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REPORT TO THE INTERIM FOUNDATION FOR JARRAH DIEBACK RESEARCH

by

W.A. Heather

Yarralumla, A.C.T.

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Executive Summary

1.0 Introduction

The budgetary details of receipts and disbursements from the Fund are given in Appendix 1. The titles of projects supported by the Foundation are listed in Appendix 2 while the research reports of recipients of support from the Foundation are set out in Appendix 3.

The material in the body of this summary is arranged under the same headings, and in the same sequence as that in the Technical Report. Hopefully this will enable the reader to refer quickly to further detail he may require.

The summary concludes with some recommendations which, apart from some rather minor points of administration, are intended to assist researchers in their current projects.

2.0 The Pathogen

Although the sporangial inducing potential of jarrah soils was at a maximum in summer, in the field, sporangial production and zoospore release, and consequently Phytophthora cinnamomi populations, in surface horizons were usually maximal in spring and late autumn when temperature and moisture conditions were optimal. In years when heavy rain occurred in summer, populations built rapidly and the pathogen survived the summer in the surface horizons.

At depth, (5-75 cm) in the soil profile, in areas with concreted lateritic caprock, sporangial production continued throughout summer and winter and consequently populations remained high.

Dispersal of the pathogen in surface horizons was very restricted, even when areas were artificially flooded during summer. In contrast,

at depth in profiles with shallow caprock, zoospores were rapidly dispersed in the lateral flow which occurred on the caprock surface.

During summer, survival of zoospores, cysts or chlamydospores in surface soils of jarrah forest is very limited. In contrast, saprophytic survival in Banksia roots, infected parasitically, is very efficient, and recolonisation of tissue may occur in the following autumn/winter. Again, conditions at depth in areas with shallow caprock are favourable throughout the year. Thus the organism, located in major sinker roots of jarrah or banksia at the surface of, or in channels in, the caprock, is well placed to sporulate and disperse when free moisture is available in the area.

While the surface of the caprock is a favourable environment for the pathogen, the surface horizons of the soils of the jarrah forest have numerous antagonistic aspects, e.g. antibiosis from rhizosphere organisms, antagonism from jarrah litter, antagonism from the roots of Acacia pulchella and mycorrhizal organisms. In ecological terms, the occurrence of P. cinnamomi at depth can be viewed as a form of escape from the antagonism of the surface horizons. It happens that this is an excellent location for the parasitism of the major roots of jarrah. The presence in this zone of the systemically, colonised roots of dead Banksia builds the inoculum potential of the pathogen and makes the infection of the major roots of jarrah inevitable.

3.0 The Host

The basic root system of jarrah with long horizontal roots, surface pads of fine roots some of which are mycorrhizal, a system of vertical sinker roots and negatively geotropic riser roots, appears suited to exploit the resources of the profile, and to enable survival over the dry summer.

The growth of non-mycorrhizal fine roots usually occurs in spring and autumn but rain in summer will also stimulate activity.

Ectomycorrhizae have been synthesised on jarrah seedlings using a number of epigeous and hypogeous basidiomycete fungi to produce the typical pyramidal form. In contrast the ascomycete Cenococcum geophilum produces a black type mycorrhiza. A succession of fungi have been recognised to form mycorrhizae as the tree ages and fungi differ in their efficiency as mycorrhizal associates.

Jarrah lacks stomatal control of water loss, hence the importance of the sinker roots to supply water from depth in the profile. Water-logging of jarrah seedlings rapidly induces symptoms of water deficiency and wilting.

While the nutritional status of jarrah soils is usually low, a combination of heavy dressings of nitrogen and phosphorus is generally necessary to produce a growth response. There is evidence of zinc deficiency affecting the growth of jarrah on certain soils.

While micropropagation of jarrah from the shoots of mature trees has proved difficult, many of the problems have been solved and plantlets have been established in the field. These have foliage characteristic of mature, not juvenile, trees and lack the lignotubers and the coppice habit of jarrah seedlings.

The occurrence of sinker roots in jarrah and in other elements of the jarrah forest, e.g. Banksia, suggests these are essential to survival of the species during summer drought. It is the attack of P. cinnamomi on these portions of the root system which induces the rapid death syndrome in jarrah dieback. The coincidence of fine root growth and reproduction of P. cinnamomi in surface horizons in spring and autumn is probably another contributor to decline in jarrah.

4.0 Host-Pathogen Relations

The inoculation of fine roots of seedlings, under optimal conditions in the laboratory, resulted in a tolerant reaction in marri but a tolerant to susceptible reaction in various plants of jarrah. This is evidence of variability in resistance of biotypes in the latter species. In the field, the inoculation of fine roots in spring frequently led to spread into the framework of the root pads but progress of the infection in the summer was usually halted, with periderm production, in roots in the upper portion of the profile.

In B. grandis systemic invasion of the root system, and of the stem, followed inoculation of larger roots. In contrast inoculation of large roots of jarrah established an infection which spread in the outer secondary phloem, but again systemic invasion did not occur and periderms were formed. Extension was most rapid with inoculation in summer, but if moisture content of the phloem fell below 85% expansion of the lesion ceased. The pathogen spread more rapidly in secondary , than in primary, roots.

Species of the Monocalyptus and Corymbia subgenera of Eucalyptus reacted with periderm formation, to different degrees, to invasion by P. cinnamomi , while species of the subgenus Symphyomyrtus appeared to be immune to infection.

Following inoculation of the fine roots of species of varying susceptibility to P. cinnamomi cell membrane damage occurred within 2 hr. in resistant/tolerant species, but only after 8 hr. or more in susceptible plants. Following infection a hypersensitive reaction occurred in some resistant species while tolerance was expressed by other resistant, and also in some susceptible, species. A susceptible species of Eucalyptus demonstrated symptoms of water deficiency 4-6 days after inoculation of the roots with zoospores, while the water relations of a tolerant species seemed unaffected by inoculation.

Overall these relationships indicate that B. grandis is the completely susceptible host of P. cinnamomi, at least in the jarrah forest environment. In contrast there is, apparently genetically based, resistance in jarrah. In addition, the environment of the surface horizons of the soils of jarrah forest on some upland sites, appeared unfavourable for unlimited lesion expansion and systemic invasion of jarrah. When considered together with the antagonism of this portion of the soil profile to the pathogen, this zone in the soil must be considered unfavourable for major disease occurrence.

Possibly epidemic disease occurs only where such environmental constraints are lacking e.g. on sites with a shallow concreted lateritic layer and in valley bottoms with their high moisture levels in surface horizons throughout the year.

5.0 The Environment

Following a legume regeneration fire, while the soil showed an immediate increase in the availability of most nutrients, the levels adjusted, over a 2-3 year period, to their pre-burn levels.

The loss of nutrients in outflow from a jarrah catchment, even following fire or logging, was insufficient to cause concern for reduced nutrient supply of the site, or for pollution of the downstream water supply. Inflow of nitrogen to the system considerably exceeded loss in the water outflow.

A growth model proposed for B. grandis indicates that a single high intensity burn, followed by normal, low intensity control fires, would maintain the population of B. grandis at a very low level i.e. a series of hot burns is not necessary to achieve this end.

Following a cool autumn burn the invertebrates of the soil returned more rapidly to their previous levels than did the litter

invertebrates. There were distinct differences in population and taxonomic constitution of the invertebrates of a dieback, compared with a healthy, jarrah forest.

6.0 The Disease

On some 400 sites, which vary in disease impact from absent, through subtle, to moderate, to high, features of the environment and vegetation have been described in detail. Analysis of these observations demonstrates that the distribution of particular impact sites is skewed towards certain vegetation, slope, aspect, soil, geological etc. characteristics. The survey of sites is continuing and when the bank of data has been increased it should be possible to predict the likely disease impact status of an at present uninfested site, should P. cinnamomi be introduced into the area at some time in the future.

This type of survey can establish the potential disease impact status at a particular point in time. However it is likely that environmental changes, or site modification, will occur over time. A study of the processes occurring within sites, i.e. establishing the mechanism by which site characteristics casually result in disease impact, will make the survey independent of a particular sampling. The hydrological features of the site, which result in water accumulation or water dispersal, are very important in the potential disease impact status of a site. Intensive monitoring of those hydrological features, over a series of rain events, in various seasons, will provide data on the processes through which a certain disease impact is achieved. Hopefully these processes could be modelled and their effect on the disease status of a site could be predicted. This modelling could be extended to predict the effect of various stand treatments or other management activity on the disease impact status of the site.

While a reasonable model has been produced for disease development on high disease impact sites - those with a shallow caprock layer - there is little information of damage to individual trees following infection on sites of lower potential disease impact. Excavation of whole trees, and detailed recording of root damage on various vegetation types, and in disease impact levels of subtle and moderate, will fill this gap in our knowledge of the disease. This information is essential for future planning as, at present, there are no reliable data on the effect of lower disease impact on even the growth and yield of individual trees and stands.

Lesion expansion following artificial inoculation has been used to study the effect of site, and features of individual sites, on pathogen development once it is established in the individual tree. For example, lesion expansion ceases when the relative water content of the phloem falls below 85%. The time at which this occurs in the summer depends on the nature of the site, in particular the water availability. The overall aim of the investigation is to understand how the resistance of jarrah may be enhanced by site selection and/or site modification.

The evidence for variation in resistance to root rot caused by P. cinnamomi among different biotypes of jarrah is encouraging. The techniques of micropropagation can be employed to screen the general population of jarrah for resistance, and subsequently to vegetatively propagate the resistant biotypes. A promising technique has been developed to use callus, produced from selected shoots, to test in vitro the relative resistance of the biotypes. For logistic and economic reasons this is preferable to testing vegetatively propagated seedlings (plantlets).

The callus technique has potential for use in determining the genetic basis of resistance in jarrah to P. cinnamomi root rot. In the immediate future it will be used to screen mother trees which, following inoculation in the field, demonstrated resistance to lesion expansion. Following the screening the selected candidates would be carried through to the plantlet stage - some 12 months plus - prior to testing for resistance in the glasshouse and finally in the field.

RECOMMENDATIONS

1. Research priorities are best set by a group of involved researchers, such as the present Dieback Research Working Group. The priorities should be reviewed at approximately two yearly intervals.
2. Because of the complexities of land use in the jarrah forest, the research priorities can only be set within the framework of the aims and priorities of management, as decided by the Department of Conservation and Land Management, and these should be made clear to groups setting the research priorities.
3. The criteria for evaluation of research proposals are clear and objective. They have a justified bias to encourage new and practical projects rather than research with pure academic value. Despite the bias, the projects have made considerable contributions to fundamental knowledge and have resulted in publications of academic, as well as practical, importance. The thrust of the evaluation criteria should be conveyed to potential applicants for funding by the Foundation.

4. All recipients of grants from the Foundation should be required to submit annual progress reports. The Foundation should ask all previous recipients to supply photocopies or reprints of publications which have resulted from research funded by the Foundation. Appendix 4 provides a list of most of the published material.

