THE ORIGIN AND DISTRIBUTION OF *PHYTOPHTHORA CINNAMOMI* RANDS IN AUSTRALIAN NATIVE PLANT COMMUNITIES AND THE SIGNIFICANCE OF ITS ASSOCIATION WITH PARTICULAR PLANT SPECIES

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Abstract

The origin, distribution, and disease association of *P. cinnamomi* in native plant communities in Australia has been examined.

The fungus was isolated from the root zones of 31 plant genera in 16 families and is widespread throughout eastern and southern Australia and south-western Western Australia.

Although the fungus is associated with disease in native plant communities it is also present in apparently non-diseased communities. Disease occurs usually only in environments disturbed by man, probably as a result of increase in population or activity of pre-existing fungal populations.

The widespread distribution of *P. cinnamomi* in native vegetation in Australia, its occurrence in remote, undisturbed areas, and the apparent balance it has achieved with plant species of differing susceptibility to disease in some natural, undisturbed areas suggests that the fungus is likely to be indigenous to eastern Australia. Further, it may be partly responsible for the localized distribution of some plant species.

I. INTRODUCTION

The soil-borne fungus *Phytophthora cinnamomi* Rands is widely distributed in Australia, in horticultural plantings (Zentmyer and Thorn 1967; Pratt and Wrigley 1970; as well as personal communications from the New South Wales Department of Agriculture, Tasmanian Department of Agriculture, Victorian Department of Agriculture, and the Queensland Department of Primary Industries), and in conifer nurseries and plantings (Oxenham and Winks 1963; Bertus 1968; and personal communications from the New South Wales Forestry Commission, and the Queensland Department of Forestry).

Little is known of its distribution and its disease significance in natural or semi-natural plant communities. Records suggest it might be a serious pathogen of native plants in a variety of natural habitats. *P. cinnamomi* has been found associated with a serious dieback disease of *Eucalyptus marginata* Sm. (jarrah) in Western Australia (Podger *et al.* 1965; personal communication from Western Australia Forests Department), mixed *Eucalyptus* spp. in eastern Victoria (Marks and Kassaby, personal communication; Forest Commission of Victoria, personal communication),

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mixed *Eucalyptus* spp. in central coastal New South Wales (New South Wales Forestry Commission, personal communication), and in native understorey shrubs in New South Wales (Fraser 1956).

The fungus is considered to induce rotting of fibrous roots leading to a decline in plant vigour and ultimately to death (Anon. 1969). The severity of disease and subsequent economic loss of hardwood timber in stands examined by the authors suggests *P. cinnamomi* is likely to be a significant factor in reducing Australian forest production. Consequently a survey was initiated to determine the origin and distribution of the fungus in native plant communities and the significance of any association of the fungus with disease of particular plant species.

The survey began in 1969 and this paper summarizes the results to August 1972. Subsequent to the development of the survey further reports were made on the occurrence of *P. cinnamomi* in native vegetation in southern Victoria (Weste and Taylor 1971) and southern Queensland (Pegg and Alcorn 1972).

II. Materials and Methods

(a) Selection of Areas

Australia's highly productive hardwood forests are situated in the coastal and semi-coastal areas of Queensland, New South Wales, Victoria, and Tasmania, and in the south-western corner of Western Australia. The forests vary from open mixed eucalypt forest to rain-forest where the majority of preferred timber species are members of the genus *Eucalyptus*.

The degree of disturbance of these forests by European man, whether by logging, burning, road construction, or by regeneration of other plant species after clearing, varies. Similarly the forests differ markedly in age and species composition and occupy a wide range of climatic environments between latitudes 17 and 43°S.

Representative areas of several major types of native vegetation were inspected by ground and aerial survey to determine the "normal" or average form of the vegetation at different stages of development and with varying degrees of disturbance. With the assistance of local forestry personnel, individual plants and groups of plants showing different types of growth aberration were located. These diseased plants exhibited specific symptoms such as leaf yellowing, decline of crown, reduction in leaf size and leaf number, loss of fine branches, excessive epicormic development, stunting, and mortality. Particular attention was given to areas showing disease symptoms similar to those previously described for diseased areas associated with *P. cinnamomi* occurrence in Western Australia, Victoria, and New South Wales (Anon. 1969).

