loh *et al.* 1984). Near-surface lateral seepage of water was increased in two mined high rainfall zone catchments monitored over the last decade (Loh *et al.* 1984). Near-surface seepage of water favours disease intensification and spread (chs 5 and 7).

Phytophthora cinnamomi affects the water budget by permanently changing the density and composition of the vegetation. Variation in the impact of the disease (chs 4 and 6) determines the magnitude of the effect. Infection with *P. cinnamomi* caused a reduction in vegetation density that was correlated with the increase in the yield of Wungong Brook fed by the affected catchment (Batini *et al.* 1980). In salt prone areas *P. cinnamomi* infection can lead to raised water tables and increased stream salinity (Shea and Herbert 1977).

SOIL TEMPERATURE

The inputs, storage, fluxes and outputs of energy are poorly understood for the dynamic processes affecting soil temperature in the jarrah forest. The soil is warmed by daily and annual cycles of radiation. Figure 14 shows changes of soil temperature with season for a study area near Dwellingup. Energy is lost through re-radiation and evaporation. The amount of energy falling on the soil surface is mainly affected by the amount of canopy cover and aspect.

Surface soil shaded by vegetation and litter is cooler than soil in the open by about 2°C in winter to about 10°C

in summer (Christensen 1975; Shea 1975; Fig. 14). However, no relationships are available to predict the effect of different levels of shading on soil temperatures in the jarrah forest. In addition little information is available on the effects of removal of cover and blackening of the soil by fire on soil temperature. Shea (1975) simulated fire by removing the litter from the soil surface and found similar cooling of the top 7.5 cm soil covered by litter compared with open ground, as that already described for shaded and open areas. Aspect also affects the amount of incoming radiation. Shea (1975) found that temperatures in the top 15 cm of soil on a south facing slope were 2-5°C cooler than those in soil on a north facing slope. Winter rains borne by cool winds from the south-west cool the soil (Shea 1975), although the relationships between rain and soil temperature have not been determined.

Once radiant energy reaches the soil surface the conduction of heat through the profile is affected by soil composition, structure and moisture content. Little is known of the effects of these factors on the conduction of heat through the soils of the jarrah forest, especially since the factors change appreciably with depth.

The gradient of soil temperature with depth is important to *P. cinnamomi* since temperature is a major stimulus to its life cycle and the fungus occurs up to 3 m below the soil surface (ch. 5). Information on changes of temperature with depth in the jarrah forest is lacking as previously reported temperatures were measured in the top 30 cm of soil (Christensen 1975; Shea 1975). In a study area near Dwellingup, temperatures in winter at 1.5 m below the soil surface were warmer and fluctuated less than those near the surface (Fig. 14). Temperatures at 1.5 m below the surface of an area with 60 per cent canopy were 2-5°C cooler than those in an area with 10 per cent canopy (Fig. 14).

Phytophthora cinnamomi infection, and also logging, mining, burning and site quality can affect the heat budget of the soil by controlling the amount of vegetation cover and shading. *Phytophthora cinnamomi* reduces crown cover by killing jarrah in the overstorey and susceptible plant species in the understorey (ch. 4). The effects of burning, logging, and mining depend on how quickly vegetative cover is re-established in affected areas. High quality sites have higher biomass and associated greater canopy density and litter cover than low quality sites. Biomass accumulation is partly dependent on soil fertility, a description of which follows.

SOIL FERTILITY

The fertility of the major soil groups of Australia is low by world standards (Leeper 1960). The nutrient stores in jarrah forest laterites are particularly poor compared with stores in other Australian forest soils (Hingston *et al.* 1981). The infertility of laterites has made them unattractive

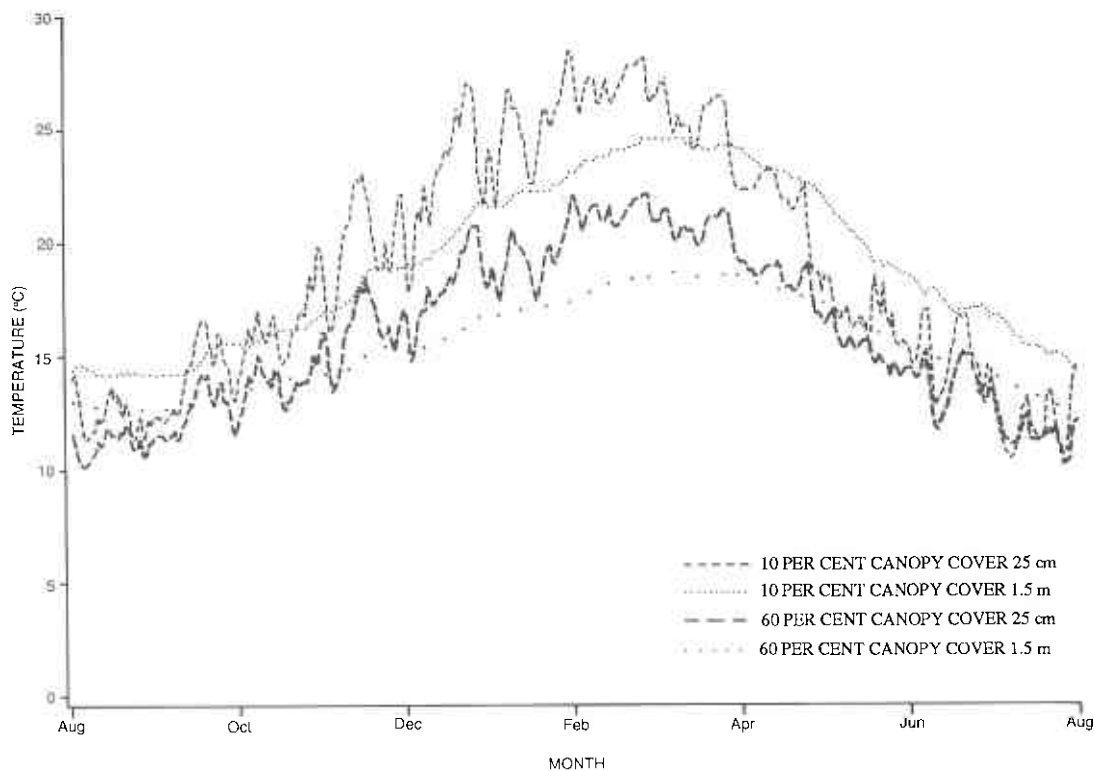


Figure 14

Daily midday soil temperature measured at 25 cm and 1.5 m below the soil surface in an area with a 10 per cent canopy cover compared with one with a 60 per cent canopy cover at a study area, 20 km south-east of Dwellingup.

for agriculture and played a part in the preservation of the jarrah forest. This has been partially negated by the low fertility favouring survival of *P. cinnamomi*, since impoverished soils do not encourage high populations of soil microflora antagonistic to the pathogen (chs 5 and 7).

The fertility of jarrah forest soils varies from the relatively fertile fine textured red earths to the infertile lateritic gravelly sands (Table 1). Variations in fertility are related to the degree of weathering; laterites have been depleted over longer periods than the freshly weathered red loams in younger parts of the landscape (Turton *et al.* 1962). Availability of phosphorus is particularly low in lateritic soils, due to long periods of leaching of weathered materials from parent rock already low in phosphorus and to fixation by iron oxides. The jarrah forest vegetation has developed specialized root systems to cope with low phosphorus availability (ch. 3). Infection by *P. cinnamomi* can be favoured or disfavoured by the particular type of specialized root system developed (ch. 5).

Later chapters refer to biological activity in the soil. Biological activity is encouraged by organic matter in the surface 30 cm soil, which in turn is influenced by the biomass of the vegetation. Organic matter content of jarrah forest soils is generally low. Lateritic soils of a Havel site-vegetation type S (ch. 3) had an organic matter content of 5 per cent in the top 5 cm, decreasing to 1-2 per cent at depths between 10 cm and 1 m (Hingston *et al.* 1981). The

higher fertility of the red loams encourages greater biomass and therefore higher organic matter and biological activity than is the case in the infertile lateritic soils (Podger 1972).

FIRE

Jarrah forest communities are highly flammable due mainly to the high content of volatile oils in leaves and the rapid accumulation of flammable litter fuels on the forest floor (Underwood and Christensen 1981). Fire is a natural part of the jarrah forest environment and plants have evolved adaptive strategies such as thick bark, dormant buds and heat triggered seed release mechanisms and dormancy to cope with it. Fire influences nutrient cycling by unlocking nutrients bound in dead tissues and encouraging the germination of nitrogen fixing legumes.

Broad-scale low intensity burns have been implemented on a regular basis to reduce the accumulation of flammable litter and the incidence of uncontrolled wild fires. Techniques developed for low intensity burns have been refined to allow manipulation of the frequency and intensity of fires in the forest.

Understorey composition that is important to survival and sporulation of *P. cinnamomi* (chs 5 and 7), is affected by fire intensity and frequency. The following chapter describes the vegetation and how it has developed in response to the environment of the jarrah forest.

The Vegetation

The diversity of the shrub layer of the jarrah forest is in contrast to the floristic paucity of the tree strata. The understorey occurs as a complex mosaic because the vegetation integrates and indicates the diversity of microclimates occurring within the forest. Systems for site-vegetation typing and the adaptation of the vegetation to the environment are described.

The northern jarrah forest viewed from the air has a remarkably uniform appearance over a vast area; jarrah crowns dominate. Marri (*Eucalyptus calophylla* Lindley) grows in association with jarrah on a range of sites but near-pure stands of jarrah are widespread. Jarrah is a remarkable species for its ability to dominate a very wide range of sites. It is only in valleys and depressions that the other eucalypt species, yarri (*E. patens* Benth.), bullich (*E. megacarpa* F. Muell.) and wandoo (*E. wandoo* Blakely), replace jarrah. Wandoo replaces jarrah on the heavier textured soils of the eastern low rainfall zone of the forest and on the slopes of monadnocks.

The forest is characteristically dry sclerophyll with a uniform overstorey dominated by jarrah, but with up to 50 per cent marri in some places. It varies in height from 25-30 m in the western part of its range to about 15 m in the eastern part and on low quality sites (Fig. 15). The small-tree understorey of 10-15 m is mainly restricted to eucalypt regeneration, *Allocasuarina fraseriana* (Miq.) L. Johnson, and two Proteaceous species, *Banksia grandis* Willd. and *Persoonia longifolia* R. Br (Fig. 15). *Banksia grandis* commonly occurs as dense thickets in the western high rainfall zone, becoming less frequent in the eastern low rainfall zone. In contrast to the floristic paucity of the tree strata, the jarrah forest floor is covered by a diverse sclerophyllous shrub layer 1-2 m in height (Havel 1975a).

The diversity of the shrub layer reflects more specific requirements for successful establishment compared with the widely distributed jarrah (Havel 1975a,b). The understorey occurs as a complex mosaic wherein the vegetation integrates and hence serves as an indicator of the diversity of environmental conditions. A change in soil type or drainage is often associated with changes in the composition of the understorey rather than obvious changes in the jarrah overstorey (Havel 1975a,b). Havel (1975a) used principal component analysis to determine the relationships between vegetation and environment. In this manner, a large number of northern jarrah forest vegetation samples were arranged into site-vegetation types based on their similarity.

SITE-VEGETATION TYPES

As noted by Havel (1979b):

Perhaps the simplest way to describe the situation is to say that the vegetation is an integral part of the landscape in which it occurs. It is shaped by the landscape, and what vegetation is found at any one locality depends on the climatic, topographic and soil conditions at that locality. It influences the landscape in that it speeds up the breakdown of rocks and slows down erosion of the soil. It should therefore not be surprising that the number of possible interactions and combinations is so great, and that it is not easy to describe them briefly and clearly.

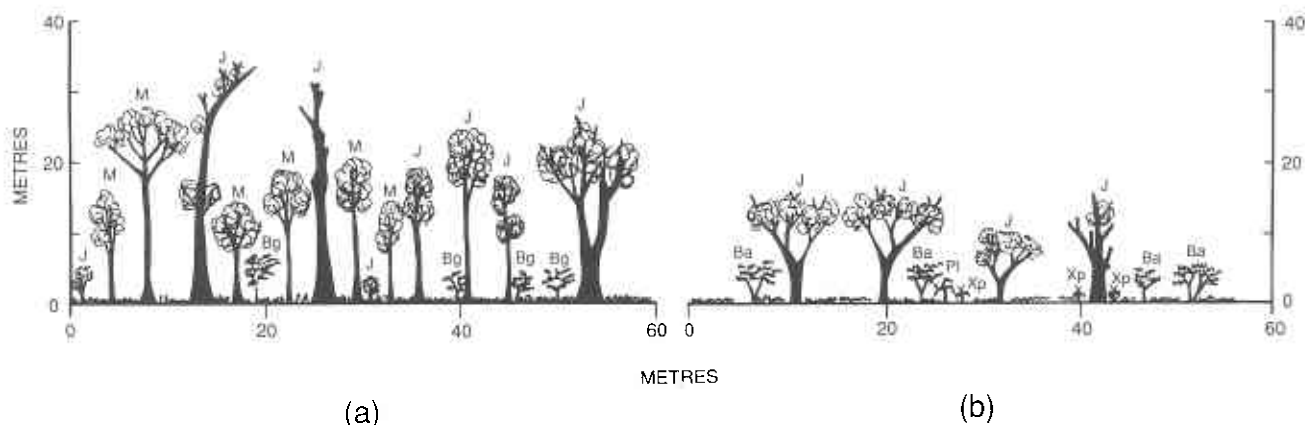


Figure 15

Profile of (a) jarrah-marri open forest and (b) jarrah-open woodland. J = jarrah, M = marri, Bg = *Banksia grandis*, Ba = *B. attenuata*, Pl = *Persoonia longifolia*, Xp = *Xanthorrhoea preissii* (McArthur and Clifton 1975).

Havel described the variation in vegetation as a four dimensional continuum in which the factors of the environment were strongly interrelated (Havel 1975a). Topography, moisture availability affected by proximity to the Scarp, the degree of leaching and fertility of the soil were the main factors influencing variation in the vegetation.

The continuum was broken into site-vegetation types, each having a characteristic group of indicator species. Table 2 gives the indicator species for the site-vegetation types of the northern jarrah forest for which jarrah dominates in the tree stratum. A general description of the Havel site-vegetation types (Havel 1975a,b) occurring on the transect through Pinjarra and Mount Wells (Fig. 6) follows.

Table 2

Havel site-vegetation types for the northern jarrah forest in which jarrah dominates in the tree stratum (Havel 1975a).

Havel Site Type	Other tree species	Indicator species usually present	Description	Soil Type
R	<i>Eucalyptus calophylla</i>	<i>Hakea lissocarpa</i> <i>Leucopogon capitellatus</i> <i>Leucopogon propinquus</i> <i>Macrozamia riedlei</i> <i>Phyllanthus calycinus</i> <i>Trymalium ledifolium</i>	Uniform to concave. Valley slopes, frequently in proximity to granite outcrops.	Grey to brown sandy loam to sandy clay with admixture of lateritic gravel.
Q	<i>E. calophylla</i> <i>E. patens</i>	<i>Acacia extensa</i> <i>Chorizema ilicifolium</i> <i>Hakea lissocarpa</i> <i>Hypocalymna angustifolium</i> <i>Leucopogon capitellatus</i> <i>Leucopogon propinquus</i> <i>Macrozamia riedlei</i> <i>Phyllanthus calycinus</i> <i>Trymalium ledifolium</i> <i>Trymalium floribundum</i>	Uniform or convex. Lower and middle slopes .	Dark brown sandy or silty over red-clay loam.
D	<i>E. calophylla</i> <i>E. patens</i>	<i>Acacia extensa</i> <i>Baeckea camphorosmae</i> <i>Dampiera alata</i> <i>Hypocalymna angustifolium</i> <i>Kingia australis</i> <i>Lepidosperma angustatum</i> <i>Leptocarpus scariosus</i> <i>Leptospermum pericalymna</i> <i>Mesomelaena tetragona</i> <i>Synaphea petiolaris</i>	Concave. Lower slopes and valley floors .	Orange-brown loam sands and sandy loams over sandy clay or secondary lateritic ironstone.
W	<i>E. calophylla</i> <i>E. patens</i>	<i>Acacia extensa</i> <i>Hakea lissocarpa</i> <i>Hypocalymna angustifolium</i> <i>Lepidosperma angustatum</i> <i>Mesomelaena tetragona</i> <i>Synaphea petiolaris</i>	Concave. Lower slopes and valley floors .	Yellow-brown or orange-brown sandy loams to loams.
P	<i>Allocasuarina fraseriana</i> <i>Banksia grandis</i> <i>E. calophylla</i> <i>Persoonia longifolia</i>	<i>Acacia browniana</i> <i>Adenanthos barbigerus</i> <i>Grevillea wilsonii</i> <i>Hovea chorizemifolia</i> <i>Lechenaultia biloba</i> <i>Lepidosperma angustatum</i> <i>Patersonia rudis</i> <i>Styphelia tenuiflora</i>	Mostly uniform. Mild, Lower and middle slopes .	Lateritic gravel with sand or loamy sand matrix, or sand with heavy gravel.
S	<i>Allocasuarina fraseriana</i> <i>Banksia grandis</i> <i>E. calophylla</i> <i>Persoonia longifolia</i>	<i>Acacia browniana</i> <i>Adenanthos barbigerus</i> <i>Hovea chorizemifolia</i> <i>Lasiopetalum floribundum</i> <i>Leptomeria cunninghamii</i> <i>Leucopogon capitellatus</i> <i>Leucopogon propinquus</i> <i>Macrozamia riedlei</i> <i>Patersonia rudis</i> <i>Phyllanthus calycinus</i> <i>Styphelia tenuiflora</i>	Uniform or convex. Mid and upper slopes, plateaus and ridges.	Yellow to orange heavy lateritic gravel with loamy sand matrix.

Table 2 cont.

T	<i>Banksia grandis</i> <i>E. calophylla</i> <i>Persoonia longifolia</i>	<i>Acacia urophylla</i> <i>Bossiaea aquifolium</i> <i>Clematis pubescens</i> <i>Hovea chorizemifolia</i> <i>Lasiopetalum floribundum</i> <i>Leucopogon capitellatus</i> <i>Leucopogon propinquus</i> <i>Leucopogon verticillatus</i> <i>Macrozamia riedlei</i> <i>Phyllanthus calycinus</i> <i>Pteridium esculentum</i>	Mainly convex . Upper slopes and ridges in strongly dissected, high- rainfall western zone.	Orange to brown gravel with sandy loam to loam matrix.
O	<i>E. calophylla</i> <i>B. grandis</i>	<i>Bossiaea ornata</i> <i>Cyathochaeta clandestina</i> <i>Conostylis setigera</i> <i>Dampiera linearis</i> <i>Lepidosperma angustatum</i> <i>Leucopogon propinquus</i> <i>Scaevola striata</i>	Uniform with lower and middle slopes in high rainfall zone.	Lateritic gravel with a sandy loam matrix.
E	<i>E. calophylla</i>	<i>Baekkea camphorosmae</i> <i>Dampiera alata</i> <i>Hypocalymma angustifolium</i> <i>Kingia australis</i> <i>Lepidosperma angustatum</i> <i>Leptocarpus scariosus</i> <i>Mesomelaena tetragona</i> <i>Synaphea petiolaris</i>	Concave. Lower slopes and depressions .	Grey, yellow or brown sands and loamy sands with admixture of lateritic gravel.
H		<i>Daviesia decurrens</i> <i>Hakea ruscifolia</i> <i>Isopogon dubius</i> <i>Lepidosperma angustatum</i> <i>Mesomelaena tetragona</i> <i>Patersonia rudis</i> <i>Sphaerolobium medium</i> <i>Stirlingia latifolia</i> <i>Styphelia tenuiflora</i> <i>Synaphea petiolaris</i>	Uniform to concave. Lower and middle slope in mildly undulating landscape.	Yellow-grey sand or loamy sand merging into lateritic gravel at depth.
F	<i>Nuytsia floribunda</i>	<i>Caustis dioica</i> <i>Leptocarpus scariosus</i> <i>Stirlingia latifolia</i>	Uniform to concave. Lower slopes and broad upland depressions.	Coarse grey sand over yellow sand.
J	<i>E. calophylla</i> <i>Banksia attenuata</i> <i>Nuytsia floribunda</i>	<i>Conospermum stoechadis</i> <i>Hibbertia polystachya</i> <i>Lepidosperma angustatum</i> <i>Leptocarpus scariosus</i> <i>Lyginia barbata</i> <i>Mesomelaena tetragona</i> <i>Styphelia tenuiflora</i>	Uniform to concave . Lower slopes and broad upland depressions.	Deep, pale yellow-grey sand, frequently underlain by lateritic gravel in sandy clay matrix at depth.
B	<i>E. calophylla</i> <i>B. grandis</i>	<i>Adenanthos obovatus</i> <i>Conospermum stoechadis</i> <i>Dasyogon bromeliifolius</i> <i>Hibbertia polystachya</i> <i>Lepidosperma angustatum</i> <i>Leptocarpus scariosus</i> <i>Lyginia barbata</i> <i>Mesomelaena tetragona</i> <i>Petrophile linearis</i> <i>Synaphea petiolaris</i>	Concave. Upland depressions Broad valley heads.	Light grey sand over grey to pale yellow sand.
M	<i>E. calophylla</i> <i>E. patens</i> <i>E. wandoo</i>	<i>Hakea lissocarpa</i> <i>Macrozamia riedlei</i>	Uniform to concave. Valley slopes in middle and upper reaches of valley in dry eastern zone.	Brown sandy loam over yellow or red-brown clay loam.
Z	<i>E. calophylla</i>	<i>Hakea lissocarpa</i> <i>Leucopogon capitellatus</i> <i>Leucopogon propinquus</i> <i>Macrozamia riedlei</i> <i>Patersonia rudis</i> <i>Styphelia tenuiflora</i>	Mainly uniform. Mainly valley slopes.	Grey-brown loamy sands to sandy loams with moderate to heavy admixture of laterite gravel, frequently over base of gravel in clay matrix.

Associated with granitic outcrops, the G site-vegetation type occurs mainly on the face of the Darling Scarp and on the monadnocks further east. The depth of soil over the granitic rock determines the structure of the vegetation. It ranges from lichen on bare rock to herbfields, shrublands and open woodlands dominated by either marri, wandoo, *Eucalyptus laeliae* F. D. Podger & Chippendale, J. or rock sheoak (*Allocasuarina huegeliana* (Miq.) L. Johnson).

The R site-vegetation type occurs on valley slopes as a fringing transition zone between granitic outcrops and laterite-mantled slopes. The soil is a relatively fertile grey to brown sandy loam to sandy clay with an admixture of gravel.

In the high rainfall zone, Q and U types occur as high quality forest on slopes of the dissected river valleys on the western edge of the Scarp. They are the best sites in terms of moisture and fertility having brown to red deep loams (Table 1). The U type has been largely cleared for agriculture with the present vegetation occurring on the periphery of former agricultural clearings. Yarrri dominates the overstorey in both types, though jarrah occurs in type Q.

Type C occurs on valley floors fringing creeks and swamps. Jarrah is not normally common in this type as the sandy loams occurring over an impeding horizon are frequently waterlogged. The chief indicators are yarrri in the overstorey and dense thickets of ti-tree (*Agonis linearifolia* (DC.) Schauer). Bullich occurs in the overstorey where the C type extends upstream in shallow valleys into the upland areas. Types W and D flank type C on valley floors and lower slopes. The yellow sandy loams of types W and D are frequently waterlogged in winter, though the soils of type W tend to be drier and more fertile than type D. Jarrah has ceased to be a major component of the overstorey in types W and D that are infected with *P. cinnamomi* (Havel 1975b).

Types P, S and T occur in the lateritic uplands of the high and intermediate rainfall zones. They occur along a topographic and fertility gradient. The infertile type P occurs as gravelly sands in mid slope positions (Table 1). It is characterized by the relative absence of the zamia palm (*Macrozamia riedlei* (Fischer ex Gaudich.) C. Gardner), *Phyllanthus calycinus* Labill., *Leucopogon capitellatus* DC. and *L. propinquus* R. Br. and the frequent occurrence of *Lepidosperma angustatum* R. Br. and *Grevillea wilsonii* Cunn. in the understorey and sheoak (*Allocasuarina fraseriana*) in the overstorey (Table 2).

Type S, flanking type P upslope, is the broadest and most common type on laterite-mantled uplands (Havel 1975b). Occurring on upper slopes, ridges and plateaux type S has higher stocking densities and the soils are more fertile (Table 1) than those of type P. The chief indicators

are *Banksia grandis*, *Persoonia longifolia* with some *Allocasuarina fraseriana* in the second storey and *Adenanthos barbigerus* Lindley, *Hovea chorizemifolia* (Sweet) DC., *Lasiopetalum floribundum* Benth., *Macrozamia riedlei*, *Phyllanthus calycinus*, *Leucopogon capitellatus*, *L. propinquus*, *Acacia preissiana* (Meissner) Maslin, *Styphelia tenuiflora* Lindley and *Patersonia rudis* Endl. in the shrub stratum (Table 2).

The soils of type T are more fertile than those of type S (Table 1), supporting high quality forest on upper slopes and ridges in strongly dissected areas of the western high rainfall zone. The incidence of type T tends to be greatest around Dwellingup. Type T shares with type S *Lasiopetalum floribundum*, *Macrozamia riedlei*, *Phyllanthus calycinus*, *Leucopogon capitellatus*, *L. propinquus*, and *Acacia preissiana*, but *A. barbigerus* and *S. tenuiflora* tend to be replaced by *Leucopogon verticillatus* R. Br., *Pteridium esculentum* (G. Forster) Cockayne, *Clematis pubescens* Huegel ex Endl. and *Acacia urophylla* Benth. ex Lindley. *Allocasuarina fraseriana* is largely absent from the second storey of type T (Table 2).

Type O lacks the presence of the defined indicator species of other types. It most strongly corresponds to type P, having sandy gravel colluvium in minor valleys and depressions within lateritic uplands. However, sites of type O tend to be moister than those of type P.

With distance east of the Scarp, type Z tends to be the 'dry' equivalent of type S, type H the 'dry' equivalent of P and E the 'dry' equivalent of type W. In the eastern low rainfall zone, type A occurs as seasonally wet, leached grey soils over an impeding horizon on flat, poorly drained floors of valleys. Type B flanks type A with type J usually occurring above B but below H on gentle slopes. Type M occupies dissected slopes with pure wandoo or admixtures of wandoo, marri and jarrah. Wandoo is dominant in pale loamy soils of type Y in broad valley floors and lower slopes.

Strelein (1988) has used methods similar to those of Havel to develop a site classification for the southern jarrah forest. The indicator species differ between the two site-vegetation classification systems because of differences in climate, soils and landform between northern and southern jarrah forest. Seventeen types were recognized based on soil moisture relations and drainage, soil structure and fertility. Types T, K, S and P are mentioned later and occur on a fertility gradient as follows.

Types T and K support good quality forest on fertile loamy soils on upper slopes. Type K has deeper loamier soils, better drainage and is more common in moderate to steeply dissected landscapes than T. Type S supports good to medium quality forest on soils less fertile than T on upper slopes. This type is variable in understorey

structure and drainage. Type P supports low to medium quality forest on relatively infertile sandy soils with poor drainage.

PLANT SPECIES RICHNESS

The flora of the south-west of Australia shows a very high level of endemism; 75-80 per cent of more than 3600 species known to occur in the region are endemic (Hopper 1979). Many species and some genera and families occur only in this region. An additional characteristic of the flora of south-western Australia is the large number of species in each genus; about 300 species of *Acacia*, 170 of *Eucalyptus*, 160 of *Melaleuca*, 120 of *Grevillea* and 80 of *Hakea* (Beard 1981).

George *et al.* (1979) used the number of plant species per 500 m² to compare the floristic richness between plant formations. Floristic richness of the jarrah forest (43 spp./plot) is greater than wandoo woodland (35 spp./plot), about the same as Eastern Australian forests and woodlands (40 spp./plot), but less than heathland (60 spp./plot). The understorey of the jarrah forest is particularly rich in members of the Myrtaceae, Papilionaceae and Proteaceae (Marchant *et al.* 1987).

The high level of endemism and speciation reflects adaptation and specialization to habitat continuity over a long geological period, isolation by barriers to migration, nutrient poor soils, recurrent climatic stress, and a mosaic of landforms (Hopper 1979). This has occurred particularly within families such as the Proteaceae, Epacridaceae, Dilleniaceae and Myrtaceae, whose species are major constituents of heath, woodlands and forests. Members of these families have adapted to poor soils and drought by specialization of root systems.

ROOT PRODUCTION AND ECOPHYSIOLOGY

Both jarrah and *B. grandis* exhibit characteristics that suggest that their success in the Darling Range is dependent on their specialized root systems. Although they are well adapted for growth and establishment on a range of sites they are vulnerable to soil disturbance, root damage and disease. Individual trees employ adaptive rooting tactics as they establish and survive on different sites. Their plasticity in coping with changes in the environment over time also varies.

Jarrah and *B. grandis* both have the capacity to produce masses of fine roots in surface soil horizons as well as at depths of 15-40 m below duricrust (Kimber 1974; Shea and Dell 1981; Dell *et al.* 1983). Fine root production is cyclical with growth cycles being analogous to that of foliage (Dell and Wallace 1983b). Fine roots are produced most readily when the soil is warm and moist and nutrient uptake is possible.

The success of jarrah and *B. grandis* in growing on lateritic soil profiles is also associated with their ability to produce extensive systems of vertical tap roots which complement the systems of lateral and surface fine roots (Kimber 1974; Dell *et al.* 1983). The vertical tap roots grow through cracks and fissures in duricrust to exploit moisture reserves in clay layers up to 40 m below the surface (Fig. 12). Lateral branching and root proliferation from the vertical tap roots occur within the duricrust and pallid clay zones. Roots of jarrah and *B. grandis* may occur together (Shea *et al.* 1983c) and the common root channels are reused by successive generations of trees (Dell *et al.* 1983).

Responses to Low Nutrition

What might appear as excessive near-surface fine root proliferation is a common feature of species endemic to areas with nutritionally impoverished soils. In response to rhizosphere micro-organisms, the roots and root hairs of a large number of genera of the Proteaceae develop into specialized structures known as proteoid roots (Lamont 1981). *Adenanthos*, *Banksia*, *Conospermum*, *Dryandra*, *Grevillea*, *Hakea*, *Isopogon*, *Petrophile*, *Stirlingia* and *Synaphea* are some of the genera which form proteoid roots. Their formation assists plants in the absorption and storage of ions such as phosphate from phosphorus deficient lateritic soils of the jarrah forest. The advantages of forming proteoid roots in nutritionally impoverished soils can, however, be negated by susceptibility to infection by *P. cinnamomi* (ch. 5).

Mycorrhizal symbiosis between plant roots and certain fungi also aids nutrient absorption from the soil. Surface roots of jarrah proliferate to produce extensive pads in which ectomycorrhizal associations occur between a number of fungi and jarrah roots (Malajczuk and Hingston 1981). The season, amount and type of surface litter and inoculum levels and type of fungal symbiont affect the formation of ectomycorrhizae (Malajczuk and Hingston 1981). The greatest number of ectomycorrhizal root tips form in the top 5 cm of soil in winter and spring. Active ectomycorrhizae were not observed in late summer and autumn (Malajczuk and Hingston 1981). In addition to aiding nutrient uptake ectomycorrhizae can help protect roots from *P. cinnamomi* infection (ch. 5).

Responses to Drought

The water relations and hence the growth and physiological characteristics of any plant species is dependent on the capabilities of its root system and on soil water availability. Jarrah and *B. grandis* have the capacity to transpire water rapidly when conditions are optimal, partly because they are successful in absorbing moisture at great depth in the profile (Doley 1967).

Low leaf water potentials are rarely recorded for *B. grandis* and its distribution is patchy in the low rainfall zone of the forest (Z and H site-vegetation types). This highly susceptible species is most common in the high rainfall zone of the jarrah forest where conditions are most favourable for *P. cinnamomi* proliferation and spread.