5. The value of some of the research could be improved if the investigators made fuller use of the advice of professional statisticians in the planning of the experiments and analysis of results. Some of the current research involves complex concepts, while other areas are yielding enormous quantities of data. In both instances the use of the appropriate statistical techniques will help to achieve the greatest value from the results.

6. The disease assessment and disease survey projects are of critical importance. The practical and aesthetic impact of dieback, at the level of the rapid death syndrome, is unquestioned. However, current opinion suggests that the areas of jarrah forest, currently potentially susceptible to this level of disease, are limited. It is essential to develop numerous parameters to assess the 'total impact' on the jarrah ecosystem of dieback at a lower level of intensity.

7. The examination of disease processes and of factors affecting host susceptibility both impinge on the concept of 'predisposition to disease'. If possible these investigations should be extended to study experimental techniques to obtain a progressive infection in the root system of jarrah.

8. The jarrah breeding programme should involve testing with isolates of P. cinnamomi of minimum pathogenic variability. This will fulfil the requirements of screening resistance candidates, and also reveal the genetic basis of resistance in jarrah and its relationship to virulence in P. cinnamomi.
9. The breeding programme needs guidance also on the parameters to be used to screen the resistance candidates. Thus the resistance, for which the programme is selecting, must have direct value for resistance in the field or it must be positively correlated with features giving that resistance.

There is a justifiable air of confidence among the researchers in the results achieved and in their ability to solve some of the major problems being investigated. Further, they have a quiet confidence that jarrah dieback does not mean the end of the jarrah forest, rather that their research will enable high impact disease to be confined to limited areas of the forest and the lower level impact on other areas to be ameliorated.

Chapter 1

INTRODUCTION

1.0 Structure of the Report.

1.0.1 Executive Summary.

This summary was prepared from the conclusions listed at the end of each Chapter which covers an aspect of the research. Thus its layout follows essentially that of the technical report. Hopefully, this will enable an interested reader to refer to a particular technical point fairly quickly. Elements of unresolved conflict, or where data were incomplete or unconvincing have been omitted from this Summary.

1.0.2 The Technical Report

While one can accept that dieback in jarrah may result from a complex of biotic, e.g. insects, soil - and air - borne fungi (14, 15, 111) and other micro-organisms and abiotic e.g. drought, waterlogging (IV) etc. agencies, I have accepted the view of the Dieback Research Working Group Report 1983, that dieback associated with P. cinnamoni warrants the highest priority in research.

In any case most of the research undertaken with Foundation support has been related to the P. cinnamoni/E. marginata complex. Thus the report is presented as a series of Chapters which have considerable inter-relations. The location of some research projects is rather arbitrary, but results, in part, from the placement of the chapters in the series. The limited comments which I have made on certain aspects of the research, on research priorities etc., are in Chapter 7. I did not wish these to become confused with the summary of the actual research reported in Chapters 2 - 6. At the end of each

Chapter I have listed what seem to be the outstanding achievements on the particular aspect of the investigation.

1.1 Administrative Details

Contributions to the Foundation up to June 1985 are listed in Appendix 1. Disbursements from the Fund commenced in the second half of 1979 and have continued to 1985. The recipients, their institutions, the period and amounts of funding are given also in Appendix 1.

The titles of those projects funded are provided in Appendix 2, while the progress and annual reports submitted to the Foundation by recipients of funds are detailed in Appendix 3 (Capitals in text). Annual reports of receipts and expenditure from the recipient's institutions are held by the Secretary of the Foundation and are not included in this report.

1.2 Technical Report Reference

Publications in proceedings of conferences, journals, departmental publications etc. which have stemmed, at least in part, from funding by the Foundation are listed in Appendix 4 (arabic numerals in the text). It will be appreciated that funds received from the Foundation were part of the total funding or support e.g. salary and research facilities, A.R.G.C. support, etc. available to most recipients. It was usually not possible to distinguish the particular portion of the total research project which was supported by Foundation grants. In Appendix 4 I have marked with an asterisk those publications where Foundation funding was a significant, direct contributor to the project. In other instances the Foundation funds were an indirect supporter, or a catalyst, in the published work. In Appendix 5 (roman

numerals in text) I have listed a miscellanea of papers submitted for publication but not as yet accepted, academic theses and reports to organisations other than the Foundation. In all instances this material was made freely available to me by the authors or their supervisors. I appreciate this assistance.

Finally, I have listed, Appendix 6, those individuals with whom I had discussions during my visit in October. These interviews provided the pers. comm. references in the text. I appreciate greatly the time and assistance which all these people gave so freely to update the research results for inclusion in the report.

1.3 Acknowledgement

I wish to thank the Secretary of the Foundation and officers of the Department of Conservation and Land Management for making my visit to Perth in October beneficial and enjoyable. In particular I want to thank Mr. M. Samon for his very practical assistance and thoughtfulness and my wife for her help with the data preparation and initial typing of the report.

Chapter 2

THE PATHOGEN

2.0 Introduction

The epidemiologically important, asexual portion of the life-cycle of the pathogen has been investigated by a number of groups. In particular the influence of environment of sporulation, dispersal, survival and population of the pathogen has been reported.

2.1 Sporulation (sporangial formation and zoospore release).

Sporangial formation is an aerobic process (A, 16, 51), which can occur in soil at field capacity (51) and is skewed towards high temperature; in soil leachates sporangial formation is optimal at 22-28°C (B). Thus, in the surface soil horizons on well drained sites in the northern jarrah forest, typically there is a peak of sporangial production in late spring with another in early autumn. Heavy rains in summer, e.g. Dec./Jan. 1982, resulted in sporangial production and release of zoospores into soil on these sites (B). In the upper soil horizons on low lying moisture gaining sites, temperature and moisture conditions are suitable for sporulation for long periods of the year (A, B). Sporulation on mycelial mats, held at -1.0 kPa soil water potential was maximal in soil cores collected in summer, intermediate in those collected in spring and low in those collected in winter or autumn (B, IX). This seasonal pattern is independent of soil type, although in a series of cores from the northern jarrah forest, sporulation was highest in a yellow sandy gravel, intermediate in a sandy loam and a black gravel and low in a red loam (B, IX). Sporulation was stimulated in a disease suppressive red earth, by

comparison with that in a disease conductive jarrah laterite, but this stimulation was inversely related to hyphal lysis in these soils (47).

Although zoospore release occurs only in saturated soil it has a similar seasonal and soil type pattern to that for sporangial induction in northern jarrah soils (A, B, IX).

In contrast to the behaviour in the surface horizons of well drained sites, sporangial production on mycelial mats exposed at a depth of 60 cm on the surface of concreted lateritic caprock was as high, or higher (period mid-April/late July) than on comparable mats exposed in the top 6 cm of such profiles (C, 65, 66). On July 29, 1983, at 120 cm in such profiles, the temperature remained above 14°C (the minimum for sporangial production) although in the surface soil it had fallen to 10°C (D). Following rain, ponding of water occurs on the surface of the caprock thus providing suitable conditions for zoospore release and dissemination in the water flow on the surface of the indurated layer (D, 66).

Stimulation of sporangial production by Penicillium spp., which dominate the rhizosphere of Banksia grandis has been reported (48). However there are several reports of suppression of sporangial production and/or zoospore release. Sporangial production was suppressed under stands of Acacia pulchella (A) while fewer sporangia were formed in soil cores collected under unburnt stands of this legume than in comparable cores from beneath unburnt B. grandis. Burning of stands resulted in fewer sporangia in soil cores, while canopy type or burning did not affect zoospore release or hypal lysis (B, I). The suppressive effect of soils from under A. pulchella was also evident in soil suspensions in which zoospore release was reduced when compared with suspensions prepared from soils under B. grandis (49). Saponins, extracted from the roots of A. pulchella, reduced considerably the

release of viable zoospore from sporangial produced in axenic culture (Kagi pers. comm.). Thus, apart from indirect environmental effects (A), A. pulchella has the potential for direct antagonism to the sporulation of P. cinnamoni.

2.2 Zoospore dispersal, encystment and germination.

In the period July 1979/May 1980 the maximum rate of movement of P. cinnamomi downslope from pieces of banksia root buried in surface horizons was 25-40 mm (A); even the spread of inoculum on infested sites heavily irrigated in late spring/summer, was slow with the recovery of few zoospores (B). In Jan/Feb 1982, following heavy rain, significant movement (75 mm) occurred downslope in surface soil from infected banksia (C). The latter observation emphasises the importance of heavy rain in late spring/summer leading to some overland flow and zoospore dispersal. Under controlled conditions dispersal is slightly more rapid in black gravel than in red loam (B, IX).

In contrast to the generally slow rate of dispersal in surface horizons, zoospores were dispersed laterally at depth following rain on sites with a shallow concreted lateritic layer (B, 65, 66). In the field, zoospores moved 50-70 cm downslope in the water flow on the surface of the caprock layer but only vertically beneath the inocultaion point when introduced into soils lacking such an impeding layer (65).

Zoospore germination is not suppressed by the absence of oxygen (IV), however actinomycetes from the rhizosphere of A. pulchella strongly inhibit cyst germination (Murray pers. comm.). Among the cations tested Calcium is unusual since in the mMolar range it promotes both zoospore encystment and cyst germination. Most other cations induce encystment only and are toxic at higher concentrations (E, 9).

Zoospores and cysts had a broad tolerance to pH (3.5-9.0) and temperature (10-26°C) (E, 9). Pectin was the only carbohydrate to promote zoospore encystment while a few proteins, e.g. histons, also performed this function. A variety of carbohydrates and amino acids stimulated cyst germination (E, 10, 33).

2.3 Survival of inoculum

2.3.1 Hyphae

Hypal lyis was most rapid in soils at or below field capacity when incubated at 25-27°C (51). While there was little lysis of hyphae by bacteria in leachates from laterites, bacteria in litter leachates extensively colonised hyphae, causing lysis (52).

2.3 Zoospores and/or cysts

After 8 weeks exposure the survival of zoospores under stands of A. pulchella was markedly reduced when compared with that under stands of B. grandis or fertilised, non legume stands (A). In contrast to normal experience the abnormal heavy rain in Dec./Jan. 1982 resulted in introduced P. cinnamomi surviving the summer in the surface of freely draining soils (B). Survival of zoospores in a Karri loam, (a suppressive red earth), was significantly reduced by comparison with that in a northern jarrah lateritic soil (F, 47). Zoospores failed to survive exposure for 4 days to an extract of non-sterile jarrah litter while an extract of non-sterile jarrah mineral soil promoted survival after 8 and 12 days (presumably the spores reproduced in this latter extract) (F). Extracts of cultures of a number of mycorrhizal fungi reduced the survival of cysts and sterilised extracts of "white", but not "black", entomycorrhizae of jarrah reduced cysts survival also (F). Although cysts germinated within 24 hr on the surface of the

basidiomycete ectomycorrhizal mantle on jarrah roots, the pathogen could not be recovered from these roots while it was readily recovered from non-mycorrhizal roots. On the mycorrhizal roots the cysts were colonised by a range of distinct bacteria and actinomycetes (43).

