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FORESTS DEPARTMENT

50 HAYMAN ROAD, COMO, WESTERN AUSTRALIA
P.O. BOX 104, COMO, 6152. TELEPHONE (09) 367 6333

Address all correspondence: Conservator of Forests
Your ref: *Our ref:* Forests Department
Enquiries: Research Station,
DWELLINGUP WA 6213.

17th March, 1983.

Dr. M. Mulcahy,
Chairman,
Research Co-ordinating Committee,
c/- Dept. of Cons. & Environ.,
"B.P. House",
1 Mount Street,
PERTH WA 6000.

Dear Dr. Mulcahy,

I enclose copies of a report on Dieback Research strategy for consideration by the Research Co-ordinating Committee and the Dieback Research Foundation.

As I indicated to you when you requested this report I consider that it would be impossible to obtain a consensus view on Dieback Research Strategy for obvious reasons.

In producing this report,however, I have consulted with the senior workers of the Dwellingup/Como research staff (Dr. Shearer, Dr. Tippett and Miss Deegan) who are working on Jarrah Dieback.

S.R. SHEA
INSPECTOR.

SRS/map

encl*.

JARRAH DIEBACK RESEARCH STRATEGY.

A INTRODUCTION.

1. The objective of this document is to provide a broad outline of what we perceive as the optimum strategy for Jarrah Dieback Research.

2. Over the period since 1965 when P.cinnamomi was identified as the causal organism of Jarrah Dieback progress towards practical control procedures has been handicapped because of our inability to understand some of the fundamental processes which cause severe disease. As a consequence the research on the problem has been necessarily broadly based.

3. Over the past two years there has been a major improvement in our understanding of the basic processes involved in the interactions between host-pathogen-environment which cause Jarrah Dieback. We are now able to focus research towards avenues which offer the most promising approaches to control.

4. In this document we have:
   - summarized the results of research which have provided a new perspective on Jarrah Dieback.
   - described the relevance of this research to the implementation of the Forests Department's recently adopted Jarrah Dieback policy.
   - defined the principal questions which need to be resolved before a rational Dieback management program can be implemented.
   - propose a research strategy.

B CURRENT STATUS OF RESEARCH.

(Details of this research are contained in Appendix A).

1). Over the period since P.cinnamomi was identified there have been two major problems.

   a). It has not been possible to explain the capacity of P.cinnamomi to cause severe disease (mass collapse of jarrah stands) on the basis of what was known of the pathogen biology and the environment in which the fungus operates.

   b). Over this period, although there has been extensive spread of the disease mass decline and death (which occurred in the period from 1945-65) has not occurred.

2). In the last two years there has been a recurrence of severe disease but this has been restricted to specific site types.

3). It has been assumed that P.cinnamomi was confined to the surface soil horizons. It has now been shown that P.cinnamomi occurs at depth on mass decline sites. On these sites impedance of water flow at a concreted layer of laterite provides conditions for reproduction and transmission of P.cinnamomi at depth.

4). It has previously been assumed that P.cinnamomi could not invade secondary tissue. This assumption has been proved to be incorrect.

5). On mass decline sites death of jarrah results from destruction of the vertical roots by P.cinnamomi where they pass through the layer of concreted laterite.

6). Jarrah appears to be relatively resistant to P.cinnamomi but under certain conditions (as yet not defined) extensive invasion of secondary tissue can occur .

C CURRENT JARRAH DIEBACK POLICY AND MANAGEMENT.

Prior to 1982 management of Jarrah Dieback was based on a policy of exclusion from forest areas which had been quarantined and, in areas outside of quarantine, minimization of spread of the fungus by implementation of hygiene practices. The objectives of quarantine were firstly, to provide an immediate reduction of the spread of the disease into the central and eastern areas of the forest and secondly, to provide an interval during which all existing infections could produce symptoms. Following a period of quarantine (3 years) it was proposed that detailed aerial photography could be employed to identify all existing infections. It was proposed that the forest could then be managed in the presence of P.cinnamomi by implementation of stringent hygiene and the total exclusion of contact between potential vectors of the disease and the identified infected areas. In 1982 the disease situation was reviewed and a new policy on Jarrah Dieback was adopted (Dieback Policy 1982). The essence of this policy is that forest operations can only occur within a forest area if the risk of introduction of the fungus, the impact of the disease on the vegetation and the consequences of loss of forest cover because of disease are acceptable.

The new policy is based on control by exclusion of the fungus from healthy forest but recognizes that it is impractical to achieve absolute control by hygiene. Accordingly the concepts of impact of the fungus on vegetation and the impact of loss of vegetation on land use values have been introduced

in the criteria used to evaluate the effect of forest operations in the presence of P.cinnamomi.

It is not the purpose of this report to consider the implications of the loss of forest cover on land use values. However, the objective of forest management is to optimize all land use values. The loss of forest cover would affect all forest uses, albeit in different ways in different site types. Part of the research strategy on jarrah dieback should be to regard maintenance of forest cover as a priority objective regardless of land use. The concept of 'impact of land use' should be seen more properly as a question for political decision - makers.

Research Questions Posed by Dieback Policy 1982.

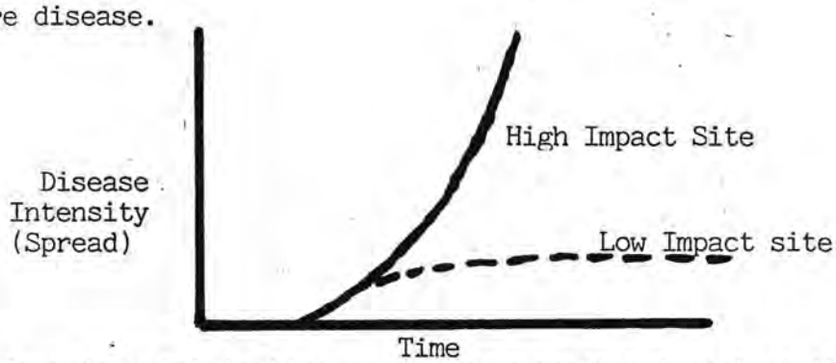
The capacity to implement the policy depends on a subjective assessment as to the level of risk which the state is prepared to accept. At one extreme it would be possible to implement the policy throughout the forest immediately with existing knowledge if a high level of risk is acceptable. Alternatively the policy could be interpreted as preventing access to any healthy forest for an indeterminate period until the potential consequences of the introduction of P.cinnamomi to any healthy forest are thoroughly understood or until research has produced management strategies which prevent P.cinnamomi causing damage.

The objective of the proposed research program is to develop a dieback management strategy which will permit utilization of the forest for multiple use purposes in perpetuity without significant impact from P.cinnamomi.

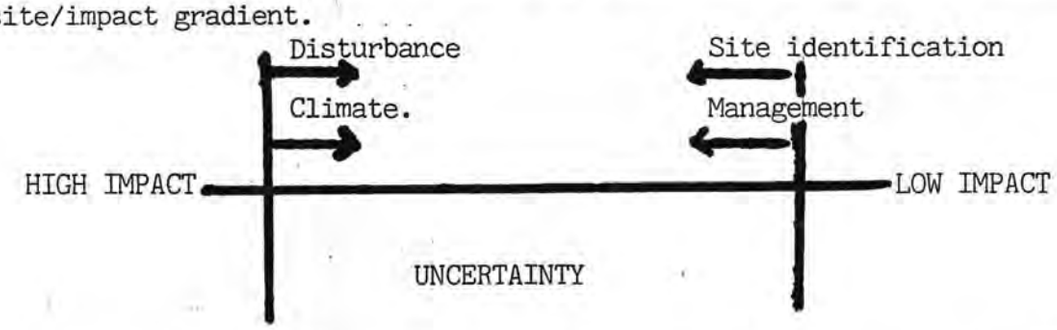
The major problems associated with implementation of Dieback policy 1982 may be summarized as follows:-

1). Hygiene, although a critical element of dieback management, will not in itself result in control of the disease in the long term because hygiene can never be absolute.

2). "The risk of introducing P.cinnamomi" cannot be evaluated without quantifying impact because on high impact sites it is probable that only small amounts of inoculum (minor breakdowns in hygiene) are sufficient to cause severe disease.



3). At this point in time we can only predict impact at the extremes of the site/impact gradient.



This means that although it is possible that a significant proportion of the forest is not subject to high impact we have to assume that it is until we can predict impact/site relationships over the whole gradient.

D RESEARCH PRIORITIES.

Given that in the long term it would be impossible to achieve control of Jarrah Dieback by a policy of total exclusion (stringent hygiene) the objectives of the research program are:-

(i) To define the relationship between site type and disease impact throughout the site/impact gradient.

(ii) Devise management strategies which will minimize damage by P.cinnamomi throughout the site/impact gradient.

(iii) Define those sites where it will be possible to manage the forest for multiple use without significant long term damage by P.cinnamomi.

It is impossible to achieve these objectives by empirical procedures because the activity of the fungus varies in space and time. Therefore it is necessary to develop procedures which can be used to predict fungal activity and the impact of the disease. This can only be achieved by developing an understanding of the processes which determine the consequences of the host-environment-interaction on different sites under varying climatic conditions.

Jarrah Dieback is a complex ecological problem and accordingly the number of basic process questions which can be posed is very large. The principal problem facing research workers who are concerned with developing a practical approach to controlling the disease in a realistic time frame has been to select research strategies which are relevant. While it is recognized that there is the potential to overlook major biological processes by constraining research to what appears to be a relevant direction, we are confident that we have identified the major questions which need to be resolved to allow a realistic dieback control management strategy to be implemented.