Jarrah can survive several months of severe drought stress, a common condition in the low rainfall zone of the forest. Although jarrah water relations parameters have been measured (Doley 1967; Carbon *et al.* 1981; Colquhoun *et al.* 1984) few studies apart from that of Carbon *et al.* (1981) have compared the performance of jarrah over a range of sites. Little is known about phenotypic differences in the performance of the species throughout its range.

Crombie *et al.* (1988) and Tippett *et al.* (1987) have compared the water status of jarrah and diurnal patterns of stomatal opening and closure on a range of Havel site-vegetation types. The following observations have been made:

- Jarrah stomata may be less sensitive to changes in humidity than other *Eucalyptus* species (Bartle *et al.* 1983¹, unpublished; Crombie *et al.* 1987). The tree responds to water stress to maintain leaf water potential above a threshold value between -2 and -2.6 MPa.

- There were no qualitative differences in the water relations of jarrah on sites with or without permanent water tables.

- Water consumption of jarrah in the eastern zone is limited by restricted water availability from early summer. This was reflected in significant differences in pre-dawn leaf water potentials and growth rates.

Water status of understorey species reflects the overall availability of water on a site as well as the root depth and ability to control water loss of each species. The only detailed study of the water relations of a range of jarrah forest understorey species was made by Crombie *et al.* (1988). Differences between a western S site-vegetation type and an eastern Z type were determined by measuring the water status of plants and soils over summer. Root depths of each species were also determined. Shallow rooted species developed more severe water deficits than did medium and deep rooted species as surface soils dried out. Water stress developed more slowly and was less severe in the deeper rooted than in the shallow rooted species.

Monitoring of water status of understorey species can now be used to compare the water status of different sites. Differences in water status may then be related to differences in the susceptibility of vegetation to *P. cinnamomi* (ch. 5).

¹Bartle, J., Giles, R. and Whitford, K. (1983), Unpublished data, File LE 310, Dwellingup Research Centre.

The Disease In The Jarrah Forest Ecosystem

The impact of introduced *P. cinnamomi* on the diverse but mainly susceptible flora of the jarrah forest is described. There is a greater appreciation that impact of *P. cinnamomi* varies from low to high impact as composition of the vegetation changes with site types. Site, climate, time since infection, human activity, susceptibility of vegetation and their interactions are some of the many factors affecting disease expression.

ASSOCIATION OF *PHYTOPHTHORA CINNAMOMI* WITH DISEASE

Phytophthora cinnamomi has been consistently associated with the death of understorey and overstorey species (Podger 1972). Moreover symptoms of disease were reproduced by inoculating unaffected jarrah forest with pure cultures of *P. cinnamomi* and soil collected from diseased forest. The fungus has not been isolated from healthy forest (Batini 1973) and unaffected forest inoculated with soil from healthy forest remained healthy (Podger 1972).

Lesions in roots of *B. grandis* and jarrah inoculated with *P. cinnamomi* were similar to those observed in infected forest and the fungus was recovered from inoculated roots. Trees girdled by the fungus following inoculation died and *P. cinnamomi* was recovered from lesioned tissue (Tippett *et al.* 1983; ch. 5). Pathogenicity tests have shown that *P. cinnamomi* is a primary pathogen in a wide range of hosts (Podger 1972; Podger and Batini 1971; Brown 1977; Tippett *et al.* 1985; Shearer *et al.* 1988).

SUSCEPTIBILITY OF SPECIES TO *PHYTOPHTHORA CINNAMOMI*

A botanist recently lamented that *P. cinnamomi* could have the same impact on the flora of the south-west of Australia as the last ice-age. There is no doubt that the composition of vulnerable communities alter dramatically once infected by the fungus. Most species of several major plant families well represented in Western Australia are highly susceptible. Although the disease has been called 'jarrah dieback' no one should be misled into believing that the fungus attacks only jarrah.

Jarrah is the only eucalypt species of the jarrah forest ecosystem killed by *P. cinnamomi* (Podger 1972). The genus *Eucalyptus* is large and susceptibility of species varies greatly (Marks *et al.* 1972; Podger and Batini 1971). Marri continues to survive long after jarrah has died in infected areas (Fig. 16). Eucalypts such as yarri and bullich that normally grow on the low lying sites of

the forest are resistant. Other species that occupy restricted well defined habitats such as karri (*E. diversicolor* F. Muell) and tuart (*E. gomphocephala* DC.) are also resistant. Jarrah can resist invasion by the fungus, but the balance between resistance and susceptibility is dependent on site and environmental conditions (ch. 5).



Figure 16

Distribution of dead and live jarrah and marri in an area infected with *Phytophthora cinnamomi* in Teesdale block near Dwellingup in February 1951. Most of the jarrah of different size classes had died in the north-west corner of the map compared with live and dead jarrah to the south. Live marri occurred throughout the area.

Species of the families Proteaceae, Epacridaceae, Dilleniaceae, Xanthorrhoeaceae and Papilionaceae make up a large component of the jarrah forest understorey and shrub layer. Many species of these families are susceptible to *P. cinnamomi*. Their deaths, in addition to that of jarrah result in an irreversible decline in the diversity of vegetation in infected sites (Fig. 17). Some understorey species, including grasses and sedges, are resistant. These and other species, such as marri, colonize old dieback sites.

Although many of the plant species are different, the disease expresses itself similarly in both Victoria and

Western Australia (cf. Weste and Taylor 1971). Members of the Proteaceae, Epacridaceae, and Xanthorrhoeaceae are the first to die when sites are infected. Most eucalypts express some resistance.

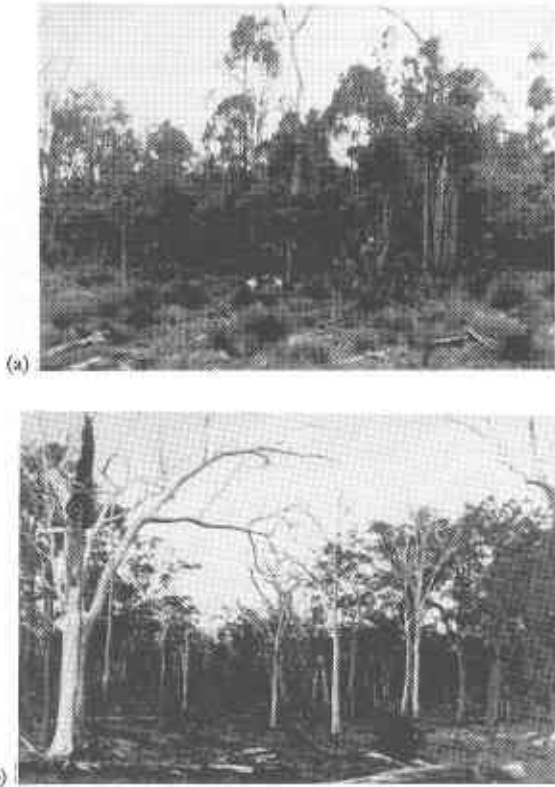


Figure 17

Impact of *Phytophthora cinnamomi* in infected areas in Teesdale block.

(a) An area infected with *P. cinnamomi* in the foreground and healthy forest with dense *Banksia grandis* in the background. Note the dead *B. grandis* in the infected area and the dense line of healthy banksia indicating the border of the infection.

(b) An infected area with standing dead jarrah. Note the reduction in cover within the infected area in the foreground in contrast to healthy forest in the background. The lower stratum in the infected area has a 'sedge' like appearance (Waring 1950).

DISEASE EXPRESSION

The appearance of infested sites varies according to the time elapsed since the fungus was first introduced. This is an important consideration when observing impact. Although *P. cinnamomi* has been present in parts of the jarrah forest for at least 50 years its introduction to some areas has been relatively recent.

The first indication that the fungus has spread into a new area is the death of the susceptible understorey species. *Banksia grandis* is considered a 'good indicator' species of disease because it is a large and obvious plant that dies rapidly once infected (Figs 17a and 19b) and is distributed over a wide range of sites throughout the high rainfall zone of the forest. A line of dead and dying

banksias often marks the 'infection front' at the edge of dieback patches (Fig. 17a). Other understorey species such as *Xanthorrhoea preissii* and *Macrozamia riedlei* may also appear yellow and chlorotic.

Jarrah in areas not infected with *P. cinnamomi* may show symptoms of crown decline, evident as a framework of branches carrying few leaves. The relative importance of fungi, insects, site, stand density, and wildfire in causing unthrifty crowns requires evaluation (Abbott and Lonergan 1986).

In areas infected with *P. cinnamomi*, jarrah exhibits a range of symptoms (chs 5 and 6) and rate of symptom expression is variable (Fig. 18). This can be partly explained by the greater resistance of jarrah than *B. grandis* to the fungus. Gradual deterioration of crowns may occur, commencing with leaf chlorosis and death of primary leaf-bearing branches. New leaves formed on epicormic shoots are reduced in size, resulting in thinning of the crown (Fig. 18). As the condition progresses both epicormic production and leaf area decline. Trees exhibiting such symptoms may survive for many years.



Figure 18

Variation in 'dieback' symptoms in jarrah in an area infected with *Phytophthora cinnamomi*. A dead tree in the background compared with an unhealthy crown with reduced leaf growth from epicormics in the middle and a healthy crown in the foreground.

Apparently healthy individuals or groups of trees can die suddenly (Fig. 19a). The tree may reshoot from epicormics along the stem, but these often do not survive the following summer. Trees of different age classes may die or the incidence of mortality may vary greatly within an area (Fig. 16). 'Islands' of survivors may exist in varying degrees of health. Alternately dead trees occur in close proximity to living trees (Fig. 16).

The impact of disease varies on different sites from no to low through to high impact as composition of the vegetation changes with site types (Havel 1979a). On high impact sites, both susceptible understorey species and jarrah are killed (Fig. 19a). The destruction and devasta-

tion is most obvious when jarrah deaths quickly follow those of the susceptible understorey species. This is most common on infertile sites with poor drainage (chs 5 and 7). On some sites infected jarrah survives despite mortalities in the understorey and impact is described as intermediate (Fig. 19b). Impact may be underestimated on sites where jarrah declines slowly (ch. 6) and monitoring is essential for accurate assessment of disease impact in many areas of the forest. On low impact sites the fungus, although present, causes no obvious damage to jarrah (Fig. 19c). Such sites generally have more fertile soils, high in organic matter; they are common south of the Preston river and in major valleys in the north.

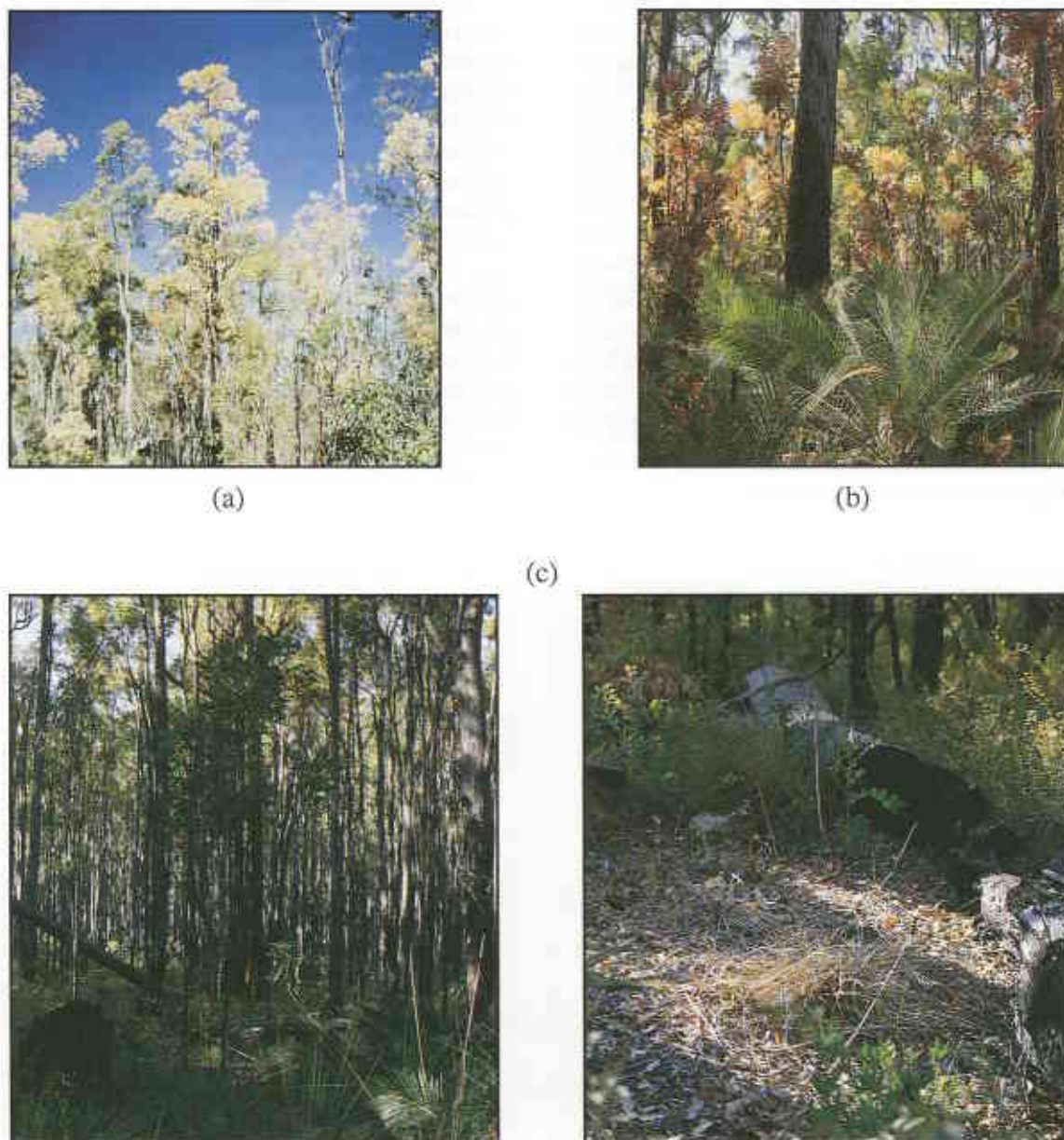


Figure 19

Variation in the impact of *Phytophthora cinnamomi* in the jarrah forest. (a) High impact. Most of the susceptible overstorey and understorey dead, (b) Intermediate impact. Susceptible understorey dead, few or no dead jarrah. (c) Low impact. Localised death of shrub stratum, little effect on the overstorey.

Many infected areas of the jarrah forest in which jarrah died in the 1950s and 1960s and early 1980s now have quite a different appearance from the original forest. Open woodlands with sedge-dominated lower stratum and regrowth marri-dominated upper stratum are characteristic of these old dieback sites. Although colonized by species such as *Dryandra sessilis* (Knight) Domin. (Rockel *et al.* 1982) and sedges, the sites have become floristically impoverished.

Climatic conditions affect the rate of disease incidence and expression and are partly responsible for epidemics. Mass death of vegetation does not occur every year, even on the most disease-prone sites. In fact 1982-1984 were the most recent years when jarrah mortality rates were high. There seems to be an association between annual rainfall, summer rainfall events and disease expression. In Victoria, Tregonning and Fagg (1984) found *Eucalyptus* mortality rates were highest in the years following heavy summer rain. This may also be true for the jarrah forest, although any relationship between jarrah deaths and rainfall has yet to be quantified.

A major problem in comparing disease impact from site to site and in predicting the long term effects of the fungus in any area is that the rate of disease development can vary. One can never be quite sure how long sites have been infected and if the disease has been fully expressed in terms of damage. Impact may worsen depending on

climate, disturbance and treatment of sites. Patterns of disease and impact reflect not only patterns of fungal spread but also differences in site conditions which affect the fungus and the susceptibility of the vegetation. Defining impact in terms of jarrah mortality therefore has limitations. Furthermore emphasis on deaths of jarrah ignores detrimental effects of disease on the understorey vegetation which suffers greatest mortality following infection.

The composition of the understorey vegetation and the establishment, spread, proliferation and impact of *P. cinnamomi* vary greatly with site. There is an obvious association between level of disease impact and composition of the understorey in some areas. Partly for this reason, the site-vegetation classifications of the jarrah forest (ch. 3) have been useful in describing disease impact. Disease impact in northern jarrah forest is generally low in U and Q site-vegetation types commonly associated with dissected river valleys of the Scarp in the high rainfall zone of the forest (Havel 1975b). Disease impact in upland northern jarrah forest is greatest in type P, varies greatly in S type forest and is low to intermediate in T type forest. The impact in southern jarrah forest is greatest in type P, variable in type S and low in types T and K (Strelein 1988). The following chapters describe how the site characteristics, which partly determine understorey composition, affect the population dynamics of the pathogen and impact of disease.

Disease Dynamics

The diversity of stimuli to which *P. cinnamomi* responds during different parts of its life cycle leads to the development of populations of the pathogen in time and space and infection of host tissue. Infection, invasion and spread of the fungus within host-tissue and the influence of environment on these processes are described. Hosts vary in the ability to resist infection, but fortunately genetic variability within the pathogen is limited. *Phytophthora* species other than *P. cinnamomi* are not ignored and the chapter finishes with a comparison of the relative importance of *Phytophthora* species occurring in the jarrah forest.

INTRODUCTION

This chapter examines the interactions that result in expression of disease. Prediction of the likely outcome of disease is not easy because disease is the cumulative effect of a series of interactions between pathogen, host and environment that mostly go unobserved. Observation is limited by the microscopic dimensions of the vegetative structures of *P. cinnamomi* which mainly occur in soil and woody tissue.

The inability to observe survival and sporulation of the pathogen and infection of the host often clouds true perceptions of the results of changes in the environment or of management practices on final disease outcome. It is therefore important that a model of the processes influencing disease progression be developed to help organise thoughts on how the disease evolves under different situations. The reference model should evolve progres-

sively as the understanding of the major components, inputs and interactions that influence development of *P. cinnamomi* in the jarrah forest environment increases.

The life cycle illustrated earlier (Fig. 3) is a simple conceptual model of disease development. Figure 20 refines this diagram to include the effect of environment on sporulation, dispersal and survival of *P. cinnamomi* and infection, invasion and symptom expression in the host. The stimuli and interactions outlined in Figure 20 are subprocesses of the diversity of microenvironments occurring within the jarrah forest ecosystem.

The asexual sporangium-zoospore cycle is emphasized in Figure 20 as it produces large numbers of infectious spores and is probably the main form of reproduction of the fungus in upland jarrah forest soils (Shea *et al.* 1980). Oospores are rarely observed and little is known of the potential contribution of chlamydospores to inoculum

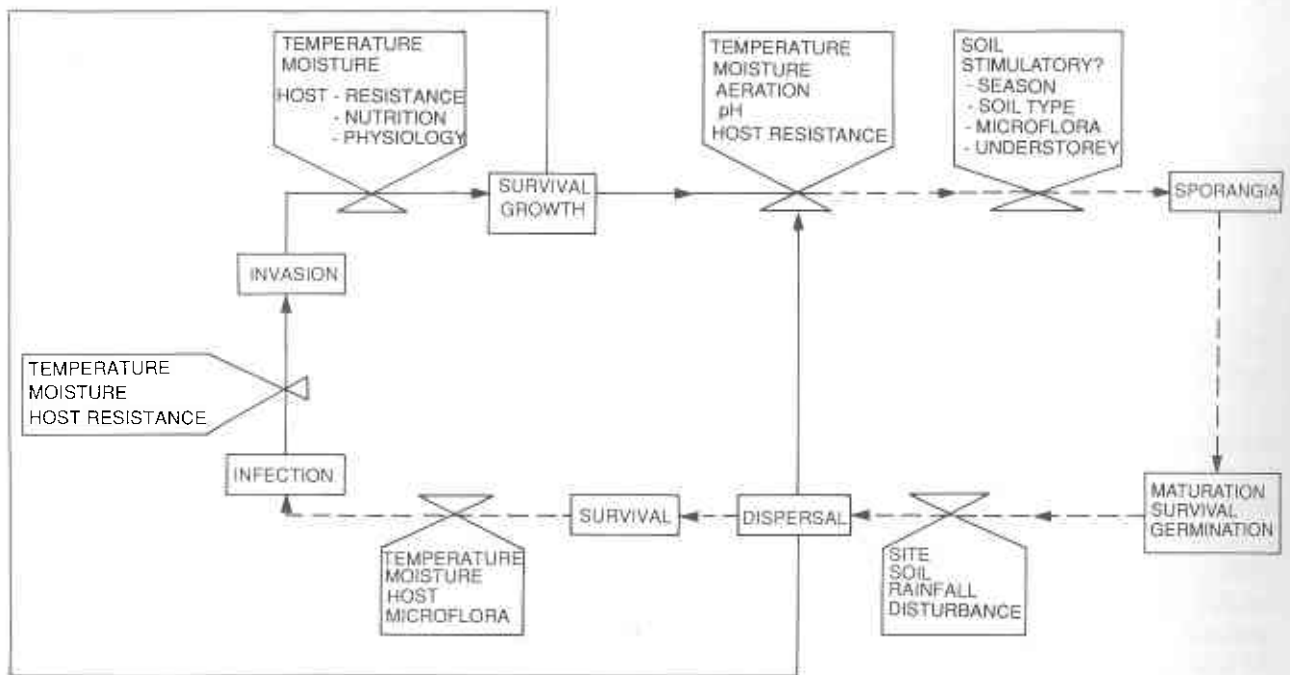


Figure 20

Life cycle of *Phytophthora cinnamomi* in the soil (---) and host tissue (—) in the jarrah forest. Events are indicated by rectangles with factors affecting the rate of development enclosed in an hour glass symbol.

survival and increase in the jarrah forest. Chlamydospores did not survive in a sandy loam after three months when moisture content was less than 3 per cent (Mircetich and Zentmyer 1966) and presumably survive dry soil conditions within living roots (Weste and Vithanage 1979).

The inability of *P. cinnamomi* to survive in dry soils was demonstrated in the early 1960s by Kuhlman (1964). Furthermore, he found that when soil moisture was not limiting, temperature was the critical factor affecting fungal development and infection in Douglas-fir forests of the Pacific north-west.

Differences in disease development between lowland and upland areas of the jarrah forest were first associated with differences in soil temperature and soil moisture availability in the late 1960s (Batini and Hopkins 1972; Batini 1973; Christensen 1975; Shea 1975). No measurements of fungal population levels were made and possible effects of the soil environment on the activity of *P. cinnamomi* in the top 30 cm of soil were inferred from pathogen-environment relationships reported in the literature. Soil moisture and temperature in moisture gaining sites were considered to be favourable for survival of the pathogen throughout the year. Surface soils of free draining upland sites were unfavourable for sporulation and survival of the pathogen in dry summers. Soils of fertile sites beneath dense canopies had soil temperature and moisture in ranges considered suboptimal for pathogen development for most of the year.

Research undertaken since the mid 1970s has aimed at determining the main processes and relationships that affect disease development and expression in the jarrah forest. The current understanding of these processes and relationships is divided into reproduction, dispersal and survival of the pathogen, the build-up of population levels of *P. cinnamomi* in jarrah forest soils, infection and invasion of host tissue and the relative importance of *Phytophthora* species.

REPRODUCTION

Spore production mainly involves stimulation and production of sporangia and release of zoospores (Fig. 20).

Sporangium Production

Unlike a number of other *Phytophthora* species, *P. cinnamomi* has very specific requirements for sporangium production. Even though temperature, moisture and aeration may be optimal for sporulation, no spores will be produced unless some inherent soil property stimulates the formation of sporangia.

The precise nature of the stimulatory factor(s) in soil is unknown but it can be influenced by soil type (Sochacki

1982) and the composition of the soil microflora (Murray 1983). Soils from jarrah forest uplands (sandy loam and sandy gravel soils from Havel site-vegetation types T and P, respectively) stimulated sporangium formation more than did a red loam soil from type Q in a dissected river valley (Sochacki 1982). For all soil types, the stimulatory capacity of the soil changed with season, being greatest in summer and least in winter.

The floristic composition of the understorey also affected the stimulatory capacity of the soil, possibly by influencing the composition of the soil microflora and chemical environment of the soil. Soil from under *B. grandis* stands stimulated greater sporangium production than soil from under *Acacia pulchella* (Cary 1982). *Penicillium* species that stimulate sporangium production by *P. cinnamomi* predominate under *B. grandis* stands but occur at low levels in soil under *A. pulchella* (Murray 1983). Reduced stimulation in soil under *A. pulchella* may also be related to changes in the chemical environment. Saponins isolated from *A. pulchella* roots suppressed sporulation of the pathogen at a concentration of 500 ppm (Alexander *et al.* 1978). It is not known how this concentration relates to levels of saponin occurring around roots of *Acacia* species in the forest.

The stimulatory factor is the most variable and least understood of the factors affecting sporulation of *P. cinnamomi* in soils of the jarrah forest. Although moisture, temperature and aeration can vary in the soil profile the amount of change is governed by physical principles. The stimulatory factor, in contrast, has a biological component that changes greatly within a small area (Murray *et al.* 1985). Prediction of pathogen development in different sites under a range of conditions requires more information on the effect of fluctuating temperature and moisture on the stimulatory capacity of soil and sporangium production with time.

Sporangium production is favoured by warm, moist and aerobic conditions in stimulatory soils (Duniway 1983). Figure 21² clearly shows greatest sporulation at temperatures between 25-30°C. Some sporangia were produced at temperatures as low as 12°C after 48 h. This has important implications to the behaviour of *P. cinnamomi* in temperature buffered environments such as those occurring at depth in the soil profile (Fig. 14). In winter, the relatively constant temperatures of 12-14°C at 1.5 m below the soil surface would favour sporulation over longer periods of time than the cooler fluctuating temperatures near the soil surface (Fig. 14). The alternation of cool wet winters and hot dry summers experienced in the jarrah forest means that warm surface soil temperatures optimal for sporulation often occur when moisture is limiting.

²Shearer, B.L. (1983), Unpublished data, File LE 425, Dwellingup Research Centre.

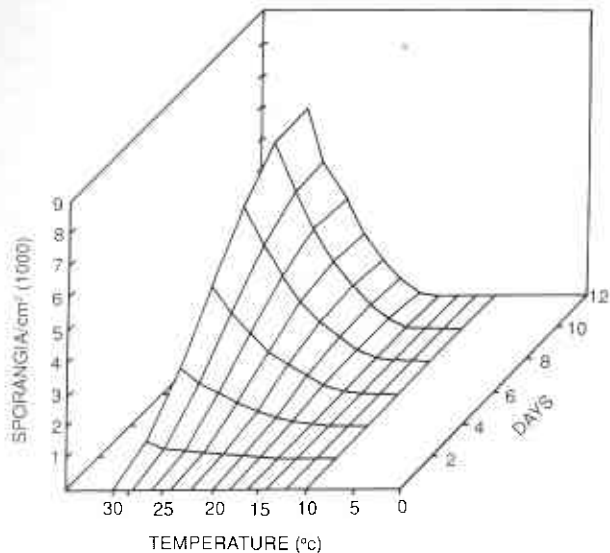


Figure 21

Sporangia of *Phytophthora cinnamomi* form more readily at warm than at cool temperatures.

Soil moisture availability is critical for the production of sporangia (Duniway 1983), but predictive moisture-sporulation relationships have not been determined for jarrah forest soils. The effect of moisture on sporulation depends on a number of factors such as soil type, texture and aeration. Gisi *et al.* (1980) observed the greatest number of sporangia of *P. cinnamomi* in a moist clay and loam soil maintained at soil matric potentials between -8 to -16 kPa. Few sporangia formed in saturated or dry soil (matric potentials 0 kPa and < -500 kPa, respectively). Sporangium formation under saturated conditions is inhibited by low oxygen concentration (Davison and Tay 1986).

Sporangium production is affected by pH (Blaker and MacDonald 1983). The pH of 5.0-6.0 recorded for surface soils of the jarrah forest (Havel 1975a) and the bauxitic zone (Dell *et al.* 1983) are optimal for sporangium production. In contrast, pH in the range 3.8-4.2 recorded in root channels in the pallid zone (Dell *et al.* 1983) are inhibitory to sporangium production (Blaker and MacDonald 1983).

Little is known of how *P. cinnamomi* sporulates on different hosts. Sporulation from infected roots of susceptible hosts, such as *B. grandis*, would contribute to the build up of inoculum in the soil around dead trees described in later sections. Pot trials have shown that the fungus can sporulate on roots of jarrah (Batini 1974; Davison and Tay 1987) and field resistant and susceptible hosts (Halsall 1978; Cahill *et al.* 1989), but how such experimental conditions relate to the field is not known. No field assessment has been made of the ability of *P. cinnamomi* to sporulate on the roots of a range of hosts.

The contribution of sporulation on the roots of resistant hosts to inoculum levels within infected areas is poorly understood.

Zoospore Release

Release of motile zoospores from sporangia is favoured by wet soil conditions and fluctuating temperatures (Duniway 1983). Floristic composition or a hot fire had no effect on zoospore release (Cary 1982). However, higher ammonium levels in soil under *A. pulchella* stands than under stands of *B. grandis* (Cary 1982) may suppress zoospore release (Tsao and Oster 1981).

Jarrah forest soil type influences zoospore release with the greatest discharge occurring in a sandy gravel from a Havel site-vegetation type P and the least in a red loam from type Q (Sochacki 1982). Irrespective of soil type, sporangia released zoospores more readily in soil collected in spring than in other seasons. Once released zoospores may be dispersed in several ways.

DISPERSAL

Effective dispersal of viable inoculum of *P. cinnamomi* is favoured by moist or wet conditions. The fungus is dispersed actively as motile zoospores in free water or passively as propagules in infected moist soil or flowing water. The fungus can also be dispersed in infected roots either actively by growth through root systems or passively in infected roots transported in soil.

Active Dispersal

Zoospores have flagellae and can swim for short distances in standing water or films of water in soil pores. Sochacki (1982) obtained a relative measure of active dispersal by applying motile zoospores on the surface of moist, intact cores of a red loam and a sandy gravel incubated under constant conditions. Using *E. sieberi* cotyledons as baits, active dispersal of *P. cinnamomi* occurred at a faster rate and over a greater horizontal distance in the sandy gravel than in the red loam. The slow rate and short dispersal distance in the red loam were attributed to fine textures and antagonistic microflora associated with this soil type. Soil texture is a very important factor affecting active dispersal; large pores in coarse-textured soils favour dispersal, while pore sizes in fine textured soils are too small to allow the passage of fungal propagules (Newhook *et al.* 1981).

The fine textures of surface loamy soils inhibit active dispersal of inoculum through undisturbed surface horizons. Thus the distribution of inoculum in undisturbed surface soil of upland infected areas is mainly confined to discrete, discontinuous foci (Shearer and Shea 1987). Inoculum levels in surface soil decrease rapidly with

distance from sources of inoculum, such as the collar of infected dead *B. grandis* (Shearer and Shea 1987). Even when sites were irrigated, inoculum was not readily dispersed through surface soil (Shearer and Shea 1987).

In contrast to fine textures, the macropore or aggregate structure of natural soils can favour dispersal of *P. cinnamomi*. Water in root channels and spaces between gravel can facilitate active as well as passive movement of fungal propagules as discussed in the next section.

Growth through roots is important for active extension of the fungus, especially upslope of infected areas (Shea and Dillon 1980). *Phytophthora cinnamomi* can grow up to 1 cm/day in roots of susceptible *B. grandis* in summer when temperatures are optimal for fungal growth (Shearer *et al.* 1987b). Thus, although activity of the fungus in dry soil can cease during summer, infection-centres continue to expand through growth of the fungus in roots of susceptible hosts. Spread of *P. cinnamomi* determined from the death of *B. grandis*, varied from 20 to 110 cm/year with an average of 77 cm/year (Shea and Dillon 1980). *Banksia grandis* removal reduced the rate of spread of *P. cinnamomi* by 12.5 per cent in comparison with untreated plots.