In other areas plants which appeared healthy or showed only slight disease symptoms were selected for study and to provide a comparison with obviously diseased plants and to obtain information on the limits of disease expression. Because of the varying crown configuration and stem form of *Eucalyptus* spp. and the poor vigour of some plants resulting from competition, fire, drought, flooding, insect predation, and soil deficiencies, disease is often a relative term.

Sample areas were located in each State essentially in the coastal and semi-coastal areas, with a further series in and near to the Australian Capital Territory, approximately 75 miles inland. The areas were deliberately widely spaced to determine as quickly as possible the extent of the topographic, geographic, and climatic distribution of the fungus and of any associated disease. Further sample areas were selected later in scattered inland areas where plant decline had been reported.

Sampling in the selected areas was based on two techniques. Firstly, samples were taken close to the base of apparently diseased plants. Secondly, a series of less-biased samples were taken at regular intervals along a transect line run through forests of different types. Usually transect lines crossed major ridges and valleys at right angles, thus traversing different topographical sites, and apparently healthy and diseased areas.

(b) Collection of Samples

Field and laboratory trials showed that although *P. cinnamomi* occurred on both large and small roots it is most easily and consistently recoverable from smaller fibrous roots and adhering soil. These roots can be obtained most efficiently from trees and large shrubs by digging to depths of 2·5–15·0 cm directly at the base of the main stem and removing the exposed roots with secateurs. Smaller shrubs and seedling plants can be dug or pulled from the soil for root removal. Usually only a single sample was taken from each plant. Implements were surface-sterilized with 70% ethanol during field sampling to avoid contamination of successive samples.

Because of the possibility of seasonal fluctuation in population or activity of *P. cinnamomi*, replicate samplings were made at different times of the year in some areas.

Individual samples were placed in sterile plastic or aluminium containers and packed in insulated boxes, for transport to the laboratory where they were examined within 1–3 days after collection. Whilst samples were usually baited within 3 days of collection, *P. cinnamomi* was isolated from samples stored for up to 21 days at 8°C prior to baiting.

About 12,000 samples were collected during a 3-year period from a zone approximately 2000 miles long and 100 miles wide extending from near Cairns in northern Queensland to the Catamaran River in southern Tasmania, and additionally from areas in South Australia, Western Australia, Northern Territory, and the Australian Capital Territory.

(c) Recovery and Identification of P. cinnamomi

P. cinnamomi was recovered from soil and plant roots by the lupin-baiting assay of Chee and Newhook (1965) as modified by the authors (Pratt and Heather 1972).

III. RESULTS

(a) Distribution of P. cinnamomi

P. cinnamomi is a relatively common component of the soil microflora in many hardwood forests in coastal and semi-coastal Australia along the 2000 mile sampling zone. It also occurs in other areas of Tasmania, Victoria, South Australia, Western Australia, and the Australian Capital Territory (Table 1; Figure 1). It occupies sites which occur from latitudes 17°S. to 43°S. and at which the average annual rainfall varies from 0·6 to 3·5 m (Table 1) and where rainfall patterns vary from summer to winter dominance. Although the fungus is recovered most frequently from coastal and semi-coastal sites it was detected up to 75 miles inland in New South Wales. It is found most commonly at moist sites such as natural drainage lines, particularly where the environment had been disturbed by man for horticultural, forestry, or urban use. Nevertheless it is found also at sites distant from cultivation and other disturbance and in south-eastern New South Wales in remote forest country apparently undisturbed by European man (Pratt et al. 1973).

The fungus was recovered from the root zone of 31 genera of plants in 16 families, particularly from members of the Proteaceae, Papilionaceae, Epacridaceae, and Myrtaceae (Table 2). It occurs in communities ranging from the dry and wet sclerophyll forests of southern, eastern, and western Australia to the edges of rain-forest in north-eastern Queensland. It is present in numerous soil types with no obvious specialization to accommodate to the different conditions, and in areas of different topography mostly below altitudes of 2000 ft, but occasionally up to 4000 ft. Soil temperature regimes where the fungus occurs vary from those of relatively low winter and medium–high summer temperatures to those of medium–high year round temperatures.