2.3.3 Chlamydospores

Chlamydospores, treated with fluorescent dyes, survived and reproduced when introduced on nylon mesh into soil, sand, gravel or glass beads at three water matric potentials. Greatest reproduction occurred in soil after 10 days while survival for 28 days occurred in the soil and in the glass beads (E, 77). In contrast, laboratory produced chlamydospores generally failed to survive when introduced into surface soil in jarrah forest even under wet conditions. However decline in population was more rapid in dry soil and over summer. There was some evidence that the inoculum occasionally infected roots and survived the summer (A).

2.3.4 Sapophytic survival in plant tissue.

On occasions survival involved reproduction, saprophytic invasion and resulting lateral spread of inoculum.

While zoospores (cysts) and chlamydospores have very limited survival in the field, P. cinnamomi is an effective survivor in tissue which it has invaded parasitically. P cinnamomi reproduced (chlamydospores) and survived for 30 days when the soft, excised, infected, primary roots of blue lupin were buried in soil (E, 76, 77). P. cinnamomi, introduced in infested banksia root pieces into plots in a regrowth jarrah stand, survived over summer (1979/80) and saprophytically reinvaded some of the banksia material in the winter of 1980 (A). The survival of P. cinnamomi was better in pots of soil

amended with banksia roots (100%), than in comparable pots amended with A. pulchella (B, I). In addition to long term survival in systemically infected dead and dying banksia (A, B) P. cinnamomi also survived over summer in the dead roots and the stem bases of Dryandra sessilis in old die back sites (58).

Excavation of roots of jarrah, exhibiting the rapid death syndrome (all located on sites with a concreted lateritic caprock 5-75 cm below the surface), demonstrated the survival of P. cinnomomi in the vertical roots both above, and within, the channels of the caprock, in some horizontal roots and on occasions in the base of the stem (B, 64, 67). The survival of P. cinnomomi in pieces of banksia was longer in black gravel than in red loam (B, X).

2.4 Populations of P. cinnamomi in soil

Despite the limitations of media containing Hymexozol for determining absolute populations of Phytaphthora spp. (69), this is the best method available and is suitable to monitor relative populations of single species between sites or, at intervals, within sites. Samplings, over an 18 month period, of surface soils of a typical dieback area on an apparently freely drained site indicated that the organism was absent from the soil in the 'old dead' zone, was at low population in the 'greenline' area but was at high population in soil adjacent to recently killed banksia. The populations peaked in late spring and autumn when higher temperatures and soil moisture were favourable for sporulation (A, 63). Studies, over a four year period, emphasised the dependence of populations in these soils on the timing of spring and autumn rains (A, B). When heavy (unseasonable) rain occurred in summer (1981/82) the fungus was present in the surface horizons of these upland sites throughout the year (B). Early autumn

rains resulted in high sporulation at the base of systemically infected banksia; this increased the population of the fungus which survived through the winter (B). Even irrigation of these sites during the summer did not cause a general spread of inoculum in the surface soil until the equivalent of 700 mm of rain had been applied to the plot. Soil population in the irrigated sites decreased rapidly when irrigation ceased in summer (63).

In contrast, populations of P. cinnamomi at the surface of the caprock in sites with a concreted lateritic layer at 5-75 cm, were relatively very high (B) and several times those in the corresponding surface horizons (B, C, 65, 66).

As would be expected features of the environment affected populations largely as a result of their effects on sporulation, survival, dispersal etc., for example when the fungus was introduced into a black gravel and a red loam in the field the population remained much higher in the former over a 100 day period (IX).

2.5 Conclusions

Although the sporangial inducing potential of jarrah soils was at a maximum in summer, in the field, sporangial production and zoospore release, and consequently P. cinnamomi populations, in surface horizons were usually maximal in spring and late autumn when temperature and moisture conditions were optimal. In years when heavy rain occurred in summer, populations built rapidly and the pathogen survived the summer in the surface horizons.

At depth (5-75 cm) in the soil profile, in areas with concreted lateritic caprock, sporangial production continued throughout summer and winter and consequently populations remained high.

Dispersal of the pathogen in surface horizons was very restricted, even when areas were artificially flooded during summer. In contrast, at depth in profiles with shallow caprock, zoospores were rapidly dispersed in the lateral flow which occurred on the caprock surface.

During summer, survival of zoospores, cysts or chlamydospores in surface soils of jarrah forest is very limited. In contrast, saprophytic survival in Banksia roots, infected parasitically, is very efficient, and recolonisation of tissue may occur in the following autumn/winter. Again, conditions at depth in areas with shallow caprock are favourable throughout the year. Thus the organism, located in major sinker roots of jarrah or banksia at the surface of, or in channels in, the caprock, is well placed to sporulate and disperse when free moisture is available in the area.

While the surface of the caprock is a favourable environment for the pathogen, the surface horizons of the soils of the jarrah forest have numerous antagonistic aspects, e.g. antibiosis from rhizosphere organisms, antagonism from jarrah litter, antagonism from the roots of A. pulchella and mycorrhizal organisms. In ecological terms, the occurrence of P. cinnamomi at depth can be viewed as a form of escape from the antagonism of the surface horizons. It happens that this is an excellent location for the parasitism of the major roots of jarrah. The presence in this zone of the systemically, colonised roots of dead Banksia builds the inoculum potential of the pathogen and makes the infection of the major roots of jarrah inevitable.

Chapter 3

THE HOST

3.0 Introduction

Investigations have concentrated on jarrah, although certain findings probably apply equally to other hosts in the northern jarrah forest, e.g. sinker type roots of B. grandis also occur in the channels of the concreted lateritic caprock. The research has yielded much fundamental data on jarrah however only that which has obvious significance to die back will be recorded in detail.

3.1 The jarrah root system.

3.1.1 Morphology and anatomy.

The root system in the surface soil horizons, with its long horizontal roots, its perennial framework roots of the extensive root pads, the ephemeral, short, fine roots, has been described (A, 61), while the anatomy of the non mycorrhizal long roots has been detailed also (22). Subsequent studies have reported the morphology and anatomy of the mycorrhizal roots (F, 20, 42).

Following the recovery of P. cinnamomi from sinker roots of jarrah (21, 64), the root distribution in the total profile, in particular the development of sinker roots from the horizontal root system, has been investigated (25). The basic roots system of jarrah with its horizontal long roots, its sinker roots and its negatively geotropic riser roots is apparently genetically determined and is only slightly modified by site; principally by compression of the system into a shallower horizon in sites with a shallow concreted lateritic layer. The horizontal system is restricted to the upper 50 cm but again this is compressed closer to the surface in soils with a shallow caprock.

The origin of the sinker roots is at random on the horizontal system and is unrelated to drainage, but the individuals which become functional depend on the channels in the caprock etc. Riser roots, from which the extensive, surface, fine root pad system is developed, are more common in deeper profiles (K). The distribution of root types in profiles on different sites is currently being investigated (K).

3.1.2 Periodicity of root growth.

Except in mid winter, non-mycorrhizal roots developed whenever their was adequate moisture in the surface profile. Thus considerable root growth occurred in spring (Sept.-Oct.) and in autumn following rain (usually May-June). The low temperatures of winter presumably prevented fine root growth. In contrast a framework of new mycorrhizal rootlets, which commenced to form in May, continued to be produced through July, i.e. this was a winter phenomenon. When 47 mm of rain occurred in February there was extensive non mycorrhizal fine root production within 2 days. The response of the jarrah root system to produce new root tissue normally in spring and autumn, with occasional production in summer following rain, coincides with the sporulation and population increase response of P. cinnamomi to similar environmental conditions. Such coincidence of activity has epidemiological significance.

3.1.3 Mycorrhizal associations.

Microbial antagonism to P. cinnamomi, and more specifically the potential of ectomycorrhiza for suppression of the pathogen, have been extensively reviewed (F, G, 39a, 40). Subsequent investigations have demonstrated high bacterial populations, many elements of which are antibiotic to species of Phytophthora and Pythium, associated with

mycorrhizal roots of E. calphylla and E. marginata (39, 40). Collections have been made of numerous epigeous and hypogeous basidiomycete fungi (G), and mycorrhizas have been synthesised on jarrah seedlings with a number of these (Malajczuk pers. comm.). There is evidence that fungi, all of which are capable of forming ectomycorrhizae with jarrah seedlings, differ in their stimulation of growth of jarrah in field trials (Malajczuk pers. comm.). There is a correlation, which holds at least to the level of genus, of the morphology of ectomycorrhizae and the taxonomic position of the fungal symbiont, e.g. the ascomycete Cenococcum geophilum forms the black type mycorrhiza while the white pyramidal type is formed by various basidiomycetes (43).

A succession of mycorrhizal fungi colonises roots of E. resinifera as the individual tree ages (28, Malajczuk pers. comm.). While there is little difference in morphology of the reaction of the root of E. marginata to eucalypt specific, or broad range mycorrhizal fungi, the roots react antagonistically to conifer specific mycorrhizal fungi (44). Strong habitat preferences have been demonstrated by various types of mycorrhizae in jarrah e.g. white and brown type mycorrhizae occurred mainly in litter and controlled burning destroyed 90% of these; black type mycorrhizae were characteristic of mineral soil (56). In addition certain basidiomycete genera occur more commonly in litter in troughs, while others fruited on the mineral soil crests, in ripped lines prepared for the rehabilitation of mined sites (28).

3.2 Physiology

3.2.1 Transpiration

E. marginata and E. calphylla showed little stomatal control of water loss, or change in leaf resistance even during summer; further

there was limited seasonal variation in xylem pressure potential. This contrasted with certain eastern states eucalypts (E. saligna, E. maculata and E. resinifera) which had marked stomatal control of water loss on summer days. E. wandoo also controlled water loss but had a xylem pressure potential much lower than the other species (13). This abnormal transpiration pattern in jarrah is not correlated with any specific anatomical feature, e.g. the leaves of jarrah are hypostomatous as are those of E. saligna and E. resinifera (57). Waterlogging of 3-4 month old seedlings of jarrah restricted water movement throughout plant within 4 days, a number of vessels were blocked with tyloses which increased in number with an increased period of waterlogging. Transpiration rates of waterlogged plants correlated with the proportion of vessels occluded by tyloses in the taproot, and the rate of wilting of seedlings depended on the duration of waterlogging (up to 16 days) and the transpiration rate (16).