Passive Dispersal - Soil

Passive dispersal, in contrast to active dispersal, can result in inoculum being transported over large distances. New infections originate from movement of inoculum in moist soil and infected plant tissue associated with disturbance by human activity. People are the main agents of dispersal and their activity is the main mechanism by which *P. cinnamomi* has been disseminated throughout south-western Australia.

Infected gravel used in road construction is a major potential source of contamination. Chlamydo spores of *P. cinnamomi* can survive and multiply for up to eight months in infected gravel free of a host (Weste and Vithanage 1979).

Before the association between *P. cinnamomi* and dieback was established, gravel for roads was unwittingly taken from areas with dead and dying vegetation. This practice dispersed inoculum of *P. cinnamomi* over large areas and initiated many new infections. Outside the area controlled by the Department of Conservation and Land Management, roads and driveways are still constructed from gravel and sand removed from private properties where deaths of susceptible species indicate infected areas or where it is not possible to assess the presence or absence of the fungus because pasture has replaced the native vegetation. Subterranean clover in pasture can be infected with *P. cinnamomi* without showing symptoms of disease (Boughton 1983).

Traffic along unsealed gravel roads is an effective mechanism of dispersal in addition to dispersal in material used in road construction. *Phytophthora cinnamomi* and *P. citricola* have been recovered from open access forest roads (Batini 1984) and *P. cinnamomi* from restricted access haul roads associated with bauxite mining (Gardner and Rokich 1987). The fungi occurred mainly in road drains from which maintenance grading could disperse infected material. Batini (1973) clearly demonstrated the ability of vehicle traffic to pick up and move infected soil.

Any activity that disturbs and moves soil, such as mining and logging, has a high potential to passively move inoculum in infected soil. Chapter 7 describes the methods developed to avoid or minimise spread associated with these activities.

Passive Dispersal - Water

Passive dispersal of *P. cinnamomi* in water has often been associated with overland flow. The fungus has been recovered in run-off water concentrated in a snig track (Palzer 1980) and in waterholes (Gardner and Rokich 1987) near Jarrahdale. Von Broembsen (1984) found *P. cinnamomi* distributed throughout the river systems of South Africa. There are a number of instances in the jarrah forest where overland flow was the main mode of transport for infections originating from road drains and this has partly contributed to the dendritic pattern of affected areas (Fig. 5).

The interpretation of how *P. cinnamomi* is dispersed in upland areas of the jarrah forest has now changed. Two research findings have highlighted the importance of lateral near-surface seepage of water, described in Chapter 2, on the dispersal of propagules of the fungus in upland areas of the jarrah forest. These are: the presence of the fungus at depth in the soil and the relationship between perching of water in upland areas and pathogen survival and dispersal, host infection and disease impact.

1. The fungus can occur at depth in the soil profile.

The supposition maintained in the literature that *P. cinnamomi* is mainly a surface soil inhabitant (Campbell 1951; Marks *et al.* 1975; Orosina and Marx 1975; Zentmyer 1980) cannot be extrapolated to the jarrah forest environment. The fungus can survive and be dispersed in jarrah forest soils up to 3 m below the soil surface (Shea *et al.* 1983c; Kinal 1986; Kinal *et al.* 1987; Shearer and Shea 1987). Passive dispersal of the fungus in water moving down root channels may be very important in distributing the fungus vertically within the soil profile. The lower limit of *P. cinnamomi* occurrence within jarrah forest soil is not known. The fungus should occur where oxygen, moisture and host tissue are present, although low pH in

the pallid clay zone may be an inhibiting factor.

2. Transient perching of water occurring in upland areas is related to pathogen survival and dispersal, host infection and disease impact.

Upland sites were once considered free draining, but Zentmyer (1969) questioned this supposition for the jarrah forest:

The attack of *P. cinnamomi* on jarrah and other hosts in what appear to be well-drained soils in a number of areas of the jarrah forest is a unique situation with respect to development of Phytophthora-induced diseases. As noted above, this may be related to the tremendous inoculum potential which could develop with the many susceptible roots throughout the soil mass. Nevertheless this would seem to provide an ideal situation for obtaining definitive information on the exact relationship between soil moisture and infection by *P. cinnamomi*. What precisely are the drainage characteristics of well-drained soils on which dieback is occurring? For how long a period does free water remain in the root zone of such soils following heavy rains? More specifically, how much water is needed for how long a period?

Answers to some of Zentmyer's questions did not become available until 1981.

Investigation of the cause of death of jarrah trees revealed the association between the behaviour of the pathogen in the soil profile and perching of water in an upland type S site. At this site, *P. cinnamomi* produced sporangia at the surface of an indurated duricrust layer which occurred at depth in the soil and zoospores were transmitted laterally in water flowing over the surface of the layer (Shea *et al.* 1983c). This significant finding linked disease development in upland areas with specific site characteristics that affected the behaviour of the fungus at depth in the soil and the infection of jarrah.

Kinal (1986) confirmed and extended these observations when he compared perching and near-surface seepage of water between hillslopes which had either a high (Havel site-vegetation type S with a W component - wS) or an intermediate disease impact (type S with a T component - tS). He showed that perching of water was related to properties of the duricrust and clay layers. In the high impact type wS area a continuous duricrust with few cracks or vertical channels (e.g. Fig. 9a) favoured perching high in the landscape. Perching below the duricrust layer also occurred on fine textured clays (Fig. 22). Deeper topsoil, cracks and well developed vertical channels in the duricrust (e.g. Fig. 9b) and coarser clay textures resulted in less perching in the type tS intermediate area, than in the high impact area (Fig. 22).

The duration of perching in the high impact area depended more on antecedent moisture conditions than on the intensity of rainfall. In mid-winter, perching occurred within 3 h of rain and was sustained for up to 5 days. Zoospores of *P. cinnamomi* were dispersed in lateral flows throughout winter (Kinal 1986).

When summer rainfall occurred, overland flows were observed but subsurface flows were absent. The dry soil inhibited infiltration of rain and absorbed any water which did enter the topsoil. Prior to this work, jarrah deaths following summer rain had been attributed to infection resulting from sporulation and dispersal stimulated by the rain. Monitoring throughout the year suggests that zoospores are dispersed in near-surface flows each winter and that temperatures at depth are sufficient for infection. Summer rainfall appears to have a greater effect on growth of *P. cinnamomi* in the host than on multiplication and dispersal of the fungus in the soil profile and on infection.

Information on near-surface hydrology explains patterns of infection that could not be accounted for by overland flow across contours and can provide estimates of rates of spread and disease expression. Ponding of water high in the landscape increases the chance of inoculum dispersal, since even small amounts of near-surface seepage of water may contribute to on-going cumulative downslope movement of the fungus (Fig. 22; Kinal 1986).

It may be concluded that lateral near-surface seepage of water is a significant factor to dispersal of

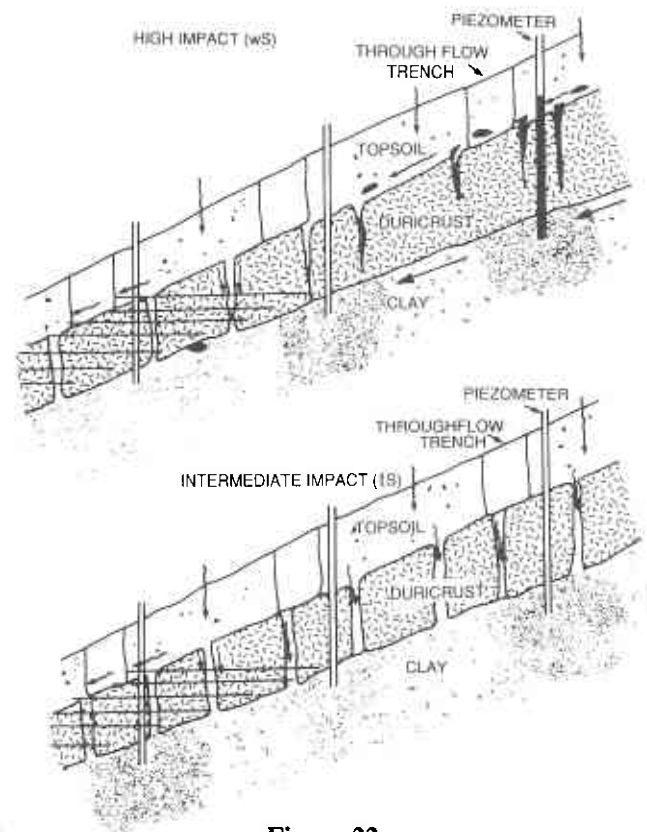


Figure 22

Schematic representation of near-surface flow of water over laterite and clay in a high and an intermediate impact area monitored by Kinal (1986). Near-surface flow of water and dispersal of *Phytophthora cinnamomi* is cumulative in the high impact wS site type, but not in the intermediate impact type tS area. - indicates recovery of zoospores (not to scale).

P. cinnamomi in any area where soils of coarse textures or aggregate structure occur above a perching layer. The perching layer can take a number of forms, ranging from clay, duricrust, hardpan, compacted gravel or a textural change. Duricrust and duplex soils would be the main soil profiles favouring perching in the western zone in the forest while in the eastern zone duplex profiles predominate (ch. 2). More information is needed on the relationship between the pore size distribution of these soils and their capacity to transmit spores.

Just as the jarrah forest is a mosaic of site-vegetation types (ch. 3), it is also a mosaic of sites with different drainage characteristics that can influence the dispersal of *P. cinnamomi*. Relatively free draining sites favouring vertical percolation of water (e.g. Fig. 11) are interspersed between sites with near-surface seepage of water, with gradations between the two extremes. Partly in association with differences in drainage, inoculum levels and infection (following sections), impact (ch. 4) and hazard (ch. 7) also occur as a mosaic within the forest.

The variation in near-surface lateral flow of water between diverse profiles in response to different climatic events and management practices within the jarrah forest is poorly understood. Near-surface flows of water need to be quantified and soil structures favouring transmission of spores identified. This would provide better estimates of the likely rate of change in disease expression on different sites as management practices and climate change.

SURVIVAL

Once dispersed, zoospores must survive to infect host tissue. Fungal propagules in inoculum foci must survive to produce new inoculum (Fig. 20). Temperature, moisture, floristic composition of the understorey, antagonistic microflora and soil type affect survival of propagules of *P. cinnamomi* in the jarrah forest.

Temperatures less than freezing or $> 35^{\circ}\text{C}$ are unfavourable to the survival of spores and mycelium of *P. cinnamomi*. Soil temperature does not adversely affect survival of *P. cinnamomi* in winters (Shearer and Shea 1987) as minimum soil temperatures experienced in the jarrah forest rarely fall below 5°C (Fig. 14). The effect of lethal temperatures in the forest is poorly understood, especially in open areas cleared for mining. Zentmyer (1980) found that mycelium growing on a nutrient medium was killed in 2-3 days at 36°C , 1-2 h at 39°C and 10-30 min at 45°C . How relevant these estimates are to the forest situation is not known since the response to lethal temperatures can be modified by soil type and organic matter content. The adverse effects of lethal temperatures in summer is confounded by low soil moisture unfavourable for survival.

Moisture is critical for the survival of *P. cinnamomi* in soil of the jarrah forest (Fig. 23), but precise information

is lacking. For the jarrah forest there is only a conceptual understanding of the relationships between moisture and survival; that is, the fungus will survive when soils are moist but not when they are dry.

A number of factors, including spore type, physical characteristics of the soil, organic matter content and soil microbiology, interact to affect the relationship between moisture and survival. Matric potentials between -2 kPa and -10 kPa did not significantly affect survival of chlamydo spores and sporangia of *P. cinnamomi* in infected jarrah root fragments in a lateritic soil. The fungus could be recovered from 70-90 per cent of these fragments after 56 days (Old *et al.* 1984b). Encysted zoospores survived for less than a week in a saturated clay loam but up to six weeks when soil moisture was controlled at -1500 kPa (MacDonald and Duniway 1979). In the same work, encysted zoospores survived 8-10 weeks in an agricultural field where moisture was uncontrolled and ranged from -700 kPa to -10 000 kPa. Soil moisture availability differs between soil type (Fig. 13) and the results of the effect of soil moisture on survival for a clay loam cannot be extrapolated to the sandy loam and sandy gravels of the jarrah forest. Prediction of survival of *P. cinnamomi* under a range of conditions requires a much better understanding of the relationships between soil moisture and survival.

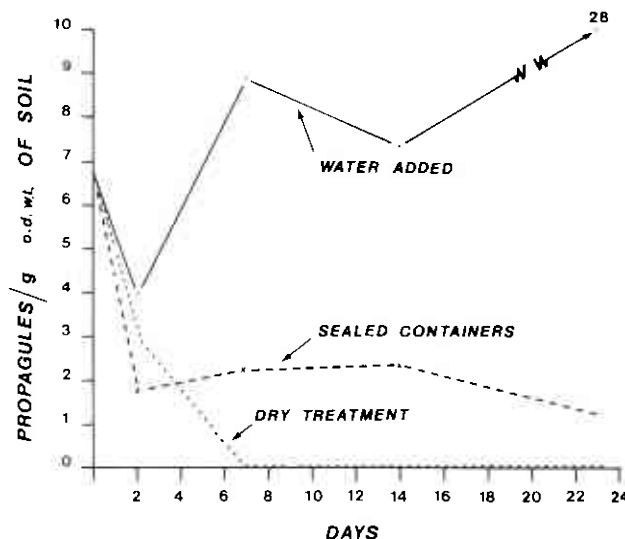


Figure 23

Phytophthora cinnamomi survived for more than a week in moist sandy loam (water added and sealed) but not in the dry treatment (Shea *et al.* 1980).

Floristic composition of the understorey greatly affects survival of *P. cinnamomi* in jarrah forest soils. Infected tissue of susceptible proteaceous hosts such as *B. grandis* and *Dryandra sessilis* provides a buffered environment for the survival of the pathogen during adverse conditions. *Phytophthora cinnamomi* survived at least one summer in the collar of infected *B. grandis*; the fungus was recovered from 50 per cent of chips from the

collar of trees that had died approximately one year prior to sampling compared with 92 per cent of chips from the collar of recently dead trees (Shea 1979b). Recovery of *P. cinnamomi* from old dead trees dropped to 17 per cent, probably because of desiccation and competition from other microorganisms. Infected *B. grandis* also provides a food base for inoculum increase when conditions are favourable.

Changes in the composition of the understorey also change the chemical and physical environment of the soil (Cary 1982). In glasshouse experiments, survival of the fungus was greatest in soil amended with *B. grandis* roots and least in soil amended with *A. pulchella* roots. Survival was inversely correlated with ammonium levels in the soil with levels as low as 2.5 ppm reducing inoculum levels in soil amended with *A. pulchella* compared with that amended with *B. grandis*. However, in the forest, differences in soil moisture beneath different vegetation types had a greater influence on survival than did ammonium levels. Changes in the physical and chemical soil environment associated with change in understorey composition affect both the quantity and composition of the soil microflora which in turn influences survival of *P. cinnamomi* (Malajczuk 1979).

The presence of bacteria, actinomycetes, fungi and amoebae in the organically rich surface soil may directly or indirectly affect survival of *P. cinnamomi* (Malajczuk 1983). They may cause lysis and perforation of mycelium and spores, and abortion and lysis of sporangia with failure of spore release. Often the mechanisms by which the microflora affect *P. cinnamomi* are not known or are counteracted by other factors. For example, hyphal lysis stimulates sporangium production (Malajczuk *et al.* 1983). Thus, although jarrah leaf litter leachates reduced hyphal survival by lysis, the production of sporangia was stimulated (Nesbitt *et al.* 1979). In some cases the effects may also be due to the absence of microbes that stimulate sporulation of *P. cinnamomi* (Murray 1983). The effect of soil microbes on survival of *P. cinnamomi* is dependent on a complexity of factors as illustrated in the following comparison between red earth and lateritic soils.

More organisms antagonistic to *P. cinnamomi* occur in a red loam than in laterite (Malajczuk 1979). However, when red loam and lateritic soil from the jarrah forest were compared, soil type did not significantly affect survival of sporangia and chlamydo spores of *P. cinnamomi* in jarrah root fragments (Old *et al.* 1984b) or encysted zoospores in soil leachates (Malajczuk *et al.* 1983). A relatively low level of organisms antagonistic to *P. cinnamomi* apparently occurs in soils of the jarrah forest (Podger 1972). The low impact of *P. cinnamomi* in red earth soils reflects the interaction of a number of factors on disease development, in addition to soil microbiology.

CHANGES IN POPULATION LEVELS OF THE PATHOGEN WITH TIME

The various components and interactions previously described are the building blocks from which disease develops in space and time. A description of how the components and interactions influence seasonal fluctuations in survival, sporulation, and inoculum density of *P. cinnamomi* in the top 10 cm, or at depth, in the soils of the jarrah forest follows.

Sporulation

In free draining surface soil the greatest number of sporangia form in autumn and spring with low numbers in winter (Fig. 24). Rain falling on warm stimulatory soil creates conditions conducive to sporangium formation in autumn. Few sporangia form in winter because the temperature of surface soil rapidly falls to suboptimal levels following cool frontal rains. Sporangia can form in the often relatively short period when soil stimulation and temperatures are increasing as the soil warms up in spring, but before the soil dries out at the start of summer. Although temperatures are optimal for sporangium production in summer the soils are generally too dry to support sporangial production unless summer rain falls.

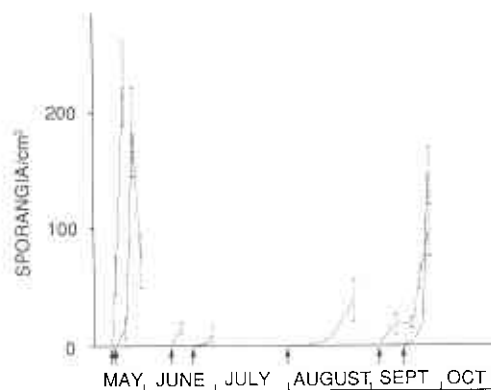


Figure 24

Greatest number of sporangia of *Phytophthora cinnamomi* formed in the top 10 cm of an upland jarrah forest site in the autumn and spring of 1978, but some also formed in winter (Shea *et al.* 1980).

Floristic composition of the vegetation can modify this seasonal pattern of sporangium formation in surface soil. The number of sporangia in soil under *A. pulchella* stands was significantly lower compared with that in soil under *B. grandis* (Shea *et al.* 1978; Murray *et al.* 1985). Suppressed sporulation under *A. pulchella* stands has been attributed to inhibition of sporulation by the cool dry conditions created by the thick legume canopy as well as the release of antagonistic compounds by the legumes and stimulation of microflora antagonistic to *P. cinnamomi* (Shea 1979a).

In a type S site sporangial production at depth in the

soil profile, just above a duricrust layer was greater and the decline in winter was less than that in surface soil (Fig. 25³). This partly reflects the more buffered temperature (Fig. 14) and moisture environment at depth. Lag times before suboptimal conditions are reached are longer at depth compared with the widely fluctuating environment at the surface. The differences in conditions between the surface and deeper soils is especially marked early in winter (Fig. 14).

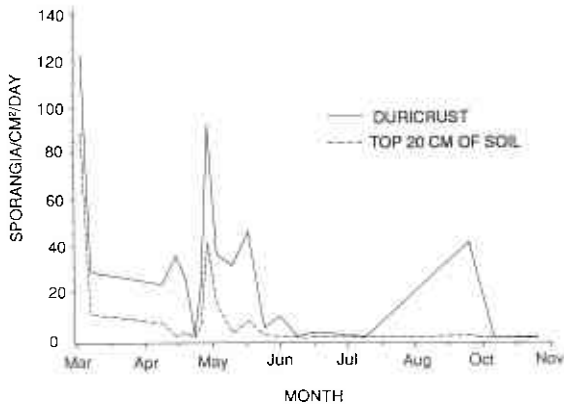


Figure 25

Sporangia production by *Phytophthora cinnamomi* in an upland type S site was greater at depth above a duricrust layer than in the top 20 cm of soil.

Inoculum Build-Up in the Soil

In Surface Soil

Viable inoculum occurs in infected, water-gaining lowland areas throughout the year (Fig. 26). This pattern of recovery reflects extended periods of moist conditions favourable for survival and maximum coincidence of warm, moist conditions favourable for sporulation.

In the surface soil of free draining upland areas, propagules surviving the dry summer in susceptible host tissue act as sources of inoculum production in autumn. Wet conditions in winter favour survival of this inoculum until spring when a return of conditions favourable for sporulation may lead to an increase in inoculum density. Inoculum levels decrease rapidly as the surface soil dries out in late spring (Fig. 26).

This seasonal pattern of inoculum increase in surface soil varies from year to year depending on the timing of opening and closing rains (Fig. 27) and changes in canopy cover. In years with late opening rain low inoculum levels occur in autumn and winter because soil moisture levels suitable for sporulation are reached when temperatures are too cool for sporulation. An early finish to the rainy season limits inoculum increase in spring as the soil dries out before stimulatory capacity and temperatures are favourable for sporulation. Late spring or summer rains

³Shearer, B.L. and Shea, S.R. (1983). Unpublished data, File LE 415, Dwellingup Research Centre.

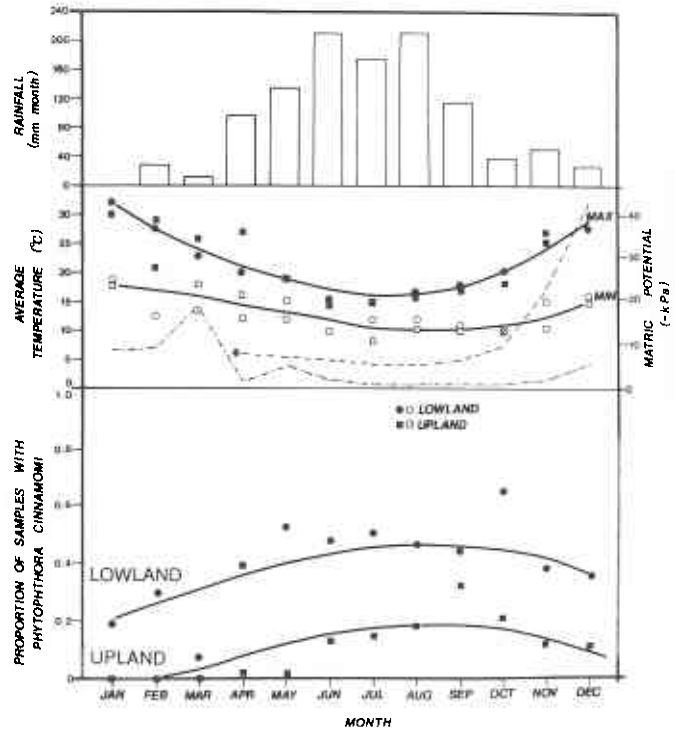


Figure 26

Phytophthora cinnamomi was recovered throughout the year from a lowland type C site but not in summer from an upland type wS-S site in the jarrah forest. Soil matrix potential for the lowland site is indicated by - - - and - - - for the upland site. Continuous lines represent predicted values from regression equations fitted to the data (Shearer and Shea 1987).

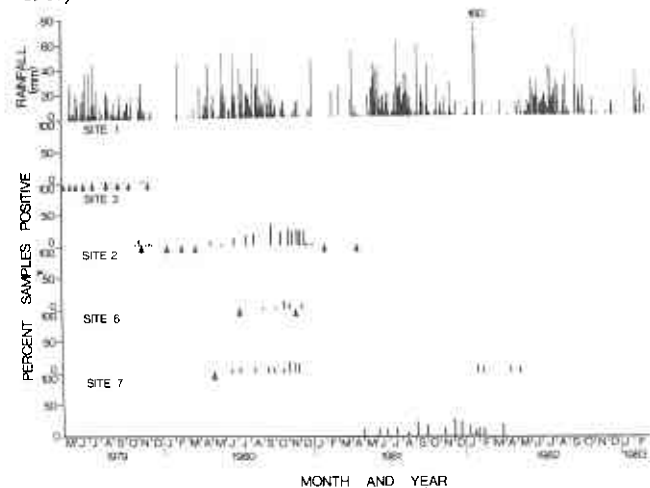


Figure 27

Seasonal variation in recovery of *Phytophthora cinnamomi* (thick bars) from surface soil of randomly sampled plots in five infected upland areas of the jarrah forest. Thin bars indicate daily rainfall for Dwellingup and arrows indicate when samples were taken but *P. cinnamomi* was not recovered. Havel site types: 1 - S; 2 - sT; 3 - sW-S; 6 - sT; 7 - S. (Shearer and Shea 1987).

allow inoculum to survive well into summer as occurred in the summer of 1981/82 (Fig. 27). Reduced canopy cover resulted in increased soil temperatures when moisture levels were favourable for survival and sporulation of *P. cinnamomi* (Christensen 1975; Shea 1975; Shea 1979a), especially at depth in the soil (Fig. 14). A small increase

in temperature towards the end of winter significantly increases the length of the period when conditions are favourable for sporulation in spring (Christensen 1975). Sustained canopy reduction extends the period of soil moisture favourable to *P. cinnamomi* development, particularly at depth in the profile (Stoneman 1988).

At Depth

Phytophthora cinnamomi survives dry summers in upland areas at depth within the soil profile (Fig. 28⁴) as well as in susceptible host tissue. Favourable moisture and temperature conditions for survival that occur in the water gaining lowland areas (Fig. 26) can be duplicated above an impeding layer at depth in upland jarrah forest soils (Fig. 28). Inoculum of *P. cinnamomi* in gravels at depth is also likely to escape antagonistic microflora that mainly occur in the organically rich surface soil (Shearer and Shea 1987). Although recovery of the fungus from deep in the profile was initially linked to high impact sites (Shea *et al.* 1983c), the fungus has been recovered at depth from site types ranging from wS to sT (Kinal 1986; Shearer and Shea 1987).

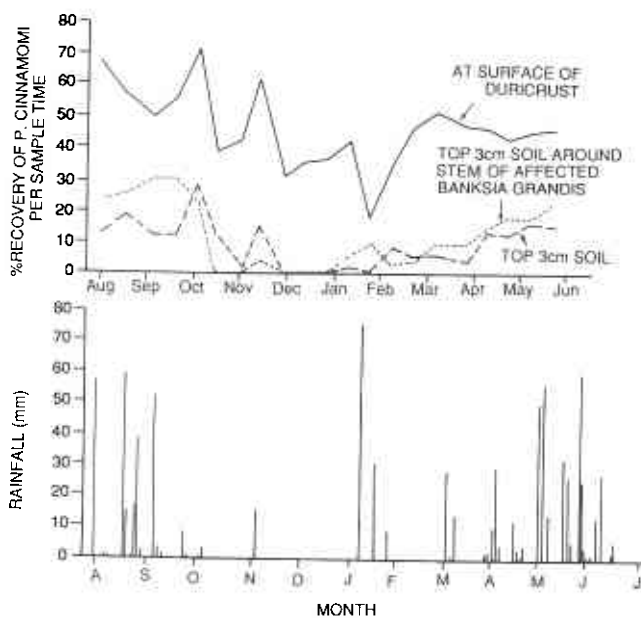


Figure 28

Phytophthora cinnamomi was recovered more frequently from soil deep within the soil profile, just above a duricrust (—) layer, than from the top 3 cm of soil sampled at random (___) or from around the collar of recently dead *Banksia grandis* (---) in an upland Havel type S site.

The recognition that an environment favourable to the pathogen can occur at depth within the soil of upland areas linked activity of *P. cinnamomi* to specific site characteristics that could be used to predict likely hazard once the fungus infected an area. Hazard rating can now be identified by using vegetation indicators that integrate

⁴Shearer, B.L. and Shea, S.R. (1983), Unpublished data, File LE 420, Dwellingup Research Centre.

site conditions (see ch. 7). There is also a much better appreciation that the jarrah forest is composed of a mosaic of hazard types ranging from low hazard fertile red earths to high hazard infertile sandy gravels.

Effect of Soil Type

In the surface layer of a Havel type Q red loam *P. cinnamomi* survived longer but inoculum density was significantly lower than in a Havel type P sandy gravel (Sochacki 1982). The higher inoculum levels in the type P sandy gravel quickly peaked but then rapidly declined relative to levels in the red loam. This illustrates how a number of soil factors can interact to influence the life cycle of *P. cinnamomi*. Low inoculum levels in the red loam were attributed to low levels of sporulation, restricted dispersal of zoospores (Sochacki 1982) and high level of antagonistic microflora (Malajczuk 1979). Stimulation of sporangia, rapid dispersal of zoospores (Sochacki 1982) and low levels of antagonistic microflora (Malajczuk 1979) encourage high inoculum levels in the type P sandy gravel. Better survival of inoculum in the red loam than the sandy gravel was attributed to the buffered environment created by the thick overstorey and high organic matter content that this fertile soil type encourages. Even though disease impact is low on the red loams, inoculum could remain viable in restricted foci in this soil type for extended periods of time.

Effect of Understorey

Changes in the composition of the understorey to one dominated by resistant *Acacia* species significantly changes the soil environment to one with a greater suppressive effect on population levels of the fungus than does simple removal of susceptible host tissue. Because the interactions between host, sites, and climatic events vary in space and time, it is often difficult to evaluate and quantify the effect of changes in understorey composition on inoculum development under the very variable conditions experienced in the forest. Thus, while in some cases inoculum levels have been less under *A. pulchella* stands than *B. grandis* (Cary 1982), in other cases no differences were observed (Shea and Shearer 1980). Generally however, reduced inoculum development under *A. pulchella*, compared with that under *B. grandis*, reflects inhibition of sporulation and survival by changes in the microbial, physical, and chemical environment described previously.

This concludes a description of the production of inoculum of *P. cinnamomi* in the environment of the jarrah forest. Movement of infected soil in association with human activity is the most important mechanism of dispersal of the fungus. Thus an understanding of the behaviour of *P. cinnamomi* in the soil environment has historically received the most research attention. However,

accumulation of knowledge has resulted in a shift in emphasis to an understanding of the factors affecting the interactions between fungus and host over time, the subject of the next section.

HOST-PATHOGEN INTERACTIONS

Disease and symptom development depend on a range of continually changing factors. Both diurnal and seasonal fluctuations in the environment affect the host and pathogen separately and also their interaction. Establishment of the pathogen in the host can also affect the physiological status of its host which in turn can alter conditions for the pathogen. Disease development and symptom expression in any host may depend on both the level of attack and the conditions which prevail as the interaction proceeds. Different levels of infection occurring at different depths in the soil may ultimately result in different amounts of damage to the host. Some plants may completely recover from infection while others may die.

To understand why and when disease develops in space and time, methods of assessing the performance of both hosts and *P. cinnamomi* under different conditions have been sought. The ways in which plants may be killed by *P. cinnamomi* have been identified. The interaction of jarrah with *P. cinnamomi* has been emphasized because of the importance of jarrah to the forest ecosystem. Progression of the disease in *B. grandis* has also been studied in detail as this host is highly susceptible and an important food base for the fungus (Shea 1979b; Shearer and Shea 1987).

Infection

The interaction between pathogen and host starts with infection. *Phytophthora cinnamomi* produces various types of spore as well as vegetative hyphae (Fig. 3), all of which may start new infections under certain conditions. Zoospores are produced in large numbers and probably initiate most infections. They are motile in water and they are attracted chemotactically to the growing tips of roots of a very wide range of plant species. They encyst and germinate to produce germ tubes which penetrate roots. Hyphae proliferate within roots macerating all un lignified and unuberized tissues and cause the roots to rot. A wide range of species is infected in the jarrah forest. However, not all the species infected are killed, as the susceptibility of species varies greatly (chs 4 and 6).

Chlamydospores and hyphae may also cause new plant infections although it is probable that the dispersal of zoospores result in rapid spread of disease, particularly where drainage favours near-surface lateral flows of water. Patterns of disease spread may thus reflect which propagules were involved. Chlamydospores, which are much

larger than zoospores, formed in buffered environments such as jarrah roots (Tippett *et al.* 1983) and water gaining areas (Schild⁵ *personal communication*). They can be spread in transported soil, gravel or root material. They germinate when conditions are favourable and may produce sporangia or directly infect roots.