1. HOST-PATHOGEN INTERACTION.

a) Jarrah - This species appears to relatively resistant to P.cinnamomi. Damage to jarrah can be placed into 3 different classes:-

1) Mass collapse and 'Rapid' death of Jarrah Stands.

The basic host processes which result in mass collapse of forest stands have been described (See Appendix A). . The principal research questions which need to be resolved with respect to this phenomenon are concerned with site which is considered in section (3).

2). Total Invasion of Jarrah.

As described above it is possible for P.cinnamomi to cause death of jarrah by destruction of the vertical roots at the interface of a soil layer which impedes water. However, we have observed situations where P.cinnamomi has been able to extensively invade the large roots and the trunk of Jarrah trees. It is possible that this is due to variation in host resistance which is based on genetic factors. However, the association of total invasion with certain sites suggests that there could be a major factor(s) operating via the environment which causes jarrah's resistance to break down.

RESEARCH QUESTION 1. What are the factors which predispose jarrah to total invasion by P.cinnamomi ?

Resolution of this question is critical because until we are able to define these factors we cannot predict the consequences of such things as site disturbance and unseasonal rainfall on Jarrah's mortality rate. We cannot predict the significance of introduction of different levels of P.cinnamomi to healthy forest areas (ie. different standards of forest hygiene) because if the trees are

potentially subject to total invasion even small quantities of inoculum could cause death.

3). Partial Damage to fine, vertical and horizontal Root system.

Although jarrah has consistently demonstrated the capacity to terminate P.cinnamomi lesions in the horizontal roots repeated attacks by the fungus could cause significant growth decrement. Partial damage of the vertical root system on intermediate sites could be the factor which results in predisposition of the trees to total invasion. Currently there are thousands of hectares of forest where P.cinnamomi is present (as indicated by death of the B.grandis understorey) but current mortality rates of jarrah are less than 1 tree per hectare per annum.

RESEARCH QUESTION 2. What is the effect of intermediate P.cinnamomi damage to jarrah roots on long term survival and growth rates?

b) Associated Hosts.

Although jarrah is the dominant overstorey species and its loss has the most impact on land use (eg. salination) the loss of other species have implication to:-

- conservation
- spread and intensification of the disease.

RESEARCH QUESTION 3. What are the relative susceptibilities of associated species; are predisposing factors involved; and what role do these species play in spread and intensification of the disease ?

c) Replacement Species.

One potential method of ameliorating the effect of Jarrah Dieback is by rehabilitation with introduced 'resistant' species. It is possible that environmental factors associated with specific sites and/or climatic conditions could reduce resistance of these species to P.cinnamomi.

RESEARCH QUESTION 4. Are there factors in the jarrah forest environment which could predispose normally resistant species to attack by P.cinnamomi ?

2. SITE -PATHOGEN INTERACTION.

If we can assume that the variation in impact of the disease which we have observed is not due to significant variation in genetic factors of either host or pathogen, then it follows that it must result from environmental factors acting via the pathogen or the host. While it is possible that extreme climatic conditions may override any site constraint and genetic variation in the host may be a factor current research indicates that site is the major factor determining impact. The effect of site on the pathogen can be divided into categories:-

a) Processes associated with mass collapse. These have been described above and in Appendix A. While it is possible to state that the principle factor affecting reproduction and spread of P.cinnamomi is the presence of a layer in the soil profile that impedes water and allows lateral transmission of zoospores, the environmental conditions which permit this to occur have not been quantified. It is possible to predict at either extreme of the site-impact gradient (Fig. 2), the effect of site on reproduction and spread of P.cinnamomi. However, it is not possible to accurately quantify these processes in a large proportion of the site types because they are affected by variation in seasonal

climatic conditions and disturbance.

RESEARCH QUESTION 5. What are the characteristics of sites which permit reproduction and lateral transmission of P.cinnamomi and how are they affected by climatic and site disturbance factors ?

b) Processes Associated with Reproduction and Spread in the surface horizon .

While it has been shown that major impacts are consequences of the site factors described in 1) above it is possible that significant damage could occur on sites in which P.cinnamomi is active only in the surface horizon. In these sites, the critical questions are how much of the root system of jarrah is exposed to and infected by P.cinnamomi, and what are the long-term effects on growth and survival of jarrah in these sites ? (See section 1-111 and Research Question 4 above). It is in these sites that management practices are likely to be most significant. Previous research has identified basic practices such as banksia reduction and legume regeneration which can be implemented and which will reduce the opportunities for build-up and distribution of inoculum.

RESEARCH QUESTION 6. What is the effect of site, seasonal climatic variation, disturbance and disease management procedures on P.cinnamomi inoculum levels in the surface soil horizons?

3. SITE IDENTIFICATION.

Our capacity to manage the forest for multiple use purposes will depend on whether we are able to predict the impact of the disease before the fungus is introduced. Questions 1 - 5 are concerned with resolving questions concerning the processes affecting impact. This will allow identification of site

characteristics associated with varying levels of impact. It is then essential to be able to identify these sites throughout the forest. Our current research indicates that a combination of geomorphological, geological and ecological mapping procedures could be used to identify sites.

RESEARCH QUESTION 7. Can procedures be developed which will permit identification of site types throughout the site/impact gradient (see Fig. 2)?

4. DISEASE MANAGEMENT PROCEDURES FOR DIFFERENT SITE TYPES.

Over the past 10 - 15 years a number of management procedures have been identified which can be used to reduce the spread and intensification of P.cinnamomi in the forest. However, apart from hygiene management it has not been possible to implement these strategies because it was not known if they would have a significant impact on the disease in the long term. This was a consequence of our inability to explain variation in disease impact.

RESEARCH QUESTION 8. What are the disease management strategies which are appropriate for each site/impact type?

E RESEARCH STRATEGY.

Current Situation

The input into jarrah dieback research can be placed into the following categories:-

1.) Forests Department

a) Dwellingup/Como Research Group - Management orientated research involving investigation of the basic relevant process affecting the host-pathogen-interaction.

This consists of:-

- 3 professional research officers(1 Foundation funded under contract).
- 6 research assistants permanent Forests Department staff)
- 2 research assistants (Foundation funded under contract).

b) Inventory and Planning - Detailed aerial detection of P.cinnamomi infection. Approximately 18 staff are engaged in Dieback Interpretation.

11) Foundation Funded Research (see previous review of this research)

1). Specific projects concerned with general Jarrah forest ecology.
2). Specific projects concerned with fungal biology, host resistance and pathogen-environment-interactions.

2). Dieback Research Organization Options.

There are three broad options:-

1). The Forests Department may decide that control of Jarrah Dieback may be achieved by a management strategy based primarily on stringent hygiene. If this is the strategy adopted dieback interpretation staff levels should be sustained at least at existing levels. Research should be directed towards resolving management questions which relate to hygiene management.

2). Maintenance of the existing management by a stringent hygiene program with continued research at the current level of staffing on a broad range of projects under the existing research structure.

3). Re-organization of the Jarrah Dieback research and management (dieback interpretation) program on an "Institute" basis.

Option 1 (management by stringent hygiene) cannot be sustained if the propositions put forward in this report are accepted. If the existing research strategy is persisted with (Option 2) we believe that although there will be progress towards resolving the questions posed above it will be slow and because of the lack of co-ordination it will be very inefficient.

We recommend that option 3 - the formation of an Institute to operate within the Forests Department - be adopted. Co-ordination of research under one organization is essential because :-

1). It is not possible to compartmentalize jarrah dieback research because of the strong inter-relationship between the major factors affecting the disease . Progress in any of the four major areas described above is dependent on resolution of key questions in the other three areas.

2). It is impossible to guide research towards a management orientated goal when major research resources are dispersed across different institutions.

3). It is essential that research be closely associated with management because:-

i) Many of the research projects require major support from management.

ii) It will ensure that the research concerned is relevant to the field problem.

iii) It will ensure rapid implementation of research findings

iv) Current dieback management practices (eg. hygiene, dieback interpretation) need to be monitored by research personnel.

4). An institute approach to Jarrah Dieback is the most efficient way to use the limited staff and financial resources which are available.

Proposed structure of Institute.

A tentative research structure is shown in Fig. 3. The key elements of the proposal are:-

1). The 'Institute' should be formed within the Forests Department since this organization is the management agency most concerned with the disease and it will be the source of most of the funds. However, it will be possible via the policy committee [A] to incorporate representatives of the Dieback Foundation and the Research Co-ordinating Committee

2). It is essential to appoint an executive officer with sufficient administrative experience and biological skills to co-ordinate the 'Institute'.

3). Three senior research scientists [C], [D], [E] are required to supervise the four maior research streams which have been documented.

