BULLETIN 85
1975

ISSN 0085—8129

ENVIRONMENTAL FACTORS OF THE NORTHERN JARRAH FOREST IN RELATION TO PATHOGENICITY AND SURVIVAL OF *PHYTOPHTHORA CINNAMOMI*

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PERTH
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SUMMARY

Soil moisture levels equivalent to "field capacity" and soil temperature levels of 15°C were assumed to be the critical limits below which infection by *Phytophthora cinnamomi* Rands does not take place. Prolonged periods during which soil moisture levels remained at "wilting point" were assumed to reduce fungal survival outside host roots.

Measurements of the soil moisture and soil temperature regimes of a range of site types in the forest demonstrated that there are two broad susceptibility zones. Lowland sites have long periods in the spring, summer and autumn months during which soil temperature and moisture levels are suitable for infection. Upland sites have relatively short periods, mainly during the spring months, when soil moisture and soil temperature are suitable. Upland sites have long periods when soil moisture levels are unsuitable for fungal survival but there are no periods when lowland sites have moisture levels critical for fungal survival.

Measurements of the soil moisture regime of the upper soil profile of a number of upland sites confirmed that they are freely drained. The maintenance of moisture levels suitable for fungal infection is dependent on consistent rainfall. Moisture measurements to 60 cm depth showed that the decrease in soil temperatures with increasing depth is not compensated by prolongation of the period when soil moisture levels are suitable for infection.

Measurements of the soil temperature regime of stands under different degrees of canopy and litter cover demonstrated that these factors have a significant effect on the period during which soil temperature and moisture levels are suitable for infection. On freely drained sites which have maximum canopy and litter cover there are no periods when both soil moisture and temperature levels are suitable for infection. Aspect has some effect on susceptibility but is not as important as canopy and litter cover.

Spatial variation in rainfall distribution may have some effect on site susceptibility. Yearly variation in rainfall distribution, however, is unlikely to have a significant effect on the susceptibility of upland sites to infection.

Measurements of fungal survival during the summer months on upland and lowland sites confirmed that the fungus is unable to survive outside host roots on upland sites during the summer but it had no difficulty in surviving on lowland sites throughout the year. Measurements of uphill rate of spread from existing infections on lowland sites over a period of five years demonstrated that average extension is usually slow. Maximum spread at isolated points and average extension on some sites is relatively high. Initial pot trials did not detect a significant effect of soil type on the ability of the fungus to infect highly susceptible species.

Forest management procedures, aimed at reducing disease spread and intensification, can be based on the results of these studies. In addition, the improved knowledge of the jarrah forest environment in relation to the disease can be used to plan further research.

Figure 1
"Dieback" destroyed forest.

ENVIRONMENTAL FACTORS OF THE NORTHERN JARRAH FOREST IN RELATION TO PATHOGENICITY AND SURVIVAL OF *PHYTOPHTHORA CINNAMOMI*

INTRODUCTION

Phytophthora cinnamomi Rands has been identified as the organism causing the disease of the Western Australian jarrah *(Eucalyptus marginata* Sm.) forest known as "jarrah dieback" (Podger et al, 1965; Podger, 1968). Extensive and intensive attempts to isolate the fungus from healthy forest have not been successful and it has been assumed that the fungus does not occur naturally in the forest.

Within one to three years after the introduction of the fungus into healthy forest, mortality occurs in the shrub and understorey layers. Death of the jarrah trees may not occur for a number of years after understorey deaths, but is complete. A few of the understorey and overstorey species are resistant to the disease. The eventual result of introduction of the fungus to a forest area, however, is the death of the commercial species (jarrah) and of the majority of the species which comprise the jarrah forest formation (Fig. 1). Observations of infected areas over a period in excess of 30 years indicate that, although there may be some regeneration of resistant species, for example marri (*Eucalyptus calophylla* R.Br.), on the infected area, there is no sustained regrowth of the suspectible species. Thus the end result is the destruction, in perpetuity, of jarrah forest on that area.

The disease occurs throughout the 1.2 million hectares of commercial jarrah forest in the south-west of Western Australia and is present on a variety of site and vegetation types. Despite its widespread occurrence, the area of affected forest is relatively small (about five per cent of the total —Forests Department Working Plans Report) and the majority of infections are located in lower topographical sites (Fig. 2). These sites carry low quality jarrah but, paradoxically, are most suited for growth of exotic species. The fungus has the capacity to destroy the forest in a range of situations (Podger, 1968) but there is evidence that the intensity of the disease varies markedly between sites. Thus, although the disease has the potential to destroy the total forest area, there is considerable opportunity for its control or at least amelioration of its effects.

Since the discovery of the organism causing the disease, numerous investigations into the host, pathogen and environmental factors of the disease complex have been initiated. This bulletin summarises investigations into the environmental factor. It is impossible to consider the host, pathogen and environmental factors of any plant disease in isolation but there is considerable justification for emphasis on the environmental aspects of this disease. In terms of practical management of the jarrah forest, control through modification of the environment appears to offer the only means by which the progression of the disease into jarrah stands can be prevented or reduced. The pathogen, although an introduced species, is extremely virulent and cannot be economically eradicated from even relatively small areas of forest. Jarrah, the dominant economic species, is uniformly susceptible to the pathogen and current research indicates that breeding for resistance is not practical.

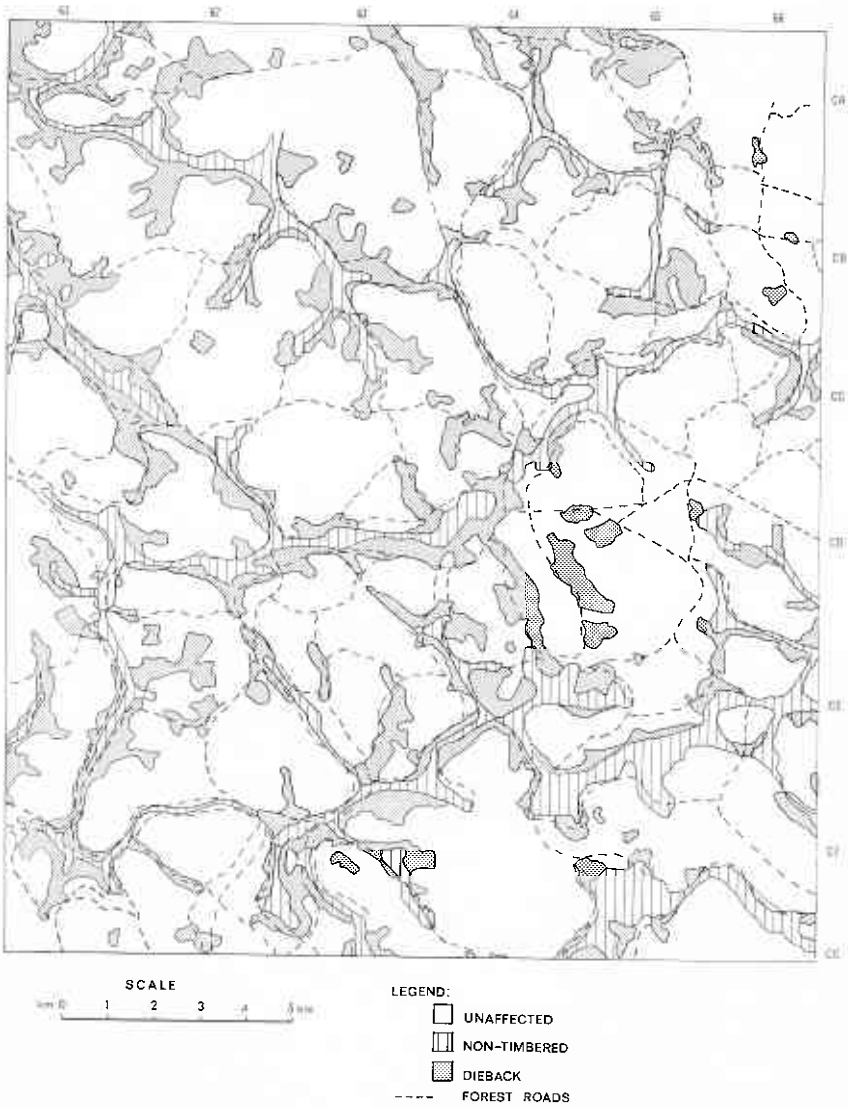

Figure 2
Typical distribution of jarrah dieback in the northern jarrah forest. (Non-timbered areas occur on lower topographical sites and hence mark drainage lines. Note close association between these sites and jarrah dieback).

Research has shown that there are some exotic eucalypt and coniferous species which are resistant to the fungus and capable of producing an economic crop. These species, however, grow most successfully on the lower topographical jarrah forest sites that carry low quality jarrah. It is possible that new economic methods of establishment, currently being investigated, will allow economic replacement of the diseased jarrah forest crop on freely drained sites with resistant economic species. It would be more desirable to retain the established jarrah crop on these sites.

Environmental studies were carried out within a 32 km radius of the town of Dwellingup, which is located in the centre of the northern jarrah forest. Hence, conclusions based on these data are only applicable to the northern jarrah forest.

Investigations of the environmental factor in the disease complex involved:

(i) Definition of the major environmental factors affecting pathogenicity and survival of *P. cinnamomi* from published data on the fungus.

(ii) Characterization of the jarrah forest environment in relation to these major factors.

(iii) Evaluation of the effect of environmental factors on fungal survival and pathogenicity by direct inoculation and measurement of disease spread.

(iv) Assessment of the implications of the study to management and future research.

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SECTION I

ENVIRONMENTAL FACTORS AFFECTING PATHOGENICITY AND SURVIVAL OF *P. CINNAMOMI*

Hepting (1964) has defined the environmental conditions required before damage can be expected by *P. cinnamomi* as follows:

Characteristic	Is this often a limiting factor?
pH range for growth and infection pH 4-8.	no
Hosts woody; great range of families.	no
Growth slow below 15°C, optimum at 27°C, nil above 34°C.	yes
Infection slight below 15°C or over 34°C	yes
Free soil moisture needed for long periods for infection.	yes
Damage rare on light soils, common on wet, heavy soils.	yes
Survival poor in soil dry for long periods.	yes
Long survival usually requires a living host.	yes

Even a superficial analysis of the jarrah forest environment in relation to the disease indicates that several of Hepting's "limiting factors" are not operating. Thus, a more critical evaluation of factors affecting survival and pathogenicity of *P. cinnamomi* is necessary.

1. FACTORS AFFECTING PATHOGENICITY

Soil moisture, soil texture and soil aeration.

Soil moisture, soil texture and soil aeration are interrelated and their effect on the pathogenicity of *P. cinnamomi* is complex. Numerous authors have shown that high soil moisture levels are required for pathogenesis (Roth and Kuhlman, 1966; Zak, 1961; Torgeson, 1954; Hine et al, 1964). The association of diseases caused by *P. cinnamomi* with conditions of poor drainage and/or excessive rainfall have been observed by Anderson (1951), Campbell and Copeland (1954), Torgeson (1954), Copeland and McAlpine (1955), and Newhook (1959). Stolzy et al (1967) showed the necessity for high moisture conditions for pathogenesis but also demonstrated that zoospore survival was inhibited at high soil moisture levels. Torgeson (1954) found that soils of moderate texture were most favourable for pathogenicity but Zak (1961) demonstrated progressively greater pathogenicity as soil texture was made heavier. Zak suggested that soil aeration was not an important factor in determining pathogenicity.

Roth and Kuhlman (1966) summarised current knowledge on the effect of soil moisture on pathogenicity. They postulated that there were two thresholds affecting pathogenesis: soil saturation which provides the stimulus for sporulation, and field capacity which enables spore migration and possibly influences infection. Data on the effect of soil moisture and associated factors on pathogenesis, however, were inadequate for critical evaluation of field conditions. The moisture characteristic curves of test soils were not specified and there was no information on the periods required for significant disease development at moisture levels above the critical minimum. In the absence of data on the moisture characteristics of test soils, a moisture content of 20 per cent may correspond approximately to "wilting point" or "field capacity", depending on soil texture and structure. Even if the moisture

characteristic curves of test soils were described, the use of static descriptions of soil moisture levels (field capacity and wilting point) was inadequate. Gardner (1960, 1968) demonstrated that both the moisture characteristic curves and soil hydraulic conductivity must be considered to define soil moisture availability adequately. Gardner's concepts have not been applied to define "water availability" for fungi.

The effects of different soil moisture regimes on pathogenicity were usually tested by adjusting the interval between watering (Zak, 1961; Roth and Kuhlman, 1966; Hine et al, 1964). Even in the driest of these treatments there were varying periods, depending on physical soil characteristics, during which the soil was between "field capacity" and saturation. Thus the interval between watering must have been much shorter than that which occurs in the field situation, to avoid drought deaths.

A comprehensive evaluation of the effects of soil moisture on pathogenicity must involve determination of the critical soil moisture levels for pathogenesis in soils with different moisture characteristics. Further, the period of time required at moisture levels above the critical level for significant infection to occur must also be assessed.

Soil temperature

Chee and Newhook (1965) established the critical temperatures for vegetative growth and sporulation. Optimum mycelial growth occurs between 26° and 28°C and growth is slow at 12°C. Sporangial production is prolific between 22°C and 28°C and negligible below 15°C and above 32°C. Kuhlman (1964) distinguished between numbers of sporangia produced and the production of zoospores capable of infection. He found infection did not occur below 15°C and was only one third as frequent at 18°C as at 20, 25, and 30°C. Studies on the effect of temperature on the number of sporangia produced, and the production of zoospore capable of infection cannot be used confidently to predict disease severity of plants grown in natural soils. Roth and Kuhlman (1966) found that Douglas-fir seedlings grown in soil temperature tanks were not infected below 15.5°C, and even at 18°C mortality only occurred in 11 per cent of the plants. Inoculum potential, zoospore motility and infectivity are probably the major factors responsible for the higher temperature requirements for disease development as distinct from spore production.

Hine et al (1964), in their investigations on heart and root rot of pineapple, demonstrated the effect of fluctuating soil temperatures on disease development. They found disease severity to be related to the number of hours that the plants were held at conditions optimum for disease development. There was only 50 per cent root destruction when the plants were alternated between 19°C and 36°C on 12 hour regimes for one month, but 100 per cent destruction occurred when the plants were kept continuously at 19°C. These studies were concerned with the upper temperature limits for *P. cinnamomi* pathogenicity and hence the data have little application to disease evaluation in temperate climates where the lower limits for disease development are more relevant. Similar studies are required to determine the effect of alternating temperature between the optimum (24°C), suboptimum (18°C) and below optimum (12°C) levels before critical evaluations of temperature climates can be made. In a Mediterranean type climate, there is considerable diurnal fluctuation in soil temperature during the spring

months. For the period of the year when soil moisture conditions are suitable for infection, there may be a total of six hundred hours during which soil temperature is above the minimum for disease development. The average period per day during which the temperature is above the critical level, however, may be only eight hours. It is unlikely that the processes involved in the production of zoospores, their transfer to the infection "court" and subsequent infection are favoured by disjunctions. Hence, the assumption that disease development is directly related to the cumulative sum of the number of hours above the critical minimum temperature probably results in an overestimate of the suitability of a particular environment for infection.

Soil microorganisms

Zentmyer (1965) showed that bacteria, notably *Chromobacterium violaceum*, stimulate initiation of the production of sporangia. Marx and Davey (1967) demonstrated that ectotrophic mycorrhizae act as deterrents to root infection by *P. cinnamomi*. Zentmyer (1963) demonstrated control of avocado root rot by incorporation of alfalfa meal into the soil and attributed this to the large increase in saprophytic fungi in the treated soils. In a later paper (Zentmyer and Thomson, 1967) it was shown that saponins could be partially responsible for control. Kuhlman (1964) showed inhibition of fungal growth was less in forest soils than in cultivated soils, but found that none of the tested soils had a lethal effect on *P. cinnamomi*. Roth and Kuhlman (1966) studied pathogenicity in eight different soils and demonstrated that the fungus was more destructive in heavier soils, but found little evidence that a saprophytic soil microflora was actively influencing damage by *P. cinnamomi*.

The influence of host susceptibility on the critical conditions required for pathogenicity.

The host, pathogen and environmental factors of the disease complex are not independent. Prediction of the degree of disease severity, in environments which are optimum, sub-optimum or marginally suitable for the fungus, cannot be made without consideration of the susceptibility of the host.

The effect of different host susceptibilities on the environmental conditions required for severe disease is illustrated by comparison between avocado and citrus. "One *Phytophthora* infection on a growing avocado rootlet destroys it, whereas in citrus massive infection is necessary for damage" (Stolzy et al, 1967).

The ease with which the fungus is able to invade the root system, the capacity of the host to regenerate roots and the host's ability to withstand stresses brought about by fungal attacks are the principal factors determining host susceptibility. The more susceptible the host is in any or all of the above respects, the lower are the environmental requirements for fungal pathogenicity and serious disease development.

2. FACTORS AFFECTING SURVIVAL

Soil microorganisms

Conflicting data on the ability of *P. cinnamomi* to survive as a soil saprophyte was presented by Kuhlman (1964) and Zentmyer and Mircetich (1965). Kuhlman found that *P. cinnamomi* was shortlived in soil, mycelial growth

did not occur through unsterilized soil and the fungus was not an aggressive saprophyte. Zentmyer and Mircetich, however, demonstrated that long persistence in the soil in the absence of a host, moderate mycelial growth through unsterilized soil and appreciable invasion of dead organic matter, particularly under conditions of high soil moisture, were possible. The contradictory data could be explained in part by the inadequacy of detection technique. Differences in the soil microorganic populations could, however, be important. In Zentmyer and Mircetich's own studies, cropping to citrus seedlings for one year eliminated the fungus. Kuhlman's studies also suggested that associated microoganisms could be important, as the soil giving the poorest recovery had been inoculated with a *Pythium* species. Zak (1961) considered the ability of the *P. cinnamomi* to survive indefinitely in soils of the south-east of the U.S.A. was due to the absence of competitive microorganisms brought about by prolonged erosion.

Soil moisture

Both Kuhlman (1964) and Zentmyer and Mircetich (1965) demonstrated that the fungus was killed by prolonged drying. Differences in the critical levels given for survival (five to ten per cent and three per cent, respectively) were undoubtedly due to different moisture characteristics of the test soils used. Mircetich and Zentmyer (1966) found oospores and chlamydospores in naturally infected avocado roots and suggested that these structures only played an important role in survival in soil when moisture content was in excess of three per cent in a sandy loam. In the absence of data on the moisture characteristic curve of test soils, the applicability of the results to other soil types is restricted. Apart from this limitation, there is no information on the *critical periods* for survival at different moisture levels. In both studies (Kuhlman, 1964; Zentmyer and Mircetich, 1965) the fungus failed to survive after two to three months drying. However, the lack of information on the rates of drying limits inferences which can be made about the length of time the fungus survived at the minimum soil moisture level, or its survival capacity for different periods at moisture levels above the critical level. An uninterrupted drying cycle of three months is rare in most temperate climates. Information on capacity of the fungus to survive for different periods at different soil moisture levels in different soil types is necessary to allow accurate evaluation of the restrictions on *P. cinnamomi* survival in temperate climates.

Soil temperature

Hine et al (1964) demonstrated that long periods of continuously high temperature (above 36°C) were necessary for inactivation of *P. cinnamomi.* Hence, in temperate climates, temperature alone probably does not affect survival because of the large diurnal fluctuation in soil temperatures in these environments.

3. SUMMARY

It is surprising that, despite the large number of investigations into the environmental factors influencing the survival of *P. cinnamomi,* these conditions have not been accurately defined. The results of some preliminary studies of the effect of the environmental factors on the fungus are reported in this bulletin and more detailed experiments have been initiated. Until more data on the factors influencing fungal pathogenicity and survival are available, it has been necessary to accept the general levels which have been published.

The major physical environmental elements controlling fungal pathogenicity are soil moisture and soil temperature. It has been assumed in the evaluation of the environmental conditions of the forest that "field capacity" is the lower soil moisture level for infection and that 12°C, 15°C and 18°C are the initial soil temperature levels below which mycelial growth, infection and significant infection, respectively, does not take place.

SECTION II

THE JARRAH FOREST ENVIRONMENT

The northern jarrah forest occurs predominantly on the uplands of an ancient, uplifted peneplain. The upland soils are lateritic podzolics underlain by mottled clay and pallid zones at depth. Downslope from the uplands, on the valley floors of the ancient peneplain, lateritic podzolic soils overlying pallid clays and deep podzolized colluvial sands are common. In some areas the rivers have incised the lateritic profile and formed younger and fresher soil material (Mulcahy et al, 1971).

The forest has a markedly Mediterranean type climate (Leeper, 1960). The average annual rainfall in some areas reaches 1 200 mm but rainfall is confined mainly to the winter months (June, July and August). There are frequent periods of 2 to 3 months in the summer during which no significant rainfall occurs. Mean minimum winter and maximum summer temperatures are approximately 5.5°C and 28.2°C respectively. Spatial and temporal variation in rainfall distribution are important factors that need to be considered.

The moisture retention properties of soil are a major factor influencing *P. cinnamomi* pathogenicity and survival (see Section I). Moisture characteristic curves of the surface horizons of the three major jarrah forest soil types are shown in Figure 3. The ability of a soil to retain a high moisture level at a range of soil potentials at the lower end of the energy scale is a criterion for suitability for *P. cinnamomi* activity. Soils with this characteristic maintain relatively high moisture levels in the intervals between rain

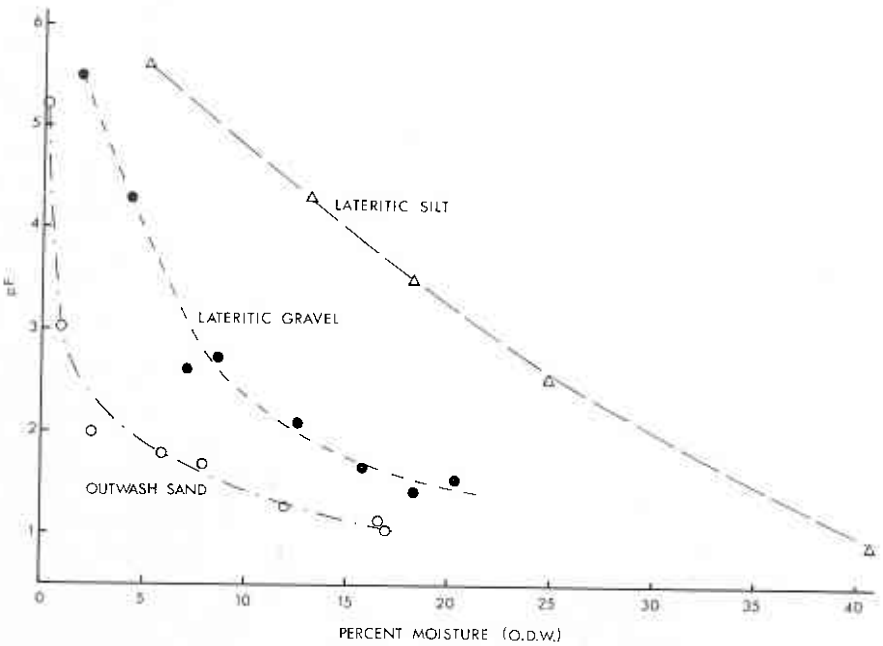

Figure 3
Soil moisture characteristic curves of the three surface horizons of major jarrah forest soil types.

and have a range of pore sizes which remain filled with water, and hence available for zoospore transport, at relatively high soil potentials. The three soils exhibit favourable (lateritic silt), intermediate (lateritic gravel) and unfavourable (sand) moisture retention for *P. cinnamomi* activity.

Field observations of the disease and evidence from the literature suggested the variation in soil temperature and moisture regimes were the principal factors affecting variation in disease distribution, intensity and spread. Consequently, an attempt was made to measure these regimes under a variety of site and stand situations which were representative of the forest environment.

The principal experimental area was located at Scarp Road in the Dwellingup Forest Division. This area provided a range of site and vegetation types that are typical of the cutover jarrah forest. The area was disease-free but was surrounded by diseased forest and thus could be inoculated without endangering large areas of healthy forest. The soil moisture and soil temperature regimes of stand and site types not represented in this study area were sampled in other areas of the forest but it was not feasible to inoculate these sites.

1. SOIL MOISTURE AND SOIL TEMPERATURE REGIMES UNDER MATURE UNEVEN-AGED CUTOVER FOREST IN DIFFERENT TOPOGRAPHICAL SITUATIONS

The experimental area was located 8 km north-west of Dwellingup, approximately 0.6 km east of the Darling Scarp. Experimental plots were located on the south-west side of a shallow valley formed by primary erosion of the ancient lateritic peneplain (Fig. 4). The site types in the experimental area were representative of the major types found in the ancient peneplain, except that there were no depositional sands.