3.2.2 Nutrition.

The level and distribution of nutrients in a jarrah ecosystem on various soil types and on upper-, mid-, and lower-slope location has been reported (N, 31). Fertilising all these sites with varying levels of nitrogen (0, 50, 200 $kgha^{-1}$) and phosphorus (0, 50, 200 $kgha^{-1}$) produced a significant increase in annual girth increment in jarrah with the combination of the two elements. The fertilising did not effect the annual girth increment of E. calophylla, Casuarina fraserana or B. grandis, associated dominants of the site, nor was the percentage cover of any of the understorey species affected (31a). Thus the perturbation of the jarrah ecosystem by fertilising was small. Further, despite the significant promotion of the growth of jarrah, the fertiliser treatment did not affect significantly the rate of lesion

extension when the jarrah was inoculated with P. cinnamomi (Hingston pers. comm.). In contrast, jarrah seedlings with the addition of a complete fertiliser minus lime and phosphate, when growing in a pallid clay, showed a definite response in shoot and root growth to fertilising with phosphate alone. A calcium phosphate dressing of 30-300 mg/kg soil produced maximum yield of seedlings (27). Soils from various sites in the jarrah forest differ considerably in fertility and consequently the growth of jarrah seedlings in pots of these soils varies, however the introduction of P. cinnamomi into the pots did not significantly depress the rate of growth of the seedlings in any soil type. The addition of macronutrients to the P. cinnamomi-infested soils increased the number of plant deaths, the number of infected plants and the level of infections in infected plants (J). It was shown in a sampling experiment that some 10-30% of total plant phosphorus in 27 month old seedlings was located in the lignotubers (26). Zinc deficiency, similar to that occurring in wheat, has been found in seedlings of jarrah growing in sand with adequate macro and micronutrients (J, 24, 74).

3.3 Vegetative Propagation.

The background literature on vegetative propagation, in particular micro-propagation, as a means of increasing the stock of selected biotypes of eucalyptus has been reviewed (7, 34, 35, 36). For jarrah the development of the techniques, media etc. for producing callus, plantlets, rooted plantlets in culture, and the transfer of these to soil involved extensive research over several years (34, 35, 36). Major problems encountered and solved were the development of callus from the axillary buds of mature shoots (explants of nodal pieces some 3-4 nodes from the apex), from anthers and from roots. In contrast to

micropropagation from seedling stages, formation of callus and induction of roots in culture from mature shoots proved difficult, and the rate of success was very low (L, M). Even when contaminant-free callus had been produced, 12 months or more were required for root induction in callus from either stamens or shoots of mature trees (36). This contrasts with callus from most eucalypt seedlings in which rooting can be induced in 1-2 months (34, 35). Plantlets of jarrah developed by micropropagation when grown in the glass house differed from seedlings in being shorter and more branched, the foliage was of the mature (not juvenile) type, and root length was shorter than that of seedlings. After two years growth in the field plantlets were taller than seedlings from the same mother tree as the plantlets, they lacked the coppice habit and lignotubers characteristic of the seedlings (M, 8).

3.4 Conclusions

The basic root system of jarrah with long horizontal roots, surface pads of fine roots some of which are mycorrhizal, a system of vertical sinker roots and negatively geotropic riser roots, appears suited to exploit the resources of the profile, and to enable survival over the dry summer.

The growth of non-mycorrhizal fine roots usually occurs in spring and autumn but rain in summer will also stimulate activity.

Ectomycorrhizae have bee synthesised on jarrah seedlings using a number of epigeous and hypogeous basidiomycete fungi to produce the typical pyramidal form. In contrast the ascomycete Cenococcum geophilum produces a black type mycorrhiza. A succession of fungi have been recognised to form mycorrhizae as the tree ages and fungi differ in their efficiency as mycorrhizal associates.

Jarrah lacks stomatal control of water loss, hence the importance of the sinker roots to supply water from depth in the profile. Water-logging of jarrah seedlings rapidly induces symptoms of water deficiency and wilting.

While the nutritional status of jarrah soils is usually low, a combination of heavy dressings of nitrogen and phosphorus is generally necessary to produce a growth response. There is evidence of zinc deficiency affecting the growth of jarrah on certain soils.

While micropropagation of jarrah from the shoots of mature trees has proved difficult, many of the problems have been solved and plantlets have been established in the field. These have foliage characteristic of mature, not juvenile, trees and lack the lignotubers and the coppice habit of jarrah seedlings.

The occurrence of sinker roots in jarrah and in other elements of the jarrah forest, e.g. Banksia, suggests these are essential to survival of the species during summer drought. It is the attack of P. cinnamomi on these portions of the root system which induces the rapid death syndrome in jarrah dieback. The coincidence of fine root growth and reproduction of P. cinnamomi in surface horizons in spring and autumn is probably another contributor to decline in jarrah.

Chapter 4

HOST - PATHOGEN RELATIONS

4.0 Infection and spread in the host.

4.0.1 Fine root (unsuberised) infection.

Initially it was hypothesised that the death of jarrah resulted from the killing of fine roots in the upper layers of the soil profile, hence the early concentration on the infection of such roots in the field and of seedling roots in the laboratory.

Inoculation (drenching) in spring, the period of fine root flush, of root pads (masses of fine roots in the surface soil horizon) of jarrah with a suspension of zoospores of P. cinnamomi resulted in significant infection of the pads; primary entry was via the distal ends of fine roots. Infection of the longer root (3-4 mm diam.) framework of the pads occurred from the root clusters. Extra-xylary spread was extensive in some roots (up to 4 mm diam.) but limited in others (J, 61). As the soil dried out in the summer, P. cinnamomi could not be isolated from the soil inoculated in spring, but the root pads, the framework roots and short laterals of the pads yielded the pathogen (61).

The inoculation, under controlled conditions in the laboratory, of the roots of 3 month old seedlings of jarrah and marri with 3-5 zoospores per root provided a clear picture of primary root infection and invasion (E). In seedlings, with root temperatures maintained at 24°C, the invasion of P. cinnamomi of marri roots ceased after 5-7 days and the lesion was shed although the fungus could be isolated subsequently from the tissue adjacent to the lesion. In jarrah the reaction varied between plants. In some the lesion continued to extend and invasion of the greater part of the root system followed, and there

was some evidence of secondary infection, while in others the organism was contained, as in marri, after some 5-7 days. Thus while marri always demonstrated a tolerant reaction at this temperature the reaction of jarrah varied from tolerant to susceptible. These reactions were temperature dependent with both species showing reduced resistance at 29°C (E, 30). Percentage roots infected, and lesion number, increased at 7 and 14 days following inoculation with P cinnamomi zoospores, when waterlogged seedlings of jarrah were compared with those in an aerobic environment (IV).

When roots, 2-3 mm diameter, were inoculated in the field at monthly intervals throughout the year, and harvested 2 months later, the fungus had always been halted by periderms at the margins of lesions up to 5 cm long. This demonstrated the resistance in these fine jarrah roots to invasion by P. cinnamomi (C, 71). The progress of infection from fine roots to major roots has yet to be established (C, Shearer pers. comm.).

4.0.2 Major root (suberised and some with secondary thickening) infection.

Following the recognition that P. cinnamomi systematically invaded B. grandis (59) and its isolation from both the stem and roots of recently killed individuals and even trees dead for two years (A, 8), the pathogen was isolated from the suberised and partly suberised roots of jarrah (63). Recoveries from woody roots of more than 2.5 cm diam. were made from both wood and bark (21, 67). Later the importance of the infection of major roots and sinker roots, in the rapid death syndrome of jarrah on sites with shallow concreted lateritic caprock, was appreciated (64). This perspective on jarrah dieback (B, 65, 66) was accompanied by investigations on the infection process in larger roots and stems (B, C, 71, 72, 73).

Following inoculation of large roots and stems with P. cinnamomi (discs of corn meal agar culture) of wounds (7 mm drill holes) lesions developed in the secondary phloem of jarrah. Fungal spread was most rapid in the outer phloem, and roots resisted tangential spread more effectively than coppice stems. The lesion spread was restricted during winter and spring by the production of necrophlactic periderms. Extension of the lesions in summer normally resulted in gum vein production, the cambium having been injured following the invasion of the inner phloem. Lesion development in coppice stems was a useful technique as it provided replication, and vertical extension was exaggerated in stems by comparison with roots (B, 73). Lesion extension in both stems and roots was at a maximum rate in summer while extension in excised roots was at a maximum at 25-30°C (B).

Under conditions of temperature optimal for growth, the extension of lesions was limited by moisture content of the bark with a linear correlation between moisture content of the bark and lesion development over a 19 day period in trees growing on sites of variable moisture availability. Lesion extension ceased when the moisture content of the bark fell below 75% (C, 70). These preliminary observations have been confirmed in a more extensive study of some 15 trees at each of 15 sites which differed in understory composition. Phloem of trees with the greatest water deficits were the least susceptible to invasion by P. cinnamomi. Even when summer temperature was favourable lesion extension ceased when the relative water content (RWC) of the phloem fell below 85%. RWC was linearly related to phloem water potential over the range 75-100% RWC corresponding to water potentials of -1.5 to 0 M Pa (XI). Intermittent halting of lesion extension by reduced phloem water content could explain the series of peridems observed around some lesions in major roots in the field (C).

When the resistance to stem inoculation with P. cinnamomi was tested in the field in some 21 eucalypt species, aggressive lesions were produced only in E. marginata. Typical lesions developed also in other species of the sub-genera Monocalyptus and Corymbia used in the rehabilitation of pits resulting from bauxite mining, but not in species of the sub genus Symphyomyrtus, most of which appeared to be immune to infection (C, 72).

The infection of secondary phloem by P. cinnamomi may eventually result in girdling of roots and stems. Despite the vulnerability of jarrah to invasion of the secondary phloem, the lesions are frequently contained by periderms at their margins. Thus lesion extension may cease, although this containment of the fungus may be only temporary and the fungus may break out under certain conditions. In some instances lesion extension ceased after 4 months but P. cinnamomi could be isolated from the lesion some 15 months later (C). When both primary and secondary roots were artificially inoculated in situ, the lesions expanded preferentially in the phloem in both instances but the lesion extension was considerably more rapid in the suberised secondary, than in the primary, roots (C, 71).

P. cinnamomi was always the most rapid invader of the stem phloem of B. grandis when stems were wounded and inoculated separately with nine species of Phytophthora. In contrast, when compared with the other species of Phytophthora, P. cinnamomi was not a more rapid invader of jarrah. The specificity of the P. cinnamomi/B. grandis relationship is further emphasised as this is the only species of Phtophthora employed which was more aggressive on B. grandis than on jarrah (C).

The rate of lesion extension in roots inoculated in winter was less than half that of inoculations made in summer, however lesion

extension rate was independent of the flowering condition of the host and was unaffected by the recent history of cool or hot burns of the site. However, while the rate of lesion extension was linearly related to temperature over the range 10-30°C with the optimum of 29.5°C, site had a significant impact on lesion length in roots. Irrespective of the time of inoculation, lesion length was greater in trees on sites considered highly susceptible to jarrah dieback (C). Such sites are typically water gaining and the effect of soil water availability on water content of the phloem is probably a partial explanation of the site relationship.