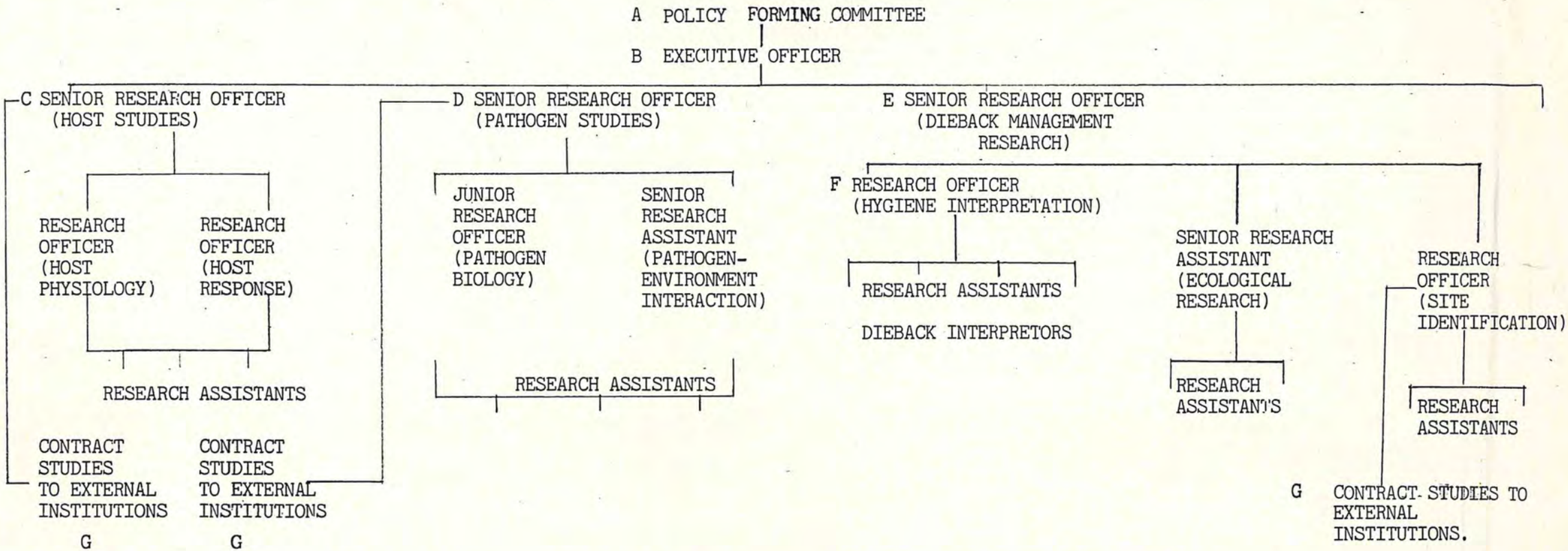
4). It is recommended that the management and inventory section of the Forests Department that is concerned with dieback interpretation [F] be incorporated into the 'Institute'.

5). It is proposed that future Foundation Funding be directed via the 'Institute' to specified and discrete research projects. [G]

It would be possible to document in more detail the components of the proposed 'Institute'. However, we believe that at this stage sufficient information

has been provided to allow the concept to be discussed and a decision made at the policy level. If the concept is approved more detailed proposals can be presented.

FIG. 3.


A POLICY FORMING COMMITTEE
B EXECUTIVE OFFICER
C SENIOR RESEARCH OFFICER (HOST STUDIES)
RESEARCH OFFICER (HOST PHYSIOLOGY)
RESEARCH OFFICER (HOST RESPONSE)
RESEARCH ASSISTANTS
CONTRACT STUDIES TO EXTERNAL INSTITUTIONS
G
CONTRACT STUDIES TO EXTERNAL INSTITUTIONS
G
D SENIOR RESEARCH OFFICER (PATHOGEN STUDIES)
JUNIOR RESEARCH OFFICER (PATHOGEN BIOLOGY)
SENIOR RESEARCH ASSISTANT (PATHOGEN-ENVIRONMENT INTERACTION)
RESEARCH ASSISTANTS
E SENIOR RESEARCH OFFICER (DIEBACK MANAGEMENT RESEARCH)
F RESEARCH OFFICER (HYGIENE INTERPRETATION)
RESEARCH ASSISTANTS
DIEBACK INTERPRETORS
SENIOR RESEARCH ASSISTANT (ECOLOGICAL RESEARCH)
RESEARCH ASSISTANT'S
RESEARCH OFFICER (SITE IDENTIFICATION)
RESEARCH ASSISTANTS
G CONTRACT STUDIES TO EXTERNAL INSTITUTIONS.

APPENDIX A.

RESEARCH NOTES

Recovery of *Phytophthora cinnamomi* Rands From Vertical Roots of Jarrah *(eucalyptus marginata Sm).*

S. R. Shea, B. Shearer & J. Tippett
West Australian Forests Department.

In 1981 it was reported that *Phytophthora cinnamomi* was recovered from the bark and wood of the large horizontal roots and, in some cases, the lower stem of jarrah (*Eucalyptus marginata* Sm) trees which exhibited a rapid death syndrome (9). This initial survey was confined to a relatively small number of trees which were located in the 'old dead zone' of *P. cinnamomi* infected areas and were scattered amongst live, apparently healthy, trees. In 1981 and 1982 several areas of *P. cinnamomi* infected forest were located where there were large numbers of dying jarrah trees and extensive mortality of the shrub and understory layer. In this note we present preliminary results from an intensive study of the distribution of *P. cinnamomi* within the root systems and lower stem of affected trees in these areas.

A total of 41 trees were excavated from 7 different areas in the forest located within a 60km radius of Dwellingup. Three of the sites were located downslope of a major site disturbance (bauxite mine or major road) which caused excessive runoff. The trees in the infected areas, which varied in size from 5 to 20 hectares, were exhibiting varying degrees of crown decline. The first observable symptom was slight chlorosis, and, in some cases microphylli. This was followed by distinct chlorosis and slight wilting followed by complete death of the crown. In some sites, trees whose crown had been killed in the previous year, formed epicormic shoots on the lower part of the bole, but these invariably died. A number of trees were observed to pass from a stage of apparently unaffected green crowns to complete death of the crowns within a period of six weeks, during the late summer and early autumn of 1982. Jarrah mortality in some sites within the affected areas occurred within two or three months of *Banksia grandis* (Willd.) deaths.

The trees sampled varied in size from small saplings to large veterans and trees in all phases of crown decline were sampled. The root systems and lower stump of affected trees were excavated by a combination of mechanical and hydraulic methods. The completeness of the excavation varied and it was impossible to excavate the trees below a concreted lateritic layer, which was present in all sites, at depths varying from 5-75cm. Following excavations the root systems were labelled, photographed and the stumps and root systems were returned to the laboratory, for analysis.

The location of lesions in the roots and the lower stump was mapped and samples were taken along the lengths of the root. The samples were cut into sections using secateurs and forceps which were flamed between samples. Sections were surface sterilized in 70 percent alcohol for 30 seconds, followed by three washes in distilled water, blotted dry on filter paper and plated on selective (10) and non-selective agar (half strength potato dextrose agar) and incubated in the dark at 25°C.

Phytophthora cinnamomi was consistently recovered from the bark and wood of the root samples of all but two trees on selective and non-selective agar. *Phytophthora cinnamomi* was more frequently isolated from fresh lesions, but it was also recovered from the dead tissue and, occasionally, healthy tissue above the lesion front. Typically *P. cinnamomi* grew vigorously from all of the root pieces plated from freshly lesioned roots. In a number of trees, lesions were observed in the lower stump and *P. cinnamomi* was recovered from this tissue. But, in a number of the trees, there were no lesions in the stump. A number of other potential plant pathogens were recovered from lesioned and dead tissue, but the rate of recovery of these fungi was relatively low in comparison to *Phytophthora cinnamomi.* (Table 1).

In several of the trees sampled, large lesions were detected and *P. cinnamomi* had extensively invaded the horizontal and vertical root systems. 'Fresh' lesion length (the distance between the active lesion front and the point where the root tissue was dry and undergoing decay) in some roots was between 150-200 cm and *P. cinnamomi* was recovered along the length of the lesion.

In the previous study (9) sampling was restricted to the horizontal root system and the lower stem of affected trees. During the initial phase of this survey sampling was again concentrated on the surface root system, and the lower stem. However, at one of the sites where large numbers of jarrah trees had died, intensive sampling of the horizontal root systems and the lower stem of ten trees in various stages of crown decline failed in give any isolations of *Phytophthora cinnamomi* and no lesions were detected. Further excavations of the root system of two trees to a depth of approximately 50-75cm below the soil surface, where a concreted lateritic layer occurred, revealed numerous vertical roots penetrating the layer through distinct 'pot holes' in an otherwise solid sheet of concreted laterite. It was only possible to obtain samples of the vertical roots penetrating these holes to depths of between 5-50cms below the lateritic layer, because of its concreted nature. However, at these depths the majority of vertical roots were found to be lesioned or dead, with active lesions extending upwards. *Phytophthora cinnamomi* was consistently recovered from these roots on selective and non-selective agar.

Following this observation ten trees on several other sites, where extensive and rapid mortality of jarrah was occurring, were excavated so that the vertical root system of the trees could be sampled. It was impossible to obtain samples of vertical roots to depths exceeding 50cm below the surface of the layer of sheet laterite and often the vertical roots could only be sampled to a depth of 5-10 cm within the layer, even with the aid of pneumatic hammers and explosives. However, *P. cinnamomi* was consistently recovered from the vertical roots sampled. (Fig. 1. Table 1.) For example, 26 vertical roots were sampled from one tree which had recently died. The majority of the roots had lesions present and frequently the point at which the root had broken off was dead. *P. cinnamomi* was recovered from all of these roots.

The length of lesions in the vertical roots varied between sites and within trees. In some of the roots the lesion extended from the point where it had broken off in the concreted lateritic layer to where it joined the horizontal root. However, there were numerous roots where the lesion was contained to a zone within 5-10 cm of where it had broken off in the layer (Fig. 2).

A number of the vertical roots which were excavated had small (<2mm in diam.) suberized roots and fine feeder roots were proliferating from the main suberized root within the root channel in the concreted lateritic layer. These roots were invariably dead and consistently yielded

TABLE 1: Recovery of potential plant pathogens from lesions on *E. marginata*.