The soils ranged from the freely drained coarse gravels of Stratum 4 to the poorly drained depositional silts of Stratum 1 (Fig. 4). Stratum 3 was freely drained and had soils similar to Stratum 4, except that the surface horizons were formed of colluvial material and massive ironstone was less prevalent. Stratum 2 was a site intermediate between the freely drained soils of lighter texture of upper strata and the poorly dained, heavy textured soils of Stratum 1.

Jarrah was the principal component of the overstorey on the upper topographical sites (Strata 3 and 4) with occasional marri. *Banksia grandis* Willd. occurred both as a scattered understorey tree and in dense thickets. *Xanthorrhoea preissii* Endl. and *Macrozamia riedlei* (Gaud.) C. A. Gardn. occurred prolifically. There were a number of shrubs but the shrub layer was discontinuous. The forest on the upper topographical sites had been managed according to a group selection system and consisted of groups of different age classes varying from poles to over-mature trees. Jarrah saplings and advance growth (regeneration) were absent (Fig. 5).

In Stratum 2, marri occurred more frequently in the overstorey and *B. grandis* formed a scattered understorey. The shrub species were similar to those on the upper strata. In Stratum 1, jarrah was absent and marri and blackbutt (*Eucalyptus patens* Benth.) formed an irregular overstorey. *B. grandis*

and *Banksia littoralis* R. Br. formed the understorey component. *X. preissii* was predominant. There were fewer shrub species but the shrub layer tended to be dense and continuous (Fig. 6).

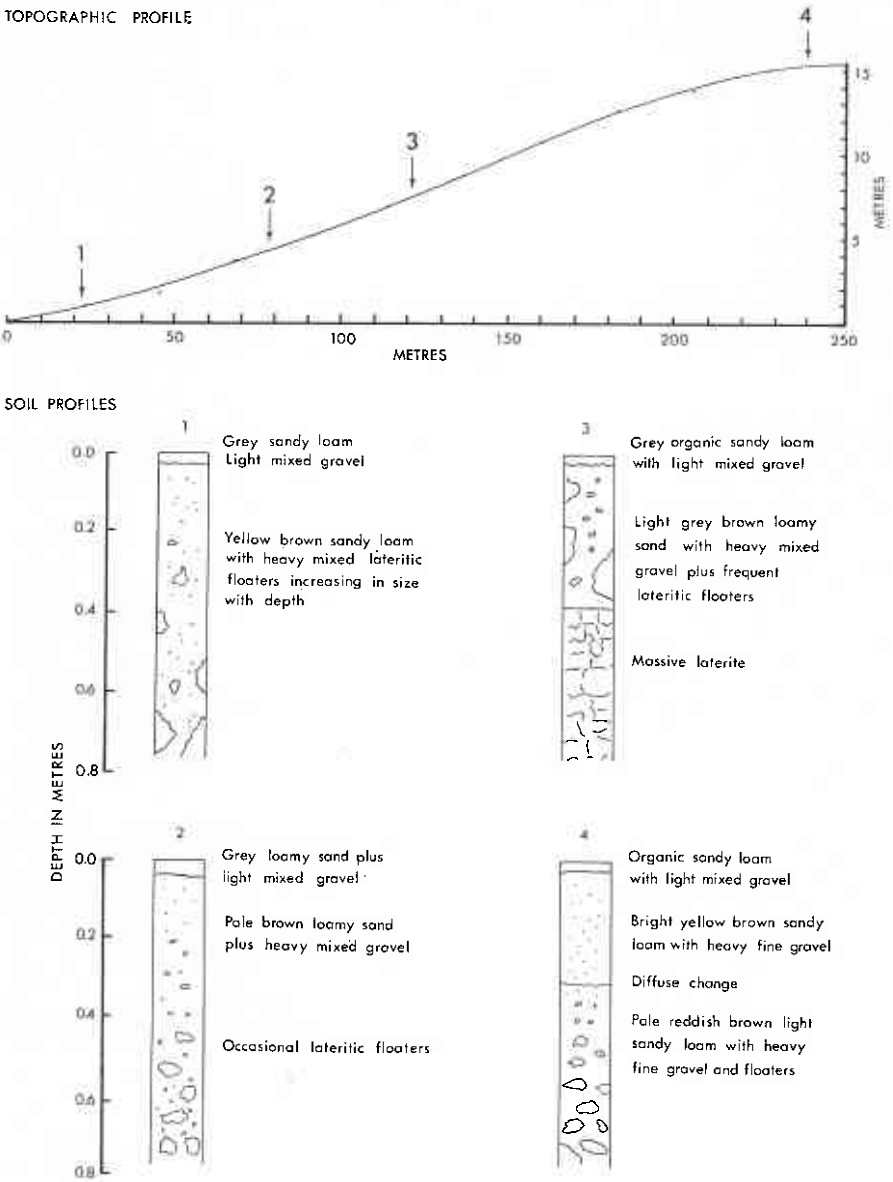

Figure 4
Topographic and soil profiles of the Scarp Road Study Area.

Figure 5

Vegetation. Stratum 4, Scarp Road Study Area.

Figure 6
Vegetation. Stratum 1, Scarp Road Study Area.

(i) PRELIMINARY MEASUREMENTS. AUGUST 1967 TO JANUARY 1968.

Procedure

Rainfall—Rain gauges were installed in three open positions on the experimental area. Rainfall was recorded weekly.

Soil moisture—The soil moisture contents of the 0 to 15 cm and 15 to 30 cm horizons were determined at three points located on a transect through the experimental area. Sample points were located at the centre of Stratum 1, on the lower third of Stratum 2 and in the centre of Stratum 4 (Fig. 4). Two samples were collected at each sampling point and horizon every week. Soil moisture content was determined gravimetrically. The approximate "field capacity" of the soil at each sampling point was obtained in the laboratory by determining the moisture content of soils after 48 hours free drainage from a saturated condition.

Soil temperature—Soil temperature at 7.5 cm depth was measured weekly at fixed positions on four sites—Stratum 2 partial canopy, Stratum 2 no canopy, Stratum 4 partial canopy and Stratum 4 no canopy. Soil temperatures were measured with dial-type metal thermometers.

Results

Spring rainfall in 1967 was below average and in October and November rainfall at Dwellingup was 40 mm less than the average.

Periods during which the soils at the sample sites remained at or above field capacity were markedly different (Fig. 7). Moisture levels in the surface

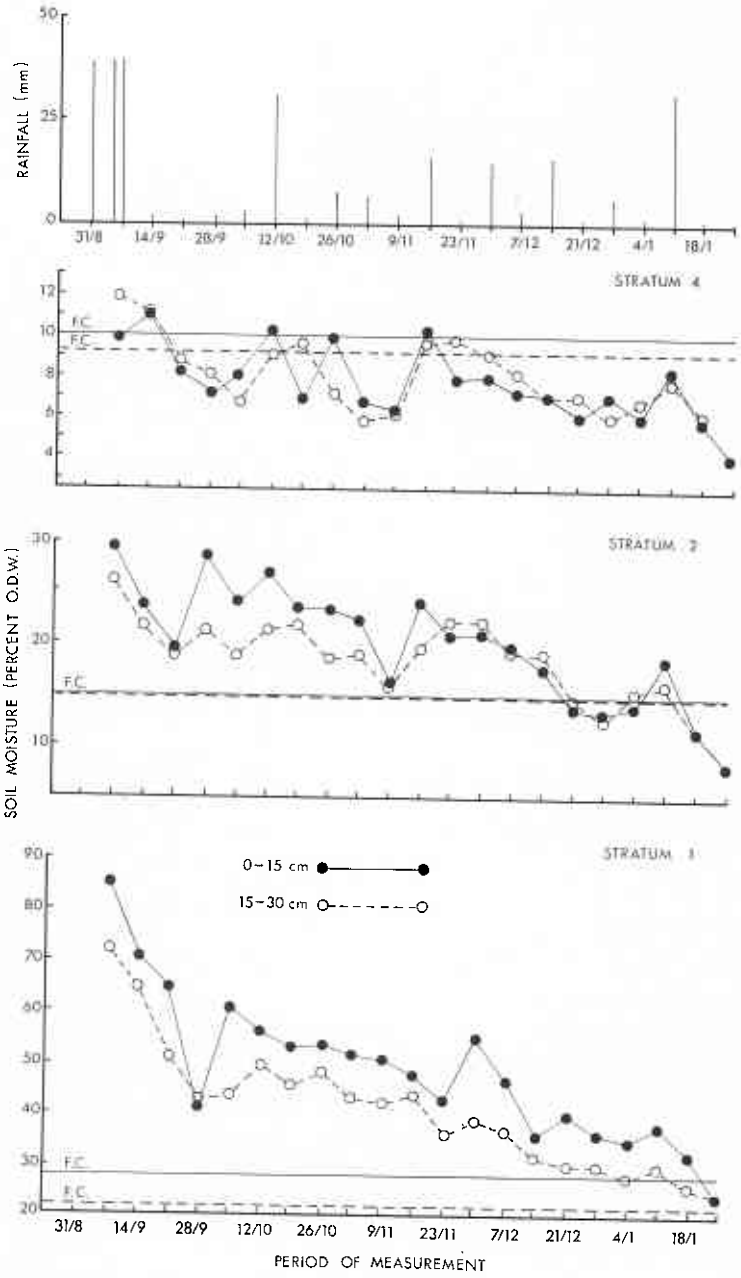

Figure 7
Weekly rainfall and soil moisture levels at the Scarp Road Study Area 31 August 1967-18 January, 1968.

horizons of Stratum 4 were above field capacity for only brief intervals during the period of measurement. Strata 1 and 2 derived moisture from both rainfall and seepage from upper topographical sites. This additional source of moisture, together with impedance to profile drainage and the high moisture holding capacities of the soils, maintained soil moisture levels above field capacity throughout most of the period of measurement.

Soil moisture trends in the 15 to 30 cm horizon were similar to those in the surface horizon, except that in Strata 2 and 4 soil moisture was depleted at slightly slower rates. Consequently, during the summer months, moisture levels in the surface horizon of these strata tended to be lower than at the 15 to 30 cm depth.

The average weekly soil temperatures at 7.5 cm depth under partial canopy and in an opening on Stratum 4 are plotted in Figure 8. Temperatures for Stratum 2 were slightly lower but showed similar trends. The data reveal a marked effect of canopy on soil temperature.

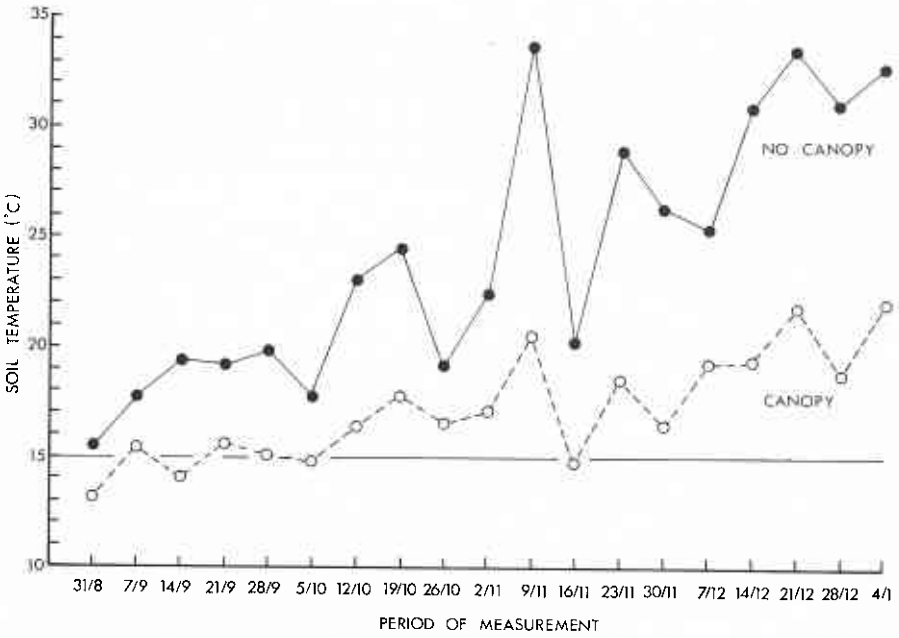

Figure 8
Average weekly soil temperatures from 31 August 1967 to 4 January 1968 at 7.5 cm under canopy and in an opening on Stratum 4. Scarp Road Study Area.

Comparison of the periods during which soil moisture and soil temperature conditions were suitable for infection in the three strata indicated that there were marked differences in their relative susceptibilities. Soil temperature levels under canopy were only slightly above the critical level for infection during the brief periods when soil moisture in Stratum 4 was not limiting. In Strata 1 and 2, however, there were long periods when soil moisture and soil temperature levels both favoured infection. The low moisture contents in

Stratum 4 during the summer months suggest that fungal survival in soil on these sites could be restricted. Soil moisture in Strata 1 and 2 never approached levels which could be considered lethal to *P. cinnamomi.*

This preliminary data suggests that differences in the susceptibility of different sites in the jarrah forest, apparent from field observation of jarrah dieback, could be partially accounted for by different soil moisture and soil temperature regimes. The lack of sampling intensity in both time and space did not permit precise evaluation of the susceptibility of the different sites.

(ii) DETAILED MEASUREMENTS. FEBRUARY 1968 TO APRIL 1969.

Procedure

Rainfall—Weekly rainfall was recorded at three open positions in the experimental area.

Soil moisture—Ten 40 m by 20 m plots were located on the experimental area. Three plots were located in Stratum 1, two plots were located in each of the intermediate sites (Strata 2 and 3) and three plots were located in Stratum 4. The plots were selected with longitudinal axes oriented along the contour Four soil samples were taken for gravimetric determination of moisture content from the 0 to 15 cm horizon in each plot at randomly located positions. The 15 to 30 cm horizon was not sampled, as the presence of massive ironstone boulders on some sites prevented unbiased sampling. Sampling was continued at weekly intervals throughout the measurement period except on plots located in Stratum 1, where sampling was discontinued during the winter months when free water occurred on the surface.

Soil moisture content was determined by oven drying at 105°C. While the soils remained moist, samples were collected with a reinforced King tube. When the soils were dry a specially reinforced soil auger was used. "Field capacity" of the freely drained soils in Sites 3 and 4 was determined by averaging the soil moisture values for the eight-week period in spring, from August 22 to October 10. The "field capacity" of the soils of the two lower sites was obtained by determining the soil moisture content after 48 hours free drainage from a saturated condition in the laboratory.

The moisture characteristic curves of soils from Strata 4 and 1 were determined using the pressure membrane apparatus.

Soil temperature—(a) Continuous measurements—Continuous recording double probe soil thermographs were located in Strata 1 and 4. At each site the probes were installed at 7.5 cm depth, either under canopy or in an opening in the forest. Standard glass soil thermometers were inserted at each probe position to check thermograph accuracy. Check readings were taken weekly at 10 a.m., 12 noon, 2 p.m., and 4 p.m., except during the winter months when readings were taken weekly at 10 a.m. and 2 p.m. During the spring months soil temperatures at 15 cm depth at the probe positions were measured weekly with dial-type metal thermometers.

At the installation site on Stratum 4, probes were located under different canopy covers—complete canopy and no canopy. It was impossible to locate the two probes on Stratum 1 under markedly different canopies and so one probe was located under partial canopy and the other in a partial opening.

(b) Weekly measurement of surface soil temperature—Soil temperatures at 7.5 cm depth were measured on six of the moisture content plots, weekly at 10 a.m., 12 noon, 2 p.m., and 4 p.m. with dial-type metal thermometers.

The thermometers were calibrated against standard soil thermometers and read at randomly located points. The six plots covered the range of moisture conditions and vegetation types represented in the experimental area.

(c) Weekly measurement at depth—Over the spring months soil temperatures at 22.5 cm and 30 cm were recorded on Stratum 4 at two positions, under canopy and in an opening. Temperatures were measured with metal thermometers inserted horizontally into the side of small pits, which were covered between measurements with thick polystyrene sheets.

Results

Rainfall—Recordings at the experimental area during 1968 (Fig. 9) corresponded closely to the rainfall measured at Dwellingup. Since the study area was within 8 kilometres of this centre the rainfall during 1968 can be compared to the long term rainfall recordings at Dwellingup. The annual rainfall received on the study area was 213 mm above the average for Dwellingup. Autumn rainfall was also above average in both March and April. October rainfall was above average but, apart from 10 mm recorded in the week ending November 21, no significant rain fell after October 31. November rainfall was slightly below average.

Soil moisture—Weekly mean soil moistures of each stratum, with levels corresponding to field capacity, are plotted in Figure 9.

Moisture trends in Strata 3 and 4 were similar. Values did not reach field capacity until April 11, after which they remained at approximately this level until the end of October. From October to April, soil moisture remained below field capacity. In both strata, soil moisture levels were approximately equivalent to wilting point by the first week in December.

Soil moisture in Stratum 1 remained consistently above field capacity from March 21 until January 30. The soil moisture data from Stratum 2 were extremely variable, reflecting the transitional nature of this zone. Moisture levels in this stratum were above or at field capacity levels from April 11, 1968 to November 21, 1968.

Soil temperature—(a) Continuous measurement—The mean difference between thermograph readings and the check thermometers was calculated for six week periods throughout the period of measurement. It rarely exceeded 1°C and was frequently less than 0.4°C. When the mean difference exceeded 0.4°C, the thermographs over the particular six week period were adjusted by correcting the soil temperatures at two-hourly intervals over the particular period of measurement.

Weekly readings of soil temperature at 15 cm depth at the two probe positions located in Stratum 1 were used to determine relationships between temperatures at 7.5 cm and 15 cm under each canopy condition. Equations for the relationships were—

$$\text{Canopy present: } Y = 3.5 + 0.69X$$

$$\text{Canopy absent: } Y = 7.0 + 0.47X$$

where Y = temp. at 15.0 cm and X = temp. at 7.5 cm.

These equations were used to estimate the temperature at 15.0 cm at each of the probe positions, for two-hourly intervals over the period of measurement. Data from the continuous recording thermographs were used to calculate the number of hours per week the temperature was above the critical level for mycelial growth (12°C), infection (15°C) and significant infection

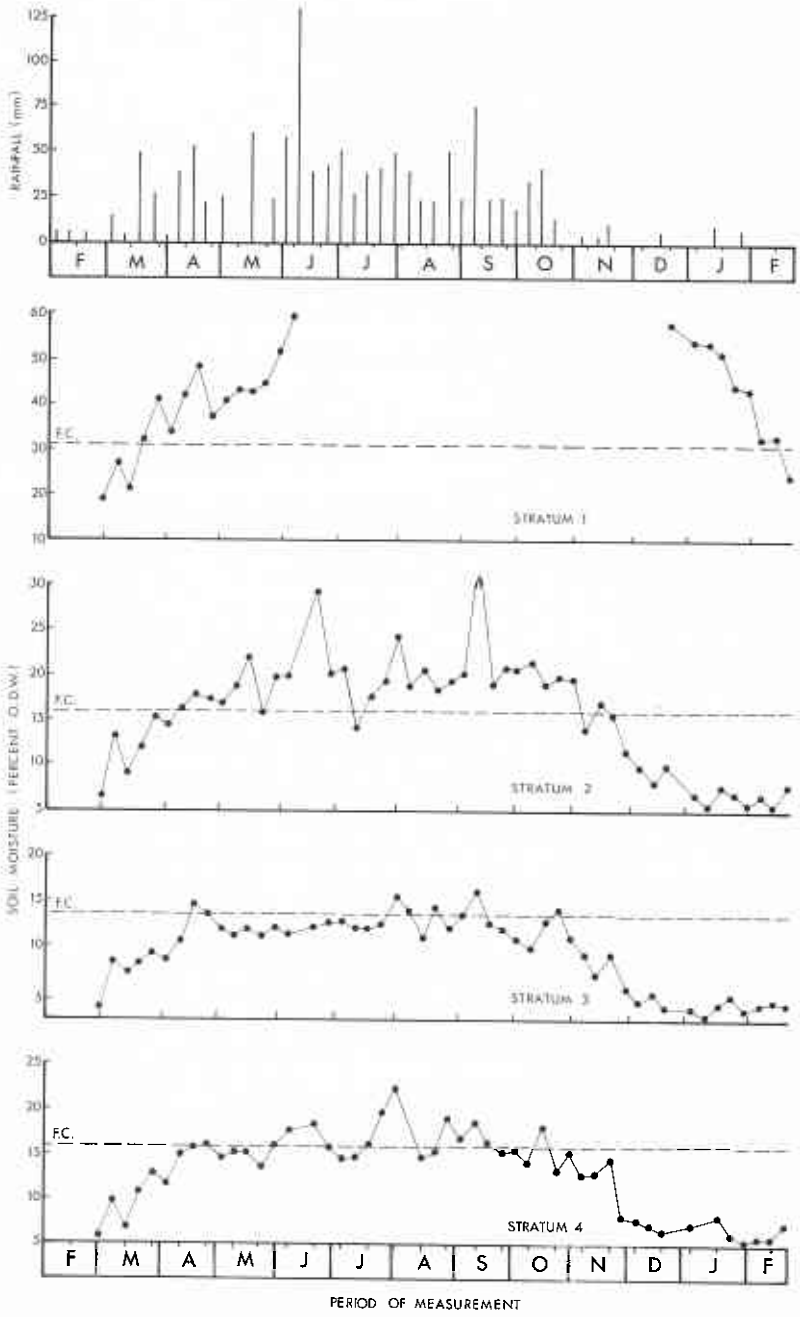

Figure 9
Weekly rainfall and soil moisture levels during 1968-1969. Scarp Road Study Area.

(18°C) (Figs. 10, 11). Data from only one of the probes located in Stratum 1 are plotted in Figures 10 and 11 as the readings of the two probes were not significantly different.

Hours per week above 12°C at 7.5 cm—Soil temperatures were rarely continuously below 12°C throughout the period of measurement. In all three sites (Fig. 10) temperatures were above 12°C for considerable periods when soil moisture levels were above field capacity. In autumn, soil temperatures remained above 12°C for shorter periods in Stratum 4 open canopy than in the other two sites, indicating greater diurnal fluctuation in soil temperatures at this site. During the winter months, the hours per week above 12°C in the three sites were similar, although there were slightly longer periods when soil temperatures remained above 12°C in the canopy-covered sites in Stratum 1. During the spring months the position was reversed, although the differences were not great. Comparison of this graph with the rainfall graph (Fig. 9) shows that soil temperatures were depressed when there was excessive rainfall.

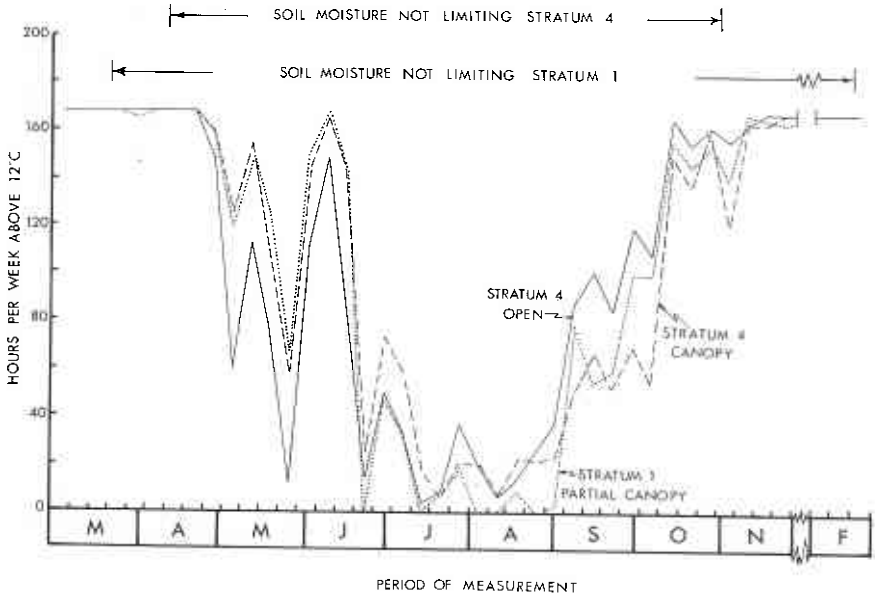

Figure 10
Number of hours per week soil temperatures at 7.5 cm were above 12°C at three locations at the Scarp Road Study Area.

Hours per week above 15°C—Soil temperatures were rapidly depressed below 15°C in all three sites once heavy and consistent rainfall occurred in late autumn (Fig. 11b). Rain falling on March 7 did not cause soil temperatures to fall below 15°C on any of the sites. Rain falling on 15th, 16th and 17th of March caused soil temperatures to be depressed for significantly longer periods under canopy on Stratum 4 than in the other two sites (Table 1). Similarly, rainfall on March 27 and March 28 caused the greatest temperature depression on the site with canopy.