Hyphal growth in roots is probably responsible for the advancement of dieback fronts upslope (Shea and Dillon 1980). Roots of different plants are often in contact and consequently the fungus may spread vegetatively from plant to plant. Jarrah roots are thought to be prone to infection when growing in close contact with roots of *B. grandis* colonized by the fungus (Shearer *et al.* 1981).

The relationships between inoculum levels and infection are poorly understood. What percentage of attempted penetrations or infections fail? For jarrah it may be high, but for highly susceptible species such as *B. grandis* the fungus may have a much higher success rate. The importance of inoculum levels and disease development for jarrah and other hosts needs to be determined to enable accurate assessments of root susceptibility to infection and the long term effects on growth.

Root Surfaces Prone to Infection

How *P. cinnamomi* infects the root system of jarrah is not known. Extensive lesions have often been observed in both large lateral and vertical tap roots, but it is uncertain how such lesions formed. Although *P. cinnamomi* can grow in the inner bark of large jarrah roots, there is no evidence that hyphae or germ tubes can penetrate outer bark (Tippett and Hill 1984). The resistance of jarrah bark to penetration or exit by the fungus is consistent with forest observations. No evidence has been found in root systems of jarrah of multiple infections or of a rapid increase in the number of points of infection. Single roots of jarrah may be extensively invaded with no sign of infections in other large roots, even those in close proximity. The fungus most likely enters through roots of primary structure or wounds and gradually progresses up to lateral roots and collars.

The bark of *B. grandis* may not afford as effective protection against *P. cinnamomi* as that of jarrah. The rapidity with which *B. grandis* is killed and the high levels of inoculum found in the vicinity of dead or dying trees (Shearer and Shea 1987) supports this idea. The bark of this banksia is much thinner than that of jarrah and old layers do not persist to form thick outer bark. In addition, the proliferation of rootlets associated with proteoid roots (Lamont 1981) of *B. grandis* are probably very susceptible to infection.

⁵Schild, D.E., Ph.D. thesis (in prep), Murdoch University, Western Australia.

Knowledge of the process by which jarrah is infected by *P. cinnamomi* will help in the assessment of forest at risk from infection. Changes in the distribution of roots and fungal propagules with depth in the soil profile will affect infection at different depths. Before this can be assessed, more information is needed on the influence of the physical environment at depth on infection.

Conditions which Favour Infection

Warm moist conditions in spring or summer not only favour the production and dispersal of zoospores but also favour the initiation and growth of fine roots (Dell and Wallace 1983b). Roots are vulnerable to infection soon after their initiation and prior to the differentiation of protective layers of bark or the development of an ectomycorrhizal cover. Some ectomycorrhizae protect roots from zoospore infection while others fail to limit infection (Malajczuk 1988). Ectomycorrhizae are most active in mid to late winter (Malajczuk and Hingston 1981) and roots may grow out of the protective cover when root growth is stimulated by warm conditions. It is therefore probable that infection of roots close to the surface is most likely to occur during spring or after periods of heavy summer rain. However, the vulnerability of fine roots to infection will also vary as the physiological status of the host changes depending on the effects of age, climate, site and disturbance.

The physiological status of the host can affect infection (Duniway 1983) but information for the forest is lacking. The water potentials of host tissues are just as likely to influence the infection process as they are to affect fungal invasion described in following sections. Levels of soluble carbohydrates and degree of lignification and suberization of tissues may also affect the progress of germ tubes originating from zoospores encysted at root surfaces. Waterlogging may be a predisposing factor to infection as flooding jarrah seedlings in containers after zoospores were released into the potting medium favoured disease development (Davison and Tay 1987).

Since the recovery of inoculum from deep (up to 3 m (Kinal 1986)) within the soil profile, speculation has increased on the importance of infection at depth. Both roots and inoculum occur at depth and as the conditions are buffered against daily and seasonal fluctuations in temperature and moisture, infection may well occur throughout the year. There is reason to believe that infection will occur at the range of temperatures known to occur at depth (Shearer *et al.* 1987b). Vertical roots were found to be girdled by the fungus when root systems were excavated on high impact sites in 1981. Since the roots broke off during excavation where they entered the top of the duricrust layer, the points of infection, which may have been within or below the duricrust layer could not be established at the time of excavation (Shea *et al.* 1982).

The vertical tap root system is the 'Achilles heel' of jarrah as it depends on this specialized root system to maintain internal water balance during dry periods (ch. 3). Infection and death of vertical tap roots reduces the uptake of water from deep sources and results in desiccation of trees (Shea *et al.* 1983c). Infection and the pattern of invasion of the collar and other parts of the root system also contribute to tree decline and death, however.

PATTERNS OF INVASION

There is considerable variation in the amount and distribution of inoculum throughout soil profiles, from site to site and with season. The patterns of fungal invasion and damage to root systems after infection can also vary. The root systems of many trees of both *B. grandis* and jarrah have been excavated over the last eight years (Dell and Wallace 1981; Shearer *et al.* 1981; Shea *et al.* 1982; Somerford *et al.* 1987).

Once infected the root systems of *B. grandis* become extensively colonized and die. The species is so susceptible to colonization that the fungus is readily isolated from both the roots and collar regions of dying trees (Shea 1979b).

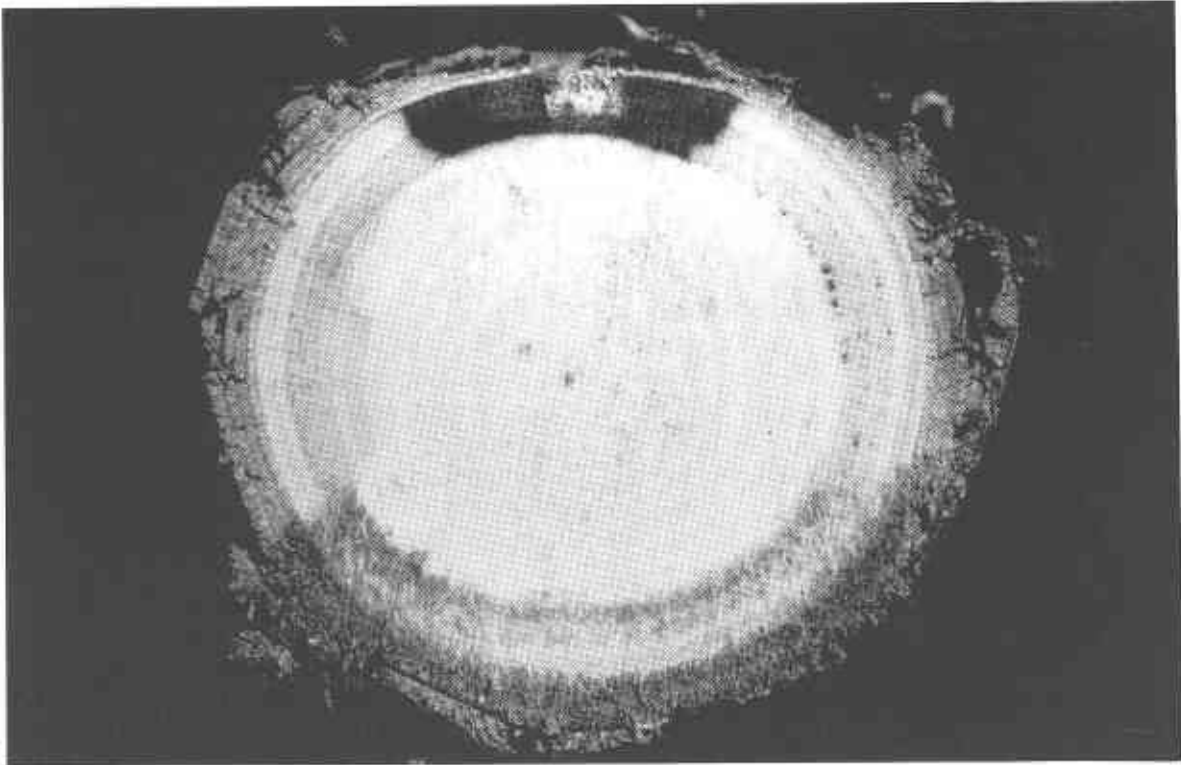
Invasion and damage in jarrah root systems are more variable than similar processes in *B. grandis* and three different patterns have been observed:

- A significant percentage of fine roots were infected and killed by the fungus with little colonization of the large laterals (Somerford *et al.* 1987);
- Vertical tap roots were girdled at depth with little damage to the lateral roots (Shea *et al.* 1982);
- Laterals were invaded culminating in the death of the trees when they were girdled at the collar (Shearer *et al.* 1981; Crombie and Tippett 1990);

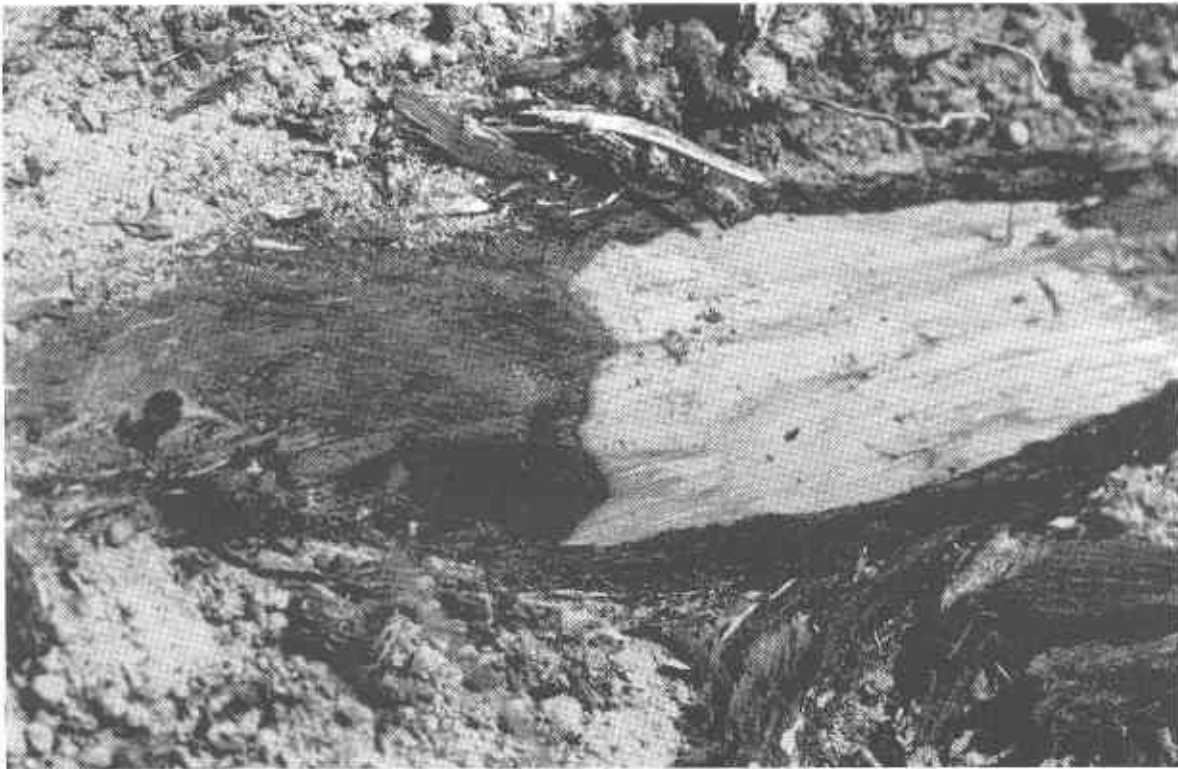
These patterns reflect differences not only in number and sites of infection, but also the interaction of factors influencing the spread of the fungus in host-tissue.

SPREAD OF THE FUNGUS WITHIN HOST-TISSUES

Once the fungus has entered the roots of a prospective host, it establishes within unligified cortical tissue and the phloem (Tippett *et al.* 1983). Advancing fronts of necrosis (lesions) caused by *P. cinnamomi* are usually observed in the secondary phloem (inner bark) of *Banksia* spp. and jarrah (Fig. 29). The inner bark is a responsive tissue and reaction zones within this tissue often mark the inhibition of the fungus. Lesions are clearly defined by new layers of bark once they have stopped extending (Tippett *et al.* 1983).



(a)



(b)

Figure 29

Typical lesions of *Phytophthora cinnamomi* in jarrah. Healthy tissue is white while infected tissue is discoloured. (a) Section of an inoculated stem showing a common pattern of inner bark (phloem) necrosis. (b) The outer bark has been removed to show a lesion in a naturally infected root.

A series of inoculations of the fungus into both stems and roots allowed lesion development to be described and compared for a number of hosts (Tippett *et al.* 1983, 1985) with the following results:

- Lesion extension in stems was generally greatest during summer;
- Fungal growth within jarrah roots and stems was often associated with kino vein development;
- The growth of *P. cinnamomi* in jarrah was often intermittent;
- Jarrah roots were rarely girdled within the first 12 months after inoculation, but could be girdled when the fungus had at least two periods of growth within the host;
- Jarrah expressed resistance to spread, but this apparently varied with season.

The ability of jarrah to resist the advance of the fungus in its roots was an important finding. It was also apparent that the resistance did not necessarily limit invasion if conditions became highly conducive to fungal growth (Tippett *et al.* 1983, 1985). Seasonal and climatic conditions were found to strongly influence the interaction between jarrah and *P. cinnamomi*, especially in the upland environment.

Although the majority of inoculation studies have been made using large woody roots (> 1 cm in diameter) one forest study involved the inoculation of fine roots in the range 1.5-2.5 mm diameter (Tippett and Hill 1984). The roots were inoculated over a period of 12 months and in the majority of roots the advance of the fungus was halted within the first 8 weeks at the end of which lesions were usually only several centimetres long. This suggests that the percentage of infections which result in extensive root damage may be low unless conditions favour maximum growth rates of the fungus within jarrah.

ENVIRONMENTAL FACTORS AFFECTING HOST-PATHOGEN INTERACTIONS

The effects of temperature, moisture, mineral nutrition and physiological status of host tissues on the interaction between *P. cinnamomi* and jarrah have been studied. *Banksia grandis* has also been included in some studies for comparison with jarrah. As *B. grandis* is much more susceptible to *P. cinnamomi* than jarrah, fungal growth rates and time of infection have less effect on the outcome of the interaction in *B. grandis* than in jarrah. Deaths of *B. grandis* occur each year whereas death of jarrah is less frequent.

Temperature

Shearer *et al.* (1987b) have determined relationships between fungal growth and temperature in the secondary phloem of *B. grandis* and jarrah. They reported that:

Most studies relating the influence of temperature to the epidemiology of *Phytophthora cinnamomi* Rands have concentrated on development of the pathogen in soil and infection of roots with little attention being given to growth in host tissue.

Grant and Byrt (1984) showed that lesions in seedling roots of marri increased in length up to 4 days after zoospore inoculation within the temperature range 14-28°C, but lesions were arrested after the initial establishment period. Lesions in roots of jarrah inoculated with the fungus increased linearly with time and rate of lesion extension increased with increasing temperature within the range 14-28°C.

Shearer *et al.* (1987b), in a series of experiments determined the temperature-growth relationships of *P. cinnamomi* in media and secondary phloem of *B. grandis* and jarrah. Growth of the fungus in intact roots in the forest was compared with growth in excised roots inoculated and incubated at constant temperatures in the laboratory. Optimal temperatures for growth of the fungus in intact roots were 25-30°C (Fig. 30). Estimates of the minimum and maximum temperature for growth were 5 and 34°C respectively (Fig. 30).

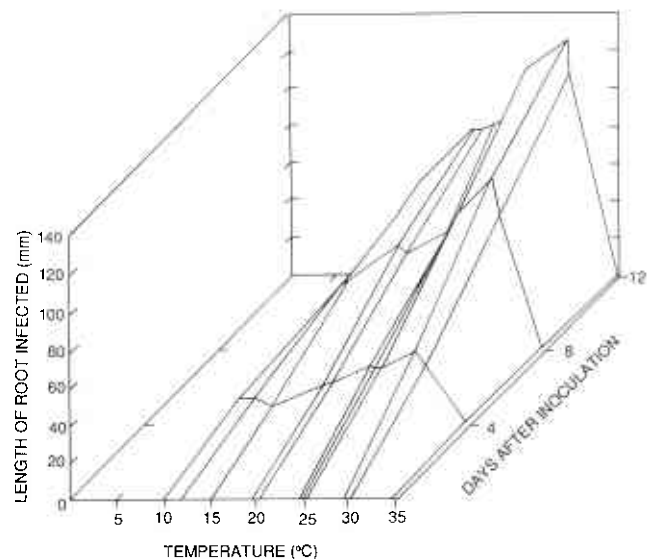


Figure 30

The optimal temperature for growth of *Phytophthora cinnamomi* in jarrah roots was 30°C (Shearer *et al.* 1987b).

The lengths of lesions which developed in roots of *B. grandis* inoculated in the forest were closely correlated with the lengths predicted using previously determined temperature-growth relationships. This research has

demonstrated how little resistance *B. grandis* offers. Temperature is the key factor determining how fast *P. cinnamomi* will grow in *B. grandis*.

Such a statement does not hold true for jarrah. Lesions that developed in jarrah roots in the forest were shorter than would be predicted if temperature only were influencing the rate of fungal growth; this was particularly the case in summer. Summer conditions may either favour the ability of jarrah to defend or may affect the water status of the trees as discussed in the next section.

Moisture

Lesions resulting from jarrah stem inoculations were often variable during summer even though temperatures were close to optimal for fungal growth. A relationship between percentage bark relative to water content and fungal growth has been demonstrated by Tippett and Hill (1983). Consequently the importance of host water status on the disease interaction was studied in more detail. Rather than confining the studies to one site type, trees were inoculated in Havel site-vegetation types P, T, H and Z (ch. 3) from October 1983 to May 1984. The fungus did not establish successfully in trees growing on the driest eastern zone type H and Z sites during February and March. Fungal establishment was successful in the wetter western zone type P and T sites with extensive lesions resulting. The trees on the latter sites differed from those on the H and Z types by maintaining high relative water contents throughout summer (Tippett and Shea 1985). As the moisture status of the trees was determined by soil water availability, site influenced the susceptibility of trees. Tippett and Shea (1985) concluded that trees suffering water stress were less susceptible to invasion than trees which were well watered.

Further studies by Tippett *et al.* (1987) confirmed that the growth rate of *P. cinnamomi* in jarrah was in part determined by the water status of phloem tissue. Predawn leaf water potentials were used to compare the water status of trees on six upland sites in the northern jarrah forest and lesion length was correlated with these values (Fig. 31). In trees growing on a Havel type Z and pS site, the relative water content of the phloem was below 85 per cent during most of the period the interaction was allowed to run and only small lesions developed (Fig. 32). When stem pieces were dried out for varying lengths of time and inoculated in the laboratory, fungal growth was found to be linearly related with tissue water potential (Fig. 33).

Nutrition

The susceptibility of jarrah to *P. cinnamomi* on sites differing in their nutritional status has been compared (Tippett *et al.* 1989). Trees growing on an infertile Havel type P site were more susceptible than those growing on a relatively fertile T site. Surface soil phosphorus levels

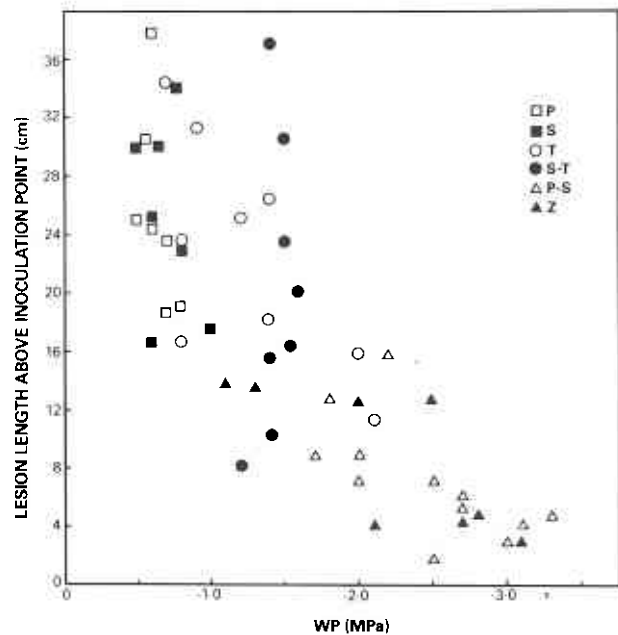


Figure 31

Lesions of *Phytophthora cinnamomi* were longer in stems of jarrah trees under least water stress (least negative leaf water potential, WP). Plots were in two areas of forest and the Havel site-vegetation types indicated. Least water stress occurred in site-vegetation types P, S and T (Tippett *et al.* 1987).

were 3-6 times higher at the type T site compared with the type P site. However, variability in the water status of the trees masked differences in susceptibility between the sites.

Calcium nutrition may affect levels of tree resistance to *P. cinnamomi*. Disease expression is generally less on calcareous red-brown loams than those on lateritic profiles (Havel 1979a). Arentz (1974) and Boughton *et al.* (1978) reported enhanced resistance of lupin and jarrah seedlings, respectively, in calcium amended media. Further study under both controlled and forest conditions is required to evaluate the importance of calcium to host plant resistance.

In Western Australia, Dell and Wallace (1983a) have been the only researchers to consider the role of micronutrients on either infection or susceptibility of jarrah to *P. cinnamomi*. They concluded that zinc applied to jarrah seedlings did not influence the amount of root damage caused by *P. cinnamomi*, but may have influenced chemotaxis of zoospores to the seedling roots.

Host Physiology and Tree Resistance

The physiological status of a host can affect how fast a fungus grows within its tissue. The previous section has described the effects of two of these factors, i.e. temperature and tissue water potential, on the growth rate of *P. cinnamomi* in host tissue. How jarrah responds to other environmental factors in relation to its ability to resist infection is poorly understood.

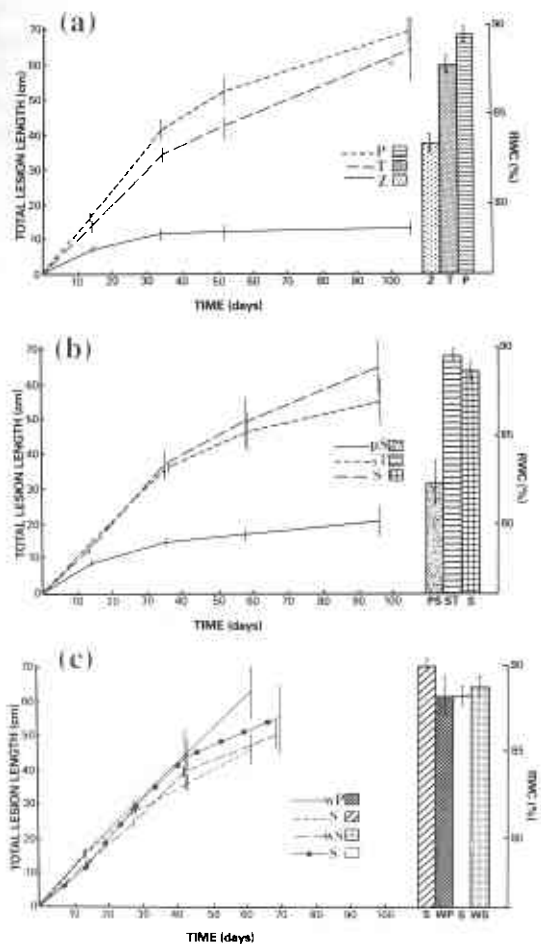


Figure 32

Growth of *Phytophthora cinnamomi* in trees at three Jarrahdale sites (a) and at seven Dwellingup (b,c) sites. Havel site-vegetation types indicated on figure. Mean relative water content (RWC) of bark was determined in February, approximately 30 days after inoculation. Lesion extension was least in the Z site trees (a) and P-S site trees (b) - the sites with the lowest RWCs (Tippett *et al.* 1987).

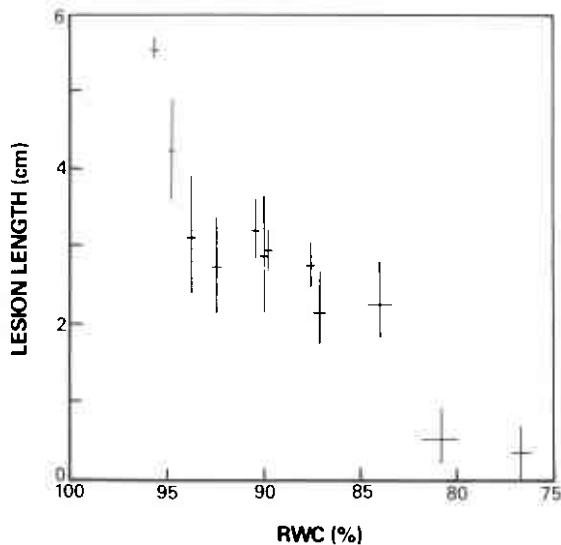


Figure 33

Lesion extension of *Phytophthora cinnamomi* in jarrah stem pieces dried and wrapped to develop varying water contents. Lesion extension was greatest in stems with the highest relative water content (RWC) (Tippett *et al.* 1987).

Competition between trees is known to affect growth rates and some aspects of the forest environment. Past and potential growth rates, growth efficiency (the annual growth of stem wood per unit of foliage) and levels of carbohydrate reserves have been related to levels of resistance. Suppressed and stressed trees may be more susceptible to some pathogens than vigorous trees (Shigo 1985). Differences in susceptibility of jarrah to *P. cinnamomi* have not been related to vigour or growth rates. Current information suggests that well watered, fast growing trees are more vulnerable to *P. cinnamomi* than stressed trees as the tissues of the former are in a state to favour fungal growth.

The ability of trees to recover from infections once the fungus has been arrested has not been assessed on a range of sites. Seasonal water stress in jarrah can result in fungal inhibition (Tippett *et al.* 1987), but Puritch and Mullick (1975) showed that the ability of some conifers to wall off infection decreased as trees became water stressed. Fast growing jarrah often have access to water over summer and avoid stress, but this does not help them resist *P. cinnamomi*; if anything, they are more vulnerable during conditions favouring most rapid fungal growth.

Shea *et al.* (1983a) examined whether tree vigour or site treatments were related to levels of jarrah resistance. Lesions in roots of trees growing in a Havel type Q loam were smaller than those in trees in a Havel type P laterite. They inoculated trees at different stages of their flowering and fruiting cycles and also trees exposed to different fire intensities. Mean lesion extension in roots was not significantly affected by the different treatments.

Tippett *et al.* (1989) in their study of 360 saplings on four sites were unable to find any relationships between lesion length and levels of ethanol-soluble carbohydrates and polyphenols in the bases of inoculated trees. The concentrations of polyphenols and carbohydrates were measured since they are substances that may directly or indirectly influence the ability of the trees to resist invasion (Tippett *et al.* 1989). No evidence was found to suggest that fast growing vigorous trees were any more able to resist invasion by *P. cinnamomi* than were suppressed saplings whose narrow bands of sapwood and secondary phloem suggested poor vigour (Tippett *et al.* 1989). The concentration of polyphenols in the phloem of large pole sized trees changed little with season whereas rates of *P. cinnamomi* lesion extension did. Results showing that trees growing on the dry eastern zone sites had higher concentrations of polyphenols than their equivalents on the wetter western sites could not be interpreted in terms of resistance to *P. cinnamomi*.

Assessment and prediction of the effects of changes in stand structure and the density and composition of the understorey on the physiology of jarrah, will help evalu-

ate the costs or benefits of different forest prescriptions. Comparison of the susceptibility of trees on different sites, on sites disturbed or undisturbed, or on sites treated silviculturally or not, depends on identifying measurable parameters that are related to tree susceptibility. Wise choice of parameters for such comparisons requires a better understanding than is presently available, of how the host responds to environmental change and the conditions that favour expression of resistance.

INTER-SPECIFIC VARIATION IN RESISTANCE

Eucalypts vary greatly in their susceptibility to *P. cinnamomi*. Forest observations (Weste and Taylor 1971; Podger 1972) and pot trials (Podger and Batini 1971; Marks *et al.* 1972; Weste *et al.* 1973) showed that eucalypt species of the sub-genus *Monocalyptus* were the most susceptible to *P. cinnamomi*. More recently the susceptibility of 21 eucalypts growing on a replanted bauxite mine pit was assessed using a wound inoculation method (Tippett *et al.* 1985). The fungus failed to establish in the inner bark of species of the sub-genus *Symphyomyrtus*, which includes wandoo, *E. laeliae* and karri. The fungus caused small lesions to form in yarri and bullich, both *Monocalypts*, and in marri of the *Corymbia*. The results were consistent with forest observations. Marri survives on infected sites, although the trees may suffer low levels of infection (Podger 1972). Bullich and yarri both colonize upslope into areas where jarrah has been killed.

Jarrah was by far the most susceptible of the *Monocalyptus* species inoculated. Hygiene procedures and attention to drainage (ch. 7) and return of uncontaminated topsoil can be used to prevent infection of areas of healthy forest mined for bauxite and ensure that jarrah can be used to replant rehabilitated mined areas. *Eucalyptus muellerana* Howitt, a *Monocalyptus* species from New South Wales and Victoria, marri and yarri are more resistant to *P. cinnamomi* than jarrah and may serve as appropriate to replace jarrah as the dominant species in infected rehabilitated mined areas. The low percentage of mortality of jarrah growing in freely drained infected rehabilitated mined areas (Alcoa 1987) may indicate that a role still exists for jarrah in these areas.

INTRA-SPECIFIC VARIATION IN THE SUSCEPTIBILITY OF JARRAH

Evidence both from experimentation and forest observations has suggested that there is genotypic variation in the resistance of jarrah to *P. cinnamomi*. Resistance assessed by measuring length of lesions induced by inoculation of trees in the forest was normally distributed (Fig. 34⁶). A

⁶Shearer, B.L. (1983), Unpublished data, File LE 442, Dwellingup Research Centre.

project to select resistant lines of jarrah has shown correlation between resistance assessed by inoculating seedlings in the glasshouse with resistance assessed in the forest (Stukely⁷ 1989, personal communication). Some resistant lines have been propagated by tissue culture methods (McComb and Bennett 1982).

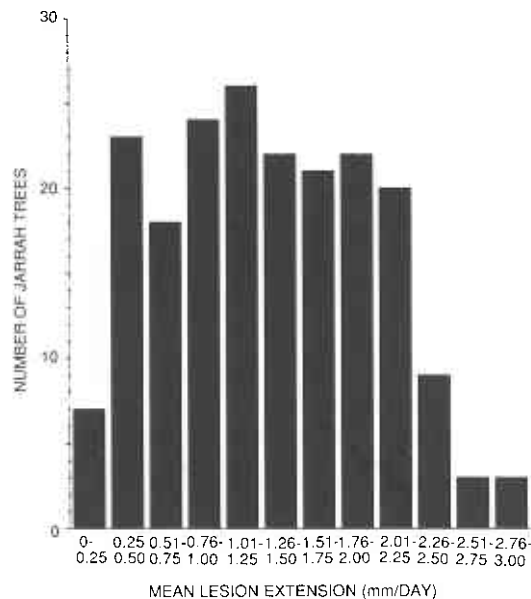


Figure 34

Variation between jarrah trees in the rate of lesion extension of *Phytophthora cinnamomi* in coppice stems inoculated in the forest. Seven trees were resistant with lesion extension rates of < 0.25 mm/day. In comparison 15 trees were very susceptible with lesion extension rates > 2.25 mm/day.

INTRA-SPECIFIC VARIATION WITHIN PHYTOPHTHORA CINNAMOMI

Selection for genetic resistant of jarrah to *P. cinnamomi* would have been little value if the pathogen had been found to be highly variable, particularly with respect to pathogenicity of isolates from different locations or different hosts. Fortunately for tree breeders, *P. cinnamomi* is a remarkably uniform species and most isolates from Australia are of the A₂ compatibility type. Isolates from a diverse range of sites and host species from around Australia have been compared by Old *et al.* (1984a). These workers used isozyme analysis to compare genetic variation with *P. cinnamomi* and concluded that:

the most significant feature of the data is that not only are single-locus genetic diversity estimates low, but the array of multilocus genotypes is very limited.