No. of Trees from which *Pestalotia* spp was recovered.	3
No. of Trees from which *Cytospora eucolypticola* was recovered.	7
No. of Trees from which *P. cinnamomi* was recovered from the stump.	13
No. of Trees from which *P. cinnamomi* was recovered.	39
Number of Trees sampled.	41
% recovery of *P. cinnamomi* from tissue with no visible symptoms.	34%
% recovery of *P. cinnamomi* from discoloured phloem.	49%
% recovery of *P. cinnamomi* from lesioned tissue.	82%
% recovery of *P. cinnamomi* from vertical roots.	66%
% recovery of *P. cinnamomi* from horizontal roots.	30%
Total number of roots yielding *P. cinnamomi*.	275
Total number of roots planted.	626

P. cinnamomi on selective and non-selective agar. *B. grandis* roots were often present in the same root channels as the jarrah roots and were infected with *P. cinnamomi*.

In all of the sites where rapid and extensive mortality of jarrah trees has been observed a concreted lateritic layer was present at depths varying from 5-75 cm. During the hydraulic excavation we observed ponding of water within the root channels in the lateritic layer (in some sites free water remained in the root channels for 48 hours before draining away) and lateral movement of water on the surface of the concreted lateritic layer. For some of the trees it is possible that *P. cinnamomi* could have invaded the vertical roots via the horizontal root system. But there were numerous examples where either the horizontal root system was not infected, or where there was a zone of uninfected vertical roots between the infection in the vertical roots within the sheet lateritic layer and the horizontal root. We conclude, therefore, that infection of the vertical roots occurred at the surface of the concreted lateritic layer or within the root channels in the layer. Part of our current research effort is directed at elucidating the factors of the physical and microbiological environment of these sites which permit extensive infection of the vertical root system of jarrah by *P. cinnamomi* at depths between 10-75 cm below the soil surface.

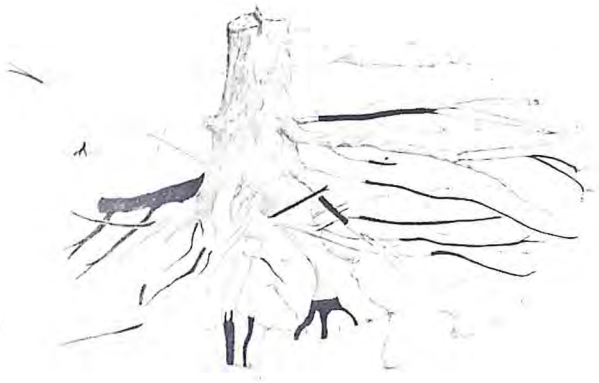


Figure 1. *P. cinnamomi* distribution in the root system of an affected tree.

Jarrah maintains a high rate of transpiration throughout the dry, summer months (December-March) (1), even though the surface (<3m) soil horizons are at soil water potentials equal to or greater than 15 atmospheres. The tree's internal water balance is maintained because of the presence of an extensive vertical root system which extracts from the ground water table and/or from the pallid clay zone of the soil profile at depths exceeding six metres (2), (8). We propose that the rapid mortality of jarrah which has been observed results from dehydration following destruction of the tree's capacity to take up water from depth in the soil profile. This could result from infection and destruction of vertical roots by *P. cinnamomi* and/or

Figure 2. *P. cinnamomi* distribution in vertical roots from affected trees. *P. cinnamomi* was isolated from blackened areas. Cross hatched areas dead tissue.

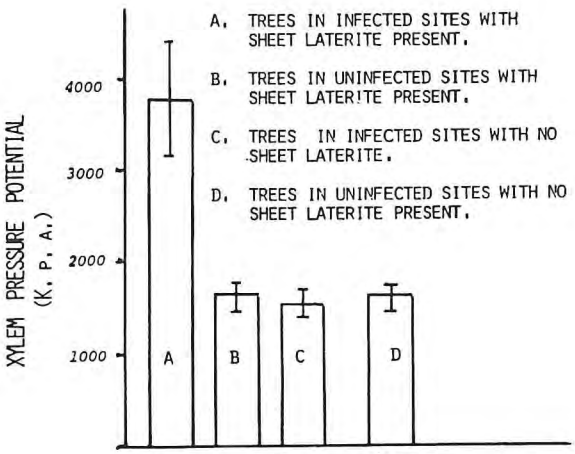


Figure 3. Xylem potentials (Kilopascals) of affected and unaffected trees. (Bars indicate 95% confidence limits.)

by extensive invasion of the horizontal roots system and the lower bole.

The water status of the affected trees supports the hypothesis that deaths result from dehydration. Xylem water potential measurements of affected trees with green crowns in the infected areas, trees in uninfected areas on the same soil type and trees from uninfected and infected areas on sites where the concreted lateritic layer was not present were recorded with a Scholander (4) pressure bomb in midsummer of 1982. A minimum of two readings were made for 12 trees from each site during mid afternoon. The trees in affected areas where sheet laterite was present had abnormally high xylem potentials but the xylem water potentials of the other categories of trees were normal. (Fig. 3).

In a number of the excavated trees there was evidence of rapid (as indicated by 'fresh' lesion length and *P. cinnamomi* recovery rates) and extensive (several horizontal roots from different parts of the same tree were infected) invasion by *P. cinnamomi*. We have difficulty in reconciling this observation with the low mortality rate and the absence of extensive lesion development in trees growing on sites where concreted sheet laterite is not present near the soil surface but which are surrounded by *B. grandis* trees which have been killed by *P. cinnamomi*. It is possible that the extensive invasion of trees by *P. cinnamomi* that we have observed is due to the presence of high levels of inoculum resulting in multiple infection. However, high inoculum levels have been recorded in the surface soils of sites where sheet laterite is not present (7), Shearer and Shea (unpublished). There may be some intrinsic site factor which causes the trees to be pre-disposed to extensive invasion by *P. cinnamomi*. But the height and diameter growth of trees growing on these sites is average for the jarrah forest and the xylem water potentials of unaffected trees, recorded in midsummer, were normal (Fig. 3). Alternatively, it is possible that the root systems and stump are pre-disposed to extensive invasion by *P. cinnamomi* following the induction of water stress caused by the destruction of the vertical root system. This is currently being investigated.

During the period from 1945 to 1965 large areas of jarrah forest were infected with *P. cinnamomi* and there was extensive mortality of jarrah (3). However, even though large areas of jarrah forest have subsequently been infected with *P. cinnamomi* (5), the rate of crown decline and mortality of jarrah trees in these areas over the past 17 years has been very low (6). It has even been difficult to detect *P. cinnamomi* in the root system of jarrah trees in infected areas (7). It has been suggested that jarrah death could be caused by attrition of the surface fine feeder root system by *P. cinnamomi* (7). This may be the mechanism by which the fungus kills some trees, but the number of trees killed following and extended period of crown decline is low and does not constitute a significant management problem. Diameter growth rates of trees in these areas is not different from trees in uninfected sites. (Shea unpublished). We conclude from the results of this study that the extensive and rapid mortality of jarrah that has been observed in the past results from invasion of the major root systems of the trees, preventing water uptake and that this is the principle mechanism by which *Phytophthora cinnamomi* kills jarrah trees.

This is the first reported occurrence of extensive, rapid, patch death of jarrah which has been observed in the last 17 years. The low rate of jarrah mortality in part could be attributed to the abnormally low rainfall which has occurred in south western Australia over this period. However, at all of the sites where extensive mortality has been observed during the current survey, which follows two years of average rainfall, a concreted sheet lateritic layer was present at depths varying between 5-75cm.

Preliminary surveys of areas where extensive mortality of jarrah was observed from 1945 to 1965 indicate that these sites had a similar soil profile. This suggests that the presence of a concreted layer of sheet laterite near the soil surface is a major factor influencing the intensification of the disease. We are currently investigating the relative importance of site and climatic factors on disease intensification. If the peculiar site characteristics we have observed are a pre-requisite for the intensification of the disease, large areas of jarrah forest may be less susceptible to *P. cinnamomi* than has previously been thought.

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THE EFFECT OF SEASON, SITE AND VIGOUR ON PHYTOPHTHORA CINNAMOMI EXTENSION IN SECONDARY TISSUE OF JARRAH (EUCALYPTUS MARGINATA)

S. R. Shea, P. M. Deegan and B. L. Shearer, Forests Department, Dwellingup, West. Australia, 6213.

Roots and stems of jarrah were wound inoculated at approximately monthly intervals from February 1981-March 1982. Rates of lesion extension in jarrah roots varied from 0.05 cm/day over a 6 week period in June 1981 to 0.24 cm/day over an equivalent period in January 1982. Rates of lesion extension in coppice stems varied from 0.03 cm/day (June 1981) to 0.54 cm/day (February 1981). Banksia roots inoculated during spring and summer showed lesion extensions of 0.27 cm/day to 0.85 cm/day. Although some seasonal variation in fungal extension could be expected due to temperature effects, this was insufficient to fully account for the seasonal variation in lesion extension. Approximately 75% of the lesions were contained within two years. Jarrah roots inoculated in September 1981 showed lesion extension during the first four months but no subsequent extension, although P. cinnamomi could be recovered from the lesions 15 months after inoculation. Inoculations of roots of trees in various flowering states at two levels of vigour showed no significant differences in lesion extension. Root inoculations in three different site types - black gravel, typical laterite and red loam - indicated some differences in rates of lesion extension, although temperature differences between the sites probably account for much of this.