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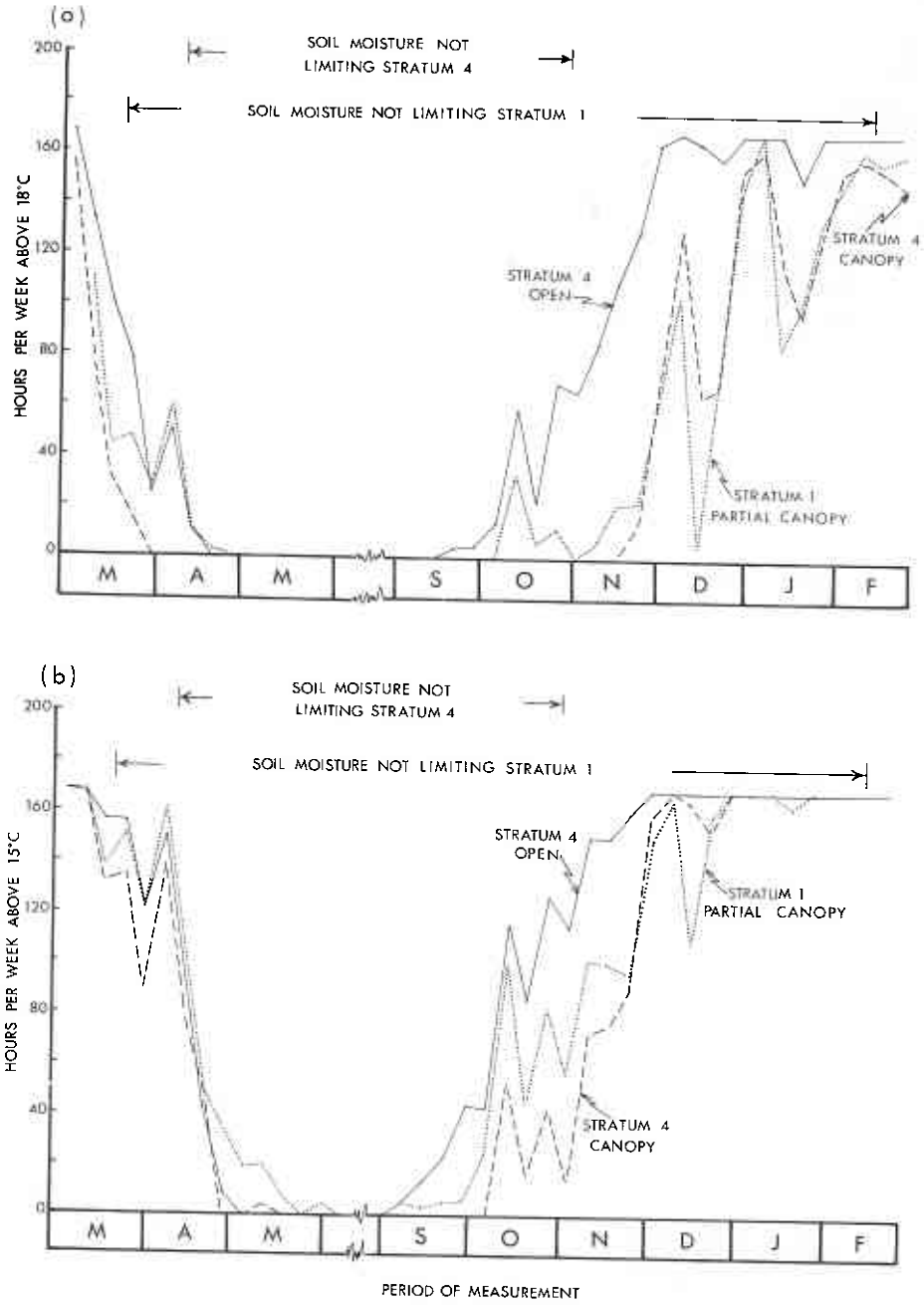


Figure 11
Number of hours per week soil temperatures at 7.5 cm were (a) above 18°C and (b) above 15°C, at three locations at the Scarp Road Study Area during 1968.

During the winter months, temperatures were consistently below 15°C on all sites. Soil temperatures commenced to rise above 15°C in the week ending on September 4, in open sites, and October 9 under canopy in Stratum 4. In spring there were significantly longer periods during which soil temperatures were above 15°C in open sites than under canopy. Rain falling on November 17 and 18 depressed soil temperature for significantly longer periods under canopy than on the other two sites (Table 1). Soil temperatures were continuously above 15°C throughout summer.

TABLE 1

Hours per day in which temperature at depth 7·5 cm exceeded 15°C under three site conditions.

Date	Stratum 4 Opening	Stratum 4 Canopy	Stratum 1 Partial Canopy
March 16	24	17	24
March 17	17	10	13
March 18	24	10	15
March 26	24	24	24
March 27	15	0	12
March 28	12	5	11
November 18	21	7	17
November 19	24	4	4
November 20	15	4	10
November 21	20	5	9

The periods during the year when soil moisture and soil temperatures were suitable for infection on the four strata were markedly different. Although the moister conditions of Stratum 1 had a cooling effect, there were still long periods during which conditions were suitable for infection. Canopy cover on Strata 3 and 4 decreased the periods when conditions for infection were suitable in spring, but not in autumn. When short, heavy showers occurred in early autumn and late spring, however, soil temperatures under canopy were less favourable for infection than soil temperatures in an opening.

Hours per week above 18°C—The number of hours per week during which soil temperatures remained above 18°C in autumn were distinctly different between the three sites (Fig. 11a). Temperatures were continuously below 18°C by the beginning of March under canopy in Stratum 4 but there were significant periods above 18°C in the other two sites, in mid April. Rainfall in the weeks ending March 7 and March 21 depressed temperatures below 18°C in the canopy situation for longer periods than in the other two sites. Soil temperatures remained continuously below 18°C in all sites throughout the winter months.

Soil temperatures began to rise above 18°C in mid-September and the first week of October, at open sites in Strata 4 and 1 respectively, but there were no periods when the soil temperatures were above 18°C under canopy until the fourth week in November. Short, heavy showers in early autumn and late spring depressed soil temperatures below 18°C for longer periods under canopy than in the open.

Soil temperatures did not remain continuously above 18°C on Stratum 4 under canopy and Stratum 1 throughout the summer months. Rain falling in January caused soil temperatures to be depressed for longer periods below 18°C in these two situations than on Stratum 4 in the open site.

The periods during the year when soil moisture was not limiting and soil temperatures were above 18°C on the four strata were markedly different (Fig. 11a). The higher soil moisture levels of Stratum 1 had a cooling effect but there were still long periods during which soil moisture was not limiting and soil temperature was above 18°C. Under canopy on Stratum 4 there were no periods when soil moisture was not limiting and temperatures were above 18°C. However, soil temperatures in an opening on Stratum 4 were above 18°C for brief periods in autumn and considerable periods in spring when soil moisture levels were not limiting. Short, heavy showers in early autumn and late spring depressed soil temperatures below 18°C for longer periods under canopy than in an opening. There were no heavy falls of rain during the summer months and hence there was no opportunity to examine the effect of heavy summer showers on the number of hours soil temperatures were above 18°C in each of the sites.

Hours per week above 15°C and 18°C at 15 cm depth—Soil temperatures at 15 cm under an opening in the canopy commenced to rise above 15°C and 18°C in the second week of September and the second week of October, respectively (Fig. 12).

Under canopy, however, although the soil temperature gradient with depth was less, soil temperatures remained continuously below 18°C throughout the period of measurement and were only above 15°C for brief periods.

(b) Weekly measurements at 7.5 cm depth—The weekly soil temperature measurement at 10 a.m. and 2 p.m. on the temperature plots in Strata 1, 2, 3 and 4 provided the same trends as for the continuous record. Sampling intensity was not adequate to show the significance of differences during the critical periods of the year and none of the plots sampled had sufficient canopy cover to demonstrate the effect of canopy on soil temperatures.

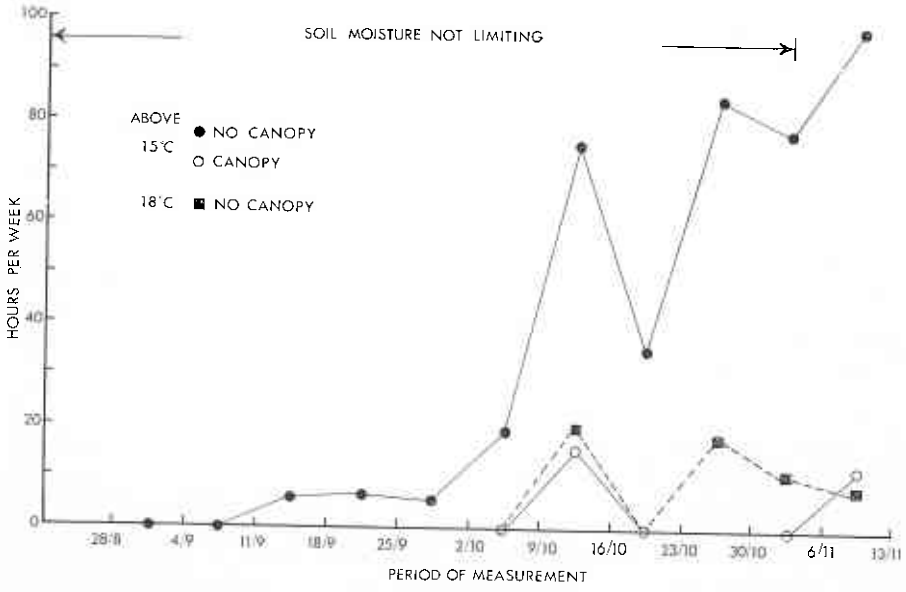


Figure 12

Number of hours per week soil temperatures at 15 cm depth were above 15°C and 18°C under canopy and in an opening at the Scarp Road Study Area during 1963.

(c) Weekly measurements at 22.5 and 30.0 cm depth—Weekly soil temperatures recorded at 4 p.m. at 22.5 and 30.0 cm depth on sites adjacent to the continuously reading station of Stratum 4 are illustrated in Figure 13. The temperature gradient with depth was greater in the open situation than under canopy.

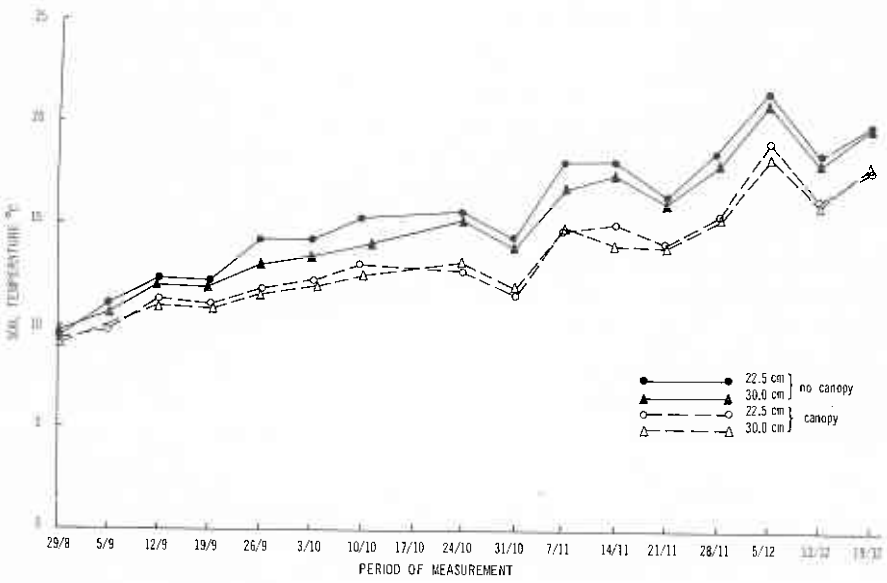


Figure 13
Weekly soil temperatures at 22.5 cm and 30.0 cm depth under canopy and in an opening at the Scarp Road Study Area during spring 1968.

Although the difference between the two sites was less with increasing depth, it was none-the-less of possible significance in relation to the critical temperatures for *P. cinnamomi* activity.

Discussion

There are three significantly different moisture zones in the experimental area—a very "wet" zone located in the valley bottom (Stratum 1), a "dry" zone on the upper topographical sites (Strata 3 and 4) and an intermediate zone between the two extremes (Stratum 2). The moisture holding capacities of the soils are high in the lowest stratum, low in the upper two strata and intermediate in Stratum 2.

Soil temperatures were affected by canopy cover, soil moisture and rainfall. Significant differences between sites can be demonstrated by continuous sampling but not by weekly point sampling.

When soil temperature and soil moisture data from the different sites are integrated (Figs. 10, 11, 12, 13), large differences in the relative susceptibility of different sites are apparent. Although the effect of complete canopy cover in Stratum 1 was not tested, it is reasonable to assume that the persistence of high soil moisture levels into mid-summer compensated for any depressive effect of soil moisture on soil temperatures. Therefore, in the lowest strata,

even under conditions of full canopy cover, there would be long periods when soil moisture and soil temperature conditions would be expected to be suitable for infection by *P. cinnamomi*. The susceptibility of Stratum 2 varies markedly, due to rapid changes in the soil moisture regime over short distances within the stratum. In the lower section of Stratum 2 (see preliminary soil moisture measurements), the level of susceptibilty would be similar to that of Stratum 1, but in the upper sections, susceptibility would be similar to that of Strata 3 and 4. In Strata 3 and 4 the maintenance of soil moisture levels suitable for infection was dependent on the input of moisture from rainfall. Susceptibility in these strata was influenced by the degree of canopy cover. In all periods when soil moisture was not limiting, except in late autumn when heavy and consistent rainfall occurred, soil temperatures were below the critical level for infection for longer periods in sites with canopy cover, than in sites without canopy cover. A relatively greater volume of roots is susceptible to infection on sites without canopy cover because the difference in soil temperature levels between the two cover types was still apparent at depths of 22.5 and 30.0 cm. Strata 3 and 4 were relatively more susceptible in spring than autumn because autumn rains had a depressive effect on soil temperature.

Soil moisture values on Strata 3 and 4 in summer approached levels which could be critical for survival of the fungus. Soil moisture values in Strata 1 and 2, however, did not approach levels which could be considered lethal to *P. cinnamomi*.

2. SOIL MOISTURE TRENDS UNDER HIGH QUALITY POLE STANDS

Studies 1 (i) and 1 (ii) at the Scarp Road experimental site indicated that moisture in soils located in upper topographical sites falls below "field capacity" before the soil temperature under canopy rises significantly above the critical level for infection. Soil moisture measurements, however, were restricted to the 0 to 15.0 cm horizon. The susceptibilty of forest growing on upper topographical sites is important, because these sites carry the highest quality forest. Therefore, a further study was conducted to provide information on soil moisture trends under even-aged high quality jarrah stands growing on upper topographical sites.

The Study Area

The experiment was located 7.5 km north-east of Dwellingup. The transect was selected on the north-east side of a flat-topped hill, which dropped to a saddle on the north-east and a small stream on the south-east side. A profile of the north-east slope of the hill showing plot location and soil characteristics is presented as Figure 14. The stand is illustrated in Figure 15.

Procedure

Four 40 m by 20 m plots were located along a transect from ridge top to the saddle (Fig. 14) and orientated so that their longitudinal axes were parallel with the contour. Soil moisture content was sampled at six randomly located positions from the 0 to 15 cm horizon on each plot over the period August 20, 1968 to December 17, 1968. Sampling of the 15 to 30 cm horizon was carried out from September 17, 1968 to December 17, 1968. The moisture content at both sampling depths on all plots was also sampled on February 2, 1969 to obtain an estimate of soil moisture levels during the period of maximum moisture stress. Samples were taken weekly except where indicated. Soil moisture content was determined gravimetrically.

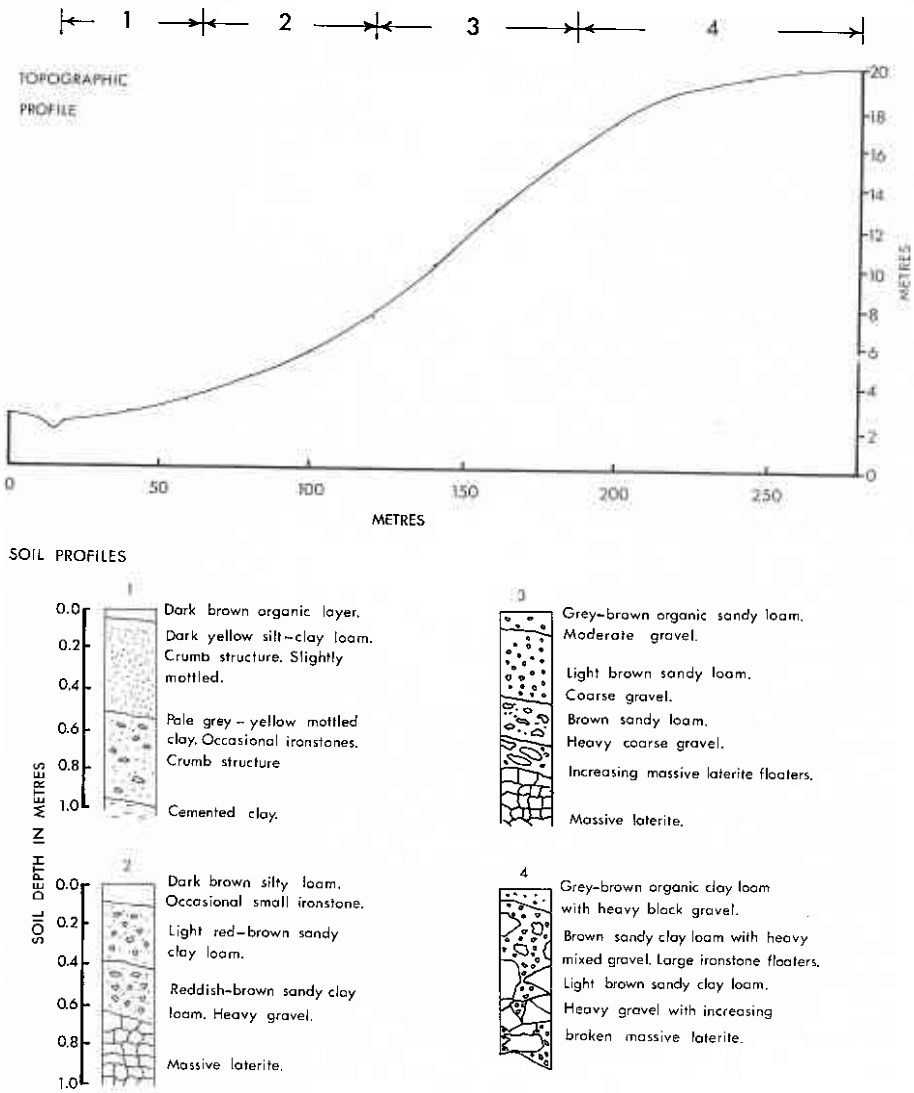


Figure 14
Topographic and soil profiles. Study Area 2.

The moisture content corresponding to field capacity was determined by averaging the weekly moisture values for each site and horizon over the periods August 29 to October 8 and September 17 to October 8 for the 0 to 15 cm and 15 to 30 cm depths, respectively.

Results

Apart from 13 mm recorded in November, there was no significant rainfall after October 22. Sixteen millimetres of precipitation were recorded at Dwellingup in mid-January.

Figure 15
Jarrah pole stand. Study Area 2.

Field capacity levels for each plot and horizon, are plotted with the corresponding moisture content data in Figure 16. Field capacity levels in plots 1, 2 and 3 were approximately the same, but the value in plot 4 was significantly higher.

Soil moisture levels were consistently below field capacity in the 0 to 15 cm horizons in all plots, as early as the first week in October (Fig. 16). Although

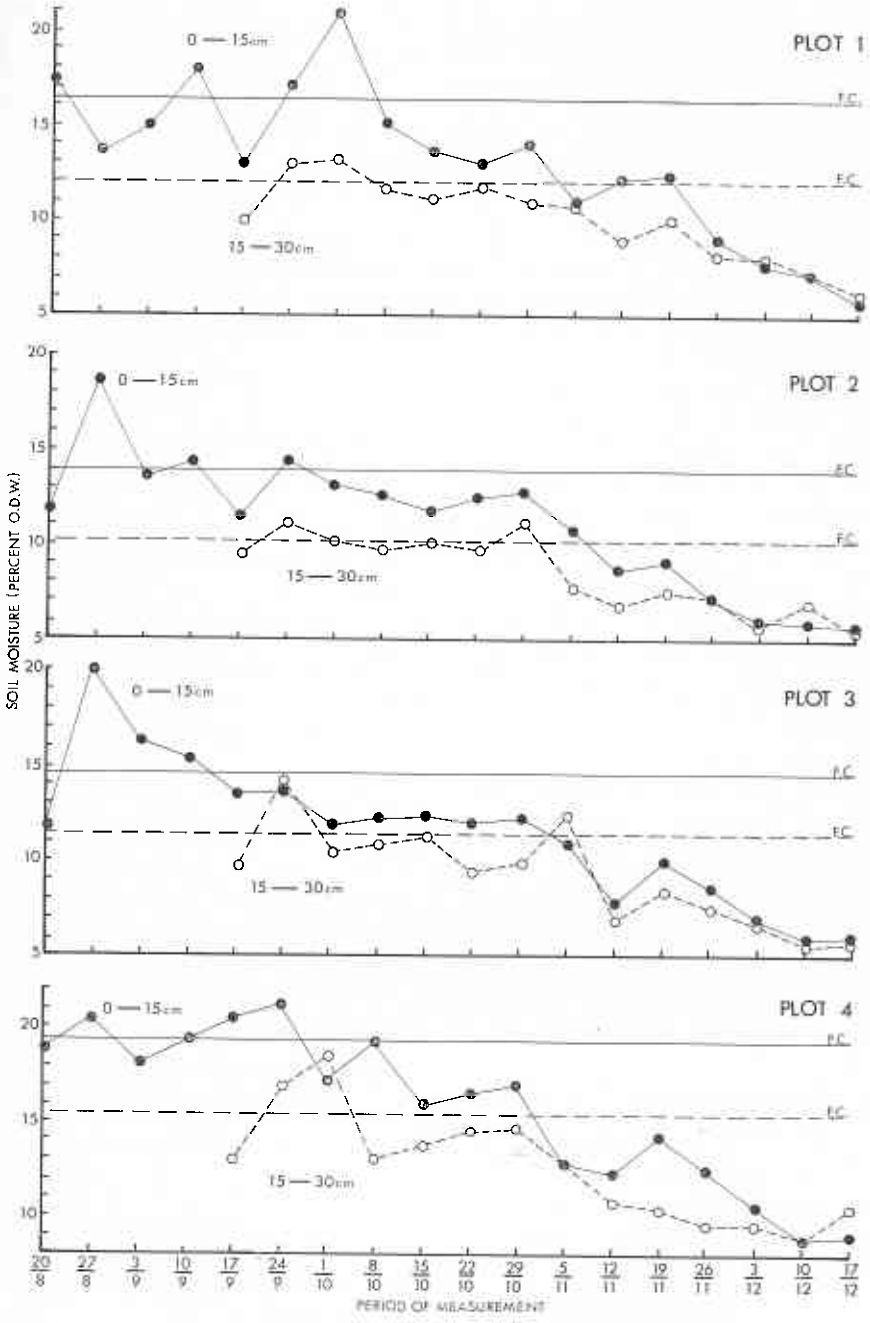


Figure 16

Weekly soil moisture levels in the 0-15 cm and 15-30 cm horizon under high quality jarrah pole stands growing on upper topographical sites during spring 1968 and summer 1968-69.

soil moisture data for the 15 to 30 cm depth were less variable than at the surface, the trends were similar. Moisture levels remained at approximately field capacity in plots 2 and 4 until the end of October but by the first week in November they had fallen significantly below field capacity. In plots 1 and 3, soil moisture remained at approximately field capacity until the first week in November. The rapid fall in soil moisture after the first week in November in plot 3 suggests that sampling bias was responsible for the higher soil moisture levels recorded in that week. The maintenance of soil moisture at approximately field capacity levels in plot 1, however, cannot be attributed to sampling error and probably reflects slight impedance and/or seepage of water from upper topographical situations on this site.

Rainfall in the week ending November 19 caused soil moisture to be higher in plots 1, 2 and 3 but the levels were still significantly below field capacity at the time of measurement. Soil moisture levels on February 2, 1969 were, in both horizons and in all plots, approximately the same as those recorded on December 17, indicating that the soils had reached maximum depletion by this date.