4.1 Histology of root infection and spread.

Studies of the histology of infection and host response were undertaken as part of the examination of lesion development. The shape of lesions in roots with secondary development reflected the pattern of periderm formation, both necrophylactic and exophylactic, the former preceded the establishment of the latter type. In infections of primary roots, the organism attacked mainly the cellulosic elements of the stele with limited growth in the cortex; lignified elements were not degraded in the stele. In roots with secondary structure, lesions were sometimes completely bounded by necrophylactic periderms, some of which extended radially inward through the cambium and into the xylem. The proliferation of P. cinnamomi in the lignified tissue of the xylem was limited. The production of exophylactic type periderms frequently occurred in the inner phloem of infected secondary roots and this resulted in shedding the infected outer phloem (B, 71).

4.2 Physiology.

Seedling roots of a number of Australian species, covering a range of susceptibility to P. cinnamomi , were inoculated with 10-15 zoospores and changes in root tissue physiology and histology observed.

Zoospores were attracted to, and infected, all species. Among the resistant/tolerant species, A. pulchella, A. melanoxylon and E. calophylla showed pronounced leakage of electrolytes from roots into a bathing fluid (indicative of root cell membrane damage) within 2 hours of inoculation. In susceptible species, including jarrah, such leakage occurred only after 8 hours following inoculation. Rapid damage to cell membranes in some host/pathogen complexes is associated with the hypersensitive response to resistant cultivars (E, 78, 79). The amount of electrolyte leakage was greater from infected roots of hypersensitive (resistant-tolerant) species than from susceptible types (E).

Although the roots of all species, with the exception of E. maculata, showed an increase in respiration following inoculation with P. cinnamomi , there was no evidence that the extent of increase was related to the susceptibility rating of the species (E, 11). The timing of respiratory rise, which can only be assessed by continuous monitoring, may be better correlated with susceptibility rating. This would be expected from the research with obligate fungal parasites such as rusts and powdery mildews.

There are only subtle differences between host species in hypal growth following penetration by cyst germ tubes. Rapid host cell necrosis and hypal lysis was observed in A. pulchella, although the pathogen on occasions continued to invade the host. Callose was produced to varying extents by all those species rated as resistant and this may slow down or restrict hyphal invastion (E). However

subsequent investigations suggest that callose formation either reduces membrane damage or prevents fungal growth (12) and the production of callose in jarrah, a susceptible species on the rating employed, has been recorded by other investigators (M).

Changes in the water relations in a susceptible (E. sieberi) host have been contrasted with those in a tolerant (E. maculata) species, following the inoculation of the roots of seedings of both species with zoospores of P. cinnamomi. In E. sieberi evapotranspiration, leaf water potential, leaf conductance, leaf relative water content and root conductance were all reduced in infected plants by comparison with uninfected controls. In E. maculata infected and uninfected seedlings behaved similarly. Thus E. sieberi, but not E. maculata, had symptoms of water stress following inoculation (E, 17, 18, 19). The changes in E. sieberi, which resulted in wilting occurred at 4-6 days after inoculation, i.e. prior to the rotting and loss of distal roots, suggesting that the wilting results from loss of permeability or hydraulic conductance following infection. Blockage of vascular tissue by tyloses could be a further factor in symptom induction (E).

4.3 Conclusions

The inoculation of fine roots of seedlings, under optimal conditions in the laboratory, resulted in a tolerant reaction in marri but a tolerant to susceptible reaction in various plants of jarrah. This is evidence of variability in resistance of biotypes in the latter species. In the field, the inoculation of fine roots in spring frequently led to spread into the framework of the root pads but progress of the infection in the summer was usually halted, with periderm production, in roots in the upper portion of the profile.

In B. grandis systemic invasion of the root system, and of the stem, followed inoculation of larger roots. In contrast inoculation of large roots of jarrah established an infection which spread in the outer secondary phloem, but again systemic invasion did not occur and periderms were formed. Extension was most rapid with inoculation in summer, but if moisture content of the phloem fell below 85% expansion of the lesion ceased. The pathogen spread more rapidly in secondary , than in primary, roots.

Species of the Monocalyptus and Corymbia subgenera of Eucalyptus reacted with periderm formation, to different degrees, to invasion by P. cinnamomi , while species of the subgenus Symphyomyrtus appeared to be immune to infection.

Following inoculation of the fine roots of species of varying susceptibility to P. cinnamomi cell membrane damage occurred within 2 hr. in resistant/tolerant species, but only after 8 hr. or more in susceptible plants. Following infection a hypersensitive reaction occurred in some resistant species while tolerance was expressed by other resistant, and also in some susceptible, species. A susceptible species of Eucalyptus demonstrated symptoms of water deficiency 4-6 days after inoculation of the roots with zoospores, while the water relations of a tolerant species seemed unaffected by inoculation.

Overall these relationships indicate that B. grandis is the completely susceptible host of P. cinnamomi , at least in the jarrah forest environment. In contrast there is, apparently genetically based, resistance in jarrah. In addition, the environment of the surface horizons of the soils of jarrah forest on some upland sites, appeared unfavourable for unlimited lesion expansion and systemic invasion of jarrah. When considered together with the antagonism of

this portion of the soil profile to the pathogen, this zone in the soil must be considered as unfavourable for major disease occurrence.

Possibly epidemic disease occurs only where such environmental constraints are lacking e.g. on sites with a shallow concreted lateritic layer and in valley bottoms with their high moisture levels in surface horizons throughout the year.

Chapter 5

THE ENVIRONMENT

5.0 Introduction

The effect of certain features of the environment on the pathogen, the host and the interaction of host and pathogen have been detailed in previous chapters and will not be canvassed here, however, a particular environmental feature may have varied effects which may be complementary or antagonistic. For example, with the reduction in soil moisture of the upper profile below field capacity in summer, the pathogen will not sporulate, there will certainly not be significant dissemination of inoculum in the undisturbed system and should the water content of the phloem fall below 85%, the extension of lesions already present in the roots should cease. All these features should contribute to reduced disease in the host. Some of these relationships will be developed further in the Chapter on disease. This Chapter will concentrate on aspects of the northern jarrah forest which have been investigated with funds provided by the Foundation but some of which have a rather indirect relationship to dieback.

5.1 Nutrient and energy flow in the jarrah forest ecosystem.

The rationale behind this research was several fold. For example, certain management practices might be introduced to avoid or control jarrah dieback, what is the likely impact of these on the jarrah ecosystem? Invertebrates are important components of soil and litter of the ecosystem, do they render the environment more or less favourable to P. cinnamomi, are they vectors of the pathogen, or do they effect the regeneration of dieback sites? Will dieback in the jarrah forest catchments lead to excessive loss of essential nutrients

from the affected site, and/or will the outflow of nutrient result in salt pollution of these streams which are portion of the metropolitan water supply? It will suffice to indicate briefly the results of some of these investigations.

5.1.1 Impact of fire - an autumn legume regeneration burn.

There was an immediate rise in pH, a doubling of total phosphorus within 2-27 days, and an increase in organic matter in the soil in 30 days, after the burn. However over the following 2-3 years the pH stabilised at its pre-fire level and soil phosphorus, organic matter, nitrogen, magnesium, potassium and calcium all decreased to approach their pre-burn levels. Presumably the decrease of mineral content of the soil reflected the uptake by the regenerating vegetation (O, P). In addition, application of phosphate following burning, stimulated the growth (biomass) of native legumes in jarrah forest (32).

5.1.2 Input-output studies of essential nutrients in catchments.

The microcatchments of the Yarragi Brook watershed are in an aggrading phase, following a control burn. An intensive study of the B. grandis component demonstrated that considerable nutrient resources, which could be made available to jarrah overstorey under an appropriate management system, are tied up in the B. grandis understorey (P, 2).

Studies of the water outflow from the Yarragil Brook watershed over a five years period established that, while the resource of total nutrient is low, the loss of essential macronutrients is very low (P). Even the logging of one microcatchment and the burning of another did not result in a loss from the system of significant quantities of nutrients, nor of increases in dissolved salts to unacceptable levels of pollution in the streams (Bell pers. comm.). The jarrah ecosystem

seems to be particularly tenacious of its mineral resource and well buffered against limited disturbance. It is unlikely that dieback in the catchment would cause serious reduction in mineral supply or pollution of the water supply (1, Bell pers. comm.). Slash burning following logging is probably the major cause of loss of nitrogen to the ecosystem.

An intensive study of the ecology of B. grandis has developed a model of the number of individuals and their size-class distribution over time, thus allowing the prediction of the effects of different burning intensities and regimes on the population of B. grandis in the northern jarrah forest. This model indicated that the B. grandis population could be considerably reduced and kept at a low level by a single hot burn follwed by a number of cooler burns at certain intervals (B, P).

Research has established also that sampling particular portions of eucalypt foliage, e.g. fully expanded leaves of current year's growth, at specific times, can indicate the nutritional status of species employed in mining site rehabilitation. Such sampling procedures indicate also deficiencies between sites in mineral availability (4).

5.2 Forest soil and litter invertebrate studies.

Monthly monitoring, over 13 months, of a jarrah forest site, subjected to a cool autumn burn, demonstrated that litter biomass, which dropped considerably following the fire, built up to 66% of its pre-fire level in the period. The burnt area had a generally increased soil and air temperature and a reduced relative humidity. The response of soil and litter invertebrates to the fire varied between taxonomic groupings from immediate density reduction, to delayed density reduction, to no effect, to increased density. The consequences of

fire were still apparent in the litter, and to a lesser degree in the soil, fauna 13 months after the fire (38). A review of the taxonomy and ecology of the soil and litter invertebrates has been published (37) and this has been extended to those characteristic of the dieback areas and to their litter decomposition in such locations (55). Studies in dieback sites indicate distinct differences in population and elements of the invertebrate fauna in these, compared with healthy sites. However, there is no evidence that elevation has significant effects on populations within these types. Further the differences between the invertebrate populations in soil and litter of suppressive and conducive soils is not significant. However the nutrient cycling by invertebrates in die back sites is worthy of further study (Majer pers. comm.).

5.3 Conclusions

Following a legume regeneration fire, while the soil showed an immediate increase in the availability of most nutrients, the levels adjusted, over a 2-3 year period, to their pre-burn levels.

The loss of nutrients in outflow from a jarrah catchment, even following fire or logging, was insufficient to cause concern for reduced nutrient supply of the site, or for pollution of the downstream water supply. Inflow of nitrogen to the system considerably exceeded loss in the water outflow.

A growth model proposed for B. grandis indicates that a single high intensity burn, followed by normal, low intensity control fires, would maintain the population of B. grandis at a very low level i.e. a series of hot burns is not necessary to achieve this end.

Following a cool autumn burn the invertebrates of the soil returned more rapidly to their previous levels than did the litter

invertebrates. There were distinct differences in population and taxonomic constitution of the invertebrates of a dieback, compared with a healthy, jarrah forest.

Chapter 6

THE DISEASE

6.0 Introduction

Research on aetiological and epidemiological aspects of the disease could proceed with confidence only following the results reported in the earlier chapters. For example, while the rapid death syndrome in jarrah was recognised as an occasional phenomenon in space and time, the model for its occurrence was developed only following the excavation of whole root systems. Research on the disease, on options for its control or amelioration, of the effects of land management activities etc., on its impact, has become more clearly defined over the past two years.