RECOVERY OF PHYTOPHTHORA CINNAMOMI FROM VERTICAL ROOTS OF JARRAH (EUCALYPTUS MARGINATA)

S. R. Shea, B. L. Shearer and J. T. Tippett, Forests Department, Dwellingup, West. Australia, 6213.

A survey of jarrah trees exhibiting a rapid death syndrome demonstrated that P.cinnamomi could be recovered from the major horizontal roots and stems of affected trees. Of 41 trees excavated at 7 different areas where there were large numbers of dying jarrah, P.cinnamomi was isolated from the major roots of 39 trees and the stems of 13 trees. A number of fungi were isolated from lesions, but the recovery rate was low in comparison to P.cinnamomi. On excavation of 12 affected trees down to concreted lateritic layer, P.cinnamomi was consistently isolated from the vertical root system. The pathogen was also isolated from primary roots proliferating in the root channels from the vertical roots growing through the concreted layer. Some lesions in the vertical roots extended to horizontal roots, but most lesions were confined to the area where the roots penetrated the channel. Xylem potential measurements of trees in infected sites over concreted laterite indicated infected trees were under severe stress. Rapid mortality of jarrah on concreted laterite sites results from invasion of the vertical root system preventing water uptake. If the peculiar site characteristics observed are a pre-requisite for the intensification of the disease, large areas of the jarrah forest may be less susceptible to P.cinnamomi than had been thought previously.

RESISTANCE OF EUCALYPTUS SPECIES TO INVASION BY PHYTOPHTHORA CINNAMOMI

Joanna T. Tippett and T.C. Hill, Forests Department, Como, Western Australia, 6152.

Eucalypts vary in their resistance to Phytophthora cinnamomi. In the most susceptible rough-barked species, Eucalyptus marginata and E. sieberi, the fungus may invade the secondary phloem of large roots and sometimes will progress up into the collar or trunk. In comparison the bark and secondary tissues of many other eucalypt species are resistant to invasion. As a result of a series of root and stem inoculations, three types of interaction between the fungus and the eucalypt species have been described. In the most resistant, smooth-barked, eucalypts the fungus failed to become established in the secondary phloem. A basic incompatibility between the fungus and these species existed. In a second category the fungus did become established, but lesions were confined and eventually shed thereby resembling the development of annual cankers. Species in this group included E. calophylla and E. patens. The most susceptible of the 20 eucalypt species inoculated was E. marginata (jarrah). Although jarrah may express resistance and lesions were sometimes arrested, this species was susceptible to rapid invasion during the summer and renewed advance of the fungus from existing lesions when conditions favoured fungal activity.

ROLE OF PERIDERM IN RESISTANCE OF ROOTS AND STEMS AGAINST FUNGAL PATHOGENS

Joanna T. Tippett and T.C. Hill, Forests Department, Como, Western Australia, 6152.

Fungal lesions in roots and stems are often confined by periderm. The formation of periderm around lesions in secondary phloem or bark is a multi-step process with various changes occurring near the infected tissue, prior to the differentiation of suberized and lignified cell layers. The changes in the tissue preceding periderm differentiation at the boundary of phloem lesions are considered as active defence processes. Examples of periderm formed in response to fungal invasion include periderm formed at root junctions isolating lateral roots, cylindral periderm formed close to the vascular cambium causing exfoliation of cortical tissues and periderm formed radially through secondary phloem lessening the risk of lesions girdling roots and stems. Rates of periderm formation in response to injury vary in roots and stems and also vary with season. Fungal lesions may be confined when rates of formation are most rapid.

VARIATION BETWEEN SEASONS AND YEARS IN INOCULUM DENSITY OF PHYTOPHTHORA CINNAMOMI IN SURFACE SOILS OF THE JARRAH FOREST OF SOUTH WESTERN AUSTRALIA

S. R. Shea and B. L. Shearer, Forests Department, Dwellingup, West. Australia, 6213.

In samples from the top 6cm of soil, P.cinnamomi has been detected in lowland moisture-gaining sites throughout the year, even during the dry summer period. In these sites the moist soil environment permits prolonged sporangial production and survival. On free draining sites, temperature and rainfall frequency have a great impact on development and survival of inoculum. Frequency of recovery for random sampling varied from 0 to 27% and were generally less than 3%. Recovery rates are greater if sampling is biased to soil near the collars of infected B.grandis. During the last 5 years of monitoring surface soil of free draining sites, inoculum was rarely detected during the dry summer months, although in one year spring and summer rains enabled survival through summer. Early autumn rains allow rapid build up of inoculum because rain falls on warm, highly stimulatory soils. The inoculum produced in autumn survives through the winter. In spring, soil inoculum increase is linked to sporulation determined by the interaction between increasing soil temperature and stimulation and decreasing soil moisture. Monitoring of population levels downslope of infected banksia indicates that extensive lateral transmission in surface soils is limited unless there is disturbance and disruption of drainage to cause overland flow.

DISTRIBUTION, REPRODUCTION AND MOVEMENT OF PHYTOPHTHORA CINNAMOMI AT VARIOUS DEPTHS OF SOIL ON SITES HIGHLY CONDUCIVE TO JARRAH DIEBACK IN SOUTH WESTERN AUSTRALIA

S. R. Shea, B. L. Shearer, J. T. Tippett and P. M. Deegan, Forests Department, Dwellingup, West. Australia, 6213.

On sites with a concreted lateritic layer, recovery of P.cinnamomi was greater above the concreted layer, 10-80cm below the surface, than in the surface 10cm of soil. From mid winter to mid summer frequency of recovery varied from 28% to 0% for random surface samples to 72% to 16% for samples at depth above the concreted layer. In summer, inoculum survived in soil over the concreted layer but not in surface soil. Recovery of the fungus in root channels was greater than from other areas of the concreted layer. Jarrah and infected B.grandis roots were found together in the channels. In autumn and spring the number of sporangia formed by mycelium on B.grandis leaf discs, was consistently greater on discs above the concreted layer than on discs in the surface soil. In transmission studies zoospores were detected in water flowing at the interface of a concreted layer 30cm below the soil surface and 2m downslope of the introduction point. On sites where no concreted layer was present the fungus was only detected in soil vertically below the introduction point. The rapid and mass death of jarrah that has been observed on some sites is a consequence of specific site characteristics which favour inoculum increase and transmission at depth and the infection and destruction of the vertical root systems of jarrah.

TEMPERATURE - GROWTH RELATIONSHIPS OF PHYTOPHTHORA CINNAMOMI IN SECONDARY ROOT TISSUE OF EUCALYPTUS MARGINATA AND BANKSIA GRANDIS

B. L. Shearer, S. R. Shea, and P. M. Deegan, Forests Department Dwellingup, West. Australia, 6213.

The effect of temperature on growth rates of P.cinnamomi in secondary root tissue of E.marginata and B.grandis was determined in excised roots over 12 days under controlled conditions and in intact roots in the field over 6 weeks. Temperature was varied in the field by repeating inoculations during the year. Growth rate of P.cinnamomi was significantly linearly related to temperature between the range 10-30 C for excised roots of B.grandis (r^2=0.97) and E.marginata (r^2=0.85) and field inoculated roots of E.marginata (r^2=0.86). The slope of the regression line relating temperature to growth rate varied from 0.45 ± 0.03 for excised B.grandis roots, 0.36 ± 0.03 for excised E.marginata roots to 0.12 ± 0.02 for intact E.marginata roots in the field. Predictions of lesion lengths from field mean daily temperature data using the E.marginata excised root temperature - growth rate relationship,were 100 to 300% greater than observed lesion lengths. Growth rates of 4 isolates in excised E.marginata roots were greater or equal to that on agar. Temperature - growth relationship derived from excised root studies may help to partition environment from host resistance effects, as the effect of active resistance mechanism would be minimal in excised roots.

THE EFFECT OF PRESCRIBED FIRE AND UNDERSTOREY ON SPORANGIAL PRODUCTION BY PHYTOPHTHORA CINNAMOMI IN SURFACE SOILS OF EUCALYPTUS MARGINATA FOREST OF SOUTH WESTERN AUSTRALIA

S. R. Shea, P. M. Deegan and B. L. Shearer, Forests Department, Dwellingup, West. Australia, 6213.

Sporangial production on banksia leaf discs was compared for sites with varying understorey, including thick stands of Acacia pulchella and of Banksia grandis. Most sporangia were produced in late spring on all sites, but acacia sites produced 10-80% of the number of sporangia produced under a banksia understorey. During winter and early spring, banksia sites which had been burnt with low intensity prescribed fire in the previous autumn showed higher sporangial production than both legume and unburnt banksia understorey sites because of higher temperatures in the blackened soil. As spring progressed and a litter layer was generally replaced on these sites, sporangial production tended to be only slightly higher than under acacia. During late spring and early summer, sites with banksia understorey which were either unburnt or burnt in spring yielded 3-4 yimes as many sporangia as other sites. The occurrence of more than 60mm of rain at the end of December enabled sporangial production to continue well into summer.