Discussion

The results of this study confirm the conclusions on the soil moisture regime of upper topographical sites in the jarrah forest summarised in Study 1 (ii) and indicate that variation in soil moisture over a range of slope positions in a uniform pole stand of high quality is minimal. The maintenance of soil moisture levels equivalent to field capacity on these sites is dependent on the consistent input of moisture from rainfall. The soil moisture trends in the 15 to 30 cm depth are particularly significant, since they indicate that these horizons fall below field capacity at the same time as, or soon after, the surface horizons.

The soil temperature measurements of Study 1 (ii) are considered applicable to this study, since the rainfall and soil moisture trends in both experimental areas were practically identical. In the absence of information on the soil moisture trends in the 15 to 30 cm horizon in Study 1 (ii), it was impossible to calculate the number of hours during which conditions were suitable for infection at a depth of 15 cm. The results of the present study, however, when integrated with the temperature data at 15 cm of Study 1 (ii), indicate that it is unlikely that significant infection occurs at this depth in upper topographical sites. The decrease in soil temperature with depth is not compensated for by an excessive prolongation of favourable soil moisture levels.

Comparison of the soil moisture levels at the end of December with those at the beginning of February shows that minimum soil moisture levels in the surface horizons are reached early in summer in freely drained jarrah forest soils. In the absence of precise data on the effect of moisture on survival of *P. cinnamomi* in soils of different textures, it is impossible to determine if the minimum soil moisture levels reached in this experiment were below the critical level for survival.

3. THE INFLUENCE OF ASPECT

Roth and Kuhlman (1966) demonstrated in Douglas-fir forests in Oregon that aspect had an important effect on the soil moisture and temperature regimes of different sites. They found that sites with southern aspects had

soil temperature regimes which were suitable for *P. cinnamomi* infection, while sites with northerly aspects did not. Soil moisture levels on southern sites were too low for infection, while on northern sites soil moisture remained above the critical level for most of the year.

Studies 1 (i) and 1 (ii) demonstrated that canopy had a significant effect on soil temperatures during the critical spring months when soil moisture levels were suitable for infection. However, as measurements were made on neutral or southerly aspects, a further study was designed to determine the effect of aspect on soil temperatures during the spring months.

Location

The experiment was located on the northern and southern slopes of the experimental area described in Study 2.

Procedure

Two, 10 metre square plots were located equidistant from the ridge top, in a mid-slope position, on the southern and northern slopes. The slope angles were 4°30′ and 6°30′ on the northern and southern plots, respectively.

The vegetation and litter were removed from both plots and from the surrounding area so that the plots were not shaded between 6 a.m. and 6 p.m. Soil temperatures at 7.5 cm and 15 cm were recorded at each site with calibrated dial-type metal thermometers at three randomly located positions. A small pit 0.6 m by 0.6 m was dug in the centre of each plot. Soil temperatures at 22.5 cm were measured by inserting thermometers horizontally into the sides of the pits at this depth. The pits were covered with thick polystyrene sheeting between measurements. Temperatures were recorded weekly at 1.30 p.m. over the period September 3 to December 17, 1968. Soil temperatures for the 7.5 cm and 15 cm depths were analysed by analysis of variance.

Results

Weekly mean temperatures at three sampling depths on each site are plotted in Figure 17. Soil temperatures at 7.5 cm were significantly different on the two sites in four of the eight weeks during which soil moisture levels were suitable for infection (assuming that soil moisture levels fell below the critical minimum after October 29—see Study 2). Soil temperatures at 15 cm depth were significantly different on the two sites in only two of the eight weeks during which soil moisture levels were suitable for infection. The significance of the difference in the soil temperatures at 22.5 cm on the northern and southern sites could not be determined, but it can be assumed that the trend of progressively less difference between the sites with increasing depth is continued. The effect of removing the canopy was to cause the soil temperatures at 7.5 cm and 15.0 cm to be above the critical level for most of the period of measurement.

Discussion

Jacobs (1955) presented data collected at Mt. Stromlo, in the Australian Capital Territory, showing influence of aspect and slope on the absorption of solar radiation. The total daily energy received in October on level ground is 684 calories per square centimetre. On northern and southern slopes of 10° the total energy is 721 and 602 calories per square centimetre, respectively. Jacobs concluded that differences due to aspect and slope are highly significant in determining soil temperatures. Apart from a few deeply dissected

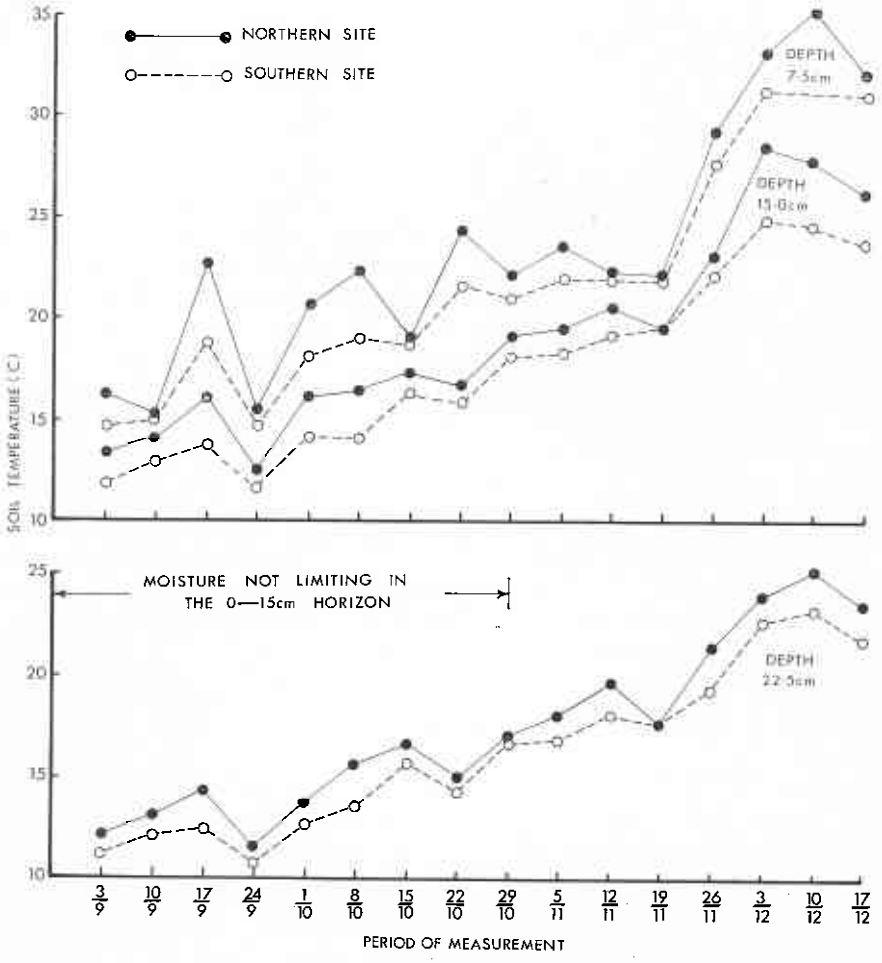


Figure 17
Weekly soil temperature trends on northern and southern aspects.

river valleys, slope angles in the jarrah forest area rarely exceed 10° and are usually less than 6°. Thus it would be expected that differences in soil temperatures due to aspects in the jarrah forest would be somewhat less than is indicated by Jacobs.

This study demonstrates that soil temperatures are higher on northern aspects and it is likely that soil temperatures on these sites would rise above the critical level for infection earlier in spring than on southern sites.

The characteristic pattern of spread of *P. cinnamomi* infections, that is upslope from moist sites, makes the effect of aspect more important. On northern slopes, because the fungus destroys the vegetation as it progresses, the sun's rays penetrate ahead of existing infection, uninterrupted by canopy, and would produce higher than normal temperatures in the infection zone.

Soil moisture measurements were not recorded in conjunction with this experiment and it is possible that the temperature effect of aspect could be offset by more rapid drying rates on northern sites.

P. cinnamomi infection may be found on all aspects (Podger, 1968). There are no data, however, on the severity of the disease on different aspects. Aspect does affect site susceptibility but this factor is not as important as moisture regime, canopy and litter cover in determining the length of the periods during which soil temperature and moisture are suitable for fungal activity.

4. THE EFFECTS OF LITTER AND CANOPY ON SOIL TEMPERATURE AND SOIL MOISTURE TRENDS UNDER HIGH QUALITY JARRAH POLE STANDS

The Scarp Road study provided data on soil moisture and soil temperature trends under mature "group selection" forest over a range of site conditions but this study area was not representative of the higher quality even-aged jarrah regrowth stands. Study 2 provided data on soil moisture trends under high quality even-age stands but soil temperatures were not measured. Both studies were conducted in areas which had been regularly prescription burnt and, consequently, the litter cover was sparse. Prescribed burning is an established management practice in the forest (Peet, 1967), and it has proved invaluable as a means of protecting the forest from uncontrolled fires. It does, however, reduce the extent of soil cover and causes marked changes in the understorey layer (Figs. 18 and 19). Thus, it was necessary to determine if burning significantly increased the susceptibility of the forest to *P. cinnamomi*.

The Scarp Road study area had been subjected to heavy selective logging over a number of years. This silvicultural treatment, which has been standard throughout the jarrah forest, creates openings in the canopy. Comparison of the soil temperature regimes of this type of forest with those of even-aged stands was necessary to evaluate the effect of "group selection" cutting on susceptibility of the forest to *P. cinnamomi*.

The soil temperature and moisture regimes under even-aged pole stands and the effect of prescribed burning on these regimes were determined in the following experiment.

The Study Area

The study area was located 16 km south-east of Dwellingup in Amphion Block, Compartment 6. The forest in this compartment was a dense, even-aged pole stand with a mean top height of 20.7 m and a basal area of 33.5 square metres per hectare (Fig. 20). The compartment had been protected from fire for a period of approximately 37 years (Fig. 18). This was in contrast to the remainder of the forest which was burnt regularly on a 4-6 year cycle (Fig. 19).

The experimental area was situated on an upper slope and hilltop. The landscape was convex in profile and sloped 3° to the south-west. Soils were freely drained lateritic podzolics derived from ancient granitic parent material. They were heavier than the gravel soils of Study 1 and massive ironstone floaters were not present in the surface horizons.

Eucalyptus calophylla was practically absent from the overstorey and did not occur on the experimental plots. *Banksia grandis* occurred in dense stands in the compartment but was not present in the experimental area. The shrub

Figure 18
Litter layer in forest unburnt for approximately 40 years.

layer was discontinuous. *Macrozamia riedlei* and *Pteridium esculentum* (Forst.) occurred abundantly and *Clematis pubescens* (Hueg.), *Hibbertia montana* (Steud) and *Leucopogon verticillatus* (R.Br.) occurred occasionally.

Procedure

The experiment had a randomised block design with five blocks and two treatments. Ten 24 m by 12 m paired plots were established in the experi-

Figure 19
Bare, blackened soil following prescribed burn.

mental area at subjectively located points. Two samples of the litter were taken at points immediately adjacent to each plot and the average litter weight per hectare was calculated.

The litter layer and all shrubs on one randomly chosen plot in each pair were removed to simulate the effect of burning. It was not possible to burn

Figure 20
Jarrah pole stand. Study Area 4.

the area because of the high moisture content of the litter layer. The litter was removed by raking and all shrubs were cut off at ground level with secateurs. Each plot was subdivided so that each block consisted of two adjacent 12 m square plots.

Rainfall—Weekly rainfall was recorded with gauges located at a fixed position on one of the subplots of one block and with two gauges which were randomly located each week on remaining subplots. Rainfall was measured in a clearing 0.4 km from the experimental area from October 23, 1968 onwards.

Soil Moisture—Soil samples of the 0 to 15.0 cm horizons were taken at two randomly located positions in each of the two extreme subplots of each block. Soil moisture content was determined by gravimetric methods. Field capacity was determined by averaging the weekly means for the eight week period from August 21, 1968 to October 16, 1968. The soil moisture content corresponding to wilting point was determined by the method of Williams and Marshall (1942).

Soil Temperature—Soil temperatures were measured in the two central subplots of each block.

(a) Continuous Measurements—A continuously recording double probe soil thermograph was installed on one of the blocks with probes located under litter and bare soil respectively at 7.5 cm depth. Weekly check readings were taken at each probe with calibrated dial-type metal thermometers.

(b) Weekly Measurements—Soil temperature at 7.5 cm depth was recorded at two randomly located positions in the two central subplots of each block with calibrated dial-type metal thermometers. One standard soil thermometer was installed at a randomly located position in each of the subplots at a depth of 7.5 cm. Soil temperature at 15.0 cm depth was recorded with dial-type metal

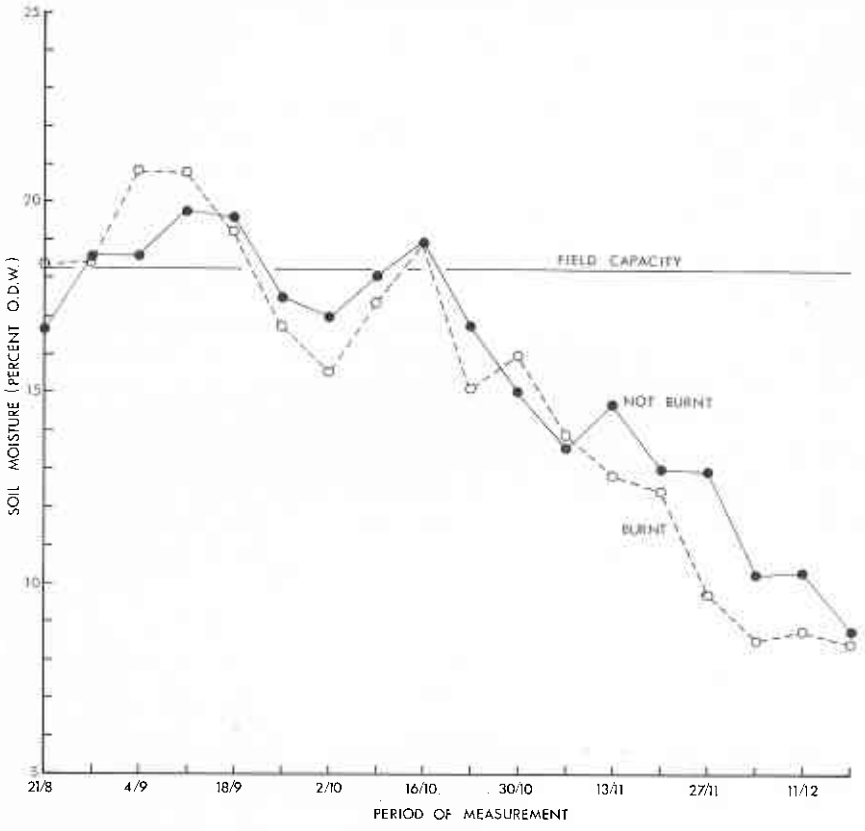


Figure 21
Weekly soil moisture levels in the 0-15 cm layer under unburnt and burnt treatments.

thermometers at points immediately adjacent to the standard soil thermometers. Soil temperatures at 22.5 cm depth were recorded with electrical resistance blocks at two randomly located fixed positions in each subplot. Two trenches were dug immediately adjacent to the five blocks. The litter was removed from around one of the trenches. Thick polystyrene sheeting was used to cover the trenches between readings. Temperatures at 30.0 cm depth were recorded by inserting metal thermometers horizontally into the sides of the trenches. All temperature measurements were carried out weekly at 1 p.m.

Results

Litter—The average litter weight measured was 16 tonnes per hectare.

Soil Moisture—The average weekly soil moisture values in both treatments are plotted, in relation to the determined field capacity, in Figure 21. Soil moisture in both treatments was below field capacity briefly at the end of September and beginning of October and consistently after October 23. Litter removal caused soil moisture to fluctuate more in response to rainfall. For the first weeks of measurement the moisture values in plots with litter removed were higher that those with litter present (Fig. 21). During drier periods soil moisture levels were slightly higher in plots with litter intact. Differences in the moisture trends of the two treatments can be explained by the buffering effect of the litter and shrub layers on soil moisture. Rainfall interception is greater and evaporation less from surface horizons in the plots with litter present. Although soil moisture levels were consistently below field capacity after October 23, it is assumed that moisture was not limiting to fungal infection until after October 30, as values were not markedly below field capacity until November 6. Soil moisture reached wilting point by mid December in both treatments.

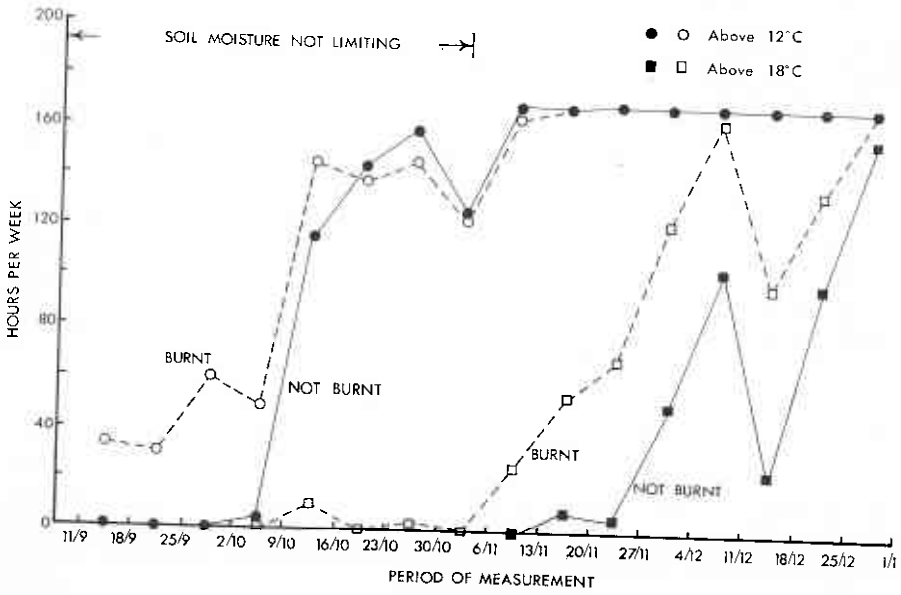


Figure 22

Number of hours per week soil temperatures at 7.5 cm depth were above 12°C and 18°C under unburnt and burnt treatments during spring 1968 and summer 1968-69.

Continuous Soil Temperature Measurement at 7.5 cm—The accuracy of the soil thermograph, as indicated by the weekly check readings, was excellent. The average departure from the check readings was less than 0.4°C and adjustment of the thermograph readings was considered unnecessary.

Data from the soil thermograph were calculated as the number of hours per week the temperature was above the respective critical levels for mycelial growth (12°C), infection (15°C) and significant infection (18°C).

(i) Hours per week above 12°C at 7.5 cm—Soil temperatures commenced to rise significantly above 12°C in early spring (Fig. 22). Initially the temperature was above 12°C for longer periods in the litter removed treatment but, later in the spring, temperatures were above 12°C for longer periods under litter. There were long periods in both treatments during which soil temperatures were above 12°C and soil moisture was not limiting.

(ii) Hours per week above 15°C at 7.5 cm—Soil temperature did not commence to rise significantly above 15°C until October 9 in both treatments. There were significantly longer periods when moisture was not limiting (during which soil temperatures were above 15°C) in the "burnt" treatment (170 hrs.) than in the "unburnt" treatment (23 hrs.). When the soils commenced to dry out, soil temperature rose rapidly and was continuously above 15° in both treatments by the week ending December 6.

(iii) Hours per week above 18°C at 7.5 cm—Soil temperature did not commence to rise significantly above 18°C until the weeks ending November 13 and December 4 in the "burnt" and "unburnt" sites, respectively (Fig. 22). Soil temperatures were above 18°C for a period of 12 hours in the "burnt" site when soil moisture was not limiting, but there was no such overlap in the "unburnt" treatments.

Weekly Soil Temperature Measurements—The mean weekly soil temperatures at 7.5, 15.0 and 22.5 cm are plotted in Figure 23.

The 95 per cent confidence intervals for results at each depth were 0.7°C, 0.4°C and 0.4°C, respectively. Data for soil temperature at 7.5 cm depth represent the means of 10 random measurements on each treatment. Mean weekly soil temperatures recorded at 30.0 cm were not statistically controlled.

Differences in the soil temperature levels under "burnt" and "unburnt" sites were statistically significant but they decreased with depth. Initially, soil temperatures at 15.0 cm were higher in the "unburnt" sites. During the period when soil moisture was not limiting, temperatures at this depth were significantly higher under "burnt" sites on only three occasions. There was no significant difference between the temperatures at 22.5 cm and 30.0 cm in "burnt" and "unburnt" treatments during the period when soil moisture was not limiting to infection.

Discussion

Although the "burnt" treatments were more sensitive to rainfall and evaporation, soil moisture levels in the two treaments were comparable in terms of their effect on fungal pathogenicity. Unseasonal rainfall, however, occurring when soil temperatures are above the critical levels for infection would be less effective in raising soil moisture above the critical limit in "unburnt" plots than in "burnt" plots because of interception by the litter and shrub layer.

The continuous temperature data indicate there were longer periods suitable for infection in the "burnt" plots than "unburnt" plots. Comparison

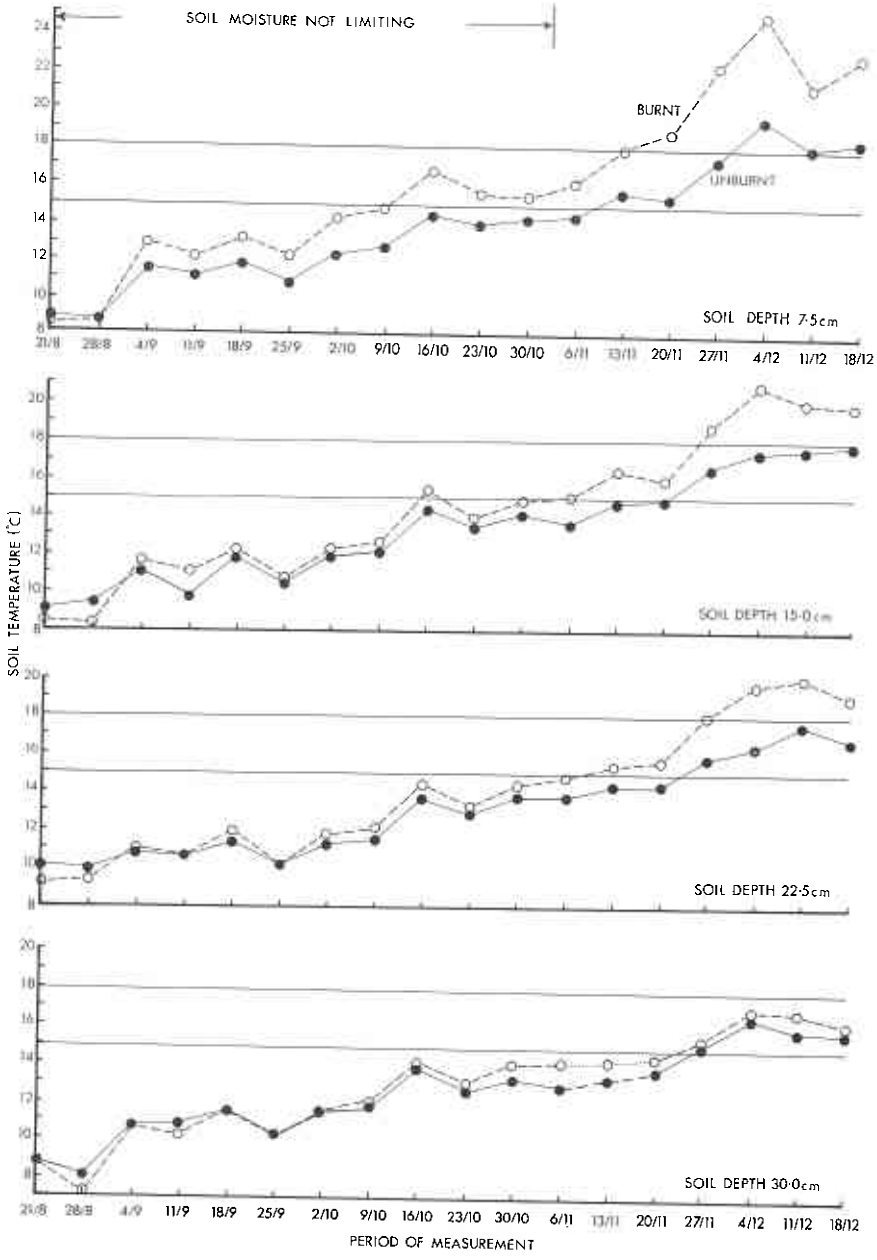


Figure 23

Mean weekly soil temperatures at 7.5 cm, 15.0 cm, 22.5 cm and 30.0 cm depth under unburnt and burnt treatments during spring 1968 and summer 1968-1969.

of the thermograph readings at 1 p.m. with the weekly readings over all plots shows that temperatures for the probe located under the "burnt" plot were slightly below the average for all the "burnt" treatment plots. Hence, it is possible that without this bias the differences between the continuous data for "burnt" and "unburnt" sites would have been greater.