They found no evidence to suggest host specificity of groups of isolates.

⁷Stukely, M. Department of Conservation and Land Management, Como Research Centre.

Some variations in morphology, growth rates and response of isolates to temperature have been recorded (Shepherd and Forrester 1977; Phillips and Weste 1985; Shearer *et al.* 1987b). Such differences are not particularly important in a management context. Morphological differences are often phenotypic rather than genotypic expressions and they do not suggest that a species has a high potential plasticity. Zentmyer (1980) reviewed variability of *P. cinnamomi* and despite some differences reported, he also commented on 'strikingly similar growth patterns' of *P. cinnamomi* isolates from around the world. As mentioned in Chapter 7, an important exception is the occurrence of strains of *P. cinnamomi* resistant to systemic fungicides (Cohen and Coffey 1986).

INTER-SPECIFIC VARIATION IN PHYTOPHTHORA SPECIES

Variation in pathogenicity is difficult to assess unless a single host plant is inoculated with a number of different isolates, or host plants of the same genotype are available. Shearer *et al.* (1988) chose to compare the pathogenicity of a number of *Phytophthora* species including *P. cinnamomi*, *P. citricola*, *P. megasperma* var. *sojae* and *P. cryptogea* A₂. Five isolates of each species were inoculated into the inner bark of *B. grandis* and jarrah. Variation in growth rates between isolates of *P. cinnamomi* and *P. cryptogea* A₂ was less than the variation for the other two species. More isolates could be tested using this method, although cloned jarrah plants, which should soon be available, would be better for pathogenicity tests. Podger (1972), in an early experiment to test the pathogenicity of 49 isolates of *P. cinnamomi*, found that all except one caused death of jarrah seedlings. If conditions are favourable, *P. cinnamomi* isolates consistently damage host plants.

THE RELATIVE IMPORTANCE OF PHYTOPHTHORA SPECIES

Twenty-three species of *Phytophthora* have been listed as having been isolated from nurseries, forests and plantations from around Australia by Podger (1979). Circumstantial evidence suggests that many *Phytophthora* species recorded in Australia have been introduced. Spread of these *Phytophthora* species must therefore be minimized.

Although much is known about *P. cinnamomi*, relatively little is known about other *Phytophthora* species in the jarrah forest. *Phytophthora citricola* probably has the greatest potential to exacerbate the problem of dieback caused by *P. cinnamomi* in the jarrah forest. Chevis and Stukely (1982) first reported that *P. citricola*, as well as *P. cinnamomi*, *P. megasperma* var. *sojae* and *P. cryptogea*, were associated with *Pinus radiata* root rot in the Donnybrook Sunklands near Busselton. Since then *P. citricola* has been frequently isolated from gravel and soil samples

collected in the jarrah forest. In 1984, 2.5 per cent of the samples tested at the Dwellingup Research Centre yielded *P. citricola* (Shearer *et al.* 1987a).

Shearer *et al.* (1987a) compared the behaviour of 8 species of *Phytophthora* in inoculated stems of *B. grandis* and jarrah in the forest. They found that *B. grandis* was more susceptible to *P. cinnamomi* than to any of the other *Phytophthora* species. *Phytophthora cactorum*, *P. cryptogea* (A₁ and A₂), *P. citricola* and *P. nicotianae* var. *parasitica* did significantly less damage to *B. grandis* than *P. cinnamomi*, but all established in jarrah. Further inoculations of jarrah, marri and *B. grandis* confirmed that *P. citricola* could establish and cause extensive lesions in jarrah (Shearer *et al.* 1988). Although marri was resistant to *P. cinnamomi*, it was susceptible to *P. citricola*. Extensive lesions up to 50 cm long had formed 12 months after inoculation.

Because of the greater resistance of *B. grandis* to *P. citricola* than to *P. cinnamomi* it is unlikely that *P. citricola* will establish in the jarrah forest to the extent of *P. cinnamomi* (Shearer *et al.* 1988). The highly susceptible *B. grandis* understorey has favoured the establishment, spread and survival of *P. cinnamomi*. Roots of *B. grandis* commonly grow in close proximity with jarrah roots and once infected, they may result in infection of jarrah (Shea *et al.* 1983c). Previous sections have described how invasion of the secondary tissues of *B. grandis* by *P. cinnamomi* favours survival of the fungus when conditions are dry.

As temperature and host water status can affect the growth rate of *Phytophthora* species, conclusions about relative susceptibility of hosts cannot be drawn unless the pathogens are tested under a range of conditions. Shearer *et al.* (1988) compared the results of *P. citricola* and *P. cinnamomi* inoculations of jarrah, marri and *B. grandis* made in summer, autumn, and winter. Growth of both *P. citricola* and *P. cinnamomi* in jarrah were least in winter and greatest in summer. In stems of jarrah and marri inoculated in winter, the growth rate of *P. citricola* was greater than that of *P. cinnamomi*. Excised roots of *B. grandis* and jarrah were inoculated in the laboratory to determine the effects of temperature on *P. cinnamomi* and *P. citricola*. Growth rates of both fungi increased with temperature up to 30°C (Shearer *et al.* 1987a).

The life cycles of *Phytophthora* species other than *P. cinnamomi* are not all equally affected by the same environment. For example, *P. citricola* persists under dry conditions, probably because it is homothallic and readily produces thick walled oospores. More details on differences between *Phytophthora* species can be found in the collection of reviews in Erwin *et al.* (1983). Further research is required to determine the relative behaviour of *Phytophthora* species in the environment of the jarrah forest and host susceptibility to infection.

Assessment of Damage

This chapter describes the consequence of pathogen development, infection and invasion described in the preceding chapter. Although disease caused by *P. cinnamomi* has been called jarrah dieback there is no denying that considerable damage is being done to the jarrah forest understorey following infection. More information is available on the damage to the jarrah overstorey than for the understorey. Root loss in jarrah from infection needs to be related to symptom expression and growth to determine the amount of root loss before the tree dies. The mechanisms whereby jarrah is killed following infection need to be determined. Assessment of jarrah mortality provides estimates of past and potential future loss through disease and is essential for determining the influence of disturbance and climatic change on disease expression.

INTRODUCTION

There are three questions to be addressed in this chapter: How much damage does *P. cinnamomi* inflict on understorey species and jarrah on different forest sites? How does the rate of mortality of host plants vary with site, season and year? What is the prognosis of disease on different forest sites? Answers to these questions are dependent on the assessment of damage to trees and understorey species on a range of sites infected by the pathogen. Disease development has to be monitored on a range of sites through periods of differing conditions before any prognosis or forecast of disease development in any area can be attempted.

Different methods of assessment have been tried. The damage caused by *P. cinnamomi* can be assessed by excavating roots and looking for lesions, a destructive and laborious process. Alternatively, non-destructive methods of assessment can be developed from the relationships between above ground symptoms and the amount of damage to root systems tested in different sites and seasons.

Damage caused by *P. cinnamomi* infection in the jarrah forest is usually equated to death of the overstorey. This approach neglects the effects of sub-lethal infections that do not cause death. Reductions in root development, decreased growth of the overstorey and health of the understorey are often ignored although such consequences of infection may be important.

DAMAGE TO THE UNDERSTOREY

A large proportion of the understorey vegetation of the jarrah forest is susceptible to *P. cinnamomi* (ch. 4). Despite this, surprisingly little information is available on the effect of infection on the composition of the jarrah forest understorey, other than the initial work of Podger (1968) (Table 3). For the jarrah forest, there is no extensive documentation of changes in understorey composition, following *P. cinnamomi* infection, compa-

rable to that undertaken in Victorian forests by Weste and Taylor (1971) and Weste *et al.* (1973).

Host lists for the jarrah forest have been compiled by Titze and Palzer (1969) from their own isolation records, pathogenicity tests, and the literature and by Gardner and Rokich (1987) from isolation records. The lists cannot be used to obtain estimates of host susceptibility because the isolation records do not separate hosts that survived from those that died following infection.

Podger (1968) assessed mortality to be greatest in plant species belonging to the Proteaceae, Papilionaceae and Dilleniaceae (Table 3). Keighery (1988) estimates that 29 of the 171 species of the Epacridaceae known to occur in south-western Australia are at risk from *P. cinnamomi*.

Havel site-vegetation types can give some idea of the potential reduction in the composition of the understorey vegetation following *P. cinnamomi* infection. Types C, M, Q and U are composed largely of resistant understorey vegetation species. A high proportion of susceptible understorey species of the families Proteaceae and Epacridaceae occur in the Havel site types B, D, E, F, J, P, O, R, S, T, W and Z (Havel 1975⁸, unpublished). These site types cover most of the laterite-mantled uplands of the northern jarrah forest (Havel 1975b). More information is available on the damage to the jarrah overstorey than for the understorey.

DAMAGE TO JARRAH

Root Infection

Fine roots

Damage to fine roots can cause symptoms which resemble nutritional deficiencies or loss of vigour. The relative amount of fine root damage compared with damage to large roots varies with host and site. Somerford *et al.*

⁸Havel, J.J. (1975), Site-vegetation types and impact of *Phytophthora cinnamomi*. Unpublished manuscript, Department of Conservation and Land Management, Library, Woodvale.

Table 3

The percentage of stocked quadrants with chlorotic or dead common species of ground flora in transects of the jarrah forest on Mt. Cook, affected and unaffected by *Phytophthora cinnamomi* in May, 1966 (after Podger 1968).

Subdivision/ Family/ Species	Affected			Unaffected		
	Occur- rence	Chlor- otic	Dead	Occur- rence	Chlor- otic	Dead
Monocotyledoneae						
Haemodoroceae						
<i>Conostylis setigera</i>	55	43	29	100	0	0
Cyperaceae						
<i>Lepidosperma angustatum</i>	70	18	29	100	33	33
<i>Tricostularia neesii</i>	70	18	6	100	0	0
Liliaceae						
<i>Lomandra</i>	55	0	7	65	0	0
Dicotyledoneae						
Goodeniaceae						
<i>Dampiera linearis</i>	90	14	0	50	0	0
<i>Lechenaultia biloba</i>	60	0	7	85	0	0
<i>Dampiera alata</i>	40	40	20	15	0	0
Proteaceae						
<i>Dryandra nivea</i>	85	43	52	100	0	50
<i>Grevillea willsonii</i>	65	0	19	100	17	0
<i>Petrophile striata</i>	60	40	40	100	0	0
<i>Adenanthos barbigerus</i>	45	45	63	100	0	0
Papilionaceae						
<i>Hovea trisperma</i>	50	8	25	100	0	0
<i>Daviesia decurrens</i>	50	42	25	85	20	0
Sterculiscaeae						
<i>Lasiopetalum floribundum</i>	70	50	44	85	0	20
Dilleniaceae						
<i>Hibbertia hypericoides</i>	50	42	50	100	0	0
Apiaceae						
<i>Xanthosia pentapeltis</i>	35	0	0	35	0	0
<i>Xanthosia candida</i>	30	25	12	35	0	0
<i>Xanthosia atkinsoniana</i>	25	33	17	35	0	0
Epacridaceae						
<i>Astroloma pallidum</i>	30	12	0	50	0	0
Rutaceae						
<i>Boronia spathulata</i>	25	0	0	50	0	0
Droseraceae						
<i>Drosera erythrorhiza</i>	25	0	0	85	0	0

(1987) have made the most recent and comprehensive study of the health and distribution of the fine roots of *B. grandis* and jarrah on six healthy and 25 infected sites. Fine root distribution and health was assessed from quadrant samples and trench faces.

Fine roots of *B. grandis* were bimodally distributed down the profile in uninfected sites, with a primary peak at about 20 cm and a secondary peak just above an impeding horizon. *Banksia grandis* fine root mortality was greater in infected than uninfected sites (Table 4).

Table 4

Percentage of fine roots of jarrah and *Banksia grandis* found dead in sites infected with *Phytophthora cinnamomi* compared with healthy sites.

Host		Infected	Healthy
<i>Banksia grandis</i>	Range	0-100	2-54
	Mean*	44 ± 8	23 ± 9
	Sites (No.)	13	6
Jarrah	Range	9-87	7-38
	Mean*	33 ± 3	17 ± 4
	Sites (No.)	25	6

* Mean ± standard error of the mean.

The occurrence of fine roots of jarrah was very variable. Most fine roots of jarrah occurred near the surface with 75 per cent of roots within the top 30 cm of soil in both infected and uninfected sites (Fig. 35). The total number of fine roots at each site excavated varied more between Havel site-vegetation types than between infected and healthy areas.

Dead fine roots of jarrah were more frequent in the infected than in the healthy sites (Table 4). *Phytophthora cinnamomi* was recovered from fine roots of jarrah even though *B. grandis* had been killed at least five years prior to sampling. This suggests that viable inoculum can persist for many years in the fine roots of jarrah.

Healthy forest trees continually shed and replace fine roots so that 30-86 per cent of fine roots may turnover annually (Fogel 1983). The exact reasons for this high turnover is little understood. The annual and seasonal death of fine roots of healthy jarrah trees has not been determined. Such information on root turnover is needed before assessing the relative importance of loss of fine roots of jarrah from *P. cinnamomi* infection to tree growth and survival.

Large roots

Root systems of 34 subdominant pole sized jarrah trees with healthy crowns were hydraulically excavated to assess the amount of damage to large roots. Of these,

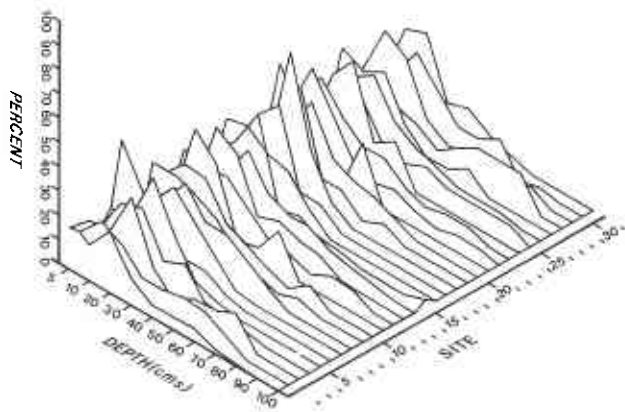


Figure 35

Distribution of fine roots of jarrah with depth.

eight were excavated in uninfected sites. *Phytophthora cinnamomi* was recovered from the large roots of 16 of the 26 apparently healthy trees on infected sites. For all trees, 66 per cent of the large roots were laterals while 34 per cent were vertical tap roots. Of the large roots from which *P. cinnamomi* was recovered (Table 5), 79 per cent were laterals and 21 per cent verticals. This is in contrast to the results from excavated trees on high impact sites where most of the recoveries were from vertical tap roots (Shea *et al.* 1982).

Although a high proportion of trees on infected sites had infected roots, the proportion of roots infected per tree was much lower (Table 5). A high percentage of infected roots were girdled by *P. cinnamomi* (45 ± 10 per cent) with considerable variation between site type and history. For example, six out of seven infected roots were girdled in a Havel type tS which had been irrigated as part of population dynamics studies (Shearer and Shea 1987). In comparison, only one out of eight infected roots were girdled by the fungus in a similar site type that had not been irrigated. The length of *P. cinnamomi* lesions varied from 1.3 to 368 cm, with 85 per cent of lesions being less than 12 cm. Approximately 75 per cent of the lesions were not contained by reactive tissue.

The occurrence of active *P. cinnamomi* lesions in the roots of a majority of apparently healthy trees on infected sites is of concern. However, the amount of root infection was relatively low compared with that observed by Shea *et al.* (1982) for recently dead trees in high impact areas. Low levels of root infection may have minimal affect on tree health unless lesions girdle the trunk collar (Fig. 39) or a significant number of vertical tap roots. How root loss relates to tree health is partly answered by work described in the next section. In sites where tree mortality is low, the long term effects of root infection on tree health and growth still need to be determined.

Table 5

Recovery of *Phytophthora cinnamomi* from large roots of live jarrah excavated in infected areas.

Tree	Total roots (No.)	Roots infected (No.)				
		Vertical	Lateral	Total	Girdled	Lesion contained
2	118	1	3	4	2	0
4	88	0	2	2	0	0
5	29	2	6	8	1	1
6	147	0	4	4	3	0
9	83	0	7	7	6	1
10	28	1	3	4	0	1
11	65	0	2	2	1	1
15	94	0	1	1	0	0
18	51	0	1	1	0	0
20	39	2	8	10	2	6
22	67	4	3	7	2	1
23	59	1	0	1	1	0
28	77	0	4	4	0	1
29	55	1	0	1	1	0
31	86	1	2	3	3	0
32	75	1	6	7	6	2

Effect of Root Loss on Jarrah

Crombie *et al.* (1987) studied the effects of root loss on the water status of jarrah. Not only did this work contribute to an understanding of symptom development in jarrah affected by *P. cinnamomi*, but also resulted in the development of methods for the non-destructive assessment of the effects on trees of severe root damage (Crombie and Tippett 1990). These methods, despite limitations, facilitate the monitoring of disease development and provide an indication of how long it takes *P. cinnamomi* to kill trees. Trees can suffer root loss for a number of years before final symptoms are expressed and death occurs. The severity of damage sustained by jarrah in areas infected by *P. cinnamomi* depends on many factors previously outlined in Chapter 5 and include genotype, abundance of inoculum in the soil, site characteristics and climate.

Jarrah has a great ability to compensate for root loss, especially when moist soil conditions prevail. Effects of root loss on tree water status were determined by progressively pruning roots from jarrah saplings (Crombie *et al.* 1987). Under moist soil conditions, night-time leaf water potentials were not reduced significantly until 80-90 per cent of roots were lost (Fig. 36). The first indication that the trees were conserving water was a reduction in water loss through stomatal closure. Root loss is understandably more critical when soils are dry (Fig. 36) and the development of water stress is more dependent on which

roots in the system have been damaged or cut. Under dry conditions, jarrah relies on deep vertical roots which tap the moist clays of the pallid zone beneath the duricrust.

Longer term responses of trees to root loss include reduction in leaf area as a result of a reduction in the rate of water uptake. Under experimental conditions, a 75 per cent reduction in functional roots was matched with a 50 per cent decrease in leaf area. Reduction of leaf area and prolonged stomatal closure during the day restricts the ability of trees to photosynthesize. Presumably growth rates are restricted by reductions in the supply of carbohydrates and cell expansion (a turgor driven process). Osmotic adjustment of cell contents to compensate for water stress and regeneration of damaged roots may also drain carbohydrates and further reduce growth.

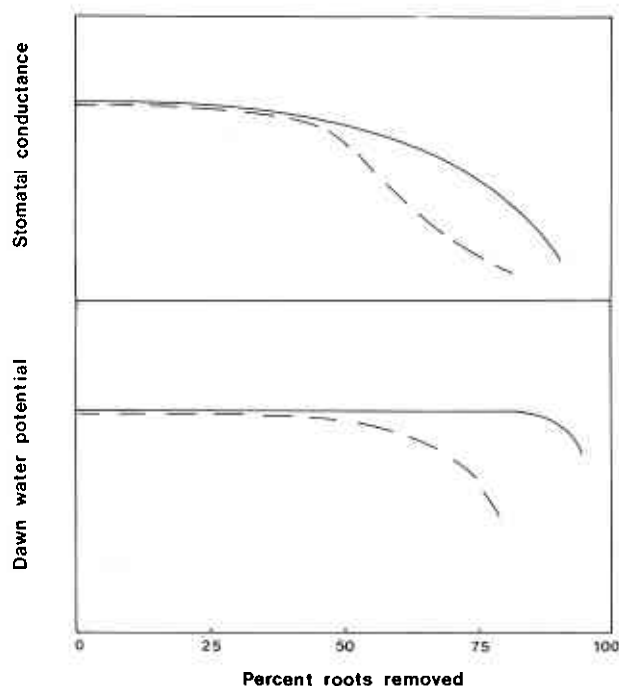


Figure 36

Decline of stomatal conductance and dawn water potentials of root pruned jarrah. The curves were derived from 13 root pruned saplings measured before and after 100 mm of rain fell during a 2-day period in February 1986 (i.e. dry (- -) and moist (—) soil conditions respectively). The greater sensitivity of water potentials and stomatal conductances of trees on dry soils to root pruning compared with similarly treated trees on moist soils demonstrates the crucial function of the deep root system of jarrah in supplying water to the crown during summer drought (Crombie *et al.* 1987).

There have been three studies of the effects of *P. cinnamomi* on the growth of jarrah. Two studies (Podger 1972; Crombie and Tippett 1990) have shown that growth rates of jarrah trees surviving on intermediate to high impact dieback sites were reduced substantially compared with apparently healthy jarrah (Fig. 37). The third study by Davison and Tay (1988), reported similar or slightly greater growth rates of jarrah on intermediate impact but heterogeneous dieback sites in comparison with

uninfected sites. The reduced tree stocking rate in their dieback sites would partly explain the observed greater growth rate in dieback areas. The effects of different levels of infection on jarrah growth requires clarification.

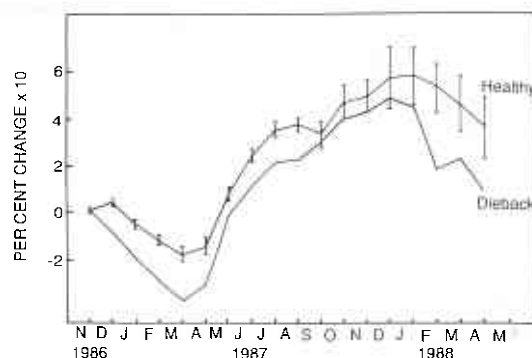


Figure 37

Changes in stem girth of dieback and healthy jarrah trees averaged over four high impact sites. Stems of dieback trees shrank more during the summers of both years (November-March) and grew less during the intervening wet winter and spring (July-October) than did healthy trees. The poor performance of dieback infected trees occurred even though stand density on dieback sites was approximately half that on healthy sites, conditions that would normally favour growth of widely spaced trees (Crombie and Tippett 1990).

MONITORING SYMPTOM DEVELOPMENT IN JARRAH

Trees in areas infected with *P. cinnamomi* may express symptoms similar to those induced by root pruning described in the previous section. Shea *et al.* (1982) found that jarrah on high impact sites had leaf water potentials significantly more negative than those of healthy trees on uninfected sites. The trees had presumably lost a high percentage of vertical tap roots and many died in the season of measurement.

Crombie and Tippett (1990) studied symptom development, and tree water status of over 200 trees on a range of infected and noninfected sites over two summers (1985-86 and 1986-87) (Fig. 38). The condition of crowns was assessed and the following measurements made:

- Predawn leaf water potentials [to assess the ability of trees to absorb water from deep in the soil profile (Fig. 38)].
- Midday leaf water potentials [to assess the ability of leaves to maintain normal water status while transpiring. This is a function of the absorption capacity of the roots, although other factors can influence midday leaf water potentials].
- Stomatal conductances at midday [to determine whether leaf water potentials were being maintained at the expense of transpiration and water loss (Fig. 38)].

Reduced transpiration would prevent development of measurable water stress in the leaves].

- Dendrometer bands [to monitor trunk growth and also shrinkage caused by water stress, and growth (Fig. 37)].
- Rainfall.

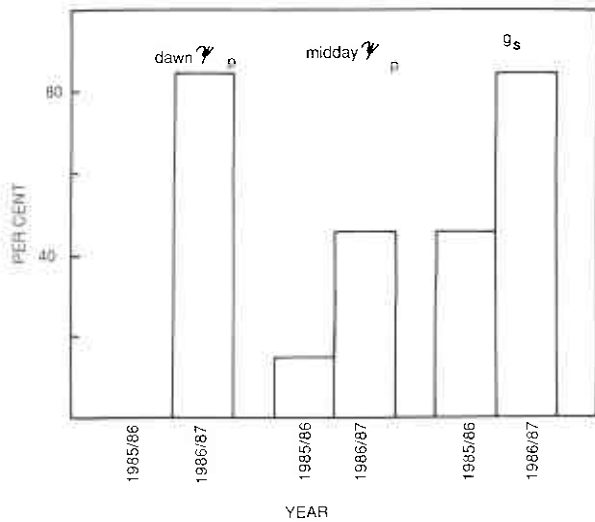


Figure 38

Percentage of sites on which relevant water relations parameters (predawn leaf water potential - dawn Ψ_p ; midday leaf water potential - midday Ψ_m and stomatal conductance - g_s) were significantly lower in groups of healthy than nearby dieback infected trees during successive summers (1985-86 and 1986-87). A greater number of significant differences in the second summer is believed to reflect the drier conditions of the second year which accentuated deficiencies in the condition of root systems of trees in the infected area compared with healthy trees (adapted from Crombie and Tippett 1990).

Stomatal conductances at midday were reduced in a number of the trees on the infected sites during 1985-86. However, it was not until the summer of 1986-87 that a large number of the trees on diseased sites suffered water stress at dawn in addition to having reduced stomatal conductances at midday (Fig. 38). Most of the trees on infected sites were able to recover overnight from daytime water stress during the first summer, but some had lost this capacity to rehydrate their tissues at night by the second summer. Trunk shrinkage, which reflected failure of stems to fully rehydrate, occurred in trees in both the control and infected sites as summer progressed but was more pronounced in the latter (Fig. 37). Trees in healthy areas grew faster than those in infected areas.

Death of jarrah was more prevalent in the spring and summer of the second year of measurement than at any other time. Root systems were excavated and *P. cinnamomi* recovered from both roots and collars of dying and dead trees. Many of the trees that died in summer 1986-87 had lesions in their roots or at the base of the trunks (Fig. 39). Eight of the trees sampled had large basal lesions extending for a metre up the trunk in one instance. Some of the lesions girdled the trunks and the trees died. In several cases some cambium remained alive and although the crowns were still active, the trees were severely water stressed. It is of interest that Shearer and Fairman⁹ (personal observations) in 1982 recovered *P. cinnamomi* from 5 m above ground level in the trunk of a live tree.

The foliage of the trees suffering water stress, including some which eventually died, was sparse and some had not produced their expected early summer leaf flush.

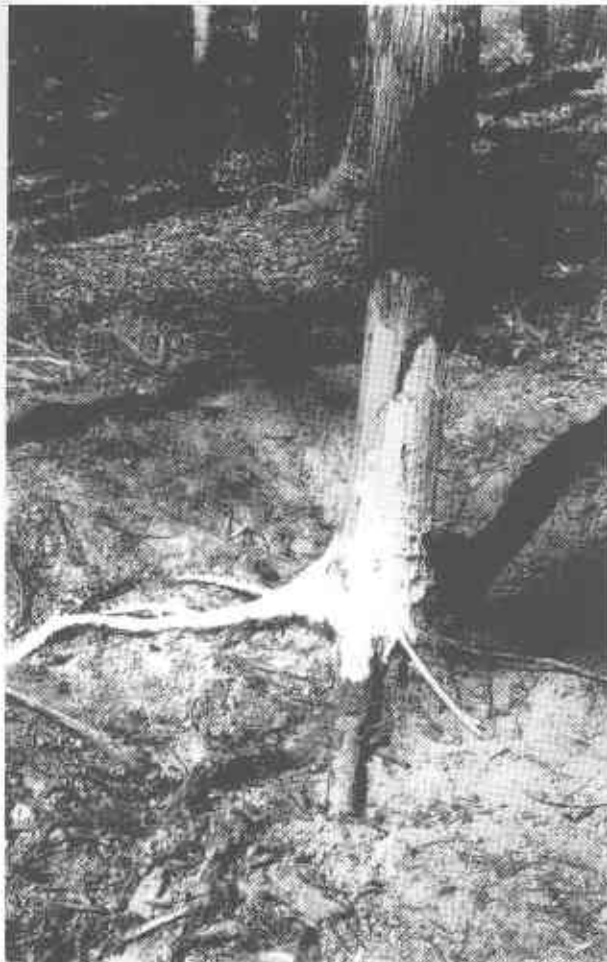
The load of seed capsules from the previous year was often moderately heavy, but this did not explain the extent to which leaves had been shed without replacement. The trees died before severe short-term leaf abscission and hence the crowns had a 'scorched' appearance of dead brown leaves when the trees finally succumbed.

Crombie and Tippett (1990) proposed that the development of severe water stress and tree deaths in the summer of 1986-87 compared with the first summer of 1985-86 was due to the climatic conditions over the two years. The summer of 1985-86 was relatively cool and mild with some rain, this was followed by a long moist spring in 1986 and then a dry summer in 1986-87. These conditions favoured fungal activity in the spring and early summer and then set a high transpirational demand with limited soil moisture in late summer.

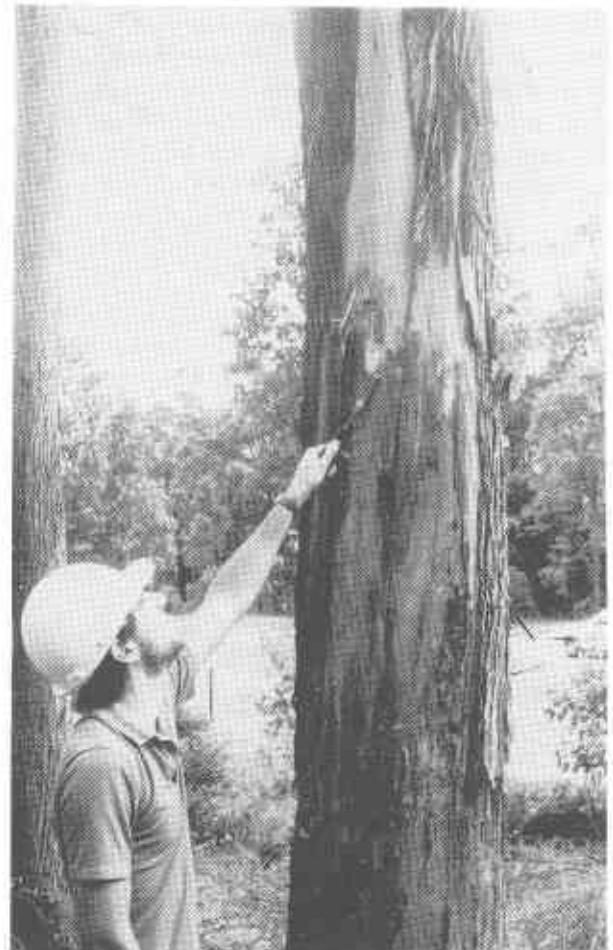
Conclusions from these studies can be summarized as follows:

- Stomatal conductance was a more sensitive indicator of root damage to jarrah than was leaf water potential.
- Lethal water stress only developed after jarrah had either lost a high percentage of roots or had been girdled at the collar.
- Jarrah is quite commonly killed by collar invasion (also Shearer *et al.* 1981).
- Extensive stem invasion can occur once the fungus has reached the collar. The fungus may grow downward into previously uninfected roots.
- It can take a number of years for *P. cinnamomi* to kill jarrah.

⁹Shearer, B.L. and Fairman, R. G., Dwellingup Research Centre.



(a)



(b)

Figure 39

The outer bark has been removed to show stem lesions of *Phytophthora cinnamomi* in jarrah. Jarrah suffering water stress as indicated by reduced stomatal conductance were often girdled at the base. (a) Area of inner bark affected by *P. cinnamomi* was painted white. (b) *Phytophthora cinnamomi* was isolated from extensive dark brown lesions in the stems of trees monitored on infected sites. The chisel indicates a lesion front between healthy white and infected discoloured inner bark.

Symptom Development in Jarrah on Upland Sites

Jarrah dies on a range of upland site types but apparently survives on others. Symptoms of *P. cinnamomi* infection in jarrah may reflect the rate of fungal invasion and the type and amount of damage. Symptoms in crowns may be subtle or obvious, they may develop slowly or be expressed rapidly.