THE EFFECT OF ACACIA PULCHELLA, A.LATERITICOLA AND BANKSIA GRANDIS ON THE INPUT OF NITROGEN INTO THE JARRAH FOREST ECOSYSTEM AND ON THE DEVELOPMENT AND SURVIVAL OF PHYTOPHTHORA CINNAMOMI

J. L. Cary, B. L. Shearer and S. R. Shea, Forests Department, Dwellingup, West. Australia, 6213.

Soil from beneath a three year old A.pulchella canopy had a higher soil total nitrogen (690 kg/ha) than soil beneath B.grandis (499 kg/ha) and A.lateriticola (420 kg/ha). Soil from beneath both burnt and unburnt A.pulchella and A.lateriticola had higher ammonia levels (5.7 ppm) than B.grandis (3.0 ppm). There was considerable variation in ammonium levels between years and within a season. Survival of P.cinnamomi in the field was not correlated with soil inorganic nitrogen or temperature, but significantly correlated with moisture. There were significantly lower numbers of sporangia formed after four days in undisturbed soil cores from beneath unburnt A.pulchella than B.grandis. There was no effect of canopy type on zoospore release or hyphal lysis. In a root amendment trial under controlled conditions 20% legume root amended soils had the highest ammonium levels and lowest P.cinnamomi levels. The fungus was suppressed in soils with ammonium levels as low as 2.5 ppm. In contrast B.grandis root amended soils had the lowest levels of ammonia and highest levels of P.cinnamomi. Ammonium levels were significantly negatively correlated with log P.cinnamomi propagules/gm dry weight soil for 5 of the 7 sampling trials. The lowest number of jarrah deaths occurred in 20% legume root amended soil.

COMPARISON BETWEEN PHYTOPHTHORA SPECIES IN RATE OF INVASION OF SECONDARY TISSUE OF BANKSIA GRANDIS AND EUCALYPTUS MARGINATA

B. L. Shearer, B. J. Michaelsen and S. R. Shea, Forests Department, Dwellingup, West. Australia, 6213.

Lesion growth rates in the secondary phloem of B.grandis stems were greatest for P.cinnamomi (6.6 mm/day), intermediate for P.cryptogea (A1) and P.nicotianae parasitica (2.4 and 1.5 mm/day) and lowest for P.cryptogea (A2), P.cactorum, P.cambivora, P.citricola and P.megasperma sojae (0.4 to 0.1 mm/day). Lesion growth rates in stem tissue in the field were less but significantly correlated with growth rates in excised B.grandis roots at 25°C (r^2=0.85). For most of the Phytophthora species, growth rates in excised E.marginata (jarrah) roots were greater than that in banksia roots. Phytophthora cinnamomi was the only species with higher growth rates in banksia than jarrah. Comparison between the Phytophthora species highlights the specific B.grandis - P.cinnamomi susceptible interaction and the importance of B.grandis as a host favourable for the survival and increase of P.cinnamomi in the jarrah forest.

THE EFFECT OF FOUR JARRAH FOREST SOIL TYPES ON DEVELOPMENT AND SURVIVAL OF PHYTOPHTHORA CINNAMOMI

S. J. Sochacki, B. L. Shearer and S. R. Shea, Forests Department, Dwellingup, West. Australia, 6213.

Using undisturbed soil cores under controlled conditions, survival of P.cinnamomi was greatest in yellow sandy gravel and sandy loam, intermediate in black gravel and least in red loam. In the field significantly less recoveries were made from red loam soil than black gravel. Sporulation and zoospore release at - 1.0 k Pa soil water potential varied seasonally, with stimulation of sporulation in all soil types being greatest in summer, intermediate in spring and low in autumn and winter. For each season, highest levels of sporulation and zoospore release occurred in yellow sandy gravel, intermediate levels in sandy loam and black gravel and significantly low levels in red loam. Movement of zoospores at - 0.5 k Pa soil water potential was significantly less in red loam than black gravel. Death rate of Banksia grandis seedlings was less in red loam than the other three soils and death rate of E.marginata did not differ significantly between soil types.

THE ROLE OF BANKSIA GRANDIS IN THE SURVIVAL AND SPREAD OF PHYTOPHTHORA CINNAMOMI IN THE JARRAH FOREST

S. R. Shea[1], D. E. Schild[2] and B. L. Shearer[1], [1]Forests Department, Dwellingup, West. Australia, 6213, [2] Department Botany, University College, Dublin.

In late summer, P.cinnamomi was detected in most of the large roots and lower stems of B.grandis which had recently died or died within 12 months of sampling. The fungus was not detected in the soil, nor in the surface roots of healthy trees nor trees dead for more than one year. Recovery rates from vertical roots were consistently higher than from surface laterals. Infected B.grandis roots and stems provide a major reservoir of inoculum, enabling survival of the fungus through the dry summer months. Under favourable soil conditions the fungus can exit as sporangia or possibly mycelium from the bark of infected banksia within 3 to 11 days. On free draining sites extension of the pathogen into the soil is limited and a wide spread is dependent mainly on mycelial growth within roots of banksia. The presence of B.grandis on highly susceptible sites contributes to the intensification and spread by permitting transmission of the fungus through vertical roots to root channels within a concreted laterite where conditions are favourable for inoculum increase and subsurface lateral spread. It is unlikely that control of P.cinnamomi in the jarrah forest will be achieved in the presence of a dense B.grandis understorey.

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Distribution, Reproduction and Movement of *Phytophthora cinnamomi* at Various Depths of soil on Sites Highly Conducive to Jarrah Dieback in South Western Australia.

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

Western Australian Forests Department, Dwellingup, Western Australia.

ABSTRACT

Phytophthora cinnamomi, which causes death of *Eucalyptus marginata* and other species in the jarrah forest of south Western Australia was recovered at a high inoculum density at depths down to 75 cm in soil immediately above a concreted lateritic layer. It was shown that the fungus can produce zoospores in soil at the interface of the lateritic layer and that zoospores are transmitted laterally in water flowing at the surface of the layer on sites of decline. It is proposed that the rapid mass decline and death of jarrah which has been observed is a consequence of these specific site characteristics which allow infection and destruction of the vertical root system of jarrah by P.cinnamomi.

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Phytophthora cinnamomi (Rands) has caused extensive mortality of jarrah (*Eucalyptus marginata Sm.*) and a large proportion of shrub and understorey components of the jarrah forest in south Western Australia over an area in excess of 200,000 ha. (5). Rapid decline and death of jarrah trees occurred primarily in 1945 - 65 although disease extension, as measured by death of the highly susceptible *Banksia grandis* (Willd) understorey, has occurred in many areas of the forest since that period.

P.cinnamomi is a soil- or water-borne fungus which is believed to be of tropical or sub-tropical origin. It is now widely distributed in temperate, sub-tropical and tropical regions of the world and it has been recovered from 967 plant species (12). The pathogen was comparatively recently introduced to south Western Australia (5). It requires warm (21 - 31°C) and wet (0.025 - 0.03) bars) soil conditions to form sporangia and free water for release and transmission of zoospores (12). Dry soil conditions reduce survival (8). A number of studies have shown

that its population density in soil decreases with depth (12).

South Western Australia has a Mediterranean climate and the jarrah forest occurs on an extensively laterized peneplain (4). In moisture gaining, poorly drained sites on the valley floors, soil moisture levels remain above critical levels for survival (6), and the fungus can be detected in the soil surface horizons through the year (Shearer and Shea, unpublished). Although the majority of these sites within the forest have been infected, the impact of the disease is limited because a number of the shrub and understorey and overstorey species are resistant to *P.cinnamomi*.

Jarrah is the dominant component of the overstorey on the ridges and divides which constitute approximately 80% of the landscape. The soils are deeply weathered infertile laterites (Fig. 1) (4). The surface horizons of these soils are suitable for sporangial formation and release only during relatively brief periods of warm wet conditions in autumn and spring (6). Overland flow of water is insignificant unless there is disturbance, and therefore lateral transmission

of zoospores in the surface horizons on these sites is negligible. During the prolonged summer dry period, water potentials of surface soil layers are less than 1.0 mPa, and survival of *P.cinnamomi* is negligible (8).

Although on upland lateritic sites the surface soil environment is only marginally favourable for *P.cinnamomi*, severe disease occurs (Fig. 2). Distribution of *P.cinnamomi* in time and space in surface (0 - 10 cm) soil horizons was monitored at a number of sites of diseased jarrah over several years but recovery rates from random soil samples rarely exceeded 10% and were usually less than 3% (8).

It was assumed that *P.cinnamomi* attacks the fine roots of susceptible *Eucalyptus* species and other hosts in the surface soil horizons (5, 8, 12). We were unable to explain how this pathogen can cause rapid and extensive mortality of jarrah trees by fine feeder root attrition because its population in the surface soil horizons of lateritic soils is so limited. *B.grandis* which forms a dense understorey in many areas of the forest is highly

susceptible to *P.cinnamomi* and is rapidly killed by the fungus (7,8). We have demonstrated consistent and rapid (0.5 - 1.4 cm per day) invasion of the xylem and phloem of the major roots and lower stem of this species (Shea and Deegan, unpublished data). Although *P.cinnamomi* can also invade the major secondary roots and lower stem of jarrah trees (10), the absence of extensive and rapid mortality of jarrah in large areas of infected forest indicated that jarrah trees normally resisted invasion of the major roots.

In a subsequent study of affected trees growing in areas where mass jarrah decline and death was occurring it was found that *P.cinnamomi* caused death of the vertical roots (Fig. 1) where they passed through root channels in a concreted lateritic layer (9). In all sites where mass decline was observed, the concreted layer was present within 1 m of the soil surface. We therefore proposed that rapid decline and death of jarrah trees resulted from destruction of the vertical root system by *P.cinnamomi* at depth in the soil profile on these specific sites. In this paper we present preliminary results from studies of the distribution, reproduction and movement of

P.cinnamomi on these sites of rapid and mass decline and death of jarrah trees.