TABLE 1

DISTRIBUTION AND DISEASE ASSOCIATION OF *P. CINNAMOMI* IN AUSTRALIA

Sites where *P. cinnamomi* was recovered from plant communities by lupin baiting

Area	Disease status		Annual rainfall (m)†	No. of effective rain days per year†
	Under-storey	Over-storey		
New South Wales				
Green Cape	+	+	0·91	114
Eden	+	+	0·91	114
Bega	+	+	0·89	88
Mogo	−	−	1·02	114
Clyde Mountain	+	−	1·14	114
Batemans Bay–Ulladulla				
(1) East	+	+	1·14	114
(2) Middle	+	−	1·14	114
(3) West	−	−	1·14	114
Penrose	+	+	0·61	108
Ourimbah*	−	+	1·30	112
Coffs Harbour	Absent	+	1·65	125
Orara	+	+	1·85	111
Pine Creek	−	−	1·65	125
Queensland				
Coolum	+	Absent	1·55	110
Kennedy	−	−	2·13	136
Bingil Bay	+	−	3·60	163
Soda Springs, Ravenshoe	−	+	1·22	117
Mill Stream, Ravenshoe	−	+	1·22	117
Victoria				
Grampians*	+	Absent	0·91	141
Brisbane Ranges*	+	+	0·71	132
Traralgon	+	+	0·76	135
Bonang–Orbost*	+	+	0·89	115
Mallacoota	+	+	0·86	101

Area	Disease status		Annual rainfall (m)†	No. of effective rain days per year†
	Under-storey	Over-storey		
Australian Capital Territory				
Condor Creek	+	+	0·81	92
Black Mountain	+	+	0·63	106
Tasmania				
Catamaran River	+	+	0·89+	158+
Dover–Hastings	+	+	0·89+	158+
Orford–Triabunna	+	+	0·66	109
Taroona	+	Absent	0·63	163
Smithton	+	+	1·08+	184
Fingal	+	+	0·76	103
Flowery Gully	−	+	0·71	135
Arthur River	+	+	1·08+	184+
Coles Bay	+	+	0·66	109
South Australia				
Belair	+	Absent	0·76	109
Western Australia				
Jarrahdale*	+	+	1·22	103
Harvey*	+	+	1·08	102
Nannup*	+	+	0·99	135
Pemberton*	+	+	1·52	194
Manjimup*	+	+	1·07	161

* Diseased area reported by other workers prior to commencement of this study.

† Nearest permanent recording station. An effective rain day is where 0·25 cm or more rain falls within 24 hr.

(b) Association of P. cinnamomi with Disease

P. cinnamomi is closely associated with the occurrence of a root-rot, decline, and dieback disease of native plants, being present in 48 of 57 diseased sites examined in all States and the Australian Capital Territory. The mechanism of its involvement in disease, and the role of other organisms, is unknown.
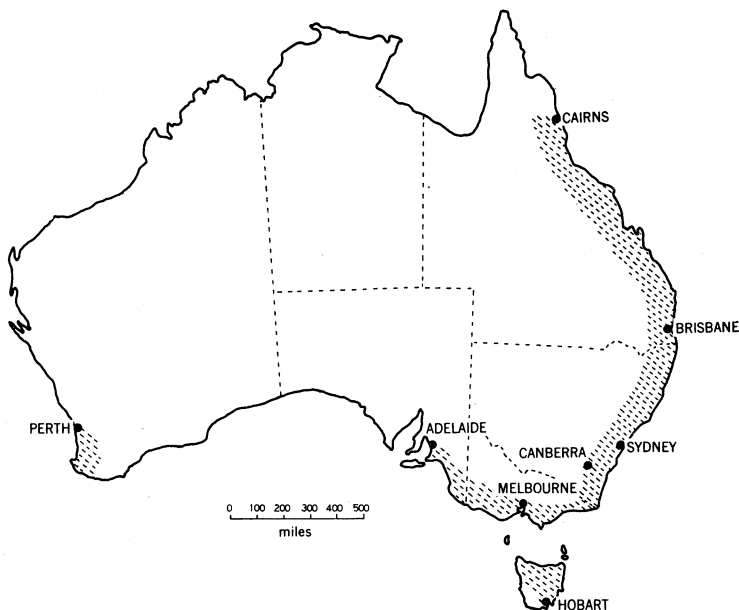

Fig. 1.—Distribution of native vegetation in Australia from which *P. cinnamomi* has been isolated. Australian National University Forestry Department sampling sites are listed in Table 1.

Manifest disease did not necessarily occur in all native communities from which *P. cinnamomi* was isolated. In numerous instances the fungus was found in the root zone of known field-resistant and field-susceptible plants (Zentmyer and Thorn 1967; Titze and Palzer 1969), yet no disease was obvious. In some of these sites there is no evidence of prior disease. Other sites have only plants of known field-resistant species which may indicate that removal by disease of certain susceptible species occurred in the past.