6.1 Survey

In earlier investigations survey was seen largely as aerial survey to recognise crown deterioration in jarrah or in the understorey, i.e. to define the distribution of the pathogen and/or the disease of dieback in jarrah. This was essentially a post-event record, and while fundamental to stand management, it did not permit prediction of the consequences in these areas, presently free of obvious disease, should the pathogen be introduced. The aim of current survey research is to associate levels of disease impact, e.g.

absent - no apparent disease e.g. stands on red loams.

subtle - random, localised disease only in herbaceous understorey.

moderate - significant dying in susceptible understorey e.g. *B. grandis*, jarrah unaffected.

high - considerable disease in overstorey i.e. dying in jarrah.

and possibly some further subdivisions of these classifications, with the total environment of the area where the disease occurs. Subsequently the environmental data can be employed to predict the potential impact in other zones of the forest, presently free of the pathogen (C, D).

A 25 page check list, which is subject to modification with experience, has been developed to describe the geology, soil, landscape and vegetation of the site on which the particular level of disease impact has been recorded. This system of recording has had considerable success, e.g. differences in vegetation, depth to caprock, type of slope have been recorded in adjoining areas (200 m radius) which were demonstrating high and subtle disease impact.

The selection of sites for assessment posed initial problems. The only criteria currently employed are that the area must be undisturbed and valley bottoms are excluded. A longer term aim of the research is to understand how disturbance can affect the potential level of disease impact on the site, hence disturbed sites are excluded while the environment of valley bottoms is favourable to reproduction and dissemination of the pathogen for long periods of the year. Except where soils are suppressive, e.g. red loam areas, it is probably not possible to avoid dieback in the valley bottoms. Finally the survey is limited to areas of jarrah forest between Mundarring and immediately south of Collie, because outside this zone the distinctions between disease levels, and also between vegetation types, are less pronounced.

To date some 400 sites have been surveyed, approximately 2 hours are required for each site (Shearer pers. comm.). The distribution of sites is concentrated in the high rainfall zone with very few in the low zone, however this merely reflects the distribution of the disease.

The sites of particular impact levels tend to be skewed towards specific features recorded in the survey. For example, on the basis of the Havel vegetation site types, the high impact type is skewed towards the P type, while the subtle and moderate types are skewed towards the S type. Again, for the T vegetation type the relative frequency is subtle moderate high, in contrast P type constitutes almost 50% of the high impact disease sites (C, Shearer pers. comm.). The association of particular elements of the vegetation with a disease impact level can be pronounced. For example, Hypocalymma augustifolium occurs on one third of the high impact sites surveyed and hence is an important pointer to a possible high impact site (C, Shearer pers. comm.). However individual species, genera etc. are not sufficient in isolation to classify the potential impact type.

Landscape and slope type are other features which show pronounced differentiation of disease impact types. For example, subtle sites are skewed towards the lower parts of the landscape while moderate and high types are more frequent on the upper positions. Again subtle types are most frequent on concave slopes, moderate on convex and high impact on concave of parallel slopes. These landscape and slope classifications emphasise the hydrological component of the environment in disease impact type. Essentially they are expressing a water accumulating, in contrast to a water distributing, site. Coarseness of the soil profile is again linked to hydrology and separates subtle from high impact sites, because this texture favours lateral flow, hence dispersal of inoculum (zoospores) and thus high impact.

An extension of this survey of sites at one point in time is to assess changes in impact over time, either from historical sources or following the imposition of a variable, e.g. logging on previously classified sites.

6.2 Processes within disease impact sites - hydrology.

This research has concentrated on monitoring variation, over time, in the physical elements of the environment, particularly temperature and moisture, and the influence of these changes on the pathogen at depth in the soil profile. The logistic problem was to perform this monitoring, involving the use of continuous automatic data collection systems, without significantly modifying the site. Because of the dearth of data on the dissemination of inoculum (zoospores) through soil profiles, particularly those in which subsurface saturated flow can occur, research has concentrated on hydrologic changes within and between different disease impact sites located in a restricted area. The Dawn Creek site, where high and moderate impact sites, infected and free of P. cinnamomi, occur on approximately the same slope and aspect, was ideal for this study.

Preliminary results from the Dawn Creek site have already been presented (Chapter 2), e.g. the relationship of temperature at depth at various times to sporulation of the pathogen. Over the next year significant results on the hydrologic behaviour following rain events will be available. The delay between a rain event, the record of soil moisture reaching saturation and flow from the series of collection trenches, varies between sites of different impact status and within a status between upper, middle and lower locations on the landscape (Kinal, pers. comm.).

The caprock surface below the disease impact sites has been mapped by probing, and the collection trenches to sample the water flow following a rain event, have been located in relation to these maps. Further the subsurface maps can be related to the configuration of the soil surface (contours at 1 m intervals required) (C, Kinal and Shearer pers. comm.). Hence the data from this research in processes can be

used to interpret the relationship between environmental features such as surface landscape, depth to caprock, surface slope, position on slope etc. to hydrologic behaviour in the profile and finally to disease impact status. Thus a causal link is provided between elements of the environment and disease impact level as recorded in the survey.

Earlier research has developed an acceptable, if slightly incomplete, model of disease development on sites (high impact) with a concreted lateritic layer at 5-75 cm below the surface (65, 66). It is believed, although there are insufficient data to establish the point, that potentially moderate impact sites form the bulk of the jarrah forest area. The immediate aim is to develop a model for disease development on such sites and hence to understand how robust and resistant to change is the present impact status of these locations. The survey and processes research, since they permit comparison between high and moderate impact sites, should help this understanding. Research on disease assessment in individual trees should contribute also to comprehending these relationships.

6.3 Disease assessment.

6.3.1 Individual tree assessment.

The excavation of whole trees on high impact sites and the isolation of P. cinnamomi from the major roots, including sinker roots, provided the basic clue to the modelling of the rapid death syndrome in jarrah (64). More recently large scale excavation of jarrah on sites other than those with concreted laterite, has yielded valuable results. On a moderate disease impact site there were fewer live fine roots per tree than in a non infected control and the difference was very pronounced at 10-20 cm deep in the profile, the zone of concentration of fine roots. The data from some 13 trees - one high impact, 11

moderate impact, one uninfected site - excavated recently, are being analysed. The research demonstrates enormous variation in the distribution of large roots between individual trees. Within the Havel vegetation sites examined (7-TS, 3-S, 2-PS) total root length appears to be related to stem diameter, while the number of sinker roots seems to be associated with the number of branches in the crown (C). This investigation is closely related to that of Dr. Dell (K). Possibly in the future a three dimensional picture of the root system of jarrah will emerge. This depth of understanding may be necessary to explain the less pronounced distinctions between disease impact types.

Finally excavation to the caprock has suggested that cementation of the laterites layer may be a dynamic system hence the interest in the project which Professor Gilkes will supervise (Appendix 2).

6.3.2 Remote sensing.

6.3.2.1 Disease Distribution

Two areas of research have been pursued in this area, reports have been submitted (Q, R), and these have been commented on by specialists in this discipline. The specialist's comments on (Q) indicate that colour infra-red film and oblique angle aerial photography are not better tools, than normal colour film, currently in use, for the detection of jarrah dieback disease by remote sensing.

Report (R) summarises an attempt to develop a spectral signature for B. grandis such that changes in this signature, due to dieback, could be recognised at an early stage, hopefully on colour infra-red film. Such an achievement would permit the earlier, and presumably more accurate, recognition of dieback by remote sensing. Again the problems involved in determining an accurate base spectral signature were such that the application of the technique to remote sensing was

not possible. The specialists in remote sensing in the Department of Conservation and Land Use seem reasonably satisfied with their present system.

6.3.2.2 Mortality rate in jarrah.

A collaborative project between Dr. Davison (Department of Conservation and Environment and Murdoch University) and the Department of Conservation and Land Management - see (IV).

The number of recent deaths of jarrah on ca. 120,000 ha of forest has been computed from aerial photographs flown between 1978 and 1983. On dieback free sites about 9 trees (range 2.6-21.4) die per 1000 ha every 6 months in contrast with the death of some 25 trees (range 9.2-34.2) per 1000 ha per 6 months on infested sites. The mortality rate for jarrah on both dieback and dieback free sites varies from year to year. Deaths may be classed as grouped (3 trees per 10 ha) or scattered and the proportion of grouped deaths is ca. 20% in both dieback and dieback free sites, while in both zones the majority of deaths in jarrah are of small trees.

6.4 Disease Resistance

6.4.1 Selection of Resistant Biotypes

There is prima facie evidence of the existence of resistance in jarrah to P. cinnamomi root rot in the rapid, systemic spread of the organism in B. grandis in the field, followed by the mass death of this species, while jarrah remains apparently unaffected on the same area, i.e. the moderate disease impact site (C). The differences between genera and species in their physiological reactions (E, 78, 79), some of which are those characteristic of resistance in other host/pathogen systems, and on the different rates of lesion expansion following stem

inoculation of certain eucalypt species (72), are again indicative of inter-genera and/or intra-species differences in resistance. The existence of intra-specific (within jarrah) variation in resistance is supported by:

a. Pronounced differences in the spread, over a 30 day period, of lesions within uniformly inoculated roots of 3 month old seedlings of jarrah, incubated in a controlled environment at 24°C (E, 30), is the most unequivocal evidence of intra-specific variation in resistance.

b. An experiment measuring the rate of lesion extension in stems - this had been shown to be more rapid than, but correlated with, the rate of lesion extension in roots (D). In this major experiment 70 trees were chosen on each of four sites, there were eight coppice stems per tree four of which were inoculated in summer and four in winter. The effect of season of inoculation was greater than that between trees within a site - inoculation in summer rather than winter resulted in longer lesions irrespective of site. However, irrespective of the site and period of inoculation, individual tree, i.e. biotype, had an effect on lesion length. There is a problem in assessing this effect as there was an evident inoculation-time x tree interaction with certain trees. In the absence of a full statistical analysis it is not clear that biotype (tree genotype) had an effect independent of its interactions).

c. In experiments where uniform inoculations of seedlings are performed it is common to find some individual plants of jarrah surviving despite the overall high mortality.

d. Occasional trees of jarrah survive on some dieback sites.

In (c), and particularly in (d), the survivors may represent disease escape rather than disease resistance.

6.4.2 Assessment of Resistant Biotypes

This research is in an early phase since it depended on the development of techniques of micropropagation to produce replicates of suspected resistant biotypes of group (c) and (d) above.

Laboratory, glasshouse and field trials using whole plantlets, with seedlings as controls, have been reported. While the results are somewhat equivocal and involve very few plantlet lines, they indicate reduced rates of disease development in certain plantlet lines and differences in mortality rates between lines. However the production of plantlets is time consuming (a minimum of 12/18 months from selection to field testing), resource and labour intensive, and expensive and hence unsuited to routine screening of biotypes for resistance.