It was impossible to burn at the time the experiment was initiated, and hence the litter and shrub layer were removed artificially. Prescribed burning temporarily removes the shrub and litter layer and causes blackening of the soil surface (Fig. 19). Thus, since the "burnt" plots were not blackened, it would be expected that soil temperature differences between actual burnt an unburnt areas would be greater than those recorded in this experiment. Prescribed burning is carried out throughout the forest on a four to six year rotation, with firing in spring or autumn. Litter fall occurs primarily in the period December to March. Autumn burning would result in no litter during the critical spring months, but the blackening effect would be removed by winter rains and there would be some regeneration of the shrub layer in the interval between autumn burning and spring. The effect of spring burning on *P. cinnamomi* infection would depend, to a degree, on whether burning was carried out prior to, or after, soil moisture levels became critical for infection. The effect of burning on soil temperatures would decrease in succeeding years after burning because of the accretion of a litter layer and the regeneration of shrub species.

Soil moisture approached levels which could be limiting to the fungus at a faster rate on the "burnt" sites, but it is unlikely that the difference would be important in terms of its effect on fungal survival.

During the spring months, soil temperatures were recorded simultaneously at the Scarp Road site (Study 1) and under even-aged pole stand forest. Comparison of the soil temperature regimes of the upper topographical sites at the Scarp Road site (Study 1—Figs. 10, 11, 12 and 13) with the soil temperatures recorded in this study (Figs. 22 and 23) gives some indication of the relative soil temperature regimes of irregular and uniform forest. The soil temperatures in the open position at the Scarp Road site rose above the critical level for infection (15°C) for significant periods in early September but the soil temperatures under the pole stand under both "burnt" and "unburnt" treatments did not reach similar levels until early October. The soil temperature regime of the canopy site on Stratum 4 of the Scarp Road study was similar to that of the pole stand "burnt" treatment but was higher than that of the "unburnt" treatment.

5. COMPARATIVE SOIL MOISTURE AND TEMPERATURE REGIMES OF *P. RADIATA* AND JARRAH STANDS

The experiments described above demonstrated the marked effect of canopy and litter cover on the periods of the year during which soil temperature and soil moisture levels are suitable for infection on freely drained sites. The range of canopy and litter cover sampled in these studies, although representative of the majority of the forest area, did not include areas of dense canopy cover. There were no jarrah forest areas which had dense cover conveniently located in the study area. Hence the effect of maximum canopy cover on the susceptibility to the fungus of freely drained sites in the study

area was determined by comparing soil moisture and temperature regimes of adjacent *Pinus radiata* D. Don and jarrah stands.

Measurement of the soil moisture and temperature regimes of a *P. radiata* stand provided some data on the potential susceptibility of plantations of this species. Newhook (1959) showed that *P. cinnamomi* was responsible for widespread *P. radiata* deaths in shelterbelts in New Zealand. The fungus also occurs in plantations but apparently does not cause widespread mortality. Newhook suggested that the difference in evapotranspiration rates of full and reduced crowns in shelterbelts and plantations, respectively, could be one of the factors responsible for the rapidity of disease development in the shelterbelt situation. Hartigan (1964) has reported dieback and mortality in *P. radiata* plantations in New South Wales associated with *P. cinnamomi*. Although mortality was low, the affected trees were salvaged as the browning, which occurs after fungal attack, "opens the way for blue stain and leads to degrade timber." Both the New Zealand and New South Wales attacks were associated with unusually high rainfall in autumn and spring, respectively.

Batini and Podger (1968) have shown that *P. radiata* and *Pinus pinaster* Ait. deaths in shelterbelts on the Swan Coastal Plain are caused by *P. cinnamomi*. To this date, there have been no reports of *P. radiata* deaths attributable to the pathogen in Western Australian plantations.

The ability of two to five-year-old *P. radiata* and *P. pinaster* to survive on old jarrah dieback sites suggests that, at least on the freely drained jarrah forest soils, *P. cinnamomi* infections are not severe enough to cause significant mortality in these species. Following Newhook's hypothesis, mortality is even less likely to occur in mature plantations because of the decreased evapotranspiration rates of individual forest trees. However, although mortalities have not occurred, and are not likely to occur in mature plantations, it is possible that the fungus could cause severe economic loss by depressing tree growth and timber degrade.

The Study Area

The experimental area was located 21 km east of Dwellingup where a trial plot of *P. radiata* was situated immediately adjacent to poor quality jarrah forest. Both pine and jarrah stands were situated on a sand flat, slightly concave in profile, which sloped gently (1.5°) to the north. The soils were of colluvial origin.

The jarrah stands were of irregular distribution with trees of pile (top height 22.6 m), pole (top height 12.2 m) and sapling (top height 1.8 m) size (Fig. 24). The understorey component was made up predominantly of jarrah saplings. *Banksia grandis* and *Persoonia longifolia* R.Br. occurred infrequently. There was no tall shrub layer and the small shrub layer was discontinuous. Litter was sparse and, although *Dryandra nivea* R.Br formed a dense carpet in some places, there were considerable areas of bare soil.

The pine stand was seven years old with a basal area of 50.5 square metres per hectare and a top height of 9.8 metres (Fig. 25). Complete canopy closure had occurred and the trees had been pruned to 2.5 m stem height. The litter layer was sparse and there were areas of bare soil.

Procedure

One plot (40 m x 20 m) was established on each of the pine and jarrah sites.

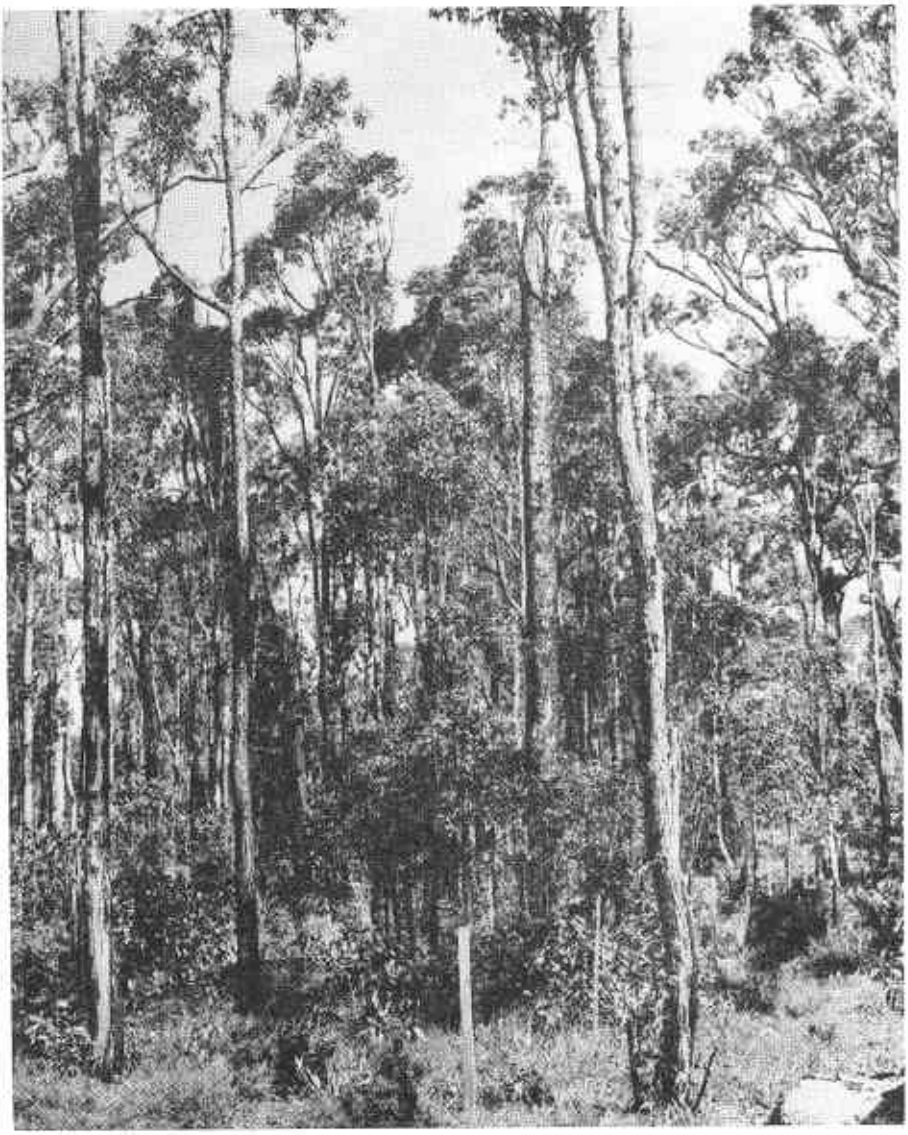


Figure 24
Irregular jarrah pole stand. Study 5.

Rainfall—As for previous studies.

Soil Moisture—The soil moisture content of the 0 to 15.0 cm and 15.0 cm to 30.0 cm horizons was sampled at six randomly located positions in each plot. Moisture contents were determined gravimetrically. The field capacity of the soils of each site and horizon were determined by averaging the respective soil moisture content during periods of average rainfall.

Figure 25
Pinus radiata stand. Study 5.

Soil Temperature—(a) Weekly Measurements—Soil temperature at 7.5 cm and 15.0 cm depths was measured weekly over the period August 21 to December 13, 1968 at 2.30 p.m. with calibrated dial-type metal thermometers, at nine randomly located positions in each plot. The temperature at 22.5 cm and 30.0 cm was determined by inserting dial-type metal thermometers horizontally into the sides of a small pit dug in the centre of each plot. The pits

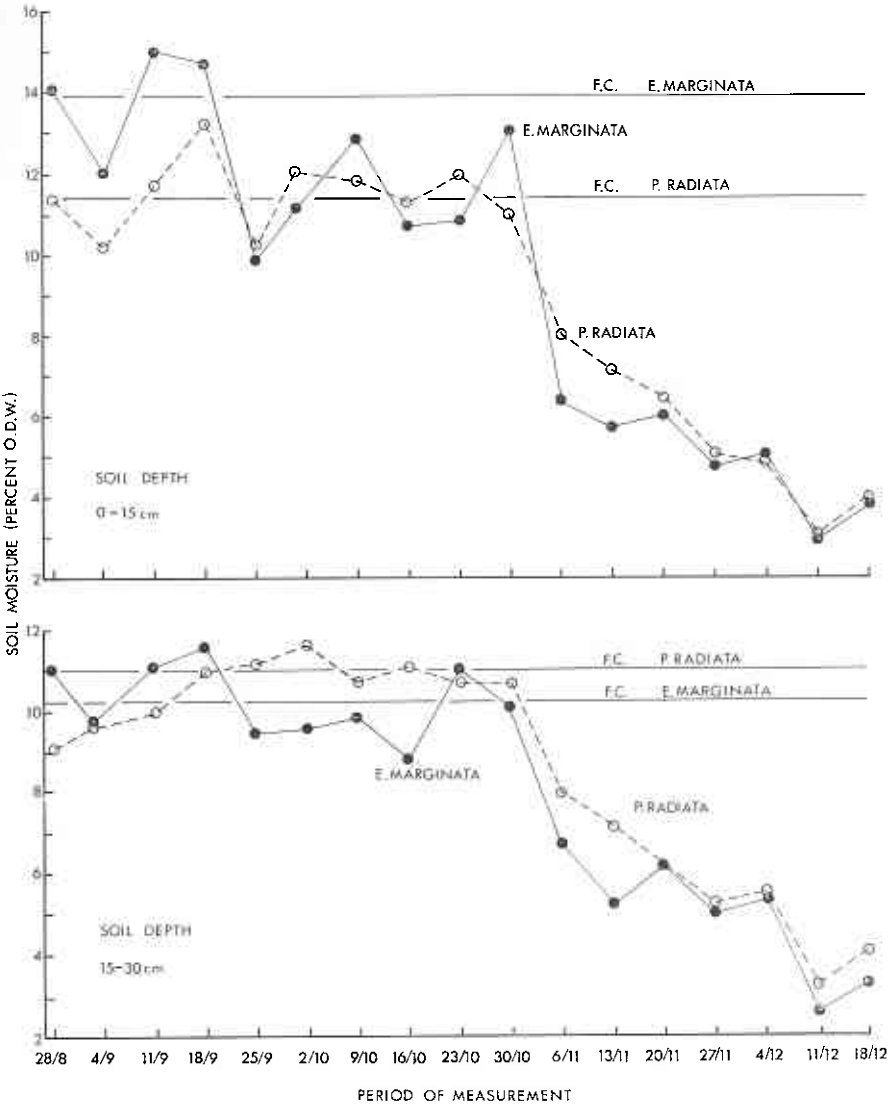


Figure 26
Weekly soil moisture levels in the 0-15 cm and 15-30 cm layers under adjacent *P. radiata* and *E. marginata* stands during spring and summer 1968.

were covered with thick polystyrene sheeting between measurements. Temperature data for the 7.5 cm and 15.0 cm depths were analysed using analysis of variance techniques.

(b) Hourly Measurements—On October 25 soil temperatures at 7.5 cm and 15.0 cm depths were recorded at six randomly located positions at hourly intervals from 10 a.m. to 4 p.m. The temperature data were subjected to analysis of variance.

(c) Continuous Measurement—Soil temperatures at 7.5 cm depth were recorded continuously with soil thermographs over the period October 9 to October 16 and October 16 to October 23, 1968 in the jarrah and pine stands, respectively. Soil temperatures at 7.5 cm and 15.0 cm depth were recorded continuously over the period November 6, 1968 to January 1, 1971 in the pine plot with a double probe soil thermograph. Continuous measurement of soil temperatures over the whole period could not be obtained because of malfunctioning instruments.

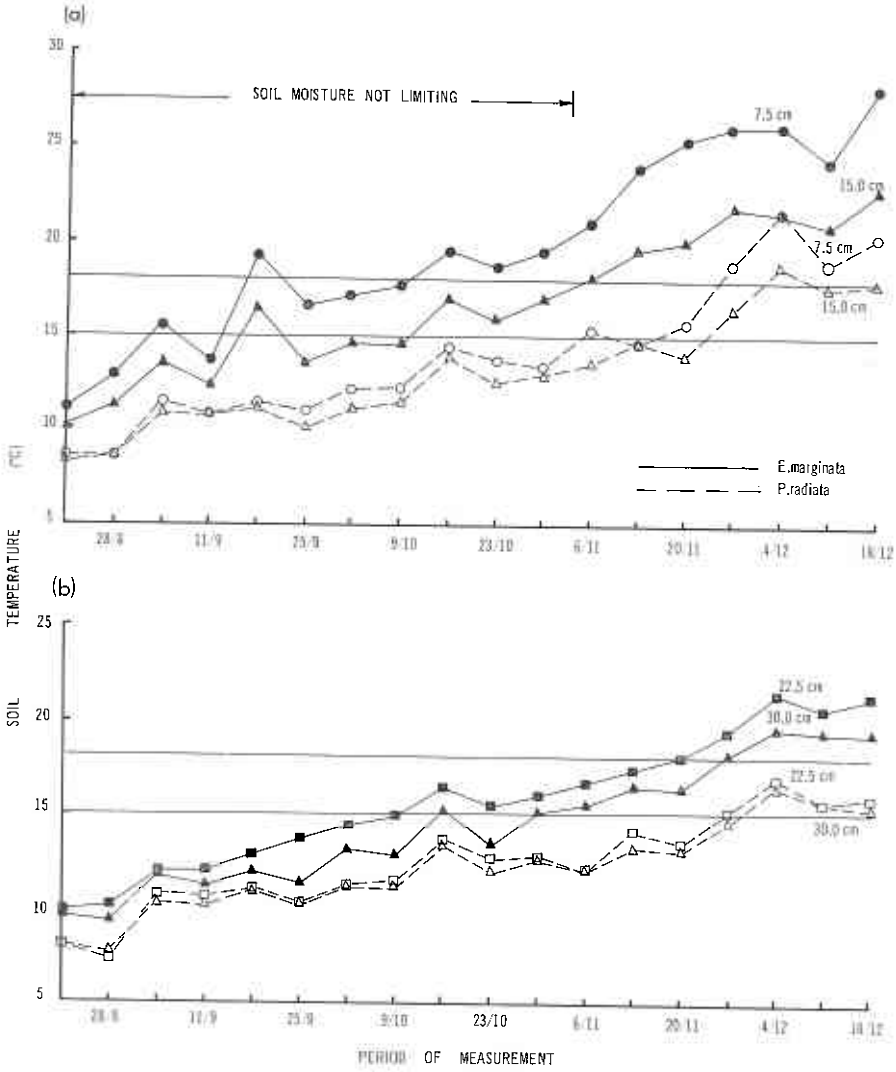


Figure 27

Average weekly soil temperatures at (a) 7.5 cm and 15.0 cm and (b) 22.5 cm and 30.0 cm, under adjacent *P. radiata* and *E. marginata* stands during spring and early summer 1968.

Results

Soil Moisture—Soil moisture in both sites and horizons was maintained at approximately field capacity up to October 30, 1968 (Fig. 26). After October 30, rainfall was almost negligible and soil moisture continued to decline rapidly until it was approximately equivalent to wilting point. The rapid rate of moisture depletion in both sites and horizons after effective rainfall had ceased indicates that the soils have low storage capacities and that the maintenance of relatively high soil moisture levels is dependent entirely on input from rainfall. The rate of moisture depletion in both horizons appeared to be slightly lower in the pine stand.

Soil Temperature—Weekly mean temperatures at 7.5 cm, 15.0 cm, 22.5 cm and 30.0 cm depths are plotted in Figure 27.

Soil temperatures under jarrah and pine were significantly different at the 7.5 and 15.0 cm depth throughout the period of measurement. The significance of the 22.5 cm and 30.0 cm temperature data could not be calculated but temperature differences at these depths, although less than at 7.5 cm and 15.0 cm, were consistent throughout the period of measurement. The differences in relation to the critical temperature conditions required for infection were highly significant.

The difference between soil temperatures on the two plots at 7.5 cm and 15.0 cm levels on the 25th October were significant at each hour during the period of measurement. Soil temperatures at 7.5 cm depth in the pine plots only rose above the critical level for two hours and at 15.0 cm depth temperatures never rose above the critical level. In the jarrah plot, soil temperatures were above the critical level for seven and four hours at 7.5 cm and 15.0 cm, respectively.

The continuous temperature data for the period November 6 to January 1 (Fig. 28) shows that even five weeks after soil moisture levels became limiting the period of time during which temperatures in the pine stand were above 15°C was only 64 and 48 hours for the 7.5 cm and 15.0 cm depth, respectively. Soil temperatures did not rise above 18°C until five and six weeks after soil moisture conditions became limiting at these depths.

Discussion

Results indicate that, during the critical spring months, environmental conditions under the *P. radiata* stand were unsuitable for infection by *P. cinnamomi*. It is possible that there are periods in the autumn when there is a coincidence of favourable soil moisture and soil temperature conditions, but the results of Study 1 (ii) suggest these periods would be very short. Comparison of the susceptibility of the pine and jarrah stands on the basis of periods during which soil temperature and soil moisture were favourable for infection demonstrates a marked effect of canopy cover on susceptibility. Not only were there much longer periods suitable for infection in the jarrah forest site, but also the volume of roots which could be attacked on the jarrah site was much greater because the soil temperature differences between plots were still significant at 15.0 cm depth. The results of this study suggest that the periods during which soil temperature levels and moisture levels would permit infection by *P. cinnamomi* on upland jarrah forest sites would be eliminated by a dense canopy cover.

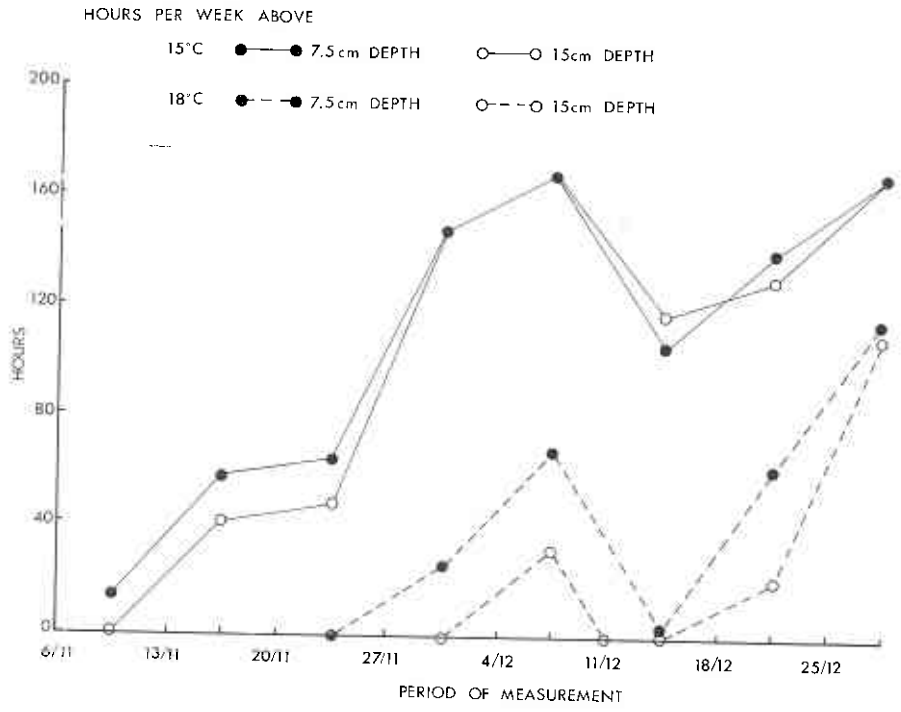


Figure 28

Number of hours soil temperatures at 7.5 cm and 15.0 cm depth under adjacent *P. radiata* and *E. marginata* stands were above 15°C and 18°C during spring and early summer 1968.

Although most *P. radiata* plantations in Western Australia are located on the fertile krasnozemic soils of the river valleys, depositional sands of the jarrah forest may eventually be used for *P. radiata* or *P. pinaster* establishment. The assumption that the results of this experiment are equally applicable to the *P. radiata* plantations growing on krasnozemic soil would appear to be valid. The river valley soils, although of heavier texture than sand, are freely drained and usually occur on steep slopes. Jarrah dieback has not caused serious damage on these sites and it is possible that they are inherently unfavourable to *P. cinnamomi*. The data derived from this experiment are only applicable to unthinned stands on which canopy closure has occurred. It is possible that heavy thinning could result in the creation of favourable temperature conditions in spring when soil moisture is not limiting. It is reasonable to conclude that *P. cinnamomi* is unlikely to cause damage in unthinned or moderately thinned *P. radiata* plantations in Western Australia growing on freely drained soils in which canopy closure has occurred.

The micro-environment of unthinned *P. pinaster* stands during the spring months would be even less suitable for *P. cinnamomi* infection because the litter layer under *P. pinaster* stands is much heavier (25 tonnes per hectare as opposed to 12.5 tonnes per hectare for ten-year-old *P. pinaster* and *P. radiata*, respectively.)

6. THE EFFECT OF VARIATION IN RAINFALL DISTRIBUTION IN SPACE AND TIME ON THE SUSCEPTIBILITY OF DIFFERENT SITES TO *P. CINNAMOMI*

It is possible that unavoidable sampling bias in time and space could result in erroneous calculations of the susceptibility of different sites assessed from soil moisture and temperature measurements. For example, Newhook (1959) found that excessive mortality in *P. radiata* shelterbelts only occurred in years when "there was abnormally heavy rewetting of soil in autumn with wet conditions continuing until spring."

Long-term records of rainfall data from selected stations in the northern jarrah forest were used to assess the effect of rainfall variation on the environmental conditions of different forest sites in relation to critical levels for fungal pathogenicity and survival.

Rainfall Variation in Space

Annual rainfall increases gradually from the coast eastwards to the Darling Scarp. From the foot of the Scarp to the top, rainfall increases rapidly. Increases in the order of 100 mm per kilometre occur where the increase in altitude is steepest. Eastwards from the top of the Scarp, annual rainfall decreases at the rate of approximately 15 mm per kilometre. The summer and winter rainfall variation in space closely follows the annual pattern. Figure 29 shows a more detailed picture of the rainfall distribution adjacent to Dwellingup (Hatch, 1964) in which the annual, spring and autumn rainfall in stations to the east and west is less than the recordings at Dwellingup.