Shea *et al.* (1982) found that the death of jarrah on high impact upland sites was caused by the fungus girdling vertical tap roots. The crowns did not show signs of gradual, progressive thinning and the trees were killed rapidly. The majority of deaths occurred during February

when conditions were desiccating and the symptoms resembled those caused by drought (Shea *et al.* 1983c). As jarrah usually dies once a high percentage of vertical tap roots are girdled or trees are girdled at the butt or root collar, the rapid death of these trees suggests a period of rapid fungal growth within the root system. Crombie and Tippett (1990) found in high impact areas that death of jarrah can also be caused by gradual decline and 'dieback' of crowns associated with cumulative root loss and decreasing tree vigour over time.

MORTALITY RATE OF JARRAH

Although the impact of *P. cinnamomi* is most evident in the death of vegetation, there has been no adequate quan-

tification of variation in rates of jarrah death in different areas and years. The Department of Conservation and Land Management has conducted an extensive large scale colour aerial photography program since the mid 1970s. Dieback mapping of operational areas has of necessity had higher priority than monitoring and no area has an extensive sequence of photographs over time. Quantification of death of jarrah would provide estimates of past and possible future loss of jarrah through disease. This would be essential for determining the influence of climatic change on disease expression, as has been done in Victoria by Tregonning and Fagg (1984).

Jarrah mortality has been assessed using:

1. Small scale black and white aerial photography. Changes in the boundaries of infected areas with high jarrah mortality have been obtained from these photographs (Van De Sande 1986).
2. Shadowless large scale coloured aerial photography for areas photographed more than once. This photography was used to quantify changes in the number of jarrah deaths with time.

Identification of individual jarrah deaths on small scale black and white photography is difficult because of the scale (up to 1 : 50 000), lack of colour, poor quality from age and use, and large gaps in time between photographs. However, the photographs are the only available continuous and long term record of deaths going back to 1961. Despite limitations, they can be used to obtain an estimate increase in the areas of jarrah deaths (Fig. 40) and the periods when most deaths of jarrah occurred (Table 6).

Based on recollections of forest personnel, it is thought that a peak in jarrah deaths occurred in the early 1960s followed by few or no deaths until those observed during 1982-1984. Monitoring of the black and white aerial photographs has not only quantified the deaths that occurred in the 1960s, but also shown that a previously unknown peak in jarrah deaths occurred in the early 1970s (Table 6). Research relating this information to rainfall and temperature records to determine the effect of climatic change on disease expression in the jarrah forest is continuing.

Figure 40 illustrates changes with time in the area of jarrah deaths in Keats forest block. In 1976 dead jarrah were confined mainly to the lower slopes of a shallow valley. By 1981 the area of dead jarrah occupied mid slopes and by 1986 there had been a dramatic extension into upper slopes.

Maps of recent jarrah deaths have been drawn from large scale shadowless colour aerial photographs of Bal-

Table 6

Summary of assessment of death of jarrah in *Phytophthora cinnamomi* infected areas assessed from black and white aerial photographs.

Plot	Year of photography										
	1958	1961	1969	1973	1976	1980	1981	1983	1985	1986	
DD6344 ^a	b	c	+ ^d	+		+	+	+		:	:
DC6562	-	-	+	+	:	+	+	+	:	:	:
DC6526	-	-	+	:	+	:	:	:	:	:	:
DC6526		+	+	+		+	+	:	:	:	+
DD6334		-	+	+		+	+	:	:	:	:
DC6311		-	+	+		:	:	+	:	+	+
DE6519	+	:	:	+	+		:	:	:	:	:
DE6411	+	+	+	+	:	+	:	:	:	:	:
DE6441	-	+	:	:	:	:	:	+	:	:	+
DF6529	+	+	+	+	+	:	:	:	:	:	:
DE6294		+	+	+		+	:	:	:	:	:
DF6512		+	:	:		:	:	+	:	+	+
DD6498		-	+		+	:	:	:	:	:	:
DE6495	-	-	-	-		+	:	+	+	:	:
DF6531		-	+	:	+	:	+	+	:	:	:
DE6488	-	+	+	+	:	:	:	:	:	:	:
DF6475		-	:	:	:	+	:	+	:	+	+
DD6494		-	+	+	:	:	:	:	:	:	:
DG6748		+	+	:	:	:	:	+	:	:	:
DH6591						+	:	:			:
DJ6655						+	+	+			+
DG6772			+	:	:	:	:	:	:	:	:
DF6715		+	+	:	+	+	+	+	:	+	+

^a Dept. Cons. & Land Management map reference.

^b No photography.

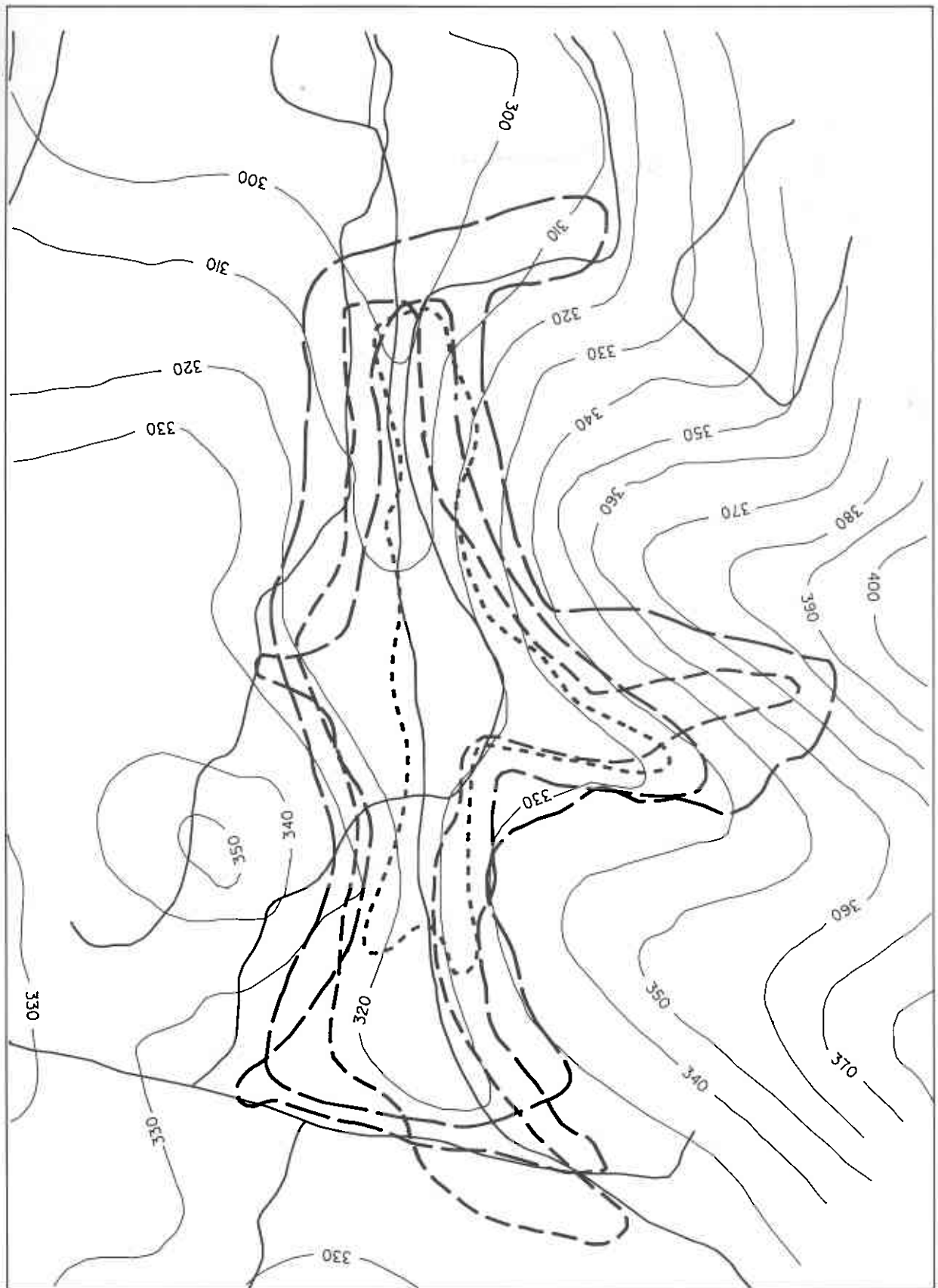
^c - No disease apparent.

^d + Plot shows reduction in jarrah canopy cover.

^e : No detectable change in jarrah canopy cover.

moral, Lang (Fig. 41) and Wilson-Whittaker forest blocks. The large scale shadowless format is the most suitable for accurate identification of individual dead trees (Bradshaw and Chandler 1978). Typically, the greatest number of dead jarrah occur in high impact areas and the dead trees tend to be in clumps (Fig. 41).

Only the blocks listed in Table 7 have had two aerial photography runs; no block has been flown more than twice. Death of jarrah recorded at the two assessment times clearly illustrates the increase in deaths following the 1982-1984 period (Table 7). Removal of dead trees by practices such as salvage logging results in an underestimation of the number of dead jarrah in Balmoral and Wilson-Whittaker blocks. This is not a factor in the research area of Lang block, where entry is restricted. Two assessments are obviously inadequate to evaluate changes in time. Lang (relatively undisturbed) and Balmoral (disturbed) provide an opportunity for coarse comparison and regular aerial photography of these blocks must be a high priority.



1976 - - - - - 1981 ————
 1980 - - - - - 1986 ————

DIEBACK RESEARCH PLOT 93

SCALE 1:8000

Figure 40
 Changes in the area of dead jarrah with time.

Table 7

Number of recently dead jarrah trees recorded in three forest blocks assessed from aerial photography on two occasions.

Forest Block	Year Photographed	Recent dead jarrah (No./100 ha of forest infected with <i>Phytophthora cinnamomi</i>)
Wilson/Whittaker	1981	4
	1985	13
Balmoral	1976	4
	1985	9
Lang	1983	5
	1984	13

PROGNOSIS

The assessment of damage and the monitoring of disease development over time will help predict future progress of disease and provide a sound basis for management decisions. Information on the effects of infection on understorey plant species in the shrub layer is lacking, particularly the effects on rare flora that may be endangered by infection. There is a need to develop databases on the susceptibility of plant species within the shrub layer to infection.

The excavation of infected root systems has recently provided valuable information about amounts of damage

to root systems on a number of sites. There is evidence from the work on jarrah that *P. cinnamomi* can remain 'dormant' in jarrah and certain conditions such as summer rain may activate fungal propagules which have persisted in tissues (Tippett *et al.* 1985). Spectacular rapid death of trees on high impact sites may also be brought on by climatic conditions which synchronize symptom expression rather than high levels of fungal activity in the soil (ch. 5). Monitoring deaths of jarrah over the last two decades has shown that the relatively few deaths observed in some years did not mean that the fungus was not infecting and invading roots, although the amount of damage is not known.

There is a particular need for assessment of the effects of *P. cinnamomi* on intermediate impact sites where jarrah may survive for long periods. The questions to be addressed include: What type of regeneration occurs on sites long infected by *P. cinnamomi* - is it from seed or old rootstocks? Is jarrah's growth affected on some sites but not others? If so, why? Are the effects of infection transitory or cumulative? How is leaf area affected and how does reduction in leaf area caused by disease relate to performance of jarrah on different types of sites?

Under the most adverse conditions, how quickly can jarrah be killed by *P. cinnamomi*? We suspect it would take at least a year, but more monitoring of the interactions over time is essential. In addition, gradual decline, where trees may take 10-20 years to succumb, may be subtle and must not be ignored.

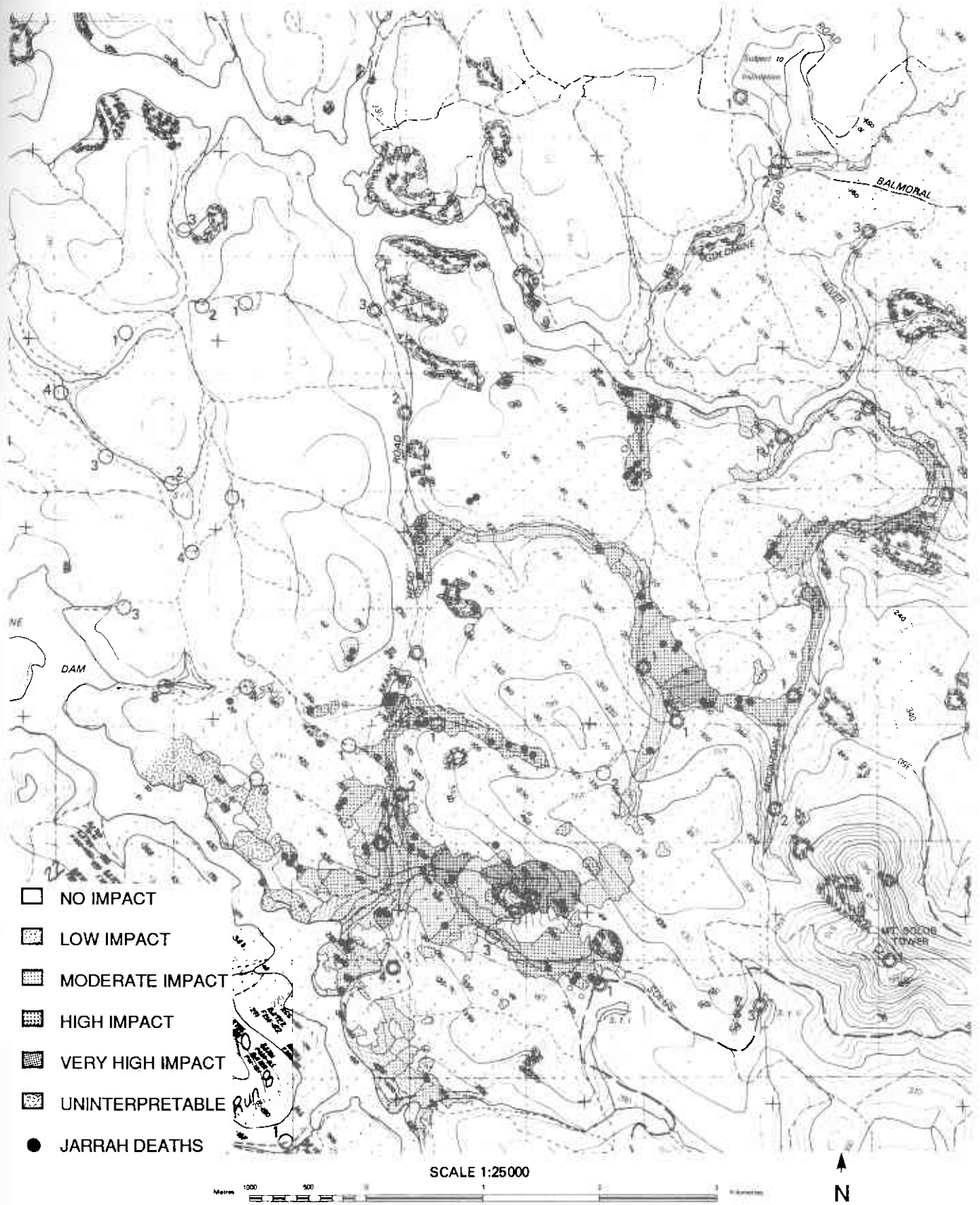


Figure 41
 Distribution of dead jarrah and areas infected with *Phytophthora cinnamnomi* in Lang block in 1984.

Disease Management

Integrated management offers the hope of exploiting the weakness of *P. cinnamomi* and enhancing resistance to disease. Hazard systems to recognize vulnerable sites and assessment of risk of spread are described. *Phytophthora cinnamomi* cannot be eradicated from infected areas but the risk of spread can be reduced by hygienic procedures. Understorey modification, stimulation of antagonistic microflora, manipulation of drainage, fungicides, selection and enhancement of resistance minimizes spread and reduces the rate of disease development.

INTRODUCTION

Disease management aims to prevent and restrict spread and intensification of the pathogen to protect conservation and economic values. Effective disease management balances the extremes between pessimism and over-optimism. 'Gloom and doom' lead to self-fulfilling prophecies; the failure to employ control measures and the actions undertaken because of a pessimistic outlook will lead to spread and intensification of disease. Over-optimism leads to a false sense of security and an under-estimation of the consequences of disease.

The manager has the opportunity to manipulate the environment to disfavour pathogen development and minimize host infection. A well conceived disease management program integrates the use of all suitable methods in a compatible manner. Such an integration must be based on knowledge of the pathogen and the cultural, site and climatic conditions under which the interaction between host and pathogen occurs. By utilizing this knowledge base, a 'package' of management options can be developed to exploit the weakness of the pathogen (ch. 5) without predisposing the host to disease.

The efficacy of disease management is judged by the extent the management either prevents, delays or reduces the rate of disease development (Fig. 42). Prevention tactics, such as hygienic procedures, do not alter the rate of disease development once established, as the environment affecting the disease is not changed by the management procedures. In contrast, procedures such as manipulation of the understorey and chemotherapy can alter the environment to disfavour the pathogen, thus delaying and reducing the rate of disease development (Fig. 42).

Disease management can be divided into four main areas as follows:

- Rating hazard (recognition of vulnerable sites);
- Assessing risk;
- Hygienic procedures;
- Manipulation of conditions to disfavour the pathogen and to enhance host resistance.

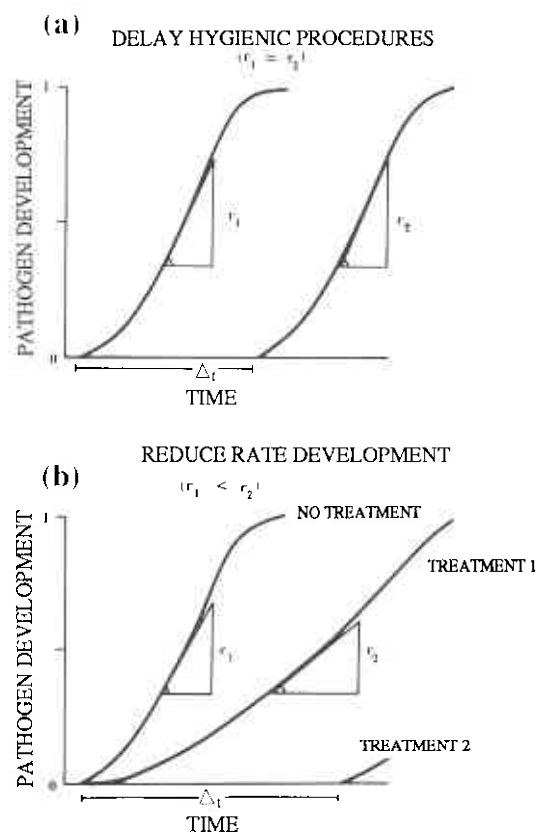


Figure 42

Influence of management on disease development.

- (a) Hygienic procedures delay the likely introduction of disease (Δt), but do not affect the rate of disease development should introduction occur.
 (b) Treatment 1 reduces the rate of disease development. Treatment 2 delays the onset of disease (Δt) and reduces the rate of development.

HAZARD RATING SYSTEM

Introduction

The concepts of hazard and risk are used extensively to classify sites according to fire danger. They have been little used to classify areas of the jarrah forest according to the consequences of *P. cinnamomi* infection. In a disease context, hazard as defined by Waters (1986):

is determined by tree, stand, site and climatic factors that influence the probability of tree mortality (and non-lethal injuries) occurring

Risk of introduction is determined by disease proximity and the type of operation planned for an area; e.g., an intermediate hazard site below an infected high hazard site would be considered a high risk.

Rating of hazard is an important part of the sound management of plant communities as it integrates disease matters with management concerns. It harmonizes management options to site type and quantifies the 'whys' and 'why nots' for operations. In a research context, a hazard rating system helps co-ordinate an understanding of host, pathogen and environment interactions and provides a data base to help objectively set research priorities. Implementation of disease management strategies requires the mapping of site hazard ratings and disease distribution. Mapping of disease boundaries is covered in the section on risk. Hazard rating systems have been developed for the northern and the southern jarrah forest.

Hazard Rating in the Northern Jarrah Forest

Earlier attempts at assigning a hazard rating to sites were based on topographic position (Batini 1973; Shea 1975; Havel 1979a). Lowland water gaining sites were rated as high hazard and high risk. Because of their low position in the landscape they were likely to be infected and conditions were favourable for fungal intensification and survival throughout the year. However, disease expression can be low in some lowland areas where conditions favourable for the growth of plants resistant to *P. cinnamomi*, such as bullich and yarri, occur. Although disease expression on upland areas was noted to be variable (Podger 1972), these areas were generally considered as low hazard in comparison with the lowland areas. Landform units were very broad with a range of hazard types occurring within a number of units.

In the course of mapping site-vegetation types, Havel (1975b) observed an association between his site-vegetation types (ch. 3) and disease impact as follows:

- Types found on dissected river valleys and relatively fertile soils, such as U, Q, T and R, were associated with low impact.
- High impact was associated with the moist type C, D, W, and E in shallow valleys and depressions, with a greater number of susceptible species in D and E than C.
- The uplands were divided into T, S, O and P along a fertility and drainage gradient. Sites of type T were the most fertile and better drained sites and were asso-

ciated with low incidence of *P. cinnamomi* (less than half the expected occurrence in the study area). Type P sites with low fertility and poor drainage were associated with high incidence (1.5 times the expected occurrence) and impact of *P. cinnamomi*. The type S was very broad and included low to high hazard.

The association between P sites and high hazard was confirmed by Shearer *et al.* (1987c). Because the broad Havel S type included low to high hazard, site quality alone could not be used to predict hazard and a system based on disease expression needed to be developed.

In the period 1982-84, high mortality of jarrah on infected sites gave the opportunity to develop a hazard system based on disease expression. At this time, an association between site factors, survival, sporulation and dispersal of the pathogen deep within the soil profile and the infection of jarrah was recognized (Shea *et al.* 1983c). There was also an appreciation that disease impact, like site-vegetation types, occurred along gradients within the forest (chs 4 and 5).

Disease expression changes with time after infection due to the various combinations of factors described in Chapter 5. Thus a high hazard site may express intermediate or low impact for a long period depending on the length of time conditions favour disease development. One difficulty in developing a hazard rating system is that disease expression must be used to identify indicators that are to predict disease expression. Thus in order to prevent underestimation of predicted hazard, it is critical that sites surveyed have equilibrated at maximum or 'true' disease expression, as occurred in 1983.

From 1983-1985 sites infected with *P. cinnamomi* were described according to disease expression, landform, geology, soils, vegetation, site history, and stand structure. The disease expression was rated according to the following scale (Fig. 19):

Low - Symptoms only evident in the shrub layer as a few scattered dead individuals. Understorey and overstorey healthy.

Intermediate - Most of the susceptible understorey species, but less than 10 per cent of the overstorey dead. Dead overstorey trees scattered throughout the site and not clumped.

High - Most of the susceptible understorey and more than 10 per cent of the overstorey dead.

It was assumed that disease was fully expressed in most of the sites and this was confirmed in subsequent analysis. Over 400 infected areas in the high and intermediate to low rainfall zones of the northern jarrah forest were surveyed since 1983 and analysed in order to identify the most effective hazard indicators.

Data from the high and intermediate-low rainfall zones were analysed separately because of differences in landform, climate and disease expression between the two areas. Vegetation was found to be a better predictor of hazard than were other site attributes measured. Plant species that changed monotonically from low to high hazard were identified. Statistical ordination techniques were used to derive scores for the plant species so that indicators of similar hazard were close together and those for dissimilar hazard were far apart in a two dimensional 'hazard space'. The presence of indicator species can now be used to assign a hazard rating to uninfected sites.

Hazard Rating in the Southern Jarrah Forest

Initially, hazard was related to soil temperature and moisture conditions favourable for infection (Christensen 1975). Water gaining and clear felled areas were identified as likely high hazard (Christensen 1975). Schuster (1978) observed a relationship between incidence and impact of *P. cinnamomi* with soil type in southern jarrah forest similar to that described for northern jarrah forest. The incidence of infection was least in red earth soil and highest in shallow duplex and gravelly sand lateritic soil. Disease symptoms were expressed in the understorey on all soil types, but the impact on the overstorey was greatest in shallow duplex and lateritic soils and least in red earths. The effect of soil type on disease hazard was related to the combined influence, in addition to soil characteristics, of drainage, canopy density, and topographic position described in previous chapters.

Grant and Blankendaal (1988) have used Strelein site-vegetation types and landform to develop a hazard rating system in the southern jarrah forest. A system using plant species indicators, similar to that described for the northern forest, has yet to be developed for the southern forest. High hazard was associated with southern types P and S and landform units Dwellingup, Trent, Ellis, Mungardup and Caldyanup. These are upland types or landform units associated with lateritic or duplex soils. Low hazard was associated with types T, S and K and the Crowea and Bevan dissected valley landform units with fertile loamy soils. Both high and low hazard were associated with the following landform units: Hester on ridge crests with gravelly-sand over duricrust; the units Collis, Mataband and Keystone with yellow duplex soils; and the Stream unit in minor valleys with swampy floors.

Site Characteristics in Relation to Hazard

Northern Jarrah Forest

The hazard rating system developed for the northern jarrah forest can help identify the major factors that can in-

fluence disease development and expression, either directly or indirectly. Parameters that change significantly with hazard rating can be projected onto the two dimensional hazard space and associations identified. System development is a continuing process and will be improved by the incorporation of new information obtained in this way. Some trends are apparent already and these are described below.

More variables were significantly related to hazard rating in the high rainfall zone than the intermediate-low rainfall zone. Geomorphology, geology, and soil properties were significantly related to hazard in the high rainfall zone. Landform and soil properties were the most important variables related to hazard in the intermediate-low rainfall zone.

Havel site-vegetation types for which more than one site was assessed show a relationship to hazard generally consistent with that observed by Havel (1975b). The high quality type Q was associated with low hazard whereas infertile or poorly drained sites such as P, W and E were associated with high hazard. Broad site-vegetation types such as S were associated with intermediate and high hazard. Sites with gravelly subsoils were associated with high hazard. This would reflect better dispersal of inoculum at depth in high than in low hazard sites.

Levels of fine root infection (ch. 6) are related to hazard. No *P. cinnamomi* was recovered from fine roots of jarrah in three infected intermediate-low hazard sites, but the fungus was recovered from fine roots in 70 per cent of infected high hazard sites.

Southern Jarrah Forest

Soil texture is strongly related to hazard in the southern jarrah forest (Grant and Blankendaal 1988). Nearly three-quarters of high impact sites had sandy soils whereas soil textures in 68 per cent of low impact sites were either loam or clay. The relationship of sandy soils and high hazard is a reflection, not only of the effects of coarse textures favouring dispersal, but also the interactions with low fertility and biomass accumulation described in previous chapters.

Mapping Hazard

Hazard has been mapped for healthy areas in the northern (Fig. 43) and the southern (Fig. 44) jarrah forest. Considerably more mapping needs to be done to estimate accurately the proportion of the uninfected landscape occupied by low, intermediate or high hazard sites. Figures 43 and 44 illustrate differences between areas in partitioning the landscape into hazard ratings. The Myara area has a much greater proportion of the landscape as high hazard than Jones catchment.

The conclusion of Weste and Marks (1987) that:

It is now considered that disease has already destroyed jarrah forests on the worst sites, such as those with perched water tables above concreted laterite, and that graveyard syndromes will not recur.

must be acknowledged to be wrong. The mapping of hazard has shown that uninfected high hazard forest still exists and may occupy a large proportion of the landscape in some areas (e.g. Fig. 43a).

Mapping of hazard allows managers to systematically predict the consequences if *P. cinnamomi* is introduced into a site. The system cannot, however, predict the effects of disturbance on hazard or how quickly hazard will be expressed after introduction of *P. cinnamomi* into a site.

ASSESSMENT OF RISK

Once an area has been mapped for disease hazard, the risk of introduction and spread of *P. cinnamomi* can be assessed from maps of distribution of disease and the type of operation planned for an area. Considerable resources have been invested by the Department of Conservation and Land Management in the accurate determination of disease distribution to enable risk to be fully assessed when managing the forest.

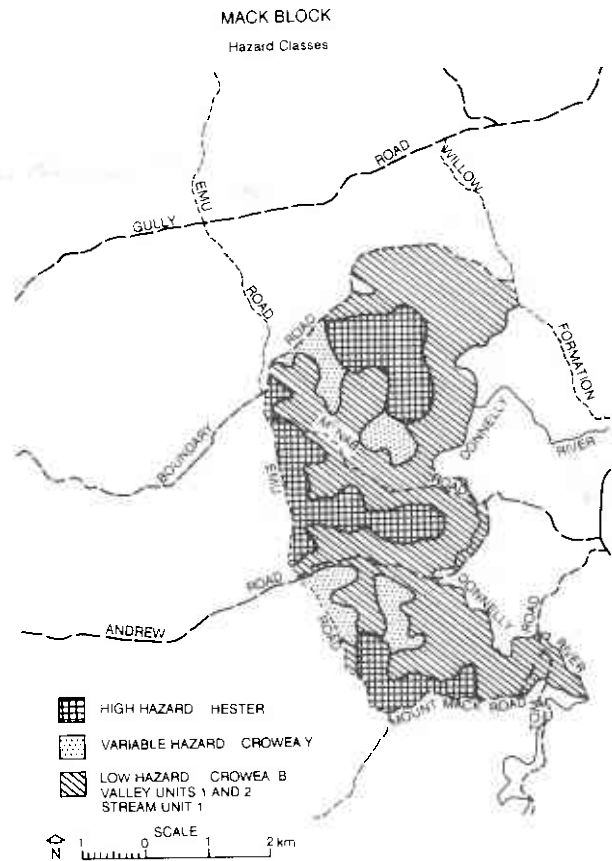
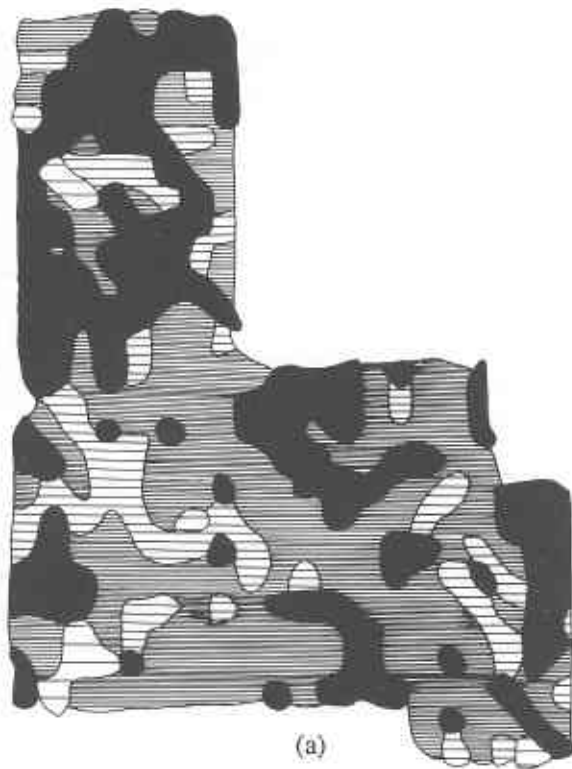


Figure 44

A map of *Phytophthora cinnamomi* hazard in Mack block in the southern jarrah forest (Grant and Blankendaal 1988).

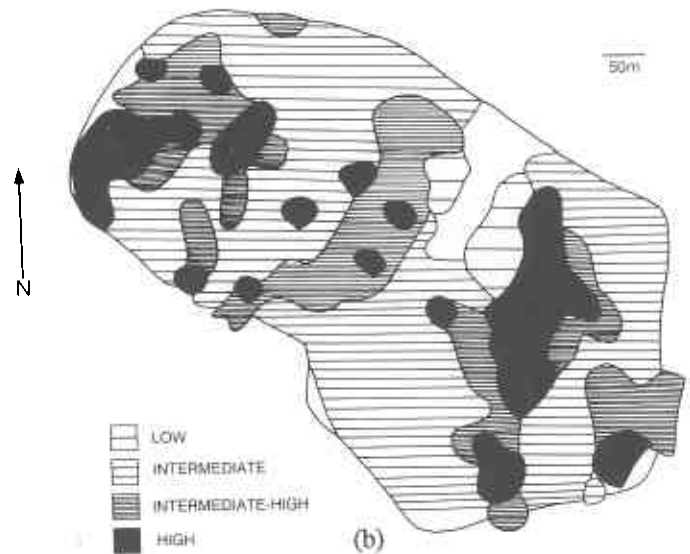


Figure 43

Mapping *Phytophthora cinnamomi* hazard in uninfected areas of (a) Myara block and (b) Jones catchment in the northern jarrah forest.