MATERIALS AND METHODS

Five plots 20 x 20 m were located in an area of forest where rapid decline and death of the jarrah overstorey, understorey and shrub layer was occurring. One similar 20 x 20 m plot was established in adjacent healthy forest. The plots were sampled three times at approximately 3 - wk intervals following the onset of winter rains in May 1982. In each plot soil from 0 - 10 cm depth surrounding the collar of 10 recently killed (leaves retained) *B.grandis* trees was sampled on each date. One soil sample was taken from each Banksia and processed separately. In addition the surface (0 - 10cm) horizon and the soil at the interface of the concreted lateritic layer was sampled, using a heavy gauge, 20-cm-diameter pipe which was driven into the soil to the laterite layer at 10 random points in each plot on each sampling date. The depth to the concreted layer was recorded at each sampling point. The samples were returned to the laboratory and immediately processed.

From each sample of approximately 3000 cm ^{3}, 5 g of soil that passed through a 2 mm sieve was placed in a glass petri dish for determination of soil moisture content, expressed as a percent of oven dry weight. Of the remaining sieved soil, 25 grams was mixed with 50 ml of distilled water and poured on a 15cm diameter petri dish containing selective (11), half strength potato dextrose agar. The plates with soil were incubated for two days in darkness at 24°C. Following incubation the soil was washed from the plates and the number of colonies of *P.cinnamomi* counted. The plates were further incubated for one day and the number of colonies recounted. The number of colonies per gram oven dry weight of soil was determined by calculating the oven dry weight of soil applied per plate from moisture content determination.

Six weeks after the onset of autumn rainfall a 12 m x 8 m plot was established in the severely diseased area. Soil samples were taken at 10-cm depth intervals to the laterite layer at each intersection of

a 1 m square grid. Following this systematic sampling the surface layer of the soil was removed and the soil in the root channels was sampled at approximately 1 m intervals along the channels. Each sample contained approximately 5000 cm^3 of soil and there was a total of 50 samples. Soil samples were assayed for *P.cinnamomi* as described above. The soil was then washed from the root channels.

Sporangial formation in the surface soil (1 - 3 cm) and at the surface of the concreted lateritic layer (2.5 - 60cm) was determined by counting sporangia formed on inoculated *B.grandis* leaf discs which had been buried in the surface soil and at the interface with the concreted lateritic layer. For this procedure, discs 4 mm in diameter were punched from new season *B.grandis* leaves and autoclaved in distilled water for 20 min at 1.05 kg/cm^2. Fifty discs were suspended in 10 ml of sterile V-8 juice (3), inoculated with 2 ml of a comminuted mycelial suspension, and incubated at 24°C in darkness for two days. Following incubation, discs with peripheral mycelium were rinsed three times in distilled water and placed between 1 cm^2 pieces of fine gauze, formed into an envelope three discs per square.

The gauze envelopes were inserted into the soil. Five series of discs (approximately 200 envelopes per series) were inserted during 2 mo after the autumn rains began in May. The discs were removed 7 to 14 days after insertion, stained and mounted, and the number of sporangia formed per disc were counted.

The capacity for lateral transmission of zoospores was determined by sampling soil at the interface with the lateritic layer 75 cm downslope of 30 cm x 30 cm trenches which had been dug to the depth of the lateritic layer and filled with 2 L of water containing approximately 10^7 zoospores. Zoospores were produced by growing mycelium in sterile V-8 juice, transferring this to 20% extract for several days, then chilling for 30 minutes. Five trials were carried out on sites with concreted laterite present and the procedure was repeated on adjacent sites where the lateritic layer was not present. Each point of zoospore introduction was matched with a plot which contained no inoculum. The soil downslope of the introduction point at the interface with the lateritic layer was sampled 24 hours after

inoculation and the presence of *P.cinnamomi* was determined using the direct plating procedure described above.

RESULTS

P.cinnamomi was detected four to eight times more frequently in soil at the interface of the concreted lateritic layer than in the surface layer (Table 1). The detection rate around the collar of recently killed *B.grandis* trees was lower (6%) than that in random surface soil samples. There was no significant difference between the density of *P.cinnamomi* propagules in surface soils and samples taken at depths considering only positive samples. *P.cinnamomi* was not recovered from the control plot. The distribution of *P.cinnamomi* in plots which were sampled on a systematic grid was similar (Figs. 3 and 4). However, the detection rate in soil samples taken from the root channels was higher than in samples from other areas on the caprock. Removal of the soil from this plot revealed numerous situations where *B.grandis* roots were occupying the same root channels as jarrah.

Sporangial formation on *Banksia* leaf discs was high during autumn (May) but decline as soil temperatures decreased. There was no significant difference (P = 0.01) between the number of sporangia formed in the soil surface and at the interface of the concreted lateritic layer. Sporangia formed at depths down to 60 cm at the interface of the lateritic layer as shown in Fig. 5 which represents the pattern of sporangial formation recorded from one of the series of discs which were inserted in June.

The fungus was consistently recovered from soil samples at the interface of the concreted lateritic layer at distances of 50 - 70 cm downslope of the zoospore introduction points 24 hr after inoculation. On sites where the concreted layer was not present the fungus was detected in soil vertically below the introduction point but not downslope. No recoveries of *P.cinnamomi* were recorded from controls. In a separate trial zoospores were detected in water flowing at the interface of a concreted lateritic layer 30 cms below the soil surface 2 m downslope from a trench which had been filled with water and

inoculated with a zoospore suspension.

DISCUSSION

It has been difficult to explain the ability of *P.cinnamomi* to cause rapid decline and death of jarrah forest on apparently free draining sites in a region which has a Mediterranean climate. The discovery that *P.cinnamomi* can occur at high densities in the soil below the surface horizons where a layer of concreted laterite is present and that zoospores of the fungus can be laterally transmitted at the interface of this layer partially resolves this question. This study together with our previous report (9) of the infection of the vertical root system of jarrah trees by *P.cinnamomi*, form the basis of an explanation of how *P.cinnamomi* can cause mass collapse of jarrah forest.

Jarrah trees depend on their vertical root system to maintain internal water balance over the extended period of annual drought because they maintain a high rate of transpiration throughout the summer months (1,2). On specific site types the presence of a

concreted layer of sheet laterite in the soil profile provides conditions conducive to the reproduction and lateral movement of *P.cinnamomi* at the surface of the layer. The vertical roots pass through the concreted lateritic layer via root channels where they commonly form fine roots. The vertical roots of the highly susceptible *Banksia grandis* understorey (7) often occur in the same root channels. The presence of infected *Banksia grandis* roots, and the fact that the root channels form depressions in the lateritic layer which accumulate water , cause zoospores to be concentrated around the vertical roots. Only relatively small extensions of *P.cinnamomi* into the vertical roots via fine roots formed in the root channels are necessary to cause death of the root at its junction with the laterite layer. Death of vertical roots results in the cessation of water uptake from deep sources and desiccation of the trees.

Preliminary surveys indicate that a large proportion of the forest area where mass decline occurred in 1947 - 1965 had soil

profile characteristics similar to those we have described, (Shea, unpublished). It is possible that large areas of forest which do not have these soil characteristics are less susceptible to *P.cinnamomi* than has previously been assumed.

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Table 1. Recovery of *P.cinnamomi* from random surface and sub-surface soil samples from a positive area undergoing mass decline.

	Surface Samples	Samples from Interface with Concreted Lateritic Layer.						
Depth (cm)	<5.0	<12	<22	<32	<42	<52	<62	Mean
Number of Samples	150	35	36	22	25	17	8	147
Percentage recovery of *P.cinnamomi*	10	40	50	68	80	71	88	61
Propagule numbers per gram O.D.W. Soil.	84[a] (0.36-1.95)[b]	0.955 (.53-2.69)	1.033 (.87-2.73)	0.689 (.5-2.73)	1.001 (.85-2.72)	0.500 (.33-1.65)	1.135 (.20-1.65)	1.129

[a] Mean of positive samples

[b] 95% asymetric confidence interval.

Fig. 1. Diagramatic representation of a Jarrah tree root system. Blackened areas of roots show infection by P.cinnamomi. (Note: roots below the concreted lateritic layer were not sampled).

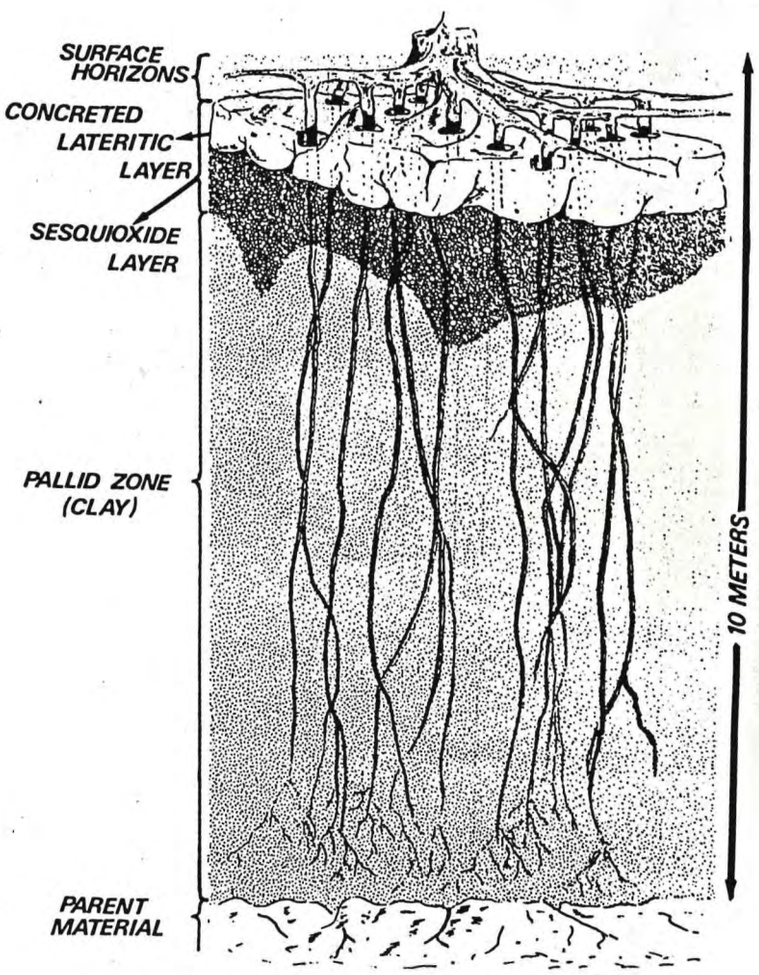

SURFACE HORIZONS
CONCRETED LATERITIC LAYER
SESQUIOXIDE LAYER
PALLID ZONE (CLAY)
PARENT MATERIAL
10 METERS

Fig. 2. Jarrah Forest exhibiting mass rapid decline and death caused by P.cinnamomi.