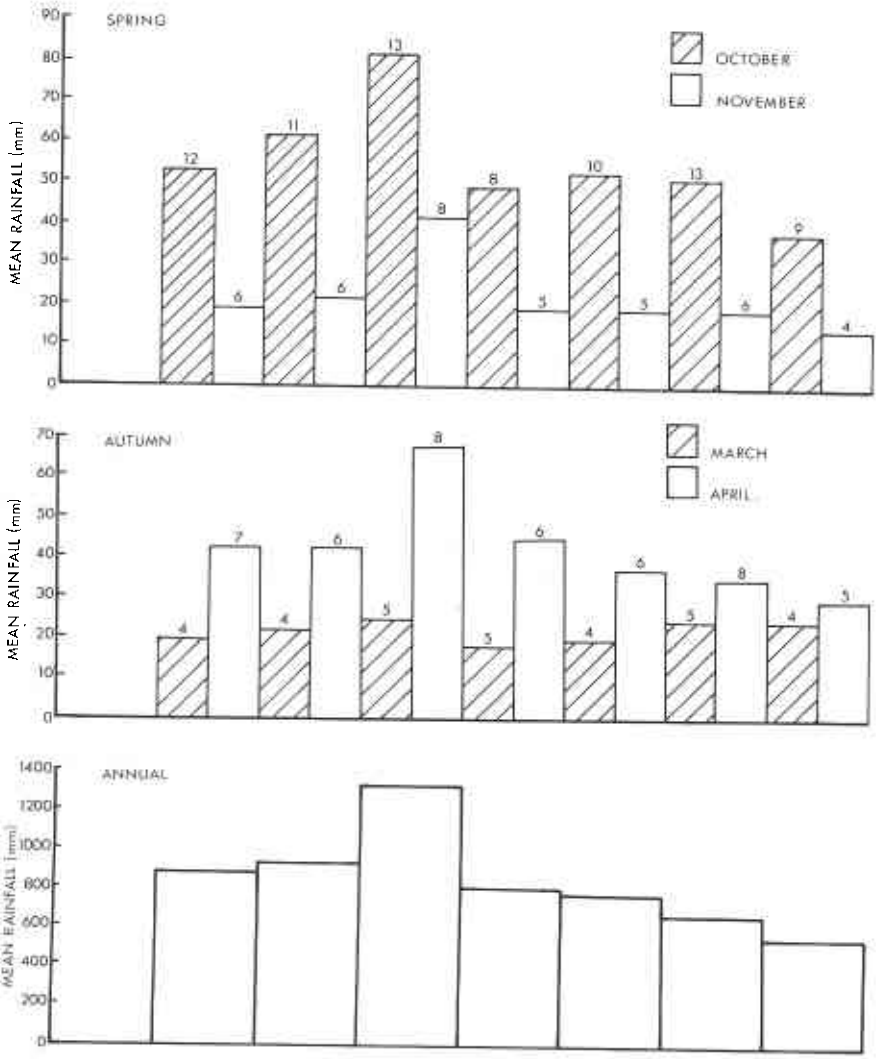
The period during which soil moisture was maintained at levels suitable for *P. cinnamomi* infection was not significantly different for the study areas, even though they were located in different rainfall zones. This was due to higher than average rainfall in the year of measurement in the eastern jarrah forest. It would be expected, however, that, over a period of years, the average periods during which conditions were suitable for infection in the lower rainfall areas would be less than in the higher rainfall areas. Accordingly, the extent of the disease should be greater in the higher rainfall areas in the west of the forest. This is, in fact, the situation, but it is impossible to directly associate the observed distribution of the fungus with variation in climate because of other factors. For example, the degree of exploitation of forest areas is also correlated with the distribution of the disease.

Rainfall Variation in Time

Variation in the seasonal and annual rainfall received in the northern jarrah forest can be expressed in two ways—

(a) Figure 30 is a graphical representation of the rainfall received and the number of rain days (days in which rainfall exceeded 0.25 mm) in winter (May to September), summer (December to February), spring (October and November) and Autumn (March and April) over the period 1934 to 1971. The data is expressed in terms of departures from the average for the 1934-1971 period.

(b) Table 2 sets out probabilities for rainfall exceeding specified levels in each month of the year for various selected stations within and adjacent to the northern jarrah forest.



STATION	MANDURAH	PINJARRA	DWELLINGUP	DUNCANS MILL	MARRADONG	WANDERING	NARROGIN
ALTITUDE (m)	4.6	8.5	271	305	305	338	339
DISTANCE FROM COAST (km)	0	22.5	41.8	66.0	75.6	98.1	143.2
PERIOD OF MEASUREMENT	1911–'40	1911–'40	1927–'53	1934–'43	1911–'40	1911–'40	1911–'40

Figure 29
Rainfall distribution at stations east and west of Dwellingup.

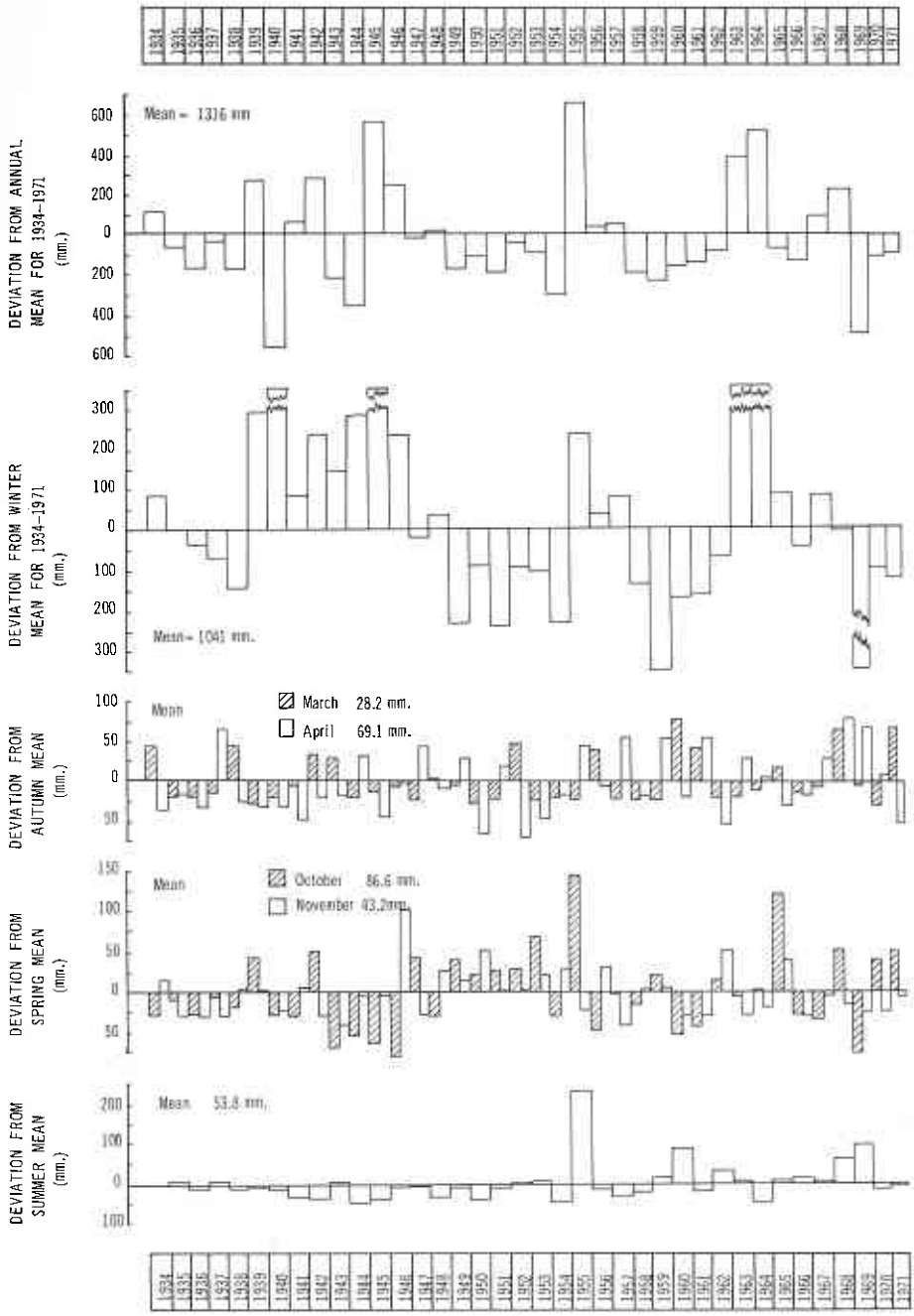


Figure 30

Annual and seasonal variation in rainfall at Dwellingup. 1934-1971.

TABLE 2

Percentage probability of receiving monthly rainfall

Line 1. Effective rainfall. Line 2. 13mm. Line 3. 25·4 mm. Line 4. 51 mm.

Station	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Bridgetown	5	8	21	62	100	100	100	100	98	96	32	7
	33	37	60	83	100	100	100	100	99	98	70	55
	16	19	42	70	100	100	100	100	97	94	46	34
	6	7	14	38	93	100	99	98	85	69	17	7
Brunswick	0	8	19	67	88	100	100	100	95	91	31	7
	23	29	53	92	100	100	100	100	98	97	73	41
	12	18	31	75	98	100	100	100	93	81	51	18
	0	7	15	37	95	100	100	98	82	75	16	4
Collie	5	6	14	66	100	100	100	100	97	93	26	4
	30	29	59	90	100	100	100	100	100	96	74	44
	17	16	39	75	99	100	100	100	96	92	45	22
	7	6	13	36	95	100	100	95	84	74	14	5
Donnybrook	0	7	21	34	100	100	100	100	96	93	30	5
	24	36	58	90	100	100	100	100	99	97	72	43
	13	17	36	76	100	100	100	100	95	92	52	22
	0	7	16	36	95	100	99	97	83	70	20	5
Dwellingup	0	4	18	69	100	100	100	100	96	87	47	10
	20	36	46	93	100	100	100	100	100	94	82	65
	4	22	34	81	100	100	100	100	96	89	66	33
	0	5	17	56	95	100	100	100	84	77	39	12
Jarrahdale	1	6	24	67	98	100	100	99	97	78	17	8
	28	27	53	83	100	100	100	100	100	96	75	51
	14	19	32	73	100	100	100	99	99	94	55	23
	5	7	15	51	94	100	100	97	87	76	18	9
Harvey	1	4	13	59	99	100	100	100	96	90	22	4
	25	29	48	85	100	100	100	100	98	96	70	41
	13	13	28	70	99	100	100	100	95	91	45	21
	1	5	10	35	95	100	100	95	83	69	21	3
Mandurah	0	3	13	52	98	100	100	100	93	68	7	2
	13	20	44	79	100	100	100	100	98	96	58	29
	4	11	28	64	99	100	100	100	93	85	32	13
	0	4	12	36	92	100	100	94	78	47	7	3
Mornington Mills	0	8	20	74	100	100	100	98	95	42	42	9
	27	44	64	93	100	100	100	100	100	98	76	52
	12	20	43	80	100	100	100	100	98	95	59	22
	0	3	16	55	100	100	100	100	90	85	26	9
Nannup	4	8	21	72	99	100	100	100	99	97	48	8
	32	28	62	90	100	100	100	100	100	100	88	63
	16	16	38	78	99	100	100	100	95	96	69	31
	4	6	13	48	94	100	100	96	91	80	27	7
Pinjarra	0	5	14	52	100	100	100	99	93	79	18	5
	21	30	45	83	100	100	100	99	98	97	64	37
	7	15	30	67	100	100	100	99	94	86	42	20
	0	5	11	30	94	99	100	96	75	50	14	7
Serpentine (Wundowie)	0	3	13	47	100	100	100	100	92	79	10	5
	24	24	40	90	100	100	100	100	96	96	65	38
	8	13	25	64	100	100	100	100	93	88	41	17
	0	3	11	34	88	100	100	96	83	64	9	7
Kalamunda	0	4	10	59	94	100	100	100	93	76	13	8
	31	27	56	88	100	100	100	100	98	98	64	49
	12	19	25	75	98	100	100	100	94	92	51	28
	2	6	15	44	92	100	100	96	87	72	17	8

(From: Climatic Survey. Region 16—South-west Western Australia. Commonwealth of Australia, Bureau of Meteorology, 1965)

(Note: Effective rainfall is that rainfall which is required to initiate and maintain plant growth above wilting point. The mean effective rainfall for any one month was determined by Prescott's formula $\frac{P}{E} \times 0.7 = 0.54$ where P = effective rainfall and E is evaporation from a free water surface.)

The effect of rainfall variation in time on fungal infection on freely drained jarrah forest sites must be considered in relation to:

(1) The periods of the year when soil temperatures are above the critical level for infection.

(2) The observed interaction between soil temperature and rainfall.

(3) The high evaporation rates during the summer months.

(4) The rainfall received in the years when soil moisture and temperature measurements were carried out in the present field studies.

The data of Table 2 indicate that inferences concerning variation in rainfall with time, based on Dwellingup, will give an overestimate of the effect of rainfall variation because the probabilities of receiving in excess of the specified totals in each month at Dwellingup are either equal to or above the majority of the other stations.

Data in Figure 30 show that most of the rainfall which occurred in years with above average rainfall could fall during the winter months. In fact, the correlation between average annual rainfall and above average rainfall in spring, autumn and summer is poor. Excessive winter rainfall would not have an important effect on the susceptibility of freely drained jarrah forest sites since soil temperatures limit infection during this season. Increased infection in moisture gaining sites would be expected, however, in years when winter rainfall was above average because of subsequent increases in mass drainage from the upper topographical sites. This is apparent from the measurements of soil moisture levels in the moisture gaining sites of Studies 1 (i) and (ii) in the years following below average (1967) and above average (1968) rainfall.

Autumn rainfall (March and April) in 1968 was the highest recorded throughout the period 1934-1971. Thus, it is reasonable to conclude that there is only a slight chance that the total number of hours during which soil moisture and soil temperature conditions were suitable for infection in autumn in 1968 would be exceeded in other years. Consistent and heavy rainfall in late autumn caused soil temperatures to be depressed in sites with and without canopy cover at approximately the same rate. Rainfall in early autumn (March and early April) usually occurs as either light showers over a number of days or heavy, isolated showers. When heavy isolated showers occur, the favourable soil moisture conditions created for the fungus are partially compensated for by the depression of soil temperatures to a level below that critical for infection. This depression of soil temperatures is more evident in sites with canopy cover.

Autumn rainfall in the northern jarrah forest is comparatively stable. Departures from the average rainfall received in March and April are small when compared to those shown by Newhook (1959). This stability, together with the observed depressive effect of autumn rainfall on soil temperatures, suggests that variation in rainfall between years in autumn is unlikely to modify conclusions drawn from soil moisture and soil temperature measurements carried out in the autumn of 1968 and 1969.

Rainfall during the early spring (October) of 1967 was below average, while in 1968 early spring (October) rainfall was considerably above average. Comparison between the soil temperatures in the two years shows that the

more favourable moisture conditions in the spring of 1968 were partially compensated for by the lower soil temperatures in that year. Thus, although October rainfall in 1968 was exceeded in three other years during the period 1934-1971, it is unlikely that there were significantly longer periods when soil moisture and soil temperatures were favourable for the fungus in these years. November rainfall in both 1967 and 1968 was below average and for this month rainfall is generally stable. When heavy rainfall does occur in November, it is usually in short, heavy downpours. Soil temperature data for November 1968 showed that when heavy rainfall did occur, soil temperatures were depressed, particularly in sites with canopy cover.

Rainfall during the summer of 1968-69 was below average and hence the effect of heavy summer rainfall on soil temperatures could not be determined. It is unlikely, however, that summer rainfall would significantly depress soil temperatures below the critical level for infection, even on sites with canopy. The average rainfall received over December, January and February in the northern jarrah forest is very low (54 mm) and evaporation rates during these months is very high. Departures from the average have been low except in the year 1955, when February rainfall was the highest ever recorded (Fig. 30). The low rainfall, high evaporation rates and small departures from the average between years suggest that summer rainfall is not important in creating favourable moisture conditions for the fungus.

Summary

(1) The soil moisture and soil temperature experiments carried out in 1967, 1968 and 1969 were located in areas representing above average, average and below average rainfall zones in the northern jarrah forest. Thus, results obtained apply to the general forest area.

(2) In years when above average rainfall occurred at Dwellingup, the excess rainfall usually fell during the winter months when soil temperatures were below the critical level for infection. Thus, although the periods when soil moisture and soil temperature were suitable for infection are likely to be increased on moisture-gaining sites in those years because of increased mass drainage, the susceptibility of freely drained sites is not likely to be affected.

(3) The comparative stability of autumn and spring rainfall at Dwellingup, the depression of soil temperatures by heavy rainfall, and the above average rainfall in the year of measurement make it unlikely that the conclusion drawn from these measurements would be markedly modified by year to year variation in autumn and spring rainfall.

(4) The low rainfall received during the summer months, the limited variation in rainfall from year to year and the high evaporation rates during these months make it unlikely that variation in summer rainfall would alter results and conclusions made from the study.

7. CONCLUSIONS

Soil moisture and soil temperature are the major environmental factors affecting *P. cinnamomi* activity. Direct measurements of these two factors over a representative range of site types in the forest provides an index of relative susceptibility. These studies have shown that the soil environments of lower topographical jarrah forest sites are very suitable for fungal activity and survival but upper topographical sites have a relatively unsuitable soil

environment both for infection and survival of *P. cinnamoni*. Soil moisture sampling over a range of upper topographical sites in the forest has demonstrated that they are dependent on consistent input of water from rainfall to maintain soil moisture levels suitable for infection. The susceptibility of these sites can be modified markedly by the degree of canopy and litter cover. Under maximum canopy cover, the soil environment of upland sites is unsuitable for sporulation and hence disease development. Aspect has some effect on susceptibility of upper topographical sites but it is not as important as canopy and litter cover. Variations in rainfall distribution in time and space are unlikely to affect the validity of the susceptibility calculations.

SECTION III

DIRECT DETERMINATIONS OF PATHOGENICITY AND SURVIVAL

Measurement of the environmental factors which influence *P. cinnamomi* activity and survival provides an index of susceptibility of different sites. The effect of differing site conditions can only be positively confirmed, however, by direct studies. Unfortunately, the fungus and the disease situation make these studies difficult to implement and long time periods are required before results are meaningful.

The results of four preliminary studies aimed at determining the influence of environmental factors on the fungus are summarised in this section.

1. THE EFFECT OF SITE, SEASON AND INOCULUM POTENTIAL ON THE ABILITY OF *P. CINNAMOMI* TO ESTABLISH INFECTIONS

A major large-scale field inoculation trial was established at the Scarp Road study area (see Section 2) in August 1967, Three metre by three metre plots with one mature *B. grandis* located in each were established on Strata 1 and 2 and Strata 3 and 4.

Three inoculum levels [0, 2 infected lupin (*Lupinus angustifolius* L.) roots and 6 infected lupin roots] and two dispersal rates (3 spots per plot and 9 spots per plot) were used to provide a range of inoculum intensity. Inoculation of both site types was carried out in each season of the year. The experiment was designed as a 3 x 2 x 4 factorial.

Assessments were carried out at 6-monthly intervals following inoculation. In February 1969, 28 of the highest inoculum level plots from each site that had been inoculated in October 1967 were sampled for the presence of the fungus using the lupin baiting technique (Chee and Newhook, 1966). A single inoculation point was withdrawn from each plot and each sample was baited twice. Positive recoveries were obtained from only 4 of the samples. In October 1969, two inoculation points in each of 50 plots were sampled and baited twice. No positive recoveries were obtained.

During autumn 1970, dieback symptoms appeared in the experimental area. The experiment was assessed in July 1971 and mortalities were recorded in inoculated plots, control plots and areas adjacent to the plots. There was evidence that there had been invasions of the disease from outside, even though at the time of establishment of the experiment the diseased area was 30-50 metres downhill from the experimental area.

Although the original objectives of this experiment were not achieved because of contamination, it has been reported here in summary form to illustrate the difficulties of obtaining, from field trials, information on the factors affecting disease severity. The principal difficulty in trials of this type is to obtain an index of fungal activity. A series of experiments was carried out in an attempt to quantify the amount of fungus in the soil, using a variety of techniques, but these were unsatisfactory. Even simple detection techniques aimed only at determining the presence or absence of the fungus failed, although large numbers of samples were taken. Thus, assessment of fungal activity is dependent on the recognition of disease symptoms in the host species. In August 1971, no symptoms could be detected in the jarrah overstorey, and understorey deaths did not occur until two and a half years after inoculation. In this period of time it is practically impossible to prevent

contamination between plots in a large trial. Despite the difficulties involved, it is obvious that field inoculation ultimately must be used to determine susceptibility. The information obtained from this trial is being used to plan future field trials.

2. SAPROPHYTIC SURVIVAL OF *P. CINNAMOMI* DURING SUMMER

Soil moisture levels on upper topographical jarrah forest sites during the summer months are approximately equivalent to lethal (low) levels reported in the literature (Kuhlman, 1964; Zentmyer and Mircetich, 1965). Soil moisture levels in lower topographical sites, however, do not approach what could be considered lethal levels in any season. The observed low occurrence of new infections on freely drained sites could at least be partially explained if soil moisture levels on these sites were lethal to the fungus during summer. Information derived from direct studies on the ability of the fungus to survive on a different jarrah forest site is essential for the planning of forest operations so that the minimum number of new infections are initiated. Consequently, the following experiment was initiated to provide some preliminary information on the ability of the fungus to survive on four different jarrah forest sites during the summer months.

Procedure

Nylon mesh bags containing 100 gm of soil infested with *P. cinnamomi* were placed in randomly located positions in four, 3 m x 3 m plots located along a transect from ridge top to valley bottom immediately adjacent to four of the soil moisture plots located in Strata 1, 2, 3 and 4 (Study 1 (ii)). The bags were placed at 7.5 cm depth and covered with soil. Samples were placed in the plots at fortnightly intervals over the period November 14, 1968 to March 20, 1969 and withdrawn one month after introduction. Immediately after the samples had been withdrawn they were tested for the presence of *P. cinnamomi* using the lupin baiting method of Chee and Newhook (1966). Samples which did not give a positive recovery of *P. cinnamomi* after the first test were rebaited. Lupins were plated regardless of the presence or absence of lesions.

The inoculum source was soil collected from fifteen naturally infected sites in the jarrah forest. This soil was thoroughly mixed and inoculated with macerated mycelium which had been grown on pea broth agar. The soil was stored in a shadehouse and kept moist. Prior to the commencement of the experiment, the soil was mixed thoroughly and twenty, 100 gm samples were baited for the presence of *P. cinnamomi*. Nineteen of the 20 samples gave positive recoveries of the fungus.

The soil was thoroughly mixed before each inoculation. Ten, 100 gm samples were baited for the presence of *P. cinnamomi* immediately after mixing.

Over the period November 14, 1968 to January 1, 1969, five bagged samples were buried at each site every 14 days and withdrawn one month later.

On January 23, 1969 a new inoculum source was prepared by mixing equal parts of infected sand, infected silt and the naturally infected soil. The infected sand and silt were derived from pots containing dead and dying *E. marginata* and *B. grandis* seedlings which had been inoculated with cultures of the fungus four months previously. At fortnightly intervals, from January 23 to February 20, 1969, ten, 100 gm samples were placed in each site.

Results

The percentage recoveries from each site in each month and the percentage recovery from the test samples, sampled prior to inoculation, are presented in Table 3.

TABLE 3

Percentage recovery of *P. cinnamomi* from infected soil samples exposed in the field for monthly periods.

Stratum	Exposure Period							Total
	14 Nov. to 12 Dec.	28 Nov. to 26 Dec.	12 Dec. to 9 Jan.	9 Jan. to 6 Feb.	23 Jan. to 20 Feb.	6 Feb. to 6 Mar.	20 Feb. to 20 Mar.	
Dry Ridge 4	0	0	0	0	10	0	50	12
Upper Slope 3	40	20	0	0	0	0	60	18
Lower Slope 2	60	40	0	40	40	80	90	58
Valley Bottom 1	60	20	40	100	80	20	90	60
Control	90	20	70	80	100	100	100	80

In Stratum 4, apart from one sample in one of the sampling periods (January 23 to February 20), all samples gave negative recoveries over the period November 14 to March 6. Similarly, in Stratum 3 no samples gave positive recoveries over the periods December 30 to March 6. The fungus was recovered consistently from Strata 2 and 1 throughout the summer months except for one period (November 12 to January 1) when the fungus was not recovered from Stratum 2.

There is an obvious correlation between the soil moisture trends in each stratum and the recovery rate (see Study 1 (i) and 1 (ii)). Stratum 2 is a transitional zone between the freely drained and moisture-gaining sites and there is considerable variation in the soil moisture levels in this stratum. This accounts for the discrepancies in the relationship between the soil moisture values and the observed high recoveries from this plot. Twenty-five millimetres of rain fell during the final sampling period (Februray 20 to March 20) and this was apparantly sufficient to cause soil moisture levels on Strata 3 and 4 to be raised above the lethal level.