Mapping Disease Distribution

In the mid 1960s disease distribution was mapped from black and white aerial photographs (Batini 1973). Diseased areas were recognized by a reduction in forest density caused by death of susceptible species and boundaries were determined. The accuracy of the maps varied from area to area depending on the original forest density and the scale and quality of the aerial photographs.

By the late 1970s the accuracy of detecting and mapping disease distribution was greatly increased by the development of 70 mm shadowless colour aerial photography (Bradshaw and Chandler 1978). Muir (1984) has given a detailed description of the methods of photography and mapping. Disease boundaries could be accurately plotted onto 1:25 000 maps following identification of dead indicator species from the film, field checking and sampling and recovery of *P. cinnamomi* in the laboratory from sampled soil and plant material. A number of susceptible indicator species were used and the patterns of death could aid in the interpretation of the presence or absence of the pathogen (Brandis 1983). Recently, mapping has been facilitated by the use of 230 mm colour shadowless aerial photographs.

Three types of map are produced: disease free area, present impact, and a hygiene map. Maps of disease free area and impact (Fig. 41) are generally not used directly by operations staff, but document the distribution and impact of *P. cinnamomi* at the time of photography. The hygiene map, drawn from the disease free map, shows disease free and uninterpretable forest, likely infected access roads and an interpretation of likely risk of disease spread, and is used to plan operations. Disease hazard maps will be prepared when the research is sufficiently advanced.

COMBINING HAZARD AND RISK

Once the hazard and disease distribution have been mapped the risk of infection and spread can be combined with hazard to determine the consequences of an operation. Figure 45 illustrates one way of representing various combinations of risk and hazard. The cumulative experience of managers and researchers will need to be combined in the development of a set of rules that will incorporate hazard and risk in a logical way. These rules need to be continually refined with experience once hazard assessment has been put into practise and as knowledge of the factors affecting disease expression increases.

There is a better idea of the consequences of introduction of *P. cinnamomi* for extreme cases such as low and high hazard than for intermediate cases. The consequences of disease compounds rapidly for high hazard sites once there is more than a very low risk of introduc-

tion of the pathogen. For low hazard sites the consequences of disease are much less and they compound at a slower rate than for high hazard. It is more difficult to predict the consequences for intermediate than for low or high hazard sites.

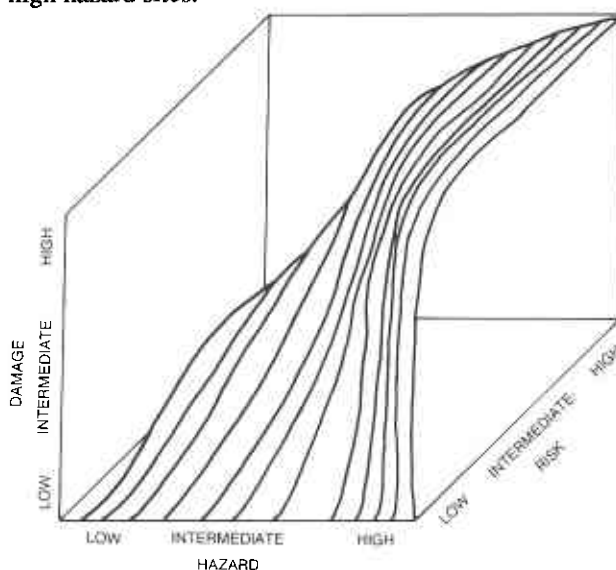


Figure 45

Combining *Phytophthora cinnamomi* hazard with risk. The surface shows the relationships between combinations of hazard and risk to the possible damage should *P. cinnamomi* be introduced into an area.

In the present systems, hazard is related to jarrah mortality and does not take into consideration deleterious effects of infection on crown vigour and growth rate of jarrah and decrease in conservation values (chs 6 and 8). Improvements in the estimation of the risk of infection can partly correct these present deficiencies in the hazard systems. However, a better estimation of risk than is presently possible requires more information on how the fungus survives and is dispersed within soil profiles.

HYGIENIC PROCEDURES

Quarantine and hygiene are aimed at preventing new infections by excluding the pathogen from an area. This will be effective if:

- The pathogen is not endemic. Evidence compiled by Podger (1972) indicates that *P. cinnamomi* was introduced into Western Australia and its spread is related to human activity.
- The distribution of the pathogen is known.
- Access can be thoroughly controlled in restricted areas.
- Operations that have high risk of spreading the disease are controlled.

Quarantine

In the mid-1970s, northern jarrah forest with little disease in environmentally sensitive salt prone areas was quarantined. In 1986, 'quarantined' forest was renamed 'disease risk area', this being the term used in the legislation.

Vehicle access was controlled by closing roads and restricting entry during periods of the year when there was a high likelihood of infected soil being picked up by machinery and when conditions would be favourable for survival and infection (ch. 5). Quarantine, by controlling people, has been an important factor in restricting the main agent of dispersal and hence the establishment of new infections in a large area of forest.

By allowing existing infections to express themselves and by reducing the establishment of new ones, quarantine aids the accurate mapping of disease distribution. It was hoped that disease distribution in all the land quarantined could be mapped from aerial photographs. This has not yet been achieved because the time required to complete the mapping was underestimated and because of the need to map areas outside of quarantine for hygienic operations.

Hygiene

Even though the term hygiene has been used more in a human rather than a plant health context, the principles are much the same. Hygiene is the application of systems or methods aimed at the preservation of health; in this case the aim is to preserve the health of native vegetation. Hygienic procedures deliberately designed to minimize the spread of *P. cinnamomi* and prevent its introduction into healthy areas have been applied to all operations in the forest, in particular fire control, road construction and maintenance, and logging. A 'belt and braces' principle (Underwood and Murch 1984) is incorporated within the hygienic procedures to minimize the consequences of accidental failure of any one element in the system.

The system has three main components:

1. Planning

Disease distribution, vegetation and topography are mapped before any activity takes place. As already described, accurate determination of disease hazard, distribution and risk is critical to the application of hygiene methods.

A series of procedures have been developed to decide whether operations may proceed and to determine the best hygiene methods to use. In 1982 the '7 way test' was introduced to determine whether an operation satisfied criteria in relation to likely introduction and spread, the vulnerability of plant communities and the likely

consequences of infection (Forests Department of Western Australia 1982). If these criteria are satisfied, options can be further checked and refined using 'hygiene failure tests' illustrated in Figure 46 (Underwood and Murch 1984) and disease hazard and risk maps.

HYGIENE - FAILURE TEST

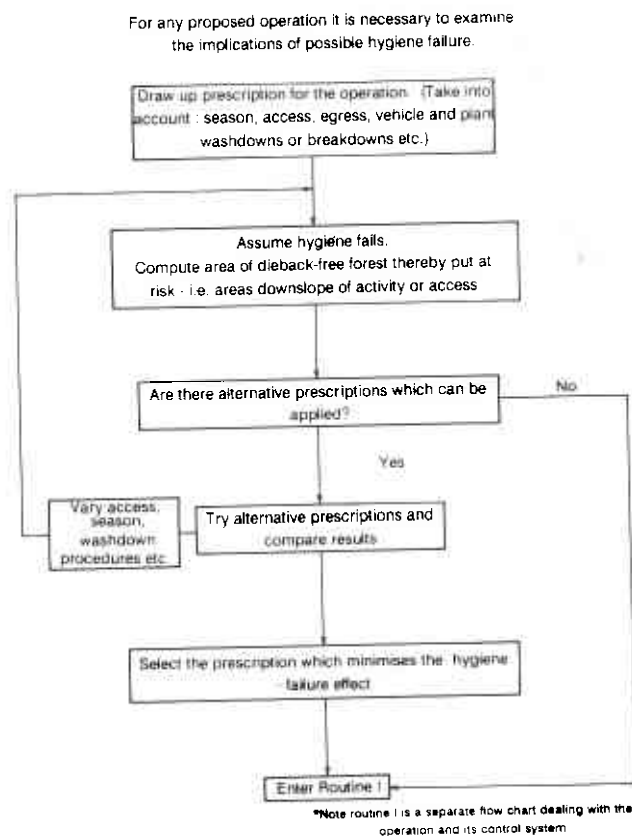


Figure 46

Hygiene failure test (Underwood and Murch 1984).

2. Exclusion methods.

● Roading

Main access roads have a high chance of being infected because they are frequently used and were probably 'open' roads with uncontrolled access by the public prior to the operation. These roads need to be isolated from the rest of an operation using washdown points and controlled access. The area of forest placed at risk of infection from newly constructed access roads is minimized by restricting roads to lower parts of the landscape. Attention must also be given to the construction of a firm road surface and diversion of drainage directly into creek systems to prevent discharge of water into forest downslope of the road.

- Washing down

Vehicle cleaning points are used to minimize dispersal of the pathogen by removing soil clinging to vehicles or machinery.

- Separation of operations

In a logging operation, snigging is separated from hauling to prevent spread of infection from roads to landings and thus into the coupe. Coupes are confined to internally draining micro-catchments to prevent spread throughout the operational area.

- Confining activities to periods of least risk

Log stockpiling during dry periods reduces the need for activity in the forest during wet periods when conditions are favourable for spread and survival.

- Access control

Strategic road closure and supervision of access during wet periods reduces activity when conditions are favourable for spread and survival of the fungus.

3. Training.

The success of hygiene methods is very dependent on the 'human element' and thus on proper training of personnel. Failures are less likely to occur if operators are aware of the biology of the fungus and the reasons for the methods used. This in turn engenders an increased public awareness of the factors affecting disease development and the likely consequences of further spread.

Application to Mining and Nurseries

The integration of the hygiene procedures described above for forest operations is also being applied to other activities such as mining, nursery care, recreation and the management of national parks. The hygienic procedures used in mine planning and operations have been adapted from forest operations, but take account of the different operational procedures specific to mining.

Hygiene is very important in nurseries because they provide the seedlings for replanting degraded areas of the jarrah forest. As conditions within nurseries are favourable for pathogen development, nursery hygiene is a necessary prerequisite for the production of *Phytophthora*-free plants. Introduction of the pathogen is prevented by controlling entry of vehicles, plants, materials and people. Incoming materials such as water, soil and equipment are sterilized before entry. Spread within nurseries can be minimized by early detection through monitoring plant health and soil testing, the use of raised, free-draining

benches and by frequent washing of pathways and utensils with disinfectants. Comparison of available disinfectants has shown that quaternary ammonium compounds were more effective against *P. cinnamomi* than the previously used chemicals (Noske and Shearer 1985).

DISFAVOURING THE PATHOGEN

Hygienic procedures delay possible introduction of a pathogen and therefore must be integrated with methods aimed at reducing the rate of disease development. Whereas hygienic procedures have been used extensively, methods to manipulate the environment to disfavour development of *P. cinnamomi* are still being developed and tested and have not yet been widely applied. Manipulation of understorey composition, stimulation of an antagonistic microflora, modification of drainage, the use of chemicals and resistant species and manipulation of conditions to enhance host resistance are the main ways pathogen development can be reduced.

Manipulation of Understorey Composition

Changing the composition of the understorey influences disease development by removing susceptible tissue and by creating an unfavourable physical, chemical and biological environment. Details have been presented in Chapter 5.

Banksia grandis is a major component of the understorey in the high rainfall zone of the jarrah forest. Increased densities of *B. grandis* have been attributed to opening up of the forest by logging together with repeated cool fires (Underwood and Christensen 1981). Reduction and maintenance of the *B. grandis* to a low density, possibly represents the understorey composition in forest of the past.

Reduction of *B. grandis* inhibits pathogen development by reducing potential sources of inoculum and susceptible tissue within which *P. cinnamomi* can survive dry summers. Changes in composition of the understorey can significantly change the soil environment and thus have a greater effect on disease development than simple removal of susceptible tissue (ch. 5). Manipulation of the understorey to protect production values cannot be undertaken in all areas, especially vulnerable communities with high conservation values.

Banksia grandis reduction can be accomplished manually by stump poisoning or by fire. Manual reduction of *B. grandis* is used in the FIRS (Forest Improvement and Rehabilitation Scheme) treatment of forested areas adjacent to areas being mined for bauxite. Burning can result in the substitution of the *B. grandis* dominated understorey by one dominated by *Acacia* species.

Using fire to manipulate understorey composition offers a management strategy to reduce disease development over large areas, but its application has not been as straightforward as initially hoped. More information is needed on the application of fire, *Acacia* ecology and follow-up methods of *B. grandis* suppression as follows.

Application of Fire

The fire must be of sufficient intensity to kill or suppress *B. grandis* and to break a heat-requiring dormancy factor in *Acacia* seed that has been buried at depth in the soil by ants (Shea *et al.* 1979). Experimental moderate intensity (600-1500 kW/m) burns under dry fuel conditions have met these requirements, but for a number of reasons, insufficient work has been done to allow the use of this technique on a wide scale. Weather conditions required to achieve these burns occur infrequently. Fires of the intensity needed to achieve significant reduction in the abundance of *B. grandis* over large areas are dangerous and difficult to control and further technical development is required (Burrows 1985). In addition, fires of this intensity can cause serious scarring and wood defects in jarrah and other *Eucalyptus* species (Burrows 1987).

Acacia Ecology

The *Acacia* species have different site preferences; for example, analysis of the survey data used to develop the northern forest hazard rating system showed that *A. pulchella* preferred fertile loamy sites. Thus after a burn the composition of the *Acacia* understorey can vary from area to area and the distribution within an area can be very patchy (McCaw 1988). Research to date has shown that an understorey dominated by *A. pulchella* can suppress activity of *P. cinnamomi*. Whether other legume species will suppress development of *P. cinnamomi* to the same extent still needs to be determined.

Sustained Suppression of *Banksia grandis*

The fire intensity recommended for suppression of *B. grandis* may not kill all stems (Burrows 1985) and it stimulates the release and germination of banksia seeds. Follow-up treatments are therefore needed, but have yet to be put into practice. Shea *et al.* (1980) simulated the effects of fire intensity and frequency on the population dynamics of *B. grandis*, but this research has not been applied to the development of follow-up prescriptions to maintain low banksia densities.

Stimulation of an Antagonistic Microflora

Microbial antagonism to *P. cinnamomi* involves a wide range of microflora and under certain conditions has an important role in the suppression of the pathogen in the soil and on the root surface (Malajczuk 1983). The

suppressive nature of the red loams of the jarrah forest can, in part, be attributed to the presence of higher levels of antagonistic microflora than in other soil types of the jarrah forest (Malajczuk 1979). The effect of manipulating the floristic composition of the understorey on the development of *P. cinnamomi* is partly due to stimulation of antagonistic microflora (ch. 5). Use of controlled introduction of selected antagonists would probably not be practical on a widescale basis, but could be used as part of the rehabilitation of degraded areas.

The populations of antagonistic microflora in soils can be influenced by fire. As previously described, fire can be used to manipulate the composition of the understorey to favour microbial populations antagonistic to *P. cinnamomi*. Fire can also influence microbial and ectomycorrhizal populations by destroying the litter layer (Malajczuk and Hingston 1981). The contention that regular burning favours *P. cinnamomi* by destroying the litter layer (Malajczuk 1983) has not been proven, but illustrates how management strategies for the jarrah forest must take into consideration all likely ramifications of an action.

Two factors very much constrain the potential for manipulating antagonistic microflora as a management tool for forested areas. Firstly, most of the microbial activity occurs in the organically rich surface soil. *Phytophthora cinnamomi* can escape this by exploiting niches at depth within the soil profile (ch. 5). Manipulation of the environment of surface soil to favour antagonists and disfavour the pathogen is difficult enough, but is likely to be impossible at depth within the soil profile. Changes in microbial populations with depth needs to be determined for the soils of the jarrah forest.

Secondly, when conditions are favourable for *P. cinnamomi* sporulation and survival the pathogen can quickly produce large numbers of infectious spores. Thus antagonists must already be at high levels or rapidly increase to high levels during these periods. Chapter 5 has already described how susceptible new roots may outgrow the protective ectomycorrhizal sheath, during periods when warm moist conditions favour sporulation, root growth and infection. A better understanding of the population dynamics of antagonists is required before manipulation of microflora can be used as a management tool.

Manipulation of Drainage

The life cycle of *P. cinnamomi* is intimately associated with moisture. Making a site drier inhibits sporulation and dispersal in the soil profile and growth in the host. The opposite occurs if the site becomes wetter (ch. 5).

Drainage from roads associated with mining and logging can affect the hydrology of forest downslope. Bren

and Leitch (1984) found that a forest road markedly influenced both stormflow and peak flow in a small catchment. The obvious intensification of dieback observed downslope of roads has been attributed to enhanced overland flow; the influence of roading on ponding and near-surface seepage of water has yet to be quantified. Factors such as position of the road in the landscape and drainage have been described in the section on hygiene.

Attention to drainage is a very important factor in the management of forested areas adjacent to bauxite mining. Near-surface seepage of water can result in intensification of disease in forested areas downslope of haul roads and bauxite mined pits. The use of well constructed sumps and the positioning of these sumps low in the landscape are being used to minimise any adverse impact of near-surface seepage. Decreasing the time period when water ponds in sumps above the forest by changes to mining schedules should also reduce the opportunity for near-surface seepage.

Depth of bauxite is directly related to the saturated hydraulic conductivity of the pallid zone (Croton and Tierney 1985) and can be used to predict potential near-surface seepage of water from a pit. Pits derived from areas with shallow bauxite layers favour near-surface seepage of water more than pits in areas with deep bauxite layers. Recent advances in rehabilitation design enable this information to be used to design appropriate drainage control procedures to restrict seepage into adjacent forest. Discharge systems are available to drain pits directly into natural water courses while improved landscape design ensures that water does not pond above impeding horizons in adjacent forest. A greater understanding of the influence of mining on hydrological processes in forest adjacent to pits will aid in the modification of the hazard rating system to take into account the effects of disturbance.

Deep percolation of water may be favoured by disrupting impeding layers that facilitate dispersal of *P. cinnamomi* in lateral near-surface flows of water in some forested areas. An indurated duricrust in a high impact area was blasted in an attempt to create an environment that was unfavourable for *P. cinnamomi* development (Bartle, in Throssell 1984). Better drainage as a result of duricrust shattering resulted in unsaturated conditions in the overburden of upslope positions, but an extension of a wedge of saturated soil in lower slope positions (Throssell 1984). Survival of jarrah planted onto the shattered and adjacent non-shattered control is being monitored. Manipulation of drainage using methods similar to this may be appropriate for areas affected by mining, but because of the amount of disturbance involved and the cost, would not be an appropriate management option for forested areas.

Chemical Control

Chemicals have been used mainly in the nursery environment to control development of *P. cinnamomi*. Fungicides fall into three classes: disinfectants, fumigants, and systemics. Disinfectants such as sodium hypochlorite, phenol based compounds, quaternary ammonium compounds, and copper sulphate can be used to eradicate inoculum from surfaces. They are extensively used to sterilize walkways and utensils in nurseries. Sodium hypochlorite is very useful for sterilizing water as, once mixed, the compound is not stable and quickly dissipates. It is used extensively to sterilize water used for irrigation, in fire fighting units, and washing down of vehicles. Most of the disinfectants are toxic to plants and cannot be used to control *Phytophthora* infection on vegetation.

Similarly, fumigants such as methyl bromide and formaldehyde, while eradicating *P. cinnamomi*, also kill vegetation. They are best used in extreme situations where total sterilization of an area is needed. Fumigants are very toxic to humans and difficult to use. Furthermore, they are nonselective and kill all organisms within the sterilized soil, including antagonistic microflora. Thus, should a *Phytophthora* species re-establish in fumigated soil, its development is often rapid due to little competition from antagonistic organisms. Use of fumigants in eradicating *P. cinnamomi* from soil needs further testing under field conditions. Hill and Tippett (1989) are evaluating fumigants in an attempt to control spot infections.

Recently a number of systemic fungicides have been found which can inhibit but not eradicate *Phytophthora* species in soil and plant tissue (Cohen and Coffey 1986). Systemic fungicides have the advantage of being translocated within a plant following absorption. Of the four main classes of systemic fungicides, metalaxyl (*N*-[2,6-dimethylphenyl]-*N*-[methoxyacetyl]-alanine methyl ester) has been used in nurseries and recently neutralized phosphorous acid (H_3PO_3) has been evaluated in the forest. Metalaxyl has a number of disadvantages, namely cost, toxicity to native plants and relatively poor mobility within the plant. In comparison neutralized phosphorous acid is cheap, has low toxicity to plants and animals and is very mobile within the plant. Recent trials where neutralized phosphorous acid was injected into *B. grandis* to control *P. cinnamomi* infection gave very encouraging results (Fig. 47¹⁰). While growth of *P. cinnamomi* lesions was inhibited in *B. grandis* injected with neutralized phosphorous acid the fungus could still be isolated from the fronts of lesions after 6 weeks. Research to determine the effect of neutralized phosphorous acid on survival of *P. cinnamomi* in infected tissue and to evaluate the use of the chemical to control localized infections, especially in areas of high conservation values, is continuing.

¹⁰Shearer, B.L. and Fairman, R.G. (1989), Unpublished data, File 77/86, Dwellingup Research Centre.

Although neutralized phosphorous acid gives, for the first time, the possibility of using a fungicide to control disease without destroying the vegetation, the chemical cannot be used indiscriminately. Frequent use may lead to the selection of strains of *P. cinnamomi* with resistance to the chemical (Cohen and Coffey 1986). In addition, not all *Phytophthora* species are equally affected by the chemical. *Phytophthora megasperma* is relatively insensitive to phosphorous acid (Dercks and Buchenauer 1987) and may be given a competitive advantage over other *Phytophthora* species in treated areas. As there are no 'backup' chemicals available, it would be irresponsible if indiscriminate application shortened the period during which phosphorous acid could be used to control *P. cinnamomi* development.

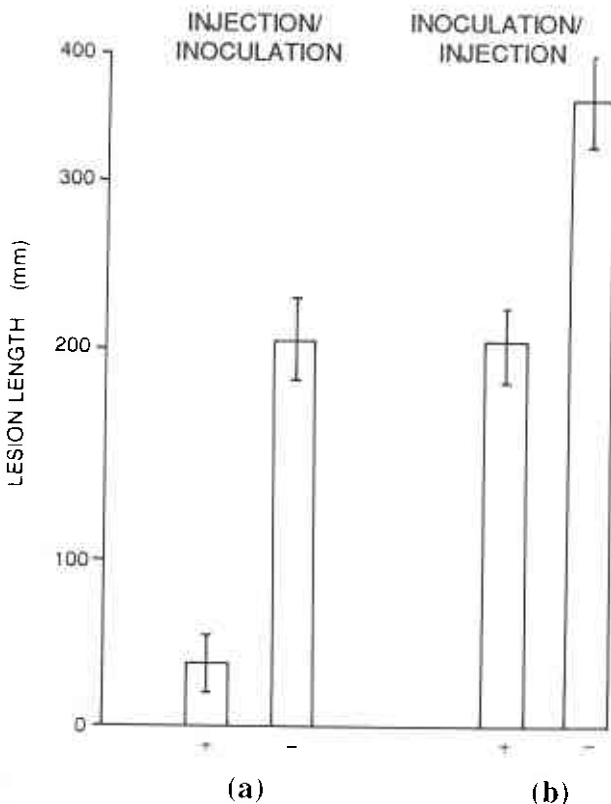


Figure 47

Lengths of lesions of *Phytophthora cinnamomi* (\pm standard error of the mean) in roots of *Banksia grandis* trees inoculated with the fungus and injected with neutralized phosphorous acid in the trunk (a) 3 weeks before and (b) 3 weeks after inoculation (+), compared with trees not injected with the chemical (-). Lesion lengths were recorded (a) 3 weeks and (b) 6 weeks after inoculation.

Use of Resistant Species

Variation in resistance to *P. cinnamomi* infection exists within the genus *Eucalyptus* (chs 4 and 5) and this has been exploited in the choice of species to rehabilitate mined and diseased areas. Because some of the introduced resistant species have failed in the northern jarrah forest, adaptation to the harsh, infertile environment of

the northern jarrah forest must be considered in addition to resistance to *P. cinnamomi*. Susceptibility to pathogens other than *P. cinnamomi* must also be considered. For example, a number of *Eucalyptus* species resistant to *P. cinnamomi* (e.g. *E. wandoo*) are very susceptible to *Armillaria luteobubalina* infection (Shearer and Tippet 1988). This is a very important factor in the selection of species for rehabilitating areas in the intermediate and low rainfall zones where impact of *Armillaria luteobubalina* is greatest.

Variation in resistance to *P. cinnamomi* infection within a species can also be exploited. Tree breeders must take considerable care in the selection of lines for propagation. Many characteristics and potential problems likely to confront the selection must be considered. Many questions must arise as to what are desirable traits. Obviously as wide a mixture of genotypes as possible should be chosen.

Lines of *Pinus radiata* showing high levels of resistance to *P. cinnamomi* have been identified and selected for use in the pine planting program (Butcher *et al.* 1984). Variation in resistance to *P. cinnamomi* infection exists within *E. marginata* and lines are being developed using tissue culture (ch. 5). Jarrah with a high level of resistance to the pathogen should be selected to maximise the proportion of selections that survive under the most adverse conditions. It is encouraging that several breeding lines selected by Stukely¹¹ (1989, personal communication) appear to express a high degree of resistance to the fungus. This research has the potential for providing selected jarrah lines for use in rehabilitation strategies.

ENHANCING HOST RESISTANCE

The manipulation of stand structure, understorey composition, soil nutrient status, and drainage may result in changes which affect resistance of jarrah to *P. cinnamomi*. Resistance is the effective response of jarrah to the fungus. Quantifying the effects of silvicultural treatments on the ability of jarrah to resist *P. cinnamomi* still proves difficult (ch. 5). A variety of resistance mechanisms may be activated at different stages of interaction of jarrah with *P. cinnamomi*, but as yet methods of enhancing the resistance of jarrah by the manipulation of site conditions are not available.

Nutrition

No guidelines can be given on fertilizing practices that may enhance resistance of jarrah to *P. cinnamomi*. Mineral nutrition can affect resistance of plants to fungal pathogens (Foster 1968), but contradictory information is available as to whether fertilizing practice can be used as

¹¹Stukely, M. Department of Conservation and Land Management, Como Research Centre.

a management tool to enhance the resistance to *P. cinnamomi*. Littleleaf disease of short leaf and loblolly pines caused by *P. cinnamomi* could be alleviated by the application of nitrogen fertilizer (Campbell and Copeland 1954). However, Hingston (1984) could find no conclusive effect of NPK fertilizer on the response of jarrah to *P. cinnamomi* and Marks *et al.* (1973) found the application of NPK fertilizer resulted in an increased amount of root damage to susceptible species in an infected area in East Gippsland.

Predisposition

The effects of different silvicultural treatments on jarrah's resistance is not known. Changes that will affect trees on different types of sites can not be predicted. More information is needed to understand how changes in stand structure and disturbance affect disease expression.

Predisposition is 'an internal degree of susceptibility resulting from external causes' (Yarwood 1959). Salinity stress predisposes ornamental plants to *Phytophthora* root rot (Duniway 1983). Whether salinity may also predispose jarrah to attack by pathogens and hasten decline needs to be determined.

Seedlings are commonly predisposed to infection by pythiaceous fungi if drainage is poor (Duniway 1983) and the same may be true for mature trees. Jarrah seedlings are sensitive to waterlogging (Brown 1977; Davison and Tay 1987). Under waterlogged conditions the ability of jarrah to resist *P. cinnamomi* may be impaired and waterlogging may predispose jarrah to infection. In contrast, water stress in jarrah can inhibit growth of *P. cinnamomi* (Tippett *et al.* 1987). Forest areas must be managed to

minimize predisposition from moisture accumulation within an area by encouraging thick overstorey or understorey canopies and by attention to drainage from roads and bauxite pits already described.

OPTIONS FOR THE FUTURE

This chapter has described the use of control strategies to restrict the spread of *P. cinnamomi* or delay and reduce the rate of disease development should the fungus infect an area. Significant progress has been made in implementing a number of hygiene procedures to prevent or delay the spread of *P. cinnamomi*. *Phytophthora cinnamomi* hazard can now be mapped for the jarrah forest, but future use will require knowledge of the effect of disturbance on disease hazard. Estimation of risk of infection by *P. cinnamomi* can be improved from a greater understanding of the factors affecting survival, sporulation and dispersal of the pathogen.

In the future, emphasis must be given to implementing control methods to reduce the rate of disease development and their integration with hygiene methods. Development of methods to control 'spot infections' must be a high priority and some progress has been made in this regard. Further ecological research is needed before fire can be used to reduce the density of susceptible hosts and encourage resistant plant species. Selections of resistant jarrah need to be increased and used to rehabilitate degraded areas of the jarrah forest. Ways of enhancing the resistance of jarrah to *P. cinnamomi* must be sought and practices predisposing jarrah to disease recognized. The next chapter discusses the most important questions research must address in order to answer these needs.

Research Priorities

The aim and character of dieback research is described. Past achievements lead to present priorities. Research up to the 1980s concentrated on the biology of the pathogen rather than the host. A balance of research emphasis between pathogen and host has been achieved since the early 1980s and priority areas for on-going research are described. Application of research results to maintaining healthy forest must be of high priority.

INTRODUCTION

The aim of dieback research in the Department of Conservation and Land Management is to predict the occurrence and development of *P. cinnamomi* under different site, climatic, and management conditions and develop methods of control. Managers of native plant communities need to predict the consequences of changes in the environment resulting from mining, logging, fire, recreation pressure, insect pests and climate on levels of disease.

The outcome of disease is determined by the interaction of many factors. As noted by Shea *et al.* (1984)

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.

Forest pathology is a complex research area in which to work. Extremes of scale must be contended with, from jarrah trees over 30 m tall that can live for centuries with years between reproductive cycles to *P. cinnamomi* inhabiting microscopic soil pores and intercellular spaces with a life span of weeks to months and a reproductive cycle of hours to days. In addition, the forest occupies a large area which includes a great diversity of microclimates affecting the host and pathogen. Large trees are difficult to work with and the soils on which they grow often have an indurated duricrust that resists penetration. The techniques needed for inoculation, excavation and assessment are therefore labour intensive and expensive. Because trees are long lived, factors affecting disease expression and controls cannot be adequately tested within a few years.

Extrapolation beyond the range of observed conditions must be on the basis of scientifically valid generalisations. This is an initial research priority, but as basic knowledge accumulates, greater priority must be given to applying the results of research to the forest.

PAST RESEARCH

There have been four broad areas of highest priority in past research: monitoring disease behaviour in relation to

environment, pathogen development in the soil, host interactions, and prediction of hazard.

Initially, greatest emphasis was given to monitoring soil temperature and moisture to identify sites and seasons when conditions were most favourable for survival and sporulation of the pathogen and infection (e.g. Christensen 1975; Shea 1975). Symptoms were used mainly to monitor changes of the pathogen with time (e.g. Shea and Dillon 1980).

With improvements in selective agars and baiting techniques, the emphasis shifted to quantifying the effects of season, site and modification of the environment through manipulation of understorey composition on population levels of *P. cinnamomi* in the soil (e.g. Shea *et al.* 1978; Shea *et al.* 1980; Shearer and Shea 1987).