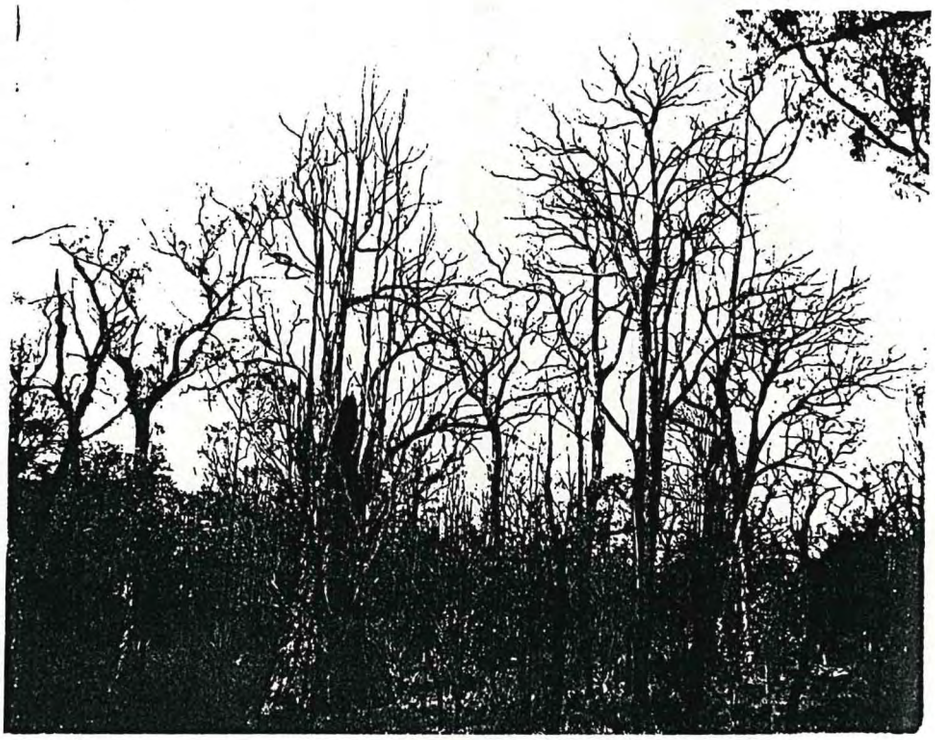


Fig. 3. Distribution of P.cinnamomi in soil above a concreted lateritic layer on a severely diseased site. (Vertical bars represent propagule numbers per gram oven dry weight).

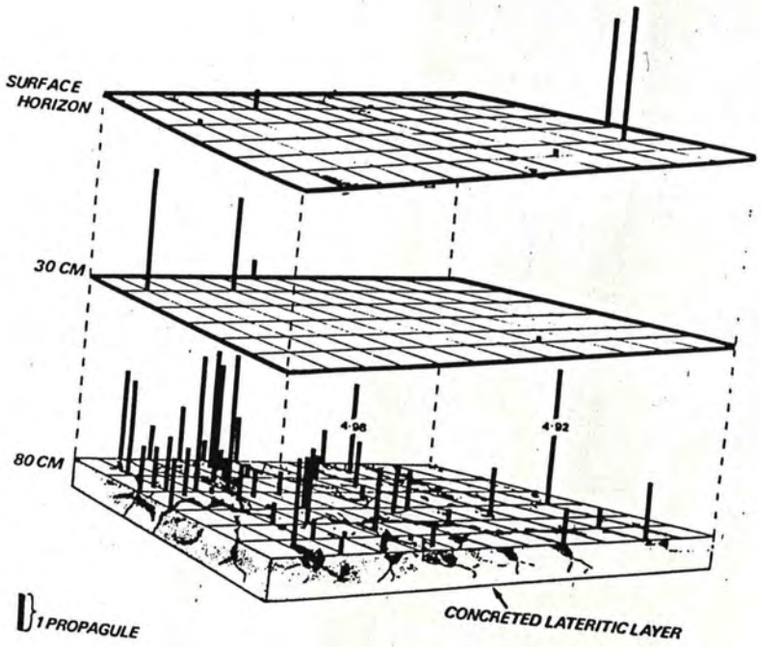

SURFACE HORIZON
30 CM
80 CM
4·96
4·92
1 PROPAGULE
CONCRETED LATERITIC LAYER

Fig. 4. Exposed layer of concreted sheet laterite forming the base of the plot shown in Fig.3. Tape denotes meter square sampling grid.

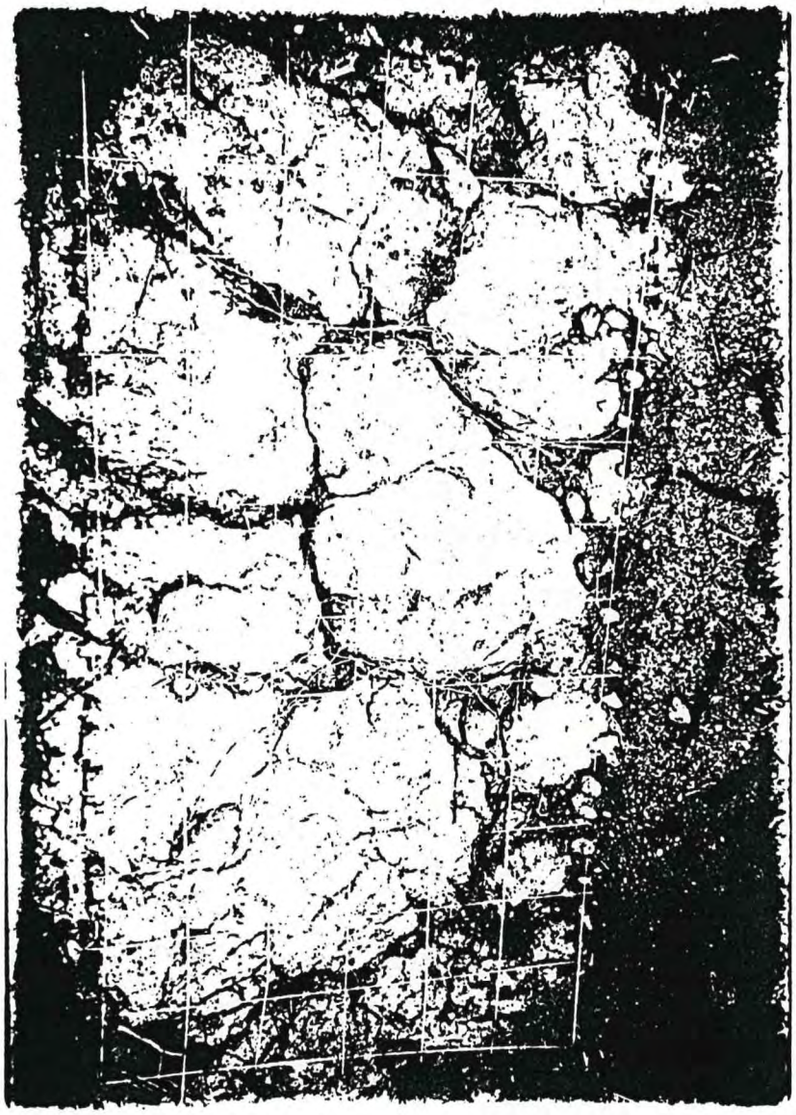
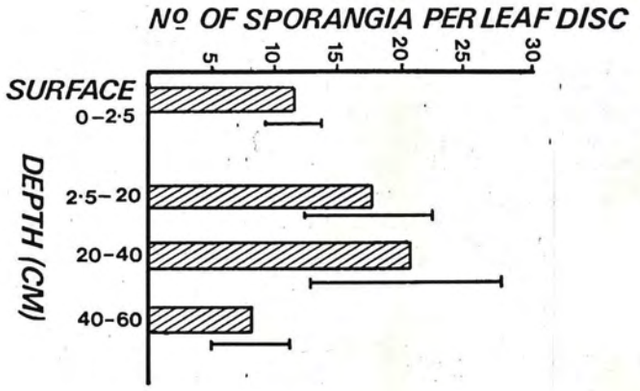


Fig. 5. Sporangia formed on Banksia grandis leaf discs in the surface soil horizon and at the interface of the concreted lateritic layer 14 days after insertion in June 1982.


Nº OF SPORANGIA PER LEAF DISC
5
10
15
20
25
30
SURFACE
0–2·5
2·5–20
20–40
40–60
DEPTH (CM)