Discussion

The results of this experiment indicate that survival of *P. cinnamomi* in soil on freely drained jarrah forest sites during the summer months is restricted by low soil moisture levels. Soil moisture levels on the lower topographical sites do not reach lethal levels during the summer.

Soil temperature is not a limiting factor. Soil temperatures, although reaching comparatively high levels (e.g. 30°C) are subject to wide diurnal fluctuation. Hine et al (1964) have shown that continuously high soil temperature levels are required before the fungus is inactivated.

The fungus is able to survive the summer months on freely drained jarrah forest sites that have established infections, since infections on such

sites persist for a number of years. This does not contradict the above data. Survival of fungal propagules in established infections probably occurs in the large roots of susceptible hosts where they are buffered from the effects of the external environment.

Although the above results suggest that survival in soil on upper topographical sites is restricted, it would be dangerous to conclude that even in the absence of susceptible host tissue the fungus will be eliminated completely on these sites because of low soil moisture levels during the summer months. The effect of different soil types on survival could not be evaluated and it is possible that in freely drained sites with heavier textured soils, soil moisture levels may not fall below the lethal level.

3. PATHOGENICITY OF *P. CINNAMOMI* IN DIFFERENT JARRAH FOREST SOIL TYPES

It was not possible to determine if differences in disease severity on different jarrah forest sites were caused by soil factors *per se*, since soil types are associated with specific topographic and vegetational characteristics.

A pot trial, incorporating the major jarrah forest soil types, was initiated to determine if there was any major factor inherent in a specific soil type that influenced *P. cinnamomi* activity.

The trial, which was carried out at the Dwellingup laboratory, was designed as a factorial with four soil types, five levels of inoculum and two moisture regimes. Each treatment was replicated three times.

Treatments

Inoculum Levels—Five levels were compared:

(1) Control

(2) 5 ml of sand mycelium

(3) 100 ml of sand mycelium

(4) 2 infected lupin *(Lupinus angustifolius)* roots

(5) 10 infected lupin roots

The sand mycelium was prepared by macerating 200 gm of mycelium, grown on pea broth agar, in a Waring blender and mixing it thoroughly with 5 000 ml of water and 5 000 cm^3 of sand.

Lupins were infected by placing them in an aerated water bath containing zoospores. A random sample of 40 lupin roots which were plated gave 61 per cent positive recoveries.

Soils—Four natural soils, whose compositions are shown in Table 4, were used.

TABLE 4

Soil compositions used to determine influence of soil type on *P. cinnamomi* activity.

Soil Type	Per cent Gravel	Per cent Fine Fraction				pH
		Coarse Sand	Fine Sand	Clay	Silt	
Sand	0	79	16	3	2	5·9
Coarse Gravel	69	63	26	4	7	6·6
Lateritic Silt	17	36	38	8	18	6·0
Krasnozem (Loam)	50	51	21	12	16	6·6

Watering—(a). Low treatment: During the first six weeks following inoculation, 150 ml of water were added to the pot saucers when wilting symptoms were observed in the plants. After six weeks the high moisture treatment was adopted.

(b) High treatment: The pots were maintained between field capacity and saturation by watering from above and below in alternative 24-hour periods.

Procedure

Ten seedlings of *Banksia grandis* were planted in each pot (22.5 cm diameter) in May 1967. The pots were inoculated in November 1967 by either mixing the sand mycelium in the surface 2.5 cm of soil or by inserting the lupin roots randomly to a depth of 2.5 cm. Pots were maintained in a shadehouse and assessed for mortalities twice weekly. Soil temperatures were recorded during the experiment.

The experiment was terminated on March 23, 1968. Whole plant dry weight, shoot dry weight and seedling height were measured. Five soil cores (1.2 cm diameter) were taken from each pot and sampled for the presence of *P. cinnamomi* by the method of Chee and Newhook (1966)).

Results

Dry Weight—Differences in height and dry weight were not significant. Measurement was complicated by the presence of dead plants in some pots.

Mortality—Three weeks after inoculation, significantly more deaths occurred in the pots with high moisture levels, inoculated with ten lupin roots. There was no significant difference between soil types.

Six weeks after treatment significantly more deaths occurred in pots with high moisture levels inoculated with ten lupin roots than in the high moisture treatment inoculated with two lupin roots. This treatment in turn had significantly more deaths than the remaining treatments. Differences between soil types again were not significant.

Twelve weeks after inoculation the interaction between inoculum level, soil type and moisture regime was significant. There were significantly more deaths in the high moisture level pots, inoculated with ten lupin roots, in all four soils and in the high water level lateritic soil, inoculated with two lupin roots, than in all other treatments (Table 5).

Soil Temperature—Soil temperatures in pots during the trial were consistently within the range favourable for zoospore production (15° to 32°C).

Recovery of P. cinnamomi—At the completion of the trial the fungus was not recovered from any of the controls or pots inoculated with sand mycelium. Positive recoveries were obtained from 50 per cent of the lupin inoculated pots in the wet treatment and from five of the dry treatment pots even though these latter contained no mortalities. At the time the experiment was sampled, it was believed that unlesioned lupin roots from the baiting process were uninfected and did not warrant plating on agar. This assumption has since been proved incorrect and if all lupin roots had been plated, recoveries could have been higher.

Discussion

The failure of the sand mycelium inoculum could have been due to excessive maceration and or dilution of the mycelium, with subsequent attack of viable macerations by other micro-organisms.

The marked differences in mortalities between the high and low moisture treatments demonstrate the favourability of high soil moisture levels for infection. No deaths which could be attributed to the inoculum occurred in the dry treatment. Those few deaths which did occur were assumed to be caused by drought, as they occurred in both inoculated and control treatments during a period when air temperatures were high. The survival of the fungus in five of the dry treatment pots and the absence of mortalities and depression in dry weight values indicate that the fungus was inactivated but not killed by the six weeks of low moisture.

The importance of level of inoculum is demonstrated in mortalities obtained for two and ten lupin roots at high water levels. The probability of infection at the lower inoculum level is diminished.

The results suggest that at high inoculum levels, with adequate soil moisture, soil type does not affect the pathogenicity of the fungus. At lower levels of inoculum, however, mortalities were significantly higher in the lateritic silt. This is probably due to more favourable moisture conditions favouring greater motility of zoospores.

TABLE 5

Mortality of *Banksia grandis* seedlings associated with variation in soil type, watering levels and inoculum levels of *P. cinnamomi*. (Twenty-five plants were used in each treatment combination and mortalities under low moisture conditions were due to drought effects.)

Inoculation Procedure	Potting Medium				Total
	Silt	Sand	Gravel	Loam	
	Low Moisture Treatments				
Control	0	0	0	1	1
5 ml Sand Mycelium	0	2	3	1	6
100 ml Sand Mycelium	0	6	0	0	6
2 Infected Lupin Roots	0	1	0	1	2
10 Infected Lupin Roots	0	0	6	2	8
Total	0	9	9	5	23
	High Moisture Treatments				
Control	0	0	5	4	9
5 ml Sand Mycelium	0	0	1	0	1
100 ml Sand Mycelium	0	0	0	6	6
2 Infected Lupin Roots	21	9	8	0	38
10 Infected Lupin Roots	21	22	24	24	91
Total	42	31	38	34	145

4. RATE OF SPREAD OF EXISTING INFECTIONS

Jarrah dieback infections are usually initiated on lower topographical sites. Spread downslope from these infections, or from infections on upper topographical sites, is rapid. The higher quality jarrah stands are located on the upper topographical sites and hence the rate of extension of the disease upslope onto these sites is of considerable importance.

Measurement of environmental factors in relation to known limits for fungal pathogenicity and survival provides some index of site susceptibity. An accurate assessment of disease susceptibility, however, can only be made by observations of fungal activity under specific environmental situations in the field. Direct inoculations of specific sites, followed by observations of disease symptoms, would appear to be the best method of assessing site susceptibility. There are, however, considerable practical difficulties in establishing, maintaining and assessing these types of experiments. Measurement of "natural" rate of spread provides an alternative method of assessing the influence of different environmental factors on fungal activity.

A series of plots was established in 1967 and 1968 to measure the rate of spread of the disease upslope from existing infections.

Procedure

Plots in which the position and condition of understorey and overstorey species in respect to a 66-110 metre baseline located at the boundary between "healthy" and dying forest, were established on 18 different locations in the forest in 1967 and 1968. Changes in the health status of the understorey and overstorey species in advance of the baseline were recorded annually. No attempt was made to observe changes in the shrub layer because of the difficulty of discriminating between deaths caused by natural seasonal mortalities and those resulting from fungal activity.

Soil, slope, aspect and position in the landform were recorded for each plot. One of two plots located adjacent to one another was treated to reduce the density of *Banksia grandis* to determine if this would reduce disease spread. All of the plots were located in positions above the moisture-gaining sites.

The annual increase in area of forest infected at each plot was measured by assuming that a line joining the most recent understorey deaths to the nearest death of the previous year defined the area of newly infected soil. The average increase in area of infected soil (infected area divided by length of plot) and the maximum linear extension for each plot were recorded each year.

Results

The annual spread of the disease, based on understorey symptoms, over five years and 18 plots is shown in Table 6.

The annual extensions of the disease over a five year period in two plots that have contrasting rates of spread, are shown in Figures 31 and 32. The average annual disease spread over all plots is shown in Figure 33. The wall of dead *B. grandis*, which occurs after extension of the disease, is shown in Figure 34.

Plot 15 (Table 6) was the only plot in which a significant change in the condition of the jarrah overstorey that could be attributed to *P. cinnamomi* was detected. Three jarrah overstorey trees died and three exhibited severe crown deterioration in the five year period.

Discussion

There is little objective data available on the rate of spread of disease from existing infections. Air photo interpretation techniques were used to obtain an average percentage increase in the area of infected forests of four per cent

TABLE 6

Rate of spread of *P. cinnamomi* infection based on understorey systems 1967–1972.

Plot No.	Linear Spread (centimetres) by Year									
	1967–68		1968–69		1969–70		1970–71		1971–72	
	Mean	Max.	Mean	Max.	Mean	Max.	Mean	Max.	Mean	Max.
1	28·2	350·0	42·3	704·1	114·7	945·5	212·4	1 609·3	70·8	603·5
2	15·7	502·9	12·7	482·8	11·5	442·6	30·2	1 026·0	....	....
3	8·2	502·9	14·3	804·0	118·7	1 146·5	45·1	523·0	26·1	442·6
4	....	....	3·0	276·6	10·5	261·5	104·8	1 026·0	100·2	543·2
5	107·8	704·1	142·8	603·5	195·1	1 066·2	7·0	221·3	60·9	482·8
6	....	....	19·1	301·8	76·2	523·0	113·1	543·2	131·8	422·5
7	24·1	844·9	3·0	352·0	472·4	502·9	132·4	1 005·8	....	....
8	10·5	352·0	51·5	744·3	16·7	342·0	31·2	502·9	40·6	502·9
9	11·3	251·5	140·0	1 347·9	6·6	342·0	406·2	1 307·6	98·0	804·7
10	43·9	955·6	9·5	704·1	68·6	663·9	119·7	1 146·7	181·0	1 307·6
11	18·9	326·9	89·7	724·2	19·5	20·1	86·5	362·1	76·5	543·2
12	100·0	502·9	180·3	855·0	....	....	....	....	....	....
13	34·8	578·4	4·6	271·6	197·6	241·4	81·3	764·4	476·4	1 287·5
14	118·1	653·8	526·9	1 659·6	265·5	1 408·2	237·0	945·5	660·6	2 756·0
15	52·7	452·6	114·1	1 086·3	18·3	422·5	86·9	1 005·9	204·0	1 609·3
16	9·5	402·4	31·0	754·4	4·4	221·3	24·3	362·1	118·9	804·7
17	4·6	125·7	....	....	....	....	....	....	244·8	1 508·8
18	....	....	95·8	1 106·4	50·3	945·5	....	....	124·9	1 106·4

per annum (Forests Department Working Plans Report). The scale of photography was 1 : 40 000 and hence the spread of the disease could only be determined from crown symptoms in the jarrah overstorey. It is logical to assume that there is a relationship between the rate of spread of symptoms in the jarrah crown and symptoms in the understorey; it is possible, however, that it varies markedly between sites. Even if this possibility is ignored, the value of four per cent per annum includes spread due to the establishment of new infections and is an average of all sites. Thus, although a useful quantity for management purposes, it is an overestimate of the unaided rate of spread of the fungus upslope from existing infections.

Measurements of the rate of spread of the disease on the basis of symptoms in the understorey, are possibly inaccurate for the same reason as measurements based on overstorey symptoms. That is, the relationship between spread of the disease based on understorey symptoms may not be directly related to spread of the fungus. Preliminary investigations carried out at Dwellingup, in an attempt to determine the distance of fungal penetration ahead of symptoms in the understorey, indicated that a large number of samples would be required. *B. grandis*, however, is highly susceptible to the fungus and over a five year period it is likely that the average rate of spread, based on symptoms in this species, would correspond closely to the actual spread of the disease.

The average rate of extension of the disease into healthy forest on 17 of the 18 plots was small. These data support the conclusion, based on measurements of the soil moisture and temperature regimes of the upper topographical sites, that the environmental conditions on these sites are only marginally suitable for the fungus. It also supports the contention that the principal cause of disease spread results from accidental contamination during forest operations.

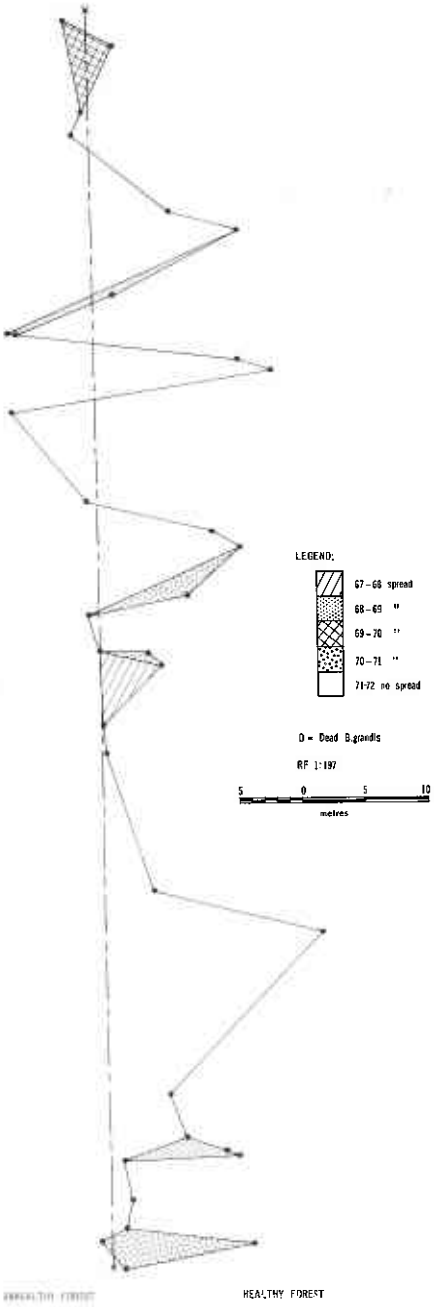


Figure 31

Spread of *P. cinnamomi* infection based on symptom development in the understorey species, over a 5 year period. Low spread rate.

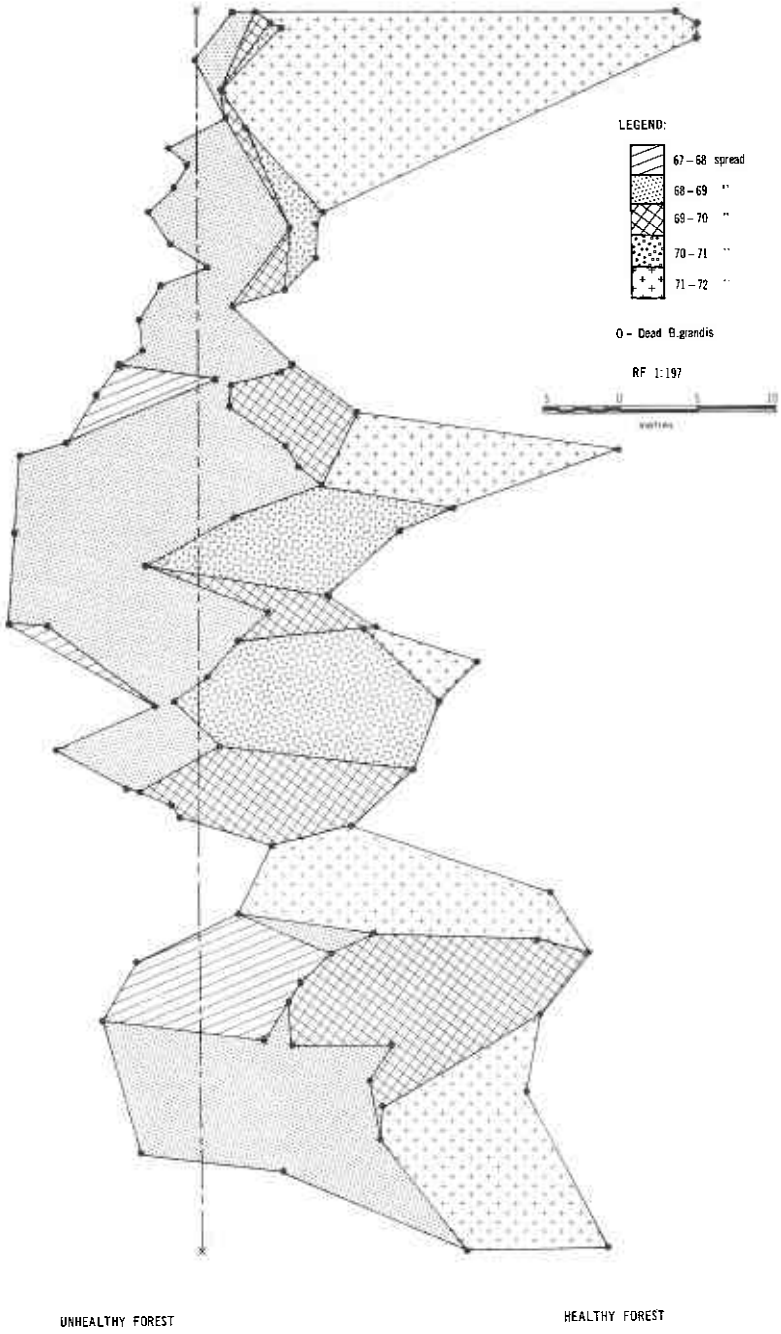


Figure 32

Spread of *P. cinnamomi* infection based on symptom development in the understorey species over a 5 year period. High spread rate.

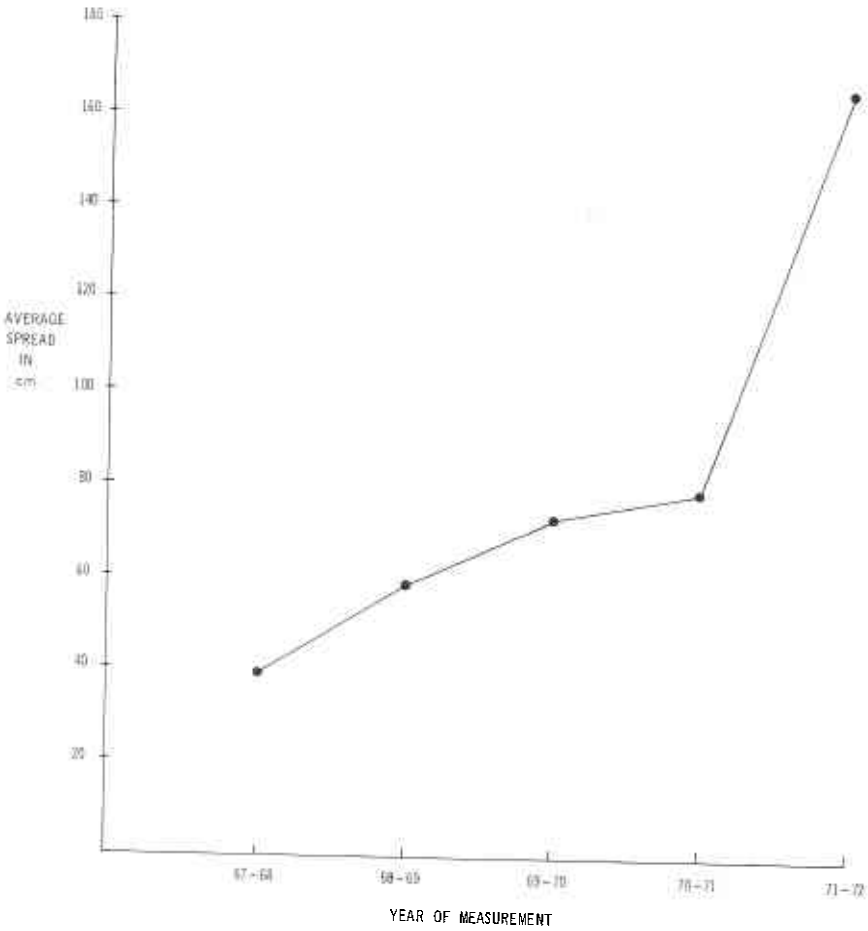


Figure 33
Mean annual linear spread of dieback infections for 19 plots over the period 1967-68 to 1971-72.

The average spread of the disease onto the upper topographical sites, however, is not insignificant to management if the large perimeter of diseased areas is considered. Relatively large extensions of the disease at isolated points along the plots indicates that under optimum conditions the extension of the disease can be rapid. This type of extension is likely to cause more rapid disease spread because on sites which slope in two directions it provides the opportunity for passive downhill spread.

In one of the plots (Fig. 32), the average spread was extensive and much greater than in any of the 17 other plots. There was no apparent site or vegetation characteristic which could explain the rapid extension of the disease in this plot. Currently, attempts are being made to determine if the chemical or microbiological characteristics of the soil on this site are different from those of the other sites.

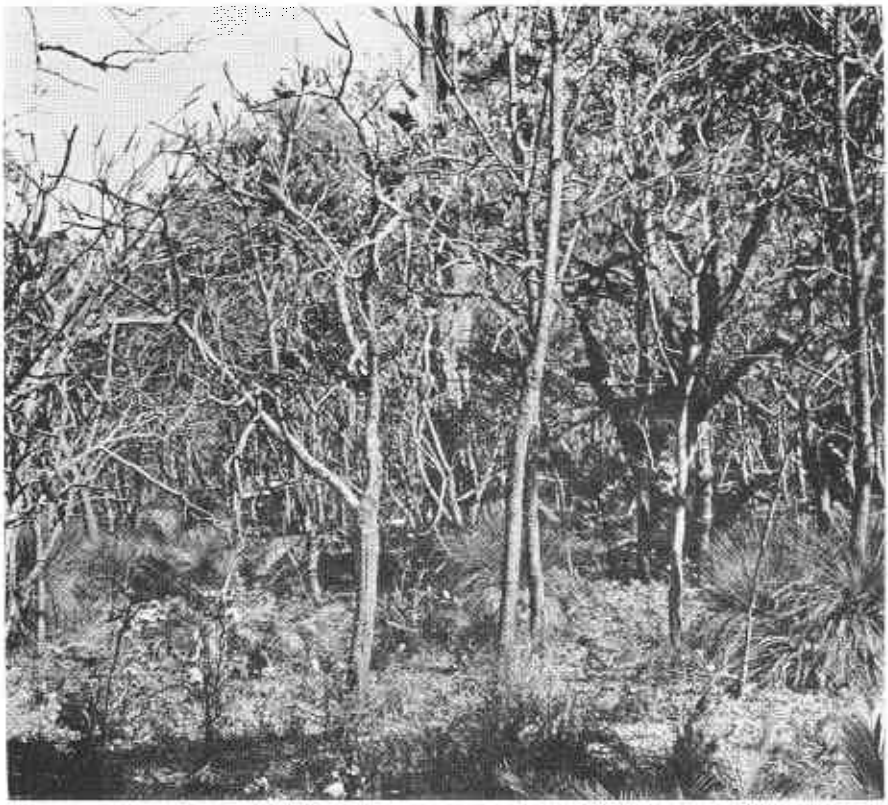


Figure 34
Dead *B. grandis* zone, which is formed following disease extension. (The "green line" occurs to the right of the photograph).

In a number of the plots the pattern of extension, that is the death of understorey species at isolated points 20-40 metres ahead of the mass of dying vegetation, suggests that the principal mechanism of spread was by way of roots and not soil. It was not, however, possible to detect any difference in the rate of extension of the disease between adjacent plots in which the banksia was thinned and unthinned.