Recently a technique has been developed to produce callus of comparable dry texture, from shoots of both various plant species differing in resistance to P. cinnamomi and of lines of jarrah believed to differ in resistance. Pieces of callus 1-2 cm in diameter were placed on medium in Petri dishes to provide a continuous surface over which the fungus could grow. These calli pieces were inoculated with pieces of a young culture of P. cinnamomi growing on Miracloth over agar. Growth of the fungus from the edge of the Miracloth was measured at regular intervals following incubation in the dark.

Up to 24 hours the extent of hypal growth correlated with the degree of susceptibility of the species from which the callus was derived. Using larger pieces of calli, measurements could be made up to 48 hours. Thus calli derived from resistant, or non host species,

supported very limited growth while prolific growth occurred on some susceptible species and on some suspected susceptible lines of jarrah. In certain instances growth on 'susceptible' lines was twice that on 'resistant' lines at 48 hours after inoculation. Strict control of the composition of the medium and selection of specific organs of the plant for propagation were essential to produce uniform calli, which in turn influenced the growth rate of the fungus, e.g. calli derived from the hypocotyl of A. pulchella supported greater fungal growth than those derived from root tissue. In certain instances the production of callose in the cells of the calli was directly correlated with the resistance of the plants from which they were derived. However differences in callose were not apparent between species of eucalyptus (VIII).

This callus technique would appear excellent for the preliminary screening of candidates for further propagation as resistant biotypes. Henceforward it is intended that candidates will be selected following field inoculation of stems. Those individuals in which lesion development is severely restricted, irrespective of effects attributable to site or season of inoculation, will be introduced into the micropropagation programme for screening as calli. Presumably those candidates which demonstrate high resistance in this preliminary screening will be carried through the programme to the plantlet stage and tested for resistance in the field.

The callus screening technique has potential also in studies of the effects of environment on levels of resistance and in investigations of the genetic basis of resistance.

6.5 Conclusions.

On some 400 sites, which vary in disease impact from absent, through subtle, to moderate, to high, features of the environment and vegetation have been described in detail. Analysis of these observations demonstrates that the distribution of particular impact sites is skewed towards certain vegetation, slope, aspect, soil, geological etc. characteristics. The survey of sites is continuing and when the bank of data has been increased it should be possible to predict the likely disease impact status of an at present uninfested site, should P. cinnamomi be introduced into the area at some time in the future.

This type of survey can establish the potential disease impact status at a particular point in time. However it is likely that environmental changes, or site modification, will occur over time. A study of the processes occurring within sites, i.e. establishing the mechanism by which site characteristics casually result in disease impact, will make the survey independent of a particular sampling. The hydrological features of the site, which result in water accumulation or water dispersal, are very important in the potential disease impact status of a site. Intensive monitoring of those hydrological features, over a series of rain events, in various seasons, will provide data on the processes through which a certain disease impact is achieved. Hopefully these processes could be modelled and their effect on the disease status of a site could be predicted. This modelling could be extended to predict the effect of various stand treatments, or other management activity, on the disease impact status of the site.

While a reasonable model has been produced for disease development on high disease impact sites - those with a shallow caprock layer - there is little information of damage to individual trees following

infection on sites of lower potential disease impact. Excavation of whole trees, and detailed recording of root damage on various vegetation types, and in disease impact levels of subtle and moderate, will fill this gap in our knowledge of the disease. This information is essential for future planning as, at present, there are no reliable data on the effect of lower disease impact on even the growth and yield of individual trees and stands.

Lesion expansion following artificial inoculation has been used to study the effect of site, and features of individual sites, on pathogen development once it is established in the individual tree. For example, lesion expansion ceases when the relative water content of the phloem falls below 85%. The time at which this occurs in the summer depends on the nature of the site, in particular the water availability. The overall aim of the investigation is to understand how the resistance of jarrah may be enhanced by site selection and/or site modification.

The evidence for variation in resistance to root rot caused by P. cinnamomi among different biotypes of jarrah is encouraging. The techniques of micropropagation can be employed to screen the general population of jarrah for resistance, and subsequently to vegetatively propagate the resistant biotypes. A promising technique has been developed to use callus, produced from selected shoots, to test in vitro the relative resistance of the biotypes. For logistic and economic reasons this is preferable to testing vegetatively propagated seedlings (plantlets).

The callus technique has potential for use in determining the genetic basis of resistance in jarrah to P. cinnamomi root rot. In the immediate future it will be used to screen mother trees which, following inoculation in the field, demonstrated resistance to lesion

expansion. Following the screening the selected candidates would be carried through to the plantlet stage - some 12 months plus - prior to testing for resistance in the glasshouse and finally in the field.

Chapter 7

COMMENTARY

Apart from some areas of administration, I have limited my comments to those which I think may be useful to the researchers and they are broad rather than matters of detail.

7.1 Administrative Aspects.

7.1.1 Research Priorities.

I believe that these are best set by a group, such as the Dieback Research Working Group, the members of which are involved in active research on projects many of which interact. I agree that these priorities should be reviewed at two yearly intervals.

It is not clear how the research priorities are set in relation to the aims of Management for the jarrah forest. Because of the complex of functions which the forest fulfils e.g. conservation, recreation, timber production, water production, bauxite mining etc., it must be particularly difficult to allocate a rating to a specific activity. For instance, does the combining of conservation and wood production in the Department of Conservation and Land Management have an immediate effect on management priorities? Does the Department hope to be able to conserve, in their present condition, currently uninfested areas of potentially high disease impact sites? Is research necessary to design a buffer of lower impact sites around such areas? Is exclusion of all activity the only option for the long term retention of these areas? Will complete exclusion conflict with purpose of conserving the areas in the first place? I have no doubt a similar set of questions could be posed, in relation to water harvesting, for the valley bottom sites.

I appreciate the difficulty of setting the aims of management, particularly when some of these are competing or mutually exclusive, but guidance on these is necessary if correct research priorities are to be set.

7.1.2 Evaluation of Research Proposals

The achievements of research, funded by the Foundation, are very impressive. In the initial stages projects were funded from a very broad area. This was justified on both academic and pragmatic grounds. In the longer term I believe it has given strength to the overall research programme. It led to interaction between individuals with very different skills and backgrounds. This mutual support built confidence in the researchers and prevented individual groups becoming sterile from lack of exchange of ideas. Over the years the funding has been restricted to a narrower field of research but much of the interchange with previous recipients of funds, has continued. Projects which received their initial impetus from Foundation support, have continued in the institutions when this support was directed elsewhere. This conclusion is very clear if one examines the list of publications (Appendix 4).

Recently the Dieback Research Working Group have set up criteria for the evaluation of research proposals (Appendix 2). I think the Chairman, and the group, are to be congratulated on setting these objective criteria. The circulation of the criteria, or a summary of their thrust, to prospective applicants would simplify the screening of applications. Quite justifiably, the criteria stress the practical aspects, and hopefully short-lead-time-application, of the results of the projects. While this limits their suitability for doctoral

research, the joint supervision facilities available make these funds attractive for partial support of Honours or Masters D gree candidates.

7.2 Technical Aspects.

7.2.1 Statistical Analysis.

In reading the reports, publications etc. I am concerned with the absence of acknowledgement of statistical advice, and indeed, in some instances, the complete absence of statistical analysis. Sometimes parametric statistical tests are employed without any indication that the data fulfilled the pre-requisites for the application of these tests. In other instances there is discussion of the impact of major elements in the data from random model experiments, although there is evidence of signficant interaction between these elements. In another instance data are analysed in blocks so arranged that the possibility of interaction of components is ignored.

These are serious shortcomings and researchers should be encouraged to enlist the help of professional statisticians in the planning of experiments and analysis of results.

The analysis of the data from the survey of the environmental components of sites of different disease impact status will be a major operation. With such data the use of principle component, or forms of vector, and multivariate analysis are certainly attractive. I do not know whether the non-random, stradified nature of the sampling renders this impossible. Further, it may be necessary to provide an arbitrary scale for certain components so that they can be included in the total analysis.

7.2.2 Parameters of Disease.

At present, evidence of an impact of non-lethal disease on the growth of jarrah is equivocal (III, IV). If such disease does not affect growth rate, or indeed a number of other desirable features of individual trees and stands, this has important management implications. It is important also, if the breeding programme is to be clear on its precise aims. For example, if sub-lethal disease significantly reduces crown density and leads to a deterioration of the site, it may be very important to select and propagate biotypes resistant to this form of disease. In contrast, if the only significant disease is that in the rapid death syndrome, is it possible to select against the disease? Has resistance in seedlings to root rot or mature host resistance to lesion extension, any significance in a disease situation where environment would seem of inordinate importance?

These questions suggest that, in the survey of moderate disease impact sites, every effort should be made to recognise additional parameters of disease e.g. predominant height, growth rates of dominant trees, etc. at this, and at lower, impact levels. These measures could be used subsequently to define, more strictly, the various disease impact levels.

7.2.3 Predisposition to Disease.

It was suggested that, while the model proposed for the rapid death syndrome was reasonably complete, an undetermined portion was the systemic invasion of secondary roots of jarrah following localised infection (Shearer, pers. comm.). The elucidation of this aspect may be very important because in it may lie the explanation of the differences between the high disease impact and other levels of disease status observed.

With certain root inhabiting fungi causing rotting in major roots of perennial hosts, progressive expansion from localised infection of major roots has been obtained experimentally only if the host is weakened, i.e. effectively it is 'predisposed' to the disease. Possibly ringbarking (not sap ringing) the individual stems, so that the roots die slowly, and presumably with decreasing resistance, might predispose the trees to systemic invasion.

The flooding of soils, and the creating of an anaerobic environment for roots, induced wilting in seedlings of jarrah (16) and of E. sieberi (E). During certain rain events flooding of profiles on both valley bottoms and on sites with shallow concreted lateritic layers could be envisaged. Flooding is another possible factor predisposing jarrah to systemic root invasion by P. cinnamomi.

7.2.4 Jarrah Breeding Programme.

This investigation is at a very interesting and critical phase. Critical because the pathology aspect of the work should be organised to yield the maximum possible value. For example, it is possible, if one uses a pathogen isolate containing numerous virulent genes, to conclude that all selections of the host are equally susceptible, whereas in fact, each selection may be susceptible to a different virulent gene(s) combination. If indeed there is a differential interaction between host and pathogen genotypes, then in establishment one should mix the host genotypes to avoid imposing a selection pressure on the population of the pathogen. In contrast, should all host genotypes be susceptible to all pathogen genotypes, then the preferred strategy in establishment may be to use only that host genotype which demonstrates the highest resistance. Thus an understanding of the nature of resistance in the system is critical.

Since the programme is screening host genotypes, this should involve screening against various pathogen genotypes. The interaction of these systems will then reveal the nature of pathogen virulence and host resistance. In effect, one is using two clonal systems, the micro-propagated calli of the host, and cultures of P. cinnamomi produced from mono-nucleate, single zoospores, the minimum genetic variability obtainable from field isolates.