In 1982, *P. cinnamomi* was found at depth within the profile, often just above a horizon that impeded vertical percolation of water in upland areas (Shea *et al.* 1983c). Emphasis was therefore given to determining the effects of soil profile characteristics on subsurface lateral movement of water, and behaviour of *P. cinnamomi* at depth in the soil (Kinal 1986). For the first time, disease behaviour in upland areas could be related to site characteristics that influenced pathogen sporulation, survival and dispersal, and the infection of jarrah. The determination of key site indicators that could be used to predict disease hazard was a high priority (Shearer *et al.* 1987c).

Research up to the 1980s concentrated on the behaviour and biology of *P. cinnamomi* with little attention being given to the physiology, growth and performance of jarrah, particularly in the presence of the fungus. In the past, conditions that favoured sporulation of the fungus in the soil and infection were often confused with those that affected symptom expression. In the first investigation of *P. cinnamomi*, Rands (1922) described invasion of woody tissue, but the relevance of this observation for *Eucalyptus* species was not appreciated until the early 1980s (Dell and Wallace 1981; Marks *et al.* 1981; Shearer *et al.* 1981). Recognition that *P. cinnamomi* could invade the woody tissue of jarrah led to greater emphasis on the interactions between host and pathogen. Lesion development and

resistance mechanisms in jarrah roots were described (Tippett *et al.* 1983, 1985; Tippett and Hill 1984) and the importance of host water status on the host pathogen interaction identified (Tippett *et al.* 1987). This work led to studies on the relationships between the ecophysiology of jarrah and infection (Crombie *et al.* 1987, 1988).

As already illustrated in previous chapters, most of the priority areas of research include factors that can be manipulated to control *P. cinnamomi*. Sufficient information is now available to recognize five areas for ongoing research (Table 8). Many areas will overlap as they include factors that have multiple effects.

ONGOING RESEARCH

Changes in Microclimate

Microclimate, the climate near and below the ground, greatly affects the rate of pathogen development and the fate of individual trees after infection (chs 5 and 6). The water status and temperature of soil and host tissue greatly influence the life cycle of *P. cinnamomi* from survival, sporulation and infection through to invasion (Fig. 20). The amount of winter rainfall influences dispersal by subsurface flow of water (Kinal 1986). Warm wet summers favour not only fungal growth but also the survival of affected trees.

The period of below average rainfall experienced since 1975 (Fig. 7) has directly influenced the relationships between moisture status of soil and host tissue and survival, growth and sporulation of *P. cinnamomi* (ch. 5). Extended periods of below average rainfall slow down the rate of disease development and personal observations over the last decade are an unreliable basis on which to predict the likely rate at which disease changes under different situations. The difficulties associated with attempts to determine past rates of disease extension have already been described in Chapter 6. Questions pertaining to future disease development can only be answered confidently by quantifying the relationships between climatic events, site and vegetation water status, water movement within a site, pathogen development and host susceptibility. Long term predictions can then be based on sensitivity analysis to determine how changes in rainfall distribution between years and seasons affect the intensification of disease.

Disease Management

Considerable progress has been made over the last decade in the development of integrated management procedures to minimise the spread and the rate of development of *P. cinnamomi* in the jarrah forest. Hygiene prescriptions will need to incorporate methods that reduce the rate of disease development such as chemical control and modification of understorey composition. Hazard and risk

Table 8

Research priority areas and questions.

Changes in Microclimate

Improve prediction of the effect of changes in microclimate on disease:

1. Determine the relationships between climatic events and the processes affecting disease development and expression;
2. Evaluate the climatic record in relation to disease expression;

Disease Management

To apply disease hazard and risk systems, specifically:

1. Incorporate the effects of disturbance on hazard;
2. Determine the relationships between the ecophysiology of jarrah forest vegetation and hazard;
3. Improve predictions of risk of introduction from quantification of modes of dispersal within the soil profile.
4. Use simple mathematics to describe disease development as an aid to predict the risk of infection and how quickly hazard will be expressed.

To assess, develop and apply methods of control to minimise new infections and reduce the rate of disease development:

1. Test efficacy of chemical control;
2. Understorey modification;
4. Rehabilitation strategies;
5. Selection of jarrah resistant to *P. cinnamomi*.

Risk of Infection

To understand the infection process, mainly:

1. The ability of a soil to stimulate sporulation;
2. The ability of *P. cinnamomi* to sporulate on roots of different hosts;
3. Survival of *P. cinnamomi* in soils of the jarrah forest;
4. Dispersal of inoculum at depth in near-surface seepage of water;
5. Relationships between inoculum levels and disease;
6. How roots of jarrah become infected;
7. Relationships between the physiological status of the host, infection and pathogen development.

Damage from Infection

To assess disease severity and conservation and economic losses:

1. Assess the rate of symptom expression;
2. Quantify understorey susceptibility to infection;
3. Determine growth and regeneration of jarrah surviving in infected sites;
4. Determine the effects of *P. cinnamomi* infection on conservation values.

Regional Differences

Apply methods and knowledge obtained for the high rainfall zone of the northern jarrah forest to other regions:

1. Develop disease risk scenarios to incorporate differences between the intermediate and low rainfall zones and the high rainfall zone;
2. Test whether information can be extrapolated between forest regions;
3. Compare the major processes affecting disease development in shrublands, woodlands and forests.

systems have been developed to aid management decisions in relation to the need, scheduling and timing of management operations. Hazard and risk system development will be an ongoing process and modifications made as a result of experience.

The hazard rating systems can predict the likely disease outcome only for undisturbed areas. The amount of disturbance varies with the size and nature of the operation affecting stand structure and the chemical and physical environment (Waring 1985). Canopy removal extends the periods when temperature and moisture are favourable for survival and sporulation of *P. cinnamomi* and infection (Christensen 1975; Shea 1975, 1979a). Monitoring the effects of these factors on disease development will aid in improvement of the hazard rating system to allow for the consequences of different intensities of management under a range of conditions. An understanding of major factors affecting hazard will help in updating the hazard rating system when management strategies are changed or are applied repeatedly over time.

Host studies showed that site factors could affect the susceptibility of jarrah to invasion by *P. cinnamomi* (Tippett *et al.* 1987). The susceptibility of jarrah and other plant species on sites of different hazard ratings needs to be assessed. On some sites disease development may be more dependent on the influence of site conditions on the pathogen than on the influence of the host (ch. 5). However, on intermediate hazard sites a number of unanswered questions remain and are described in the following section on damage. Monitoring the physiological status of host plants on different sites under different conditions can help in the understanding of why, when and for how long some plant species are vulnerable to infection and invasion.

Data gathered from monitoring the water status of a range of plants with different rooting depths, at different sites, can also help to explain the drainage characteristics of different sites. Vegetation can be monitored to help explain how different soil profiles respond to rainfall. The plants that grow on a particular site can be used as indicators of the physical environment of the soil.

Once the major factors affecting hazard have been identified, the information on pathogen development and host susceptibility can be applied through simple mathematics to test 'what if' scenarios in relation to management options. Development of a water movement-dispersal and a survival-sporulation model is continuing. Greatest emphasis must be placed on developing and verifying models to help test assumptions and give indications of probable rates of change of disease development under a range of conditions.

Estimation of risk requires accurate predictions of survival, sporulation and the likely spread of *P. cinnamomi* from sources of infection. Hazard does not include estimates on how quickly disease will be expressed and this deficiency can be partly addressed from an understanding of factors affecting risk of infection. Near-surface ponding and lateral seepage of water is an important stimulus to survival, sporulation, and dispersal (ch. 5). It is now appreciated that interactions between components of the hillslope hydrological cycle are important to disease development, but few of the flows between components (Fig. 48) have been quantified in relation to disease. The investigation of Kinal (1986) has quantified lateral flow of water and recovery of *P. cinnamomi* in response to winter and summer rain events for one year at two sites. A wider data base is required to prevent future management practices changing the water balance within a site to favour disease.

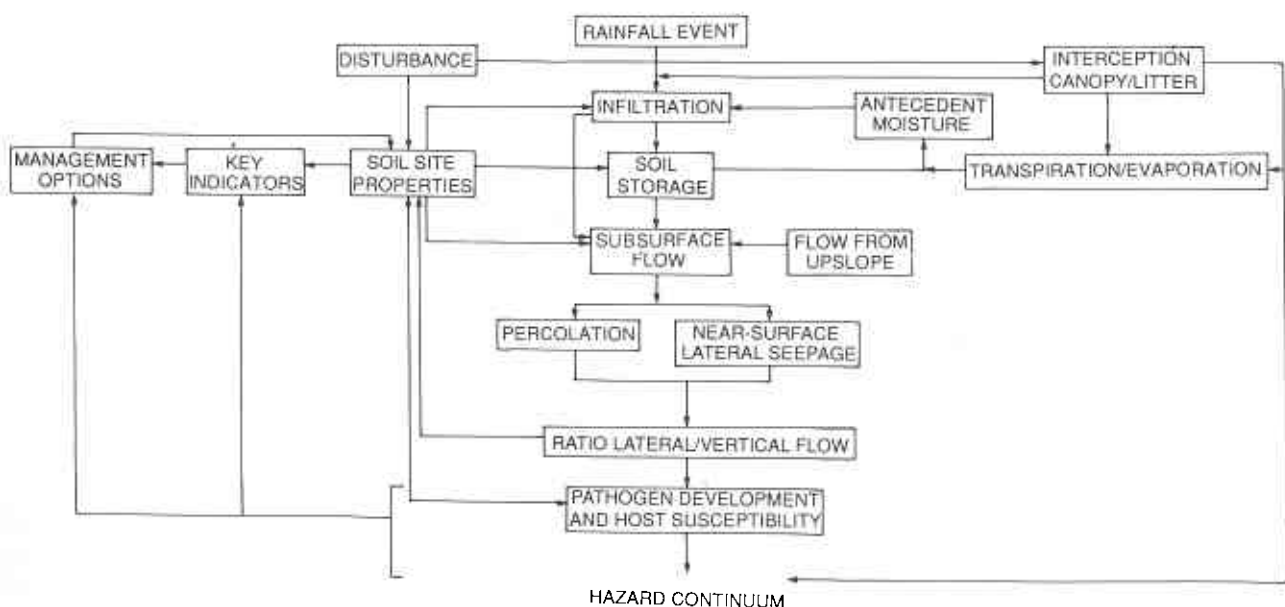


Figure 48

Components of the hillslope hydrological cycle important to development of *Phytophthora cinnamomi* in soils of the jarrah forest.

The efficacy of various treatments to reduce inoculum levels requires assessment as a management tool. Control of 'spot infections' has been identified by managers as the area of high research priority (Byrne 1984). Chapter 7 outlined projects where methods to control *P. cinnamomi* are being evaluated. Further evaluation of chemicals and other methods must be a high research priority to ensure that managers are provided with as many options as possible to reduce the spread and development of *P. cinnamomi*.

In the late 1970s and early 1980s, replacement of the susceptible *B. grandis* understorey by *Acacia* species offered hope as a means of reducing disease development. Application of the concept to the field has since suffered from a shortage of cost effective techniques. Removal of a susceptible *B. grandis* understorey can reduce inoculum foci and removes a mechanism whereby the fungus can survive dry summers (Shea 1979b; Shearer and Shea 1987). Further research is needed into cost effective methods of reducing the density of *B. grandis* without causing unacceptable damage to jarrah and conservation values. The role of understorey species other than *B. grandis* as hosts and the ecological effects of changes in understorey composition needs to be determined.

Rehabilitation prescriptions for infected areas are being modified to incorporate the local effects of landscape on drainage, rather than a blanket prescription for whole areas. Information on factors affecting hazard must be incorporated into ways of counteracting the detrimental effects of infection on stand structure and productivity.

Risk of Infection

The risk of infection broadly includes the biology of *P. cinnamomi* in the soil and its interaction with the host plant and soil biota (Fig. 20). Considerable attention has been given to understanding the infection process (ch. 5), but many questions remain unanswered (Table 8, ch. 5). Although a difficult area experimentally, it is vital that the relationships between environmental factors, sporulation, survival and infection are determined to improve the precision of risk rating systems for managers.

Damage from Infection

Considerable progress has been made in the understanding of why jarrah is vulnerable to *P. cinnamomi* on certain sites and how *P. cinnamomi* actually kills trees (chs 5 and 6). An accurate description of the interactions and the damage and symptoms caused by the fungus is fundamental information. The assessment of damage and the monitoring of disease development over time will also provide a sound basis for management decisions.

It must be realized that an understanding of the phenology, growth and physiology of jarrah forest plant species is essential to sustain a healthy forest despite the pressures and many types of disturbances to the ecosystem. The response of the jarrah forest ecosystem to different forms of disturbance or silvicultural treatments needs to be predicted on different sites with or without the fungus present. It is far too soon to say we know enough about the interactions between *P. cinnamomi* and host plants.

Parameters which integrate the effects of environmental variables on trees should prove to be most useful for comparing differences between trees on different sites. Growth rate integrates the growing conditions experienced by trees. Other parameters can integrate environmental effects over different time spans. Daily and seasonal fluctuations in environmental or physiological variables can either cause undesirable variation in readings or are indicative of different levels of stress.

There is an obligation to monitor changes in the jarrah forest ecosystem caused by *P. cinnamomi*. An accurate record of disease development can help predict future progress of the disease. It can also give a better inventory than is available at present of the mortality of jarrah and the understorey in infected areas. The comparative ecology of infected and healthy areas also needs assessing.

There is a particular need for assessment of the effects of *P. cinnamomi* on intermediate impact sites where jarrah survives. The questions to be addressed include: What type of regeneration occurs on sites long infected by *P. cinnamomi* - is it from seed or old rootstocks? Is the growth of jarrah affected by infection on some sites but not others? Are the effects of infection transitory or cumulative? How is leaf area affected and how does reduction in leaf area caused by disease relate to performance of jarrah on different types of sites?

The understorey of the jarrah forest suffers greatest damage from infection by *P. cinnamomi* (chs 4 and 6). Despite this, the susceptibility of understorey plant species other than *B. grandis* has been largely ignored. There is an urgent need for information on the susceptibility of understorey plant species to *P. cinnamomi* infection. Plant species that *P. cinnamomi* infection threatens with extinction must be identified.

Regional differences

Most of the information relating environment to disease development has come from investigations in the high rainfall zone. Potential spread and intensification of dieback in the intermediate-low rainfall zone needs to be evaluated. Decreasing rainfall (Fig 6), occurrence of *B. grandis*, laterite formation (Fig 10), and disturbance

from human activity with distance east of the Scarp would contribute to a lower incidence of *P. cinnamomi* in jarrah forest in the east than in the west. However, an increasing proportion of duplex soils with sands over clay in shallow valleys would favour disease development in eastern rather than western forest. Infected areas with high mortality of jarrah along Albany Highway and the Muja to Perth power line attest to the potential high impact of *P. cinnamomi* in the intermediate-low rainfall zone. Reduction in crown cover from disease and the associated reduction in transpiration in salt prone areas has obvious implications to the quality of groundwaters in the metropolitan catchments in the eastern jarrah forest. The potential area vulnerable to *P. cinnamomi* needs to be determined from hazard mapping. Relationships between environment, sporulation and spread of the fungus, and infection of jarrah need to be determined for the soil profiles in the intermediate-low rainfall zone.

Most of the research on *P. cinnamomi* in south-western Australia has been carried out in the northern jarrah forest. Because of the differences in climate, topography and soils, results from the northern forest cannot be directly extrapolated to southern jarrah forest. The effect of southern sites and climate on sporulation and dispersal of *P. cinnamomi* and symptom expression in jarrah needs to be determined.

Although *P. cinnamomi* has mainly been associated with jarrah dieback, it is a destructive pathogen in woodlands and shrublands that have a high proportion of susceptible species (Podger 1968; Shearer and Hill 1989). In the Stirling Range National Park infection by *P. cinnamomi* threatens susceptible endemic species with extinction. The landforms and depositional soils of the coastal plain and south coast are very different from those of the Darling Scarp. Although coastal soils are often consid-

ered to drain freely, they do have textural changes, clay layers and iron hard pans that perch shallow groundwater tables and favour survival and reproduction of *P. cinnamomi* at depth in the soil profile (Shearer *et al.* 1989). Emphasis must be given to studies on host susceptibility and pathogen dynamics in woodlands and shrublands and the findings used to develop risk and hazard rating systems for these areas.

TOWARDS THE FUTURE

The stimuli and flows in the life cycle of *P. cinnamomi* (Fig. 20) are subprocesses of the flows and interactions that occur within the jarrah forest environment (e.g. Fig. 48). Research has identified the major stimuli and flows that are important to pathogen dynamics and disease expression, but precise information on relationships is lacking. This review has highlighted the areas where more research is continuing.

The aim outlined at the beginning of this chapter can be accomplished if high priority is given to quantification of the main relationships between environment and development and expression of disease and the incorporation of the information in a form to test 'what if' options. Within future investigations, balance between research on the host and pathogen and conservation and production values must be maintained. As the understanding of processes increases, benefits will flow into improvement of hazard and risk systems and the development of integrated methods of control. The information can also be used to develop data bases and user friendly systems that can be interrogated by managers to aid in the planning operations that minimise the spread and intensification of *P. cinnamomi* in the native plant communities of south-western Australia.

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Glossary

Definition of terms as they have been used in the text. Terms already defined in the text are not included.

antagonism: A general name for associations of soil microorganisms disfavoured reproduction and survival of *P. cinnamomi*.

asexual: Vegetative reproduction without gametes or sex organs.

bauxite: Laterite high in aluminium and low in iron and silicate, mined for its aluminium content.

cementation: The process of precipitation of a binding material, commonly iron oxide, around grains or minerals in rocks.

chemotaxis: Attraction of zoospores to roots due to chemical stimuli.

chlamydospore: A thick walled spore approximately 40 µm (0.04 mm) in diameter produced vegetatively by the rounding up of a cell or cells.

conductive: Innate property of soil to stimulate formation of sporangia by *Phytophthora cinnamomi*.

control: The prevention of or reduction in the spread of a pathogen or development of disease, resulting in protection of plant health.

Corymbia: A subgenus of the *Eucalyptus* containing the woody-fruited bloodwoods. The subgenus comprises about 35 species of mainly small trees and includes marri. The subgenus is noted for the prevalence of red kino (gum) veins and pockets in the wood and hence the name bloodwood.

Darling Scarp: The dissected western margin of the Great Plateau, being clearly defined between Latitude 31°30' and 33°30', but difficult to recognise further north or south.

dendritic: A tree-like pattern of drainage.

dieback: Progressive deterioration of tree crowns from the top down due to death of leading twigs and branches. In Western Australia often associated with infection by *Phytophthora cinnamomi*, but can also be caused by other pathogens that infect roots (e.g. *Armillaria luteobubalina*) and cause cankers on branches (e.g. *Botryosphaeria ribis*).

Dilleniaceae: The family occurs mainly in Australia and tropical America. Mainly trees and shrubs, sometimes woody vines or herbs. Leaves simple, alternate, with or without stipules. Flowers either bisexual or unisexual, sepals 5; petals usually 5 but sometimes fewer; stamens numerous arranged spirally, sometimes coalescent basally; carpels several; ovules 1-several. Fruit a follicle or berry-like. (e.g.) *Hibbertia*.

disease: A harmful alteration of the normal physiological and biochemical development of a plant.

disinfectant: A substance for the destruction of pathogenic micro-organisms.

dispersal: The movement of propagules of a pathogen from the place where they were formed or where they may survive to the place where they may infect.

dolerite: A medium-grained basic intrusive igneous rock occurring in dykes.

duricrust: Describes the lateritic crust of varying hardness found at or near the surface which provides a measure of protection to the underlying material and limits the downward percolation of rainwater.

dyke: A vertical or highly inclined sheet of rock formed when molten rock material from the interior of the earth has forced its way towards the surface through a cleft or by melting a passage for itself and has cooled and solidified.

ecosystem: A functional system which includes the organisms of a natural community together with their environment.

ectomycorrhiza: The beneficial association between the roots of plants and fungi where the fungal hyphae form a closely-woven envelope covering the root apex and penetrating to a limited extent between the cortical cells. Usually formed by basidiomycete fungi.

encysted: A zoospore that has lost motility by withdrawal or shedding of the flagella and has rounded off.

endemic: The occurrence of a plant or pathogen confined to a particular area.

Epacridaceae: A large family centered in Australia. Shrubs or small trees with small, simple heath like alternate leaves. Flowers commonly bisexual, rarely unisexual with a fleshy cushion of tissue growing from the receptacle below the ovary which the stamens and

sometimes the petals are attached. Sepals 4 or 5 and persistent; petals 4 or 5, coalescent and the corolla tubular; stamens 4 or usually 5, the anthers 1-chambered, splitting lengthwise, the ovary 1-10 chambered. Fruit a capsule or a drupe with 1-5 seeds. (e.g.) *Leucopogon*, *Styphelia*.

epidemic: An increase in disease in a population of plants in time and space.

exclusion: Control of disease by preventing its introduction into disease-free areas.

ferruginous: Containing iron.

fertility: Pertaining to the level of soil nutrients needed for plant growth. A relatively fertile soil has higher level of essential nutrients than a relatively infertile soil.

fine roots: Roots < 10 mm in diameter.

floristic: Pertaining to the plant population of an area.

fumigant: A substance used in the vapour phase to kill plant pathogens.

fungus: One of the lower forms of plant life that lack chlorophyll and being incapable of manufacturing its own food, derives energy from dead or living plant or animal tissue.

fungicide: A chemical that kills or inhibits fungi.

genotype: The type of genes present in an organism.

germ tube: The initial, simple filament formed by a fungus spore when it begins to grow (germinate).

gravel: A deposit of rounded stones high in iron and aluminium oxides formed from the weathering of laterite and mixed with finer material such as clay or sand by the action of moving water.

Havel site-vegetation types: Definition of sites in the northern jarrah forest by a set of vegetation indicator species that were identified from test surveys to occur within a corresponding range of environmental conditions. The site types are designated by letters of the alphabet (Table 2).

host: The plant which is invaded by a pathogen and from which the pathogen derives its energy.

host range: The various kinds of plants that may be affected by a pathogen.

hydraulic conductivity: The volume flux of water resulting from unit gradient in hydraulic potential in the particular soil and water situation under consideration.

hydrology: The study of water, especially in relation to its occurrence in the soil.

hyphae: Threadlike strands or filaments that constitute the body (mycelium) of a fungus. Some hyphae are specialized for penetrating host tissue or producing spores.

impact: The effect of disease on plant health.

infection: The process of establishing a pathogenic relationship with a host.

infection front: The outer active edge of an infected area indicated by recent death of susceptible hosts.

infiltration: The passage of water through the surface of the soil via pores or small openings into the soil mass.

inoculation: The processes of introducing infectious material (inoculum) on or into a host for the purpose of producing infection or testing susceptibility to infection.

inoculum: Portions of any pathogen capable of being disseminated and of initiating disease.

inoculum density: Propagules of a pathogen per unit of soil.

inter-specific: Between different species.

intra-specific: Among members of a single species.

ironstone: Laterite containing a high proportion of iron oxide.

isolate: A pure culture of a fungus or micro-organism.

kaolin: A clay material usually white or nearly white in colour that is low in iron and derived from hydrous aluminium silicates.

lateral root: Roots that extend horizontally in the soil from the stem collar and often buttress the tree.

laterite: A general term referring to residual deposits rich in hydrated iron and aluminium oxides formed on exposure to alternate wetting and drying in warm, humid conditions.

leaf water potential: A measure of the availability of water in the plant compared to that of pure water at the surface of the earth and includes the effect of solutes, pressure and height on water availability. For

- convenience water potential is usually expressed as a pressure, equivalent to that required to move water from pure water at the surface of the earth to the point of measurement. Because plants usually take up water if it is available, plant water potential is nearly always negative. Droughted plants have lower (i.e. more negative) water potentials than well watered plants.
- lesion:** A well-marked but limited diseased-area of part of a host (Fig. 29).
- lignified:** Tissue in which complex aromatic compounds have been deposited in cell walls of sclerenchyma, xylem vessels and tracheids making them strong and rigid.
- mating type:** Refers to self sterile types which require the interaction of two compatible types for sexual reproduction. In *P. cinnamomi* the mating types are designated as A_1 and A_2 .
- matric potential:** The energy needed to move water in soil relative to a hypothetical reservoir of pure and free water at atmospheric pressure, at the same temperature as soil water and at a given and constant elevation measured in kilo pascals (kPa). A negative pressure potential results from the capillary and adsorptive forces due to the soil matrix. As the water content of a soil decreases, the remaining water is held by progressively stronger forces and the amount of work necessary to move water in the soil must increase.
- microflora:** The bacteria, actinomycetes, fungi and algae that occur in the soil.
- monadnock:** A residual hill of exposed granite which stands above the general level of a landscape because its rock has been more resistant to weathering than the rock of the surrounding country.
- Monocalyptus:** A subgenus of *Eucalyptus* with buds having a single cap which covers the stamens and 2 contiguous vertical rows of ovules on the placenta. It is the second largest subgenus consisting of about 100 species which include many important timber species such as jarrah.
- mycelium:** A mass of fungal hyphae forming the body of the fungus.
- Myrtaceae:** The family includes about 2500 species distributed widely through the tropics, but particularly abundant in Australia. Shrubs or trees. Leaves simple, usually opposite, entire, leathery, markedly aromatic producing essential oils. Flowers bisexual, radially symmetrical with sepals, petals and stamens growing from the floral cup fused to the ovary; sepals usually 4-5 (in *Eucalyptus* small or wanting); petals usually 4-5 (in *Eucalyptus* forming a cap which falls away as the flower bud opens); stamens numerous, carpels 3 or more, often 4, the ovary 1 chambered, ovules 2-many per carpel. Fruit a berry or a capsule, often dehiscent apically about the attachment of the floral cup or tube. (e.g.) *Darwinia*, *Hypocalymma*, *Leptospermum*, *Eucalyptus*.
- niche:** Used to describe the constellation of ecological factors which specify how a species makes its living in the world.
- oomycete:** Consists of fungi which reproduce asexually by means of biflagellate zoospores borne in sporangia of various types.
- oospore:** A thick-walled spore approximately 40 μm (0.04 mm) in diameter and formed in a fertilized oogonium.
- overstorey:** Tree species that form the upper canopy.
- overland flow:** Originates from rain which fails to infiltrate the mineral soil surface.
- Papilionaceae:** The family is distinguished by the butterfly-like appearance of flowers. Herbs or shrubs or trees with simple or compound leaves. Sepals 5, more or less joined in a tube, petals 5 overlapping and free with the upper exterior one forming the standard, the two lateral (wings) more or less parallel with each other, the lower two are joined by their lower margins into a keel; stamens inserted within the petals, often 10, mostly all perfect; anthers mostly open lengthways. Fruits usually a legume or indehiscent, sometimes jointed and breaking up into seed segments; seeds without or with a very scanty endosperm. (c.g.) *Bossiaea*, *Hovea*.
- pathogen:** Any organism or factor causing disease.
- pathogenicity:** The process of being able to cause disease.
- peneplanation:** The action by which a land surface is changed almost to a plain by erosion.
- percolation:** Movement of water through the soil.
- phenotype:** Expression of the genes in an organism in response to the interaction with the environment.
- phloem:** The principle food-conducting tissue of the vascular plant situated just below the outer bark.
- phytophthora:** (*phyton*, a plant; *phthora*, destruction) Many species in this genus are destructive parasites of

- economic plants. Hyphae typically branch at right angles and are often constricted at the base. Some species (e.g. *P. cinnamomi*) frequently produce hyphal swellings. Hyphae asexually produce oval shaped sporangia which germinate directly by a hypha or indirectly by segmentation of the protoplasm into zoospores. Following release, the motile ovoid biflagellate zoospores swarm for some time, come to rest, encyst and germinate. Sexual reproduction is by means of fertilization of an oogonium by an antheridium borne on the same or different hyphae and formation of an oospore.
- phytotoxicity:** When an applied chemical damages a plant.
- plant community:** Aggregation of plants characterized by a distinctive combination of two or more ecologically related species.
- proteoid root:** Intense local lateral root production by many of the Proteaceae to form a dense mat of roots in the surface soil.
- Proteaceae:** The family includes about 50 genera and 1000 species occurring mainly in arid regions of the Southern Hemisphere. Commonly trees or shrubs. Leaves alternate entire to bipinnate; stipules none. The flower is a floral cup (ovary not fused to it) with a long coloured floral tube, 4-numerous; sepals coalescent, petal like and coloured; stamens opposite the sepals; ovary 1 chambered, the ovules 1-many each with 2 outer coatings. A dry fruit formed from a single carpel containing more than one seed and splitting open along a suture. (e.g.) *Banksia*, *Grevillea*, *Hakea*.
- quarantine:** Restriction of entry of vehicles into designated areas of forest.
- regeneration:** The renewal of a forest by self-sown seeds, lignotubers, and advanced growth or coppice.
- relative water content (RWC):** The ratio of the amount of water held in a sample compared with the amount held when the sample is fully hydrated (turgid) by standing in water; usually expressed as a percentage. RWC calculated as:

$$\text{RWC}(\%) = 100 \times \frac{(\text{Sample fresh weight} - \text{sample dry weight})}{(\text{Sample turgid weight} - \text{sample dry weight})}$$
- resistance:** Ability of a host plant to suppress or retard activity of a pathogen.
- sporangium:** An oval or ellipsoid spore sac approximately 57 x 33 μm (0.057 x 0.033 mm) that vegetatively produces spores within a wall.
- sporulation:** The process of spore production.
- stomatal conductance:** The ease with which water vapour or gas may diffuse from the spaces inside leaves, through the stomatal pores in the leaf surface to the outside air and vice versa. Stomatal conductance is controlled by the operation of the stomata which close in response to water stress.
- survival:** The ability of individuals of a population to withstand adverse conditions.
- susceptibility:** The capacity of a plant to become infected by a pathogen or to be affected by a disease.
- sympiosis:** A reasonably long-lasting relationship in which two, or occasionally more, different species live in immediate proximity and derive reciprocal benefits from their interactions.
- Symphyomyrtus:** A botanically complex subgenus of *Eucalyptus* in which the buds of all species have two caps. The outer cap sheds early in the development of the buds of most of the species leaving an obvious scar which is retained until flowering, while a number of species retain both caps up to the flowering stage. It is the largest subgenus consisting of about 330 species, including wandoo.
- symptoms:** Usually a visible reaction of a plant to a pathogen or abiotic agent.
- systemic:** Pertaining to a chemical which spreads throughout the body of a plant following absorption through roots or foliage.
- throughflow:** Downslope flow of water occurring physically within the soil profile, usually under unsaturated conditions.
- tissue culture:** The growth of tissue cells in artificial media.
- topography:** The general configuration of the land surface including its relief.
- transpiration:** The process by which water vapour leaves the foliage or other parts of a living plant and is released to the atmosphere.
- understorey:** The lower stratum of a multi-storeyed forest.
- upland:** The higher ground of a region in contrast to valleys, plains or other low lying land.
- vertical tap roots:** Major roots of jarrah and *Banksia grandis* which descend vertically from lateral roots and able to draw on for summer transpiration, the large water stores held deep in the soil profile.

water status: A general term describing the levels of water supply in the plant relative to what is presumed to be optimal. Low water status equates to a general condition of drought and presumed stress caused by lack of water in tissues.

Xanthorrhoeaceae: 'grass tree' like perennials; rootstock a thick woody persistent underground stem base or rhizome; stem, when present, sometimes tall and woody, simple or little branched; leaves mostly linear. Flowers bisexual or dioecious, usually small, rarely large and solitary, in a spike, a cluster of associated

spikes or in a dense cluster or head. Perianth mostly dry and glumaceous, rarely coloured, of 6 segments in two whorls. Stamens 6, three outer more or less free; anthers 2 locular; ovary superior, 3-locular. Fruit deciduous along the middle of the back of each chamber, or rarely a seeded nut. Seeds with rather hard endosperm and straight embryo. (e.g.) *Xanthorrhoea*.

zoospore: A motile spore approximately 10µm (0.01 mm) in diameter produced asexually within a sporangium and released in free water.