The results of this trial emphasise the difficulties of quantifying fungal activity on different site types. Symptom development in the overstorey is usually very slow and even the susceptible understorey species do not exhibit the effects of the disease rapidly. Although the disease is widespread, the opportunities to establish plots in which symptom development can be readily observed over a period of years, without disturbance, are small.

5. SUMMARY

Assessments of the effect of environmental factors on fungal pathogenicity and survival by direct field inoculations are difficult because there is no reliable practical method of quantifying fungal populations. Symptom development in the understorey and overstorey may involve long time periods during which

the probability of contamination is high. The results of field saprophytic survival trials and measurement of the rate of disease spread on to upland sites supports the conclusion, formed on the basis of direct measurements of the soil moisture and temperature regimes of these sites, that they are relatively unfavourable for pathogenicity and saprophytic survival. There is, however, some evidence that factors other than soil moisture and soil temperature affect the spread of the disease on some upland sites. Preliminary trials indicate soil type does not affect fungal pathogenicity except by its effect on soil moisture regime.

SECTION IV

THE ENVIRONMENT AND POTENTIAL FOR DISEASE

Measurements of the major environmental factors affecting *P. cinnamomi* pathogenicity and survival and direct studies of fungal activity in the field and laboratory have established the following facts.

(1) A combination of a high capacity for water retention, mass drainage from upper topographical sites and poor internal drainage results in the soils occupying lower topographical jarrah forest sites maintaining moisture levels above the critical levels for infection for long periods into the summer.

(2) The upland soils of the jarrah forest have a moderate moisture retention capacity, are freely drained and are dependent on rainfall to ensure maintenance of moisture levels suitable for infection.

(3) There are long periods during which soil moisture and temperature conditions are suitable for infection on lower topographical sites but, even in the most open canopy situations on upper topographical sites, the period when infection can occur is relatively small. On upper topographical sites during winter, soil temperatures are below the levels which permit infection. During summer on these sites, soil moisture levels limit both survival and infection.

(4) Soil moisture regimes on freely drained sites over a range of stand types, soil types and slope positions are relatively uniform to a minimum depth of 60 cm in terms of the critical moisture levels for infection by *P. cinnamomi*. Soil moisture depletion occurs rapidly after the cessation of significant rainfall early in summer and, for most of the summer and early autumn, soil moisture levels approach or reach soil potentials corresponding to wilting point.

(5) Environmental conditions in the soils that occur on lower topographical sites permit survival throughout the year, but on upper topographical sites fungal survival outside the host roots is restricted during the summer months.

(6) There are longer periods in spring than in autumn when soil moisture and soil temperature conditions are suitable for infection. Heavy autumn rainfall, which is necessary to raise soil moisture to levels suitable for infection, causes soil temperatures to be depressed below the critical levels for infection.

(7) The periods during which soil moisture and temperature levels are suitable for infection on upper topographical sites are markedly influenced by canopy and litter cover. Under conditions of maximum cover there are no periods when soil moisture and soil temperature levels are suitable for infection.

(8) Aspect has some effect on the susceptibility of sites but is not as important as soil moisture regime and canopy and litter cover.

(9) Rainfall variation between years does not have a significant effect on the susceptibility of upper topographical sites to infection. There is some evidence that differences in rainfall distribution within the forest area could affect susceptibility.

(10) The overall *average* rate of unaided spread upslope from existing infections is low. On some sites, however, average and maximum extension rates are high. Linear extensions of the disease of 20 to 30 metres per year, *at points* along the perimeter of diseased areas, are common. This type of spread suggests that the principal mode of unaided spread is by way of very susceptible host root systems.

Measurements of soil moisture and temperature regimes of a range of sites within the forest have demonstrated that there are two major zones that have markedly different susceptibilities to the disease. Lower topographical sites have long periods during which *P. cinnamomi* infection can take place, but on upper topographical sites the environment for both infection and survival is only marginally suitable. The broad-scale pattern of distribution of the disease, that is its predominance on lower topographical sites (Fig. 2), is explained by this study. The fungus, however, can survive and cause mortalities on upper topographical sites to a degree which is difficult to explain by their calculated susceptibility. Hence it is necessary to consider the effect of other factors of the environment to explain the occurrence and activity of the disease on upland, freely drained sites.

1. THE IMPORTANCE OF OTHER ENVIRONMENTAL FACTORS

The Effect of Host Susceptibility

The degree of host susceptibility appears to be a major factor influencing the speed and intensification of the disease on sites which have environments that are only marginally suitable for *P. cinnamomi* activity. The large numbers of highly susceptible species in the understorey and shrub layer of the forest provide a dense mat of susceptible roots which act as channels for fungal spread. The presence of a dense mat of susceptible roots possibly reduces the periods during which the fungus would have to survive and sporulate in the soil. The observed pattern of spread of the disease and the direct measurements of the soil environment external to the host roots, which indicated that it was only marginally suitable for fungal activity and survival, support the hypothesis that the existence of a highly susceptible species in the understorey and shrub layer of the forest is a major factor permitting the disease to spread and cause mortality on upland jarrah forest sites.

Although a number of the shrub and understorey species of the forest are highly susceptible and have root systems which can be completely invaded by the fungus, there is circumstantial evidence that the commercial species, jarrah, does not have the same degree of susceptibility. The ability of jarrah trees to survive for long periods after the understorey and shrub layer species have died indicates that mortality results from repeated infection of the fine roots, rather than invasion of the total root system.

Artificial Spread

Prior to the discovery of the causal agent responsible for jarrah dieback, the fungus was spread artificially during normal forest operations. For example, road making material was frequently obtained from jarrah dieback areas. These practices, particularly when they cause infections on upper topographical sites, resulted in large extensions of the disease. Massive artificial spread of the disease has undoubtedly been a major factor contributing to its spread and intensification on upland sites.

Unknown Factors

The intensity of disease on the upland jarrah forest sites is much greater than that of diseases caused by *P. cinnamomi* in similar environments. The ability of the fungus to spread and cause significant mortality on sites which are only marginally suitable for fungal activity would be attributed to the above two factors. There is some evidence, however, that factors other than these contribute to the severity of the disease on upland lateritic soils. The absence of significant disease development on the krasnozemic soils that occur in the younger river valleys and the variation in rate of disease development and extension on different upland sites supports the hypothesis that other unknown factors are operating.

It is even difficult to explain why jarrah mortality occurs at all on upland sites. If invasion of the major jarrah roots does not occur, then the fungus must affect the trees by destruction of their fine unsuberised roots. The effect of removal of these roots on the tree's water supply during the summer months must be negligible, since the upper profile, to a minimum depth of 60 cm, does not have available water during the majority of the summer. Preliminary studies of jarrah root systems (Kimber, 1974), have shown that jarrah root systems contain vertical sinker roots which may extend to approximately 17 m below the soil surface to the water table. These roots are unlikely to be affected by the fungus and they must be the major source of soil moisture during the summer months. The complete removal of the fine feeder roots would prevent nutrient uptake but even in the most favourable situations (minimum canopy and litter cover), fungal activity is restricted to the top 15 cm of soil because soil temperatures, during the period when soil moisture is not limiting, decrease with increasing soil depth. Thus, unless the source of nutrient supply or presence of fine roots is completely restricted to the zone where fungal activity can occur, the impact of the fungus should not be sufficient to cause mortality.

2. MANAGEMENT AND RESEARCH IMPLICATIONS

The principal obstacle to the derivation of methods for controlling the disease is the difficulty of obtaining a quantitative measure of disease severity in different field situations. Massive artificial spread of the fungus has ensured that the disease is present in almost all site and vegetation types. It is significant that the fungus can establish infections throughout the forest, but the presence or absence of the disease provides no index of disease severity. A lengthy time period is required before an accurate evaluation of disease severity can be made from observations of symptom development in the vegetation. Even then, most observations of symptom development must be based on the highly susceptible understorey or shrub layer and these species are themselves a factor of the environment which contributes to the severity of the disease. Symptom development in jarrah crowns is impossible to distinguish from attrition due to natural factors and jarrah mortality may not take place until up to thirty years after understorey and shrub deaths have occurred.

Thus, in the short term, the effect of different management practices on disease spread and intensification can only be assessed by determining their effect on the soil environment. Long term experiments involving direct inoculation ultimately may provide conclusive evidence that specific management practices reduce the spread and intensification of the disease. The current

magnitude of the disease situation and its potential for more serious development make it necessary to make interim recommendations to management that, in part, result from logical extrapolation of the preliminary investigations rather than from direct experimental evidence.

Recognition of Variation in Site Susceptibility

This study has demonstrated that there are two markedly different susceptibility zones in the forest. Lower topographical sites have conditions that are suitable for fungal pathogenicity and survival for long periods during the year. Upland sites are only marginally suitable for the fungus. Management and research approaches to disease control will differ according to the susceptible zone.

There is no possibility that environmental modification of lower topographical sites will significantly affect their susceptibility. Thus the only method of restoring these sites to productivity is by planting resistant species. Fortunately, these sites do not support high quality jarrah stands and they are well suited for the growth of exotic species.

The relatively unfavourable conditions for fungal activity on upland sites, the existence of high value stands and the difficulties of replacing jarrah with an alternative, productive crop justify research and management approaches primarily aimed at protecting the existing crop from the disease rather than replacing it.

Prevention of Disease Spread by Artificial Inoculation

The data from rate of spread studies of unaided disease spread indicate that, if "man-carried" disease extension can be eliminated, the progression of the disease into healthy stands will be greatly reduced. Information on the jarrah forest environment, and the environmental factors influencing the fungus, form a basis for simple hygiene proposals, which should have a large impact on the spread and intensification of the disease. In brief, restriction of movement of vehicles between infected and healthy forest, washing of vehicles to remove infected soil and the restriction of logging activities in high value forest areas to the summer months will greatly reduce the probability that new infections will be introduced.

Manipulation of the Forest Canopy to Reduce Site Susceptibility

Measurements of the soil moisture and temperature regimes of upland jarrah sites, under conditions of maximum canopy and litter cover, indicate that under these conditions fungal pathogenicity should be reduced to insignificant levels. The production of a uniform even-aged forest, as opposed to a "selection type" uneven-aged forest, would improve canopy cover and hence reduce soil temperature during the critical spring months. The fungus can cause death of jarrah growing in even-aged stands, so it is evident that, even though disease severity will be reduced, the conversion to uniform stands will not eliminate the disease. The poor shading characteristics of jarrah crowns make it unlikely that the degree of canopy cover necessary to eliminate periods of coincidence of moisture and temperature conditions, suitable for fungal infection, will be achieved by silvicultural treatment of the jarrah overstorey. Heavy litter will reduce disease severity by reducing soil temperatures in spring but it is unlikely that conditions which *completely* prevent fungal activity will be achieved and the maintenance of large unburnt areas in the forest is impractical. The degree of canopy cover estimated necessary

to prevent fungal activity, however, can occur in the forest. High intensity fires frequently result in the occurrence of dense understorey stands of a number of species belonging to the family *Papilionaceae*. Following the severe Dwellingup wildfire during 1961, a dense understorey of "fireweed" species developed over large areas of the forest. In Figure 35 a stand of *Bossiaea aquifolium* Benth., which originated after the Dwellingup fire, is illustrated to demonstrate the degree of canopy cover which results from the growth of "fireweed". It was impracticable to measure soil temperature and moisture regimes under stands of this type but it is reasonable to assume that under a uniform forest, with maximum jarrah overstorey canopy and a "fireweed" understorey, the soil temperature and moisture regimes would be similar to those of the *P. radiata* stand which was sampled (Study II-5).

Future research may provide the techniques necessary to promote "fireweed" in selected areas, at least to reduce the extension of the disease from existing infections into high quality sites. It may also be possible to reduce fungal activity on infected upland sites to levels that are not damaging to the commercial crop.

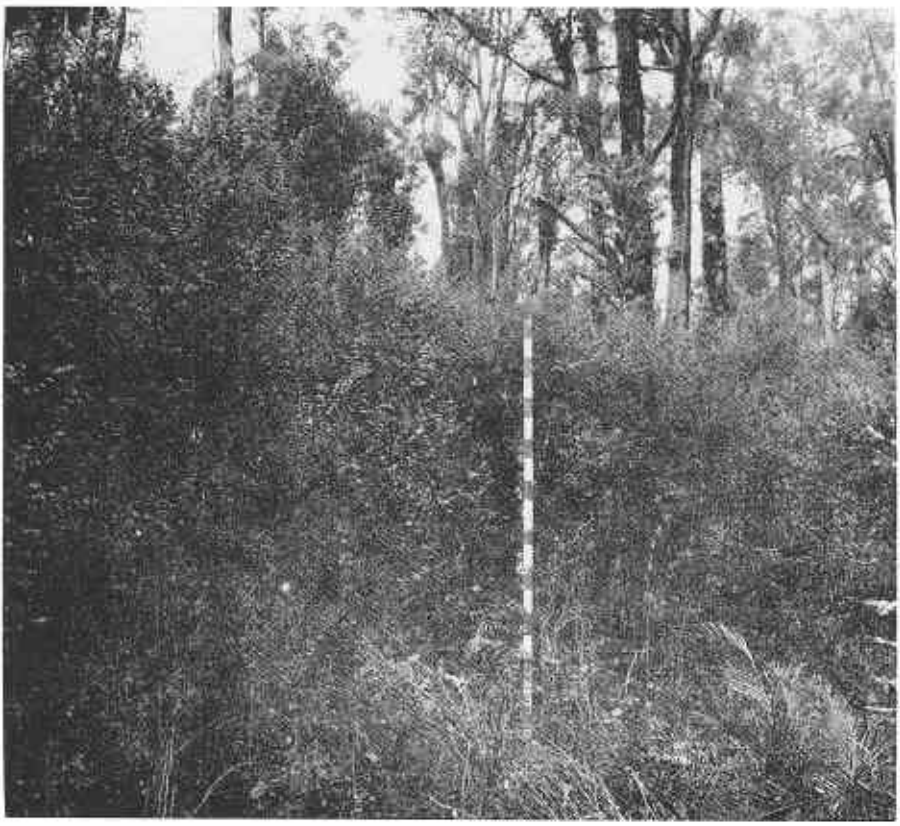


Figure 35
Dense canopy cover from understorey of dense *B. aquifolium*, which originated after severe fire.

Reduction of Density of Highly Susceptible Host Species

The structure and composition of the jarrah forest prior to exploitation was very different to that of the existing forest. Reports from early forest surveyors and examination of remnant virgin stands confirm that the understorey was sparse and the forest was "park like". This contrasts markedly with the current structure of a large area of the forest (Fig. 36), which has a dense understorey component comprising principally *B. grandis*. The cause of the change in structure of the forest is unknown. Reduction in competition from the overstorey, disturbance and the absence of high intensity fires, however, are probably three major factors which have favoured the development of the *B. grandis* understorey. The rapid symptom development in this understorey species following introduction of the fungus confirms that it is highly susceptible to the fungus. Its removal would reduce disease spread.

In the short term, poisoning with herbicides in small areas could remove the understorey. The cost of this treatment over a large area, and the possibility that re-treatment of poisoned areas would be necessary, make this method impractical on a large scale. There is evidence that high intensity fires cause marked changes in the compo ition and structure of the understorey and shrub layer. Further research is necessary to determine the prescription of burning intensity and frequency which would bring about the desired changes without damaging the jarrah overstorey.

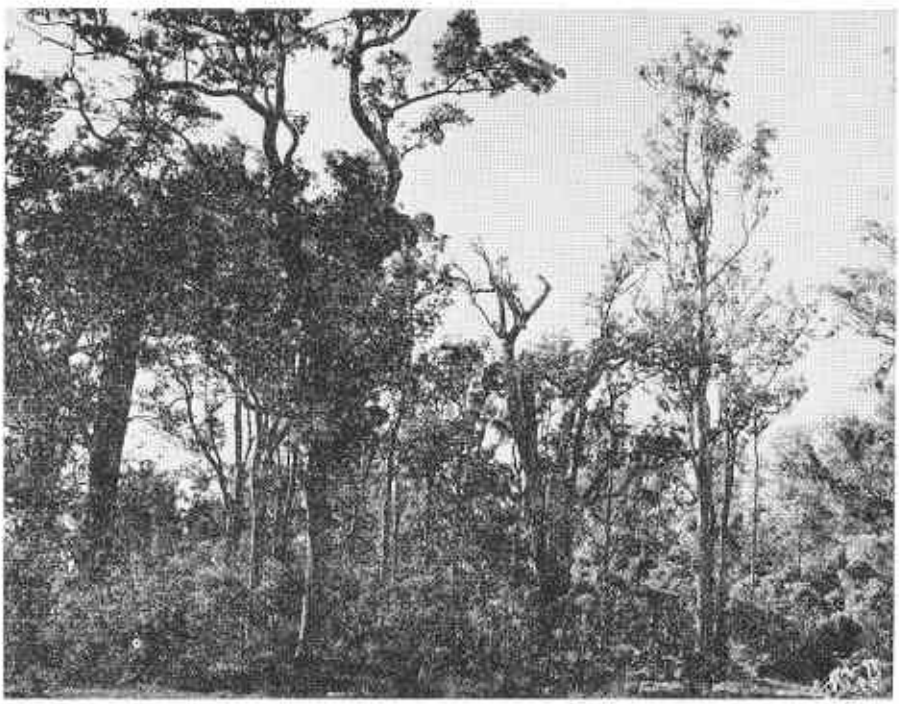


Figure 36
Healthy forest showing typical irregular stand structure, which results from "group selection" management.

3. CONCLUSIONS

An understanding of the effect of environmental factors on the disease agent is an essential pre-requisite to the initiation of control measures. It also provides basic data from which research projects aimed at resolving specific aspects of the disease complex can be planned. This study has defined the jarrah forest environment in relation to the environmental factors affecting *P. cinnamomi* pathogenicity and survival.

The principal conclusion of the study is that the forest is not uniformly susceptible to the fungus. In fact the results suggest that on upland sites, which are the principal areas of high quality forest, the soil environment is only marginally suitable for fungal pathogenicity and survival. Thus although the fungus has the ability to devastate upland jarrah forest, minor changes in the environment of this forest could be sufficient, if not to eliminate their susceptibility to the disease, at least to reduce it markedly.

ACKNOWLEDGEMENTS

The study was carried out under the direction of Dr. E. R. Hopkins. Mr. P. C. Kimber, Mr. J. J. Havel and Mr. A. L. Clifton provided advice and assistance at various stages of the study.

The staff of the Forest Research Institute, Kelmscott, in particular Mr. D. Darling, provided assistance with the preparation of inoculum and media plates.

Mr. M. J. Dillon and Mr. R. J. Kitt provided technical assistance in the field and laboratory.

Miss L. R. Hayes provided invaluable technical assistance and typed the manuscript.

LITERATURE CITED

Anderson, E. J. (1951). The *P. cinnamomi* problem in pineapple fields of Hawaii. Phytopathology. 41, 1-2.

Batini, F. and Podger, F. D. (1968). Shelterbelt mortalities on the Swan Coastal Plain. Aust. For. Res. 3, 39-45.

Campbell, W. A. and Copeland, O. L. Jr. (1954). Littleleaf disease of shortleaf and loblolly pines. U.S. Dept. Agric. Circ. No. 940.

Chee, K. H. and Newhook, F. J. (1965). Improved methods for use in studies on *Phytophthora cinnamomi* Rands and other Phytophthora species. N.Z. J. Agric. Res. 8, 88-95.

Chee, K. H. and Newhook, F. J. (1965). Variability in *Phytophthora cinnamomi* Rands. N.Z. J. Agric. Res. 8, 96-103.

Chee, K. H. and Newhook, F. J. (1966). Relationship of microorganisms to sporulation of *Phytophthora cinnamomi* Rands. N.Z. J. Agric. Res. 9, 32-43.

Copeland, O. L. Jr. and McAlpine, R. G. (1955). The interrelations of littleleaf, site index, soil and ground cover in Piedmont Shortleaf pine stands (in S. Carolina and Georgia). Ecology 36, 635-640.

Gardner, W. R. (1960). Dynamic aspects of water availability to plants. Soil Sci. 89, 63-73.

Gardner, W. R. (1968). Availability and measurement of soil water. *In* Water Deficits and Plant Growth. Vol. I. Ed. Kozlowski.

Hatch, A. B. (1964). The interaction between forest floor dynamics and soil properties in *Eucalyptus marginata* Sm. forests. M.Sc. Thesis, University of Sydney.

Hartigan, C. (1964). Some observations on the effect of *Phytophthora* in Monterey Pine. For. & Timb. Sydney, Aug., 5-6.

Hepting, G. H. (1964). Climate and forest diseases. *In* Annual Review of Phytopathology. Vol. 1.

Hine, R. B., Alaban, C. and Klemmer, H. (1964). Influence of soil temperature on root and heart rot of pineapple caused by *Phytophthora cinnamomi* and *Phytophthora parasitica*. Phytopathology. 54, 1287-1289.

Jacobs, M. R. (1955). Growth habits of the Eucalypts. For. & Timb. Bur. Commonwealth Government Printer, Canberra.

Kimber, P. C. (1974). The root system of jarrah (*Eucalyptus marginata*). Research Paper No. 10. Forests Department of Western Australia.

Kuhlman, E. G. (1964). Survival and pathogenicity of *Phytophthora cinnamomi* in several western Oregon soils. For. Sci. 10, 151-158. Published also as Tech. Pap. Ore. Agric. Exp. Sta. No. 3839.

Leeper, G. W. (1960). Climates. *In* The Australian Environment, third edition (revised).
C.S.I.R.O. in association with Melbourne University Press.

Marx, D. H. and Davey, C. B. (1967). Ectotrophic mycorrhizae as deterrents to pathogenic root infections. Nature, Lond. 213, 1139.

Mircetich, S. M. and Zentmyer, G. A. (1966). Production of oospores and chlamydospores of *Phytophthora cinnamomi* in roots and soil. Phytopathology. 56, 1076-1078.

Mulcahy, M. J., Churchward, H. M. and Dimmock, G. M. (1972). Landforms and soils on an uplifted peneplain in the Darling Range, Western Australia. Aust. J. Soil Res. 10, 1-14.

Newhook, F. J. (1959). The association of *Phytophthora spp.* with mortality of *Pinus radiata* and other conifers. I. Symptoms and epidemiology in shelterbelts. N.Z. J. Agric. Res. 2, 808-843.

Peet, G. B. (1967). Controlled burning in the forests of Western Australia. Forests Department, Perth, Western Australia. Pap. 9th Commonw. For. Conf., New Delhi 1968.

Podger, F. D. (1968). Aetiology of jarrah dieback. M. Sc. Thesis, University of Melbourne.

Podger, F. D., Doepel, R. F. and Zentmyer, G. A. (1965). Association of *Phytophthora cinnamomi* with a disease of *Eucalyptus marginata* forest in Western Australia. Plant Dis. Reptr. 49, 943-947.

Roth, L. F. and Kuhlman, E. G. (1963). Field tests of the capacity of Phytophthora root rot to damage Douglas-fir. J. For. 61, 199-205.

Roth, L. F. and Kuhlman, E. G. (1966). *Phytophthora cinnamomi,* an unlikely threat to Douglas-fir forestry. For. Sci. 12, 147-159.

Stolzy, L. H., et al (1967). Oxygen diffusion, water, and *Phytophthora cinnamomi* in root decay and nutrition of avocados. J. Amer. Soc. for Hort. Sci. 90, 67-76.

Torgeson, D. (1954). Root rot of Lawson cypress (*Chamaecyparis lawsoniana*) and other ornamentals caused by *P. cinnamomi.* Contr. Boyce Thompson Inst. 17, 359-373.

Williams, R. F. and Marshall, T. J. (1942). Determination of the permanent wilting percentage of soils. J. Aust. Inst. Agric. Sci. 8, 109-111.

Zak, B. (1961). Aeration and other soil factors affecting southern pines as related to littleleaf disease. Tech. Bull. U.S. Dept. Agric. iii-30.

Zentmyer, G. A. (1963). Biological control of Phytophthora root rot of avocado with alfalfa meal. Phytopathology. 53, 1383-1387.

Zentmyer, G. A. (1965). Bacterial stimulation of sporanguim production in *Phytophthora cinnamomi.* Science. 150, 1178-1179.

Zentmyer, G. A. and Mircetich, S. M. (1966). Saprophytism and persistence in soil by *Phytophthora cinnamomi.* Phytopathology. 56, 710-712.

Zentmyer, G. A. and Thompson, C. R. (1967). The effect of saponins from alfalfa on *Phytophthora cinnamomi* in relation to control of root rot in avocado. Phytopathology. 57, 1278-1279.

27448/2/75—500 WILLIAM C. BROWN, Government Printer, Western Australia