Disease is most severe in areas with an average rainfall between $0 \cdot 6$ and $1 \cdot 3$ m per annum and where the average number of effective rain days per year varied between 101 and 135, and the predominant climatic pattern is winter rainfall followed by summer drought.

P. cinnamomi is more frequently recovered from samples in the upper 15 cm of soil taken directly at the bases of diseased plants than from deeper or more distant root zones. Wet rather than dry soils yielded the greatest percentage recovery.

TABLE 2

DISTRIBUTION AND DISEASE ASSOCIATION OF *P. CINNAMOMI* IN AUSTRALIA:
ASSOCIATED PLANT SPECIES

Plant species with root zones from which *P. cinnamomi* was recovered by lupin baiting

Host	Area	Disease status
Pteridophyta		
DICKSONIACEAE		
Pteridium sp.	Vic.	—
P. esculentum (Forst. f.) Nakai	N.S.W.	—
Spermatophyta—Gymnospermae		
CYCADACEAE		
Macrozamia communis L. Johnson	N.S.W.	+
M. reidlei (Gard.) C. A. Gard	W.A.	+
Spermatophyta—Angiospermae—Monocotyledones		
IRIDACEAE		
Patersonia sericea R. Br.	N.S.W.	+
LILIACEAE		
Xanthorrhoea sp.	N.S.W.	+
X. australis R. Br.	Vic.	+
X. preisii Endl.	W.A.	+
Spermatophyta—Angiospermae—Dicotyledones		
CASUARINACEAE		
Casuarina sp.	N.S.W.	+
C. cunninghamiana Miq.	N.S.W.	+
C. cunninghamiana Miq.	Qld.	—
C. fraseriana Miq.	W.A.	+
C. stricta Ait.	Tas.	+
C. torulosa Ait.	Qld.	—
COMPOSITAE		
Cassinia sp.	A.C.T.	+
Cassinia sp.	Vic.	+
C. aculeata (Labill.) R. Br.	Tas.	+
CYPERACEAE		
Lepidosperma laterale R. Br.	Tas.	+
EPACRIDACEAE		
Cyathodes glauca Labill.	Tas.	+
Epacris impressa Labill.	Tas.	+
Leucopogon lanceolatus R. Br.	N.S.W.	+
Monotoca glauca (Labill.) Druce	Tas.	+
FAGACEAE		
Nothofagus cunninghamii (Hook.) Oerst.	Tas.	+
HALORRHAGACEAE		
Haloragis teucrioides (DC.) Schlecht.	Tas.	+
LEGUMINOSAE: MIMOSACEAE		
Acacia sp.	Vic.	+
Acacia sp.	Qld.	—
A. dealbata Link.	Tas.	+
A. diffusa Lindl.	A.C.T.	+
A. verticillata Willd.	Tas.	+

TABLE 2 (*Continued*)