I believe those involved in the breeding programme would benefit from the continuing advice of specialists in the genetics of host-pathogen relations. This is a complex area and one in which there is considerable research activity resulting in new concepts and proposed applications.

7.3 Conclusions.

I was very impressed with the abilities and the achievements in research, of the investigators supported by the Foundation, and of their collaborators. The list of published material, particularly, when one realises that some of these authors are teachers as well as researchers, is very impressive.

Some seven years ago I would have regarded P. cinnamomi as a most unpredictable organism and very unsuitable for controlled experimentation. Now I find these researchers handling this pathogen with confidence, in complex field experiments. The confidence is well placed for they are obtaining significant, reproducible results. Their confidence is a measure of the success achieved over the past six years, and the Foundation has contributed significantly to that achievement.

Appendix 1

Dieback Research Fund-Receipts and Disbursements

Contributions to the Dieback Research Fund to 17-6-85	$
Alcoa	768,290.50
Worsley	182,075.00
Forest Products Association	106,844.00
Wesfi	13,000.00

Disbursements to authorised projects		$
Dr D Bell	University of Western Australia 8/8/79 - 21/7/81	50,000.00
Dr R Kagi	Western Aust. Instit. Technology 21/11/79 - 24/3/81	44,000.00
Dr F Hingston	C.S.I.R.O. Inst. of Earth Resources 14/8/79 - 18/6/82	44,000.00
Dr S Shea Mr J Titze	Forests Dept. Western Australia C.S.I.R.O. Div. For. Research 18/10/79 - 28/6/84 - 17/6/85	408,552.00
Dr B Dell	Murdoch University 14/8/79 - 1/9/83 25/5/84 - 15/6/84 - 17/6/85	112,285.00
Prof D O'Connor	Murdoch University 19/3/80 - 11/3/83	29,000.00
Dr J Majer	West Aust Inst. Technology 14/8/79 - 11/3/83	48,120.60
Dr B Grant Dr G Weste	University of Melbourne 10/2/81 - 7/9/82	70,795.00
Dr N Malajczuk	C.S.I.R.O. Inst. of Earth Resources 23/4/80 - 18/6/82	67,500.00
Dr E Davison	Murdoch University 24/7/81 - 13/8/82	38,000.00

		$
Dr J McComb Dr E Davison	Murdoch University 5/11/81 - 17/11/83 - 17/6/85	114,906.00
Prof Gilkes	University of Western Australia 30/6/84 - 17/6/85	10,645.00 10,645.00

Appendix 2

Criteria Used to Evaluate Projects

Criteria not necessarily listed in order of priority:

1. Is the investigation new?
2. Is the investigation a collaborative study?
3. Can application of results be made in the short or long term?
4. Are aims achievable?
5. Scientific merit:
   - 5.1 Sound hypothesis?
   - 5.2 Quality of investigation?
   - 5.3 Methods?
   - 5.4 Group does not have expertise to judge - need for an external referee.
6. Does the proposal conform with priorities set by the working group?
7. Performance of previous fund applicants:
   - 7.1 Did they achieve original aims?
   - 7.2 Progress made.
   - 7,3 Application of results, including publications.
8. Are funds available from alternate sources?
9. Budget and duration.
10. Specific comments or recommendations in relation to proposal.

Appendix 3

Reports to the Interim Foundation for Jarrah Dieback Research

A Forests Department of W.A. and C.S.I.R.O. Div. Forest Research, Kelmscott: Progress Report to the Interim Foundation for Dieback Research Period June 1979 - Dec 1980. S.R. Shea, B.L. Shearer, J. Titze and M. Dudzinski.

B Forests Department of W.A.: Annual Report to the Interim Foundation for Dieback Research. Period 1981/82. S.R. Shea, B.L. Shearer and J.T. Tippett.

C Forests Department of W.A.: Annual Report to the Interim Foundation for Dieback Research. Period 1982/83. B.L. Shearer and J.T. Tippett.

D Forests Department of W.A.: Annual Report to the Interim Foundation for Dieback Research. Period 1983/84. B.L. Shearer and J.T. Tippett.

E University of Melbourne: Progress report to the Interim Foundation for Dieback Research. Period 1980/81. B.R. Grant and G. Weste.

F C.S.I.R.O. Division of Land Resources Management: Progress Report to the Interim Foundation for Dieback Research, period May 1980 - Dec 1980. N. Malajczuk.

G C.S.I.R.O. Division of Land Resources Management: Progress Report to the Interim Foundation for Dieback Research. Research period 1980/81. L. Sanfelieu and N. Malajczuk.

H Murdoch University: Progress Report to the Interim Foundation for Dieback Research, period 1979-80. B. Dell, School of Environmental and Life Sciences.

J Murdoch University: Progress Report to the Interim Foundation for Dieback Research, period Aug 1979 - Aug 1982. B. Dell, School of Environmental and Life Sciences.

K Murdoch University: Progress Report to the Interim Foundation for Dieback Research, period Feb 1984 - Oct 1985. B. Dell, School of Environmental and Life Sciences.

L Murdoch University: Progress Report to the Interim Foundation for Dieback Research, period July 1982 - June 1983. E.M. Davison and J.A. McComb.

M Murdoch University: Progress Report to the Interim Foundation for Dieback Research, period July 1983 - June 1984. E.M. Davison and J.A. McComb.

N C.S.I.R.O. Division of Land Resources Management: Progress Report to the Interim Foundation for Dieback Research, period Aug 1979 - Dec 1980. F. Hingston.

O University of Western Australia: Progress Report to the Interim Foundation for Dieback Research, period Aug 1979/July 1980. Dr D.T. Bell.

P University of Western Australia: Progress Report to the Interim Foundation for Dieback Research, period Aug 1980/July 1981. Dr D.T. Bell.

Q Murdoch University: Report to the Jarrah Dieback Foundation. "The use and evaluation of oblique aerial photography for environmental monitoring with special reference to colour infra-red photography and micro-densitometry". 1983. M. Cannon.

R Murdoch University: Report to the Jarrah Dieback Foundation. Preliminary investigation into the reflectance of Banksia grandis. D. O'Connor.

S Hunt Steering Committee Project 8 - Jarrah Dieback Research Progress Report to the Interim Foundation for Dieback Research. Period to Feb 1982.

T Department of Conservation and Land Management. Progress Report to the Interim Foundation for Dieback Research. Period to 1984. J. Havel 1984.

U Dieback Research Working Group. Review of Jarrah Dieback Research Priorities - 1983. B. Shearer, B. Dell, K. Sivasithamparam, J. Tippett.

Appendix 4

Proceedings of Conferences, articles in journals and departmental publications

Note: Items marked with an asterisk (*) stemmed from research supported at least in part by funds from the Dieback Research Foundation.

1* Barry, S.J. and Bell, D.T. (1983) Water and nutrient balance in northern jarrah forest catchments pp. 110-17. In Water Research Foundation of Australia. Water Quality - Its Significance in Western Australia. Perth, W.A. 13-14 October 1983.

2* Bell, D.T. and Barry, S.J. (1981) Nitrogen economy in jarrah forest catchments. In Managing the nitrogen economies of natural and man-made forest ecosystems. Ed. Rummery and Hingston. C.S.I.R.O. Perth.

3* Bell, D.T. and Koch, J.M. (1980) Post-fire succession in the northern jarrah forest of Western Australia. Aust. J. of Ecology 5: 9-14.

4 Bell, D.T. and Ward, S.C. (1984) Foliar and twig macronutrients (N, P, K, Ca and Mg) in selected species of Eucalyptus used in rehabilitation: sources of variation. Plant and Soil 81: 363-376.

5 Bell, D.T. and Ward, S.C. (1984) Seasonal changes in foliar macronutrients (N, P, K, Ca and Mg) in Eucalyptus saligna Sm and E. wandoo Blakley growing in rehabilitated bauxite mine soils of the Darling Range, Western Australia. Plant and Soil 81: 377-388.

6* Bennett, I. and McComb, J. (1982) Propagation of jarrah (Eucalyptus marginata) by organ and tissue culture. Aust. For. Res. 12: 121-127.

7* Bennett, I.J., Tonkin, C.M., Wroth, M.M., Davison, E.M. and McComb, J.A. (1986) A comparison of growth of seedlings and micropropagated Eucalyptus marginata (jarrah) 1. Early growth to 2 years. Forest Ecol and Manag. (in press).

8 Blowes, W.M., Heather, W.A., Malajczuk, N. and Shea, S.R. (1982) The distribution of Phytophthora cinnamomi Rands at two sites in South Western Australia and at Durras in South Eastern New South Wales. Aust. J. Bot. 30: 139-145.

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Appendix 5

Papers submitted for publication, academic thesis, reports to organisations other than the Foundation.

I Cory, J.L. (1982) Native legumes of the Eucalyptus marginata Donn. ex. Sm. forest in relation to nitrogen and Phytophthora cinnamomi Rands. Hons thesis Murdoch Univ.

II Darling, D.D. (1980) Bioassay of root extracts and leachates with Phytophthora cinnamomi using polycarbonate micro-filtration membranes as a mycelial support. Phytoph. Workshop A.S.P.P. Conf. May 1980.

III Davison, E.M. (1984) Annual report to the Department of Conservation and Environment 1983/84.

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VI Legge, N.J. and Grant, B.R. (1984) Cellular responses of roots of field susceptible and field resistant eucalypts to infection by Phytophthora cinnamomi. Aust. J. Bot.. (in press)

VII McComb, J.A. and Wroth, M. (1986?) Vegetative propagation of Eucalyptus resinifera and E. maculata using coppice cuttings and micropropagation. Aust. For. Res. (submitted).

VIII McComb, J.A., Hinch, J.M. and Clarke, A.E. (1986?) Expression of field resistance in callus tissue inoculated with Phytophthora cinnamomi. Phytopathol. (submitted).

IX Socahacki, S.J. (1982) A comparative study of four jarrah forest soil types in relation to Phytophthora cinnamomi Rands. Hons. thesis, Murdoch Univ.

X Tippett, T., Crombie, D.S. and Hill, T.C. The effect of phloem water relations on the growth of Phytophthora cinnamomi in Eucalyptus marginata. (Final draft stage).

Appendix 6

Individuals with whom I had discussions in Western Australia Oct. 21-30

Department of Conservation and Land Management

Mr. J. Havel	Perth
Dr S. Shea	Perth
Mr L. Hammond	Perth
Dr J. Tippett	Perth
Dr B. Shearer	Dwellingup
Mr J. Kinal	Dwellingup

C.S.I.R.O. Division of Forest Research

Dr D. Murray	
Dr N. Malajczuk	previously officers of Division of Land Resources Management
Dr F. Hingston	

University of Western Australia

Dr D. Bell
Dr K. Sivasithamparam
Miss A. Koening (Professor Gilkes)

Murdoch University

Dr E. Davison
Dr J. McComb
Dr B. Dell
Dr I. Bennett

West Australian Institute of Technology

Dr R. Kagi
Dr J. Majer
Mr A. Postle