Host	Area	Disease status
LEGUMINOSAE: PAPILIONACEAE		
Bossiaea microphylla J. E. Smith	N.S.W.	—
Daviesia mimosoides R. Br.	A.C.T.	+
D. ulicifolia Andr.	N.S.W.	—
Dillwynia retorta (Wendl.) Druce var. phylicoides (A. Cunn.) J. Thompson	A.C.T.	+
Oxylobium ellipticum (Labill.) R. Br. ex Ait.	Tas.	+
O. ilicifolium (Andr.) Domin.	N.S.W.	+
Pultenaea cunninghamii (Benth.) Williamson	N.S.W.	+
P. daphnoides Wendl.	Tas.	+
P. daphnoides Wendl.	S.A.	+
P. reticulata Sm.	W.A.	+
P. gunnii Benth. or *Aotus villosa* Sm.	Tas.	+
MYRTACEAE		
Thryptomene calycina (Lindl.) Stapf.	Vic.	+
Tristania conferta R. Br.	N.S.W.	+
Subgenus *Corymbia*		
Eucalyptus calophylla R. Br. & Lindl.	W.A.	—
E. gummifera (Gaertn.) Hochr.*	N.S.W.	+
Subgenus *Symphyomyrtus*		
Eucalyptus diversicolor F. Muell.	W.A.	—
E. globulus Labill.	Tas.	+
E. grandis Hill ex Maiden	N.S.W.	—
E. mannifera Mudie subsp. *maculosa* (R. T. Bak.) L. Johnson	A.C.T.	—
E. saligna Sm.*	N.S.W.	+
E. saligna Sm.	N.S.W.	—
E. viminalis Labill.	A.C.T.	—
E. viminalis Labill.	Tas.	+
Subgenus *Monocalyptus*		
Eucalyptus acmenioides Schau.	Qld.	+
E. amygdalina Labill.	Tas.	+
E. baxteri (Benth.) Maiden & Blakely	Vic.	+
E. dives Schau.	A.C.T.	+
E. eugenioides Sieb. ex Spreng.	Qld.	+
E. globoidea Blakely	N.S.W.	+
E. macrorhyncha F. Muell. ex Benth.	A.C.T.	+
E. marginata Donn. ex Sm.	W.A.	+
E. obliqua L'Herit.	Tas.	+
E. obliqua L'Herit.	Vic.	+
E. obliqua L'Herit.		
E. pilularis Sm.	N.S.W.	+
E. piperita Sm.	N.S.W.	+
E. radiata Sieb. ex DC.	Vic.	+
E. regnans F. Muell.	Tas.	+
E. rossii R. T. Bak. & H. G. Sm.	A.C.T.	+
E. sieberi L. Johnson	N.S.W.	+
E. sieberi L. Johnson	Vic.	+
E. sieberi L. Johnson	Tas.	+
PITTOSPORACEAE		
Marianthus procumbens (Hook.) Benth.	N.S.W.	—

TABLE 2 (*Continued*)

Host	Area	Disease status
PROTEACEAE		
Adenanthos obovata Labill.	W.A.	+
Banksia sp.	Vic.	+
Banksia sp.	N.S.W.	+
Banksia caleyi R. Br. or *B. baueri* R. Br.	S.A.	+
B. grandis Willd.	W.A.	+
B. integrifolia L. f.	Qld.	+
B. marginata Cav.	Vic.	+
B. marginata Cav.	Tas.	+
B. serrata L. f.	N.S.W.	+
Grevillea sp. aff. *G. alpina* Lindl.	A.C.T.	+
Hakea sericea Schrad.	A.C.T.	+
Isopogon (?) *anethifolius* (Salisb.) Knight	N.S.W.	+
Persoonia sp.	N.S.W.	—
P. longifolia R. Br.	W.A.	+
RHAMNACEAE		
Pomaderris apetala Labill.	Tas.	+
RUTACEAE		
Phebalium squameum (Labill.) Engl.	Tas.	+

* Insect associate at Ourimbah, N.S.W. (personal communication from New South Wales Forestry Commission).

(c) *Disease Symptoms*

The general symptoms of the disease associated with the presence of *P. cinnamomi* include leaf yellowing, leaf shedding without replacement, microphylly, epicormic shooting, stunting, loss of fine branches—occurring first in the upper crown but later extending throughout the plant and to the larger branches, and finally mortality of the whole plant. Fine roots appear rotten, particularly at the tips, but many larger roots seem sound.

Some plants, particularly understorey shrubs and seedling eucalypts, but occasionally more mature eucalypts such as *E. macrorrhyncha* and *E. sieberi*, die within a few days of the initial onset of symptoms. Plants dying in this manner often retain dead leaves and branches for some time in striking contrast to adjacent plants with apparently healthy foliage.

Other plants, typically more mature eucalypts, may remain obviously diseased for many years and decline gradually. Some specimens of *E. marginata*, *E. obliqua*, *E. regnans*, and *E. sieberi* examined were reputed to have shown definite symptoms of disease for 15–20 yr prior to death. The gradual loss of leaves from all branches, followed by repeated epicormic shooting amongst the lower branches, results in "stag-headed" trees with bare branches in the upper crown and thicker foliage below. Diseased trees are sometimes difficult to detect in the forest except where they occur in groups.

It is difficult to distinguish damage caused by *P. cinnamomi* from that due to other causes. Further it is not always possible to state emphatically that disease,

in the sense of plant mortality or reduced growth, is occurring in a particular forest stand.

For these reasons the disease has been referred to as one "associated with the presence of *P. cinnamomi*".

(d) Plants Affected by Disease

The disease associated with the presence of *P. cinnamomi* can affect understorey and overstorey plants either together or separately. The list in Table 2 is far from complete since plants of other understorey species affected were not formally identified at sampling.

Plants of all ages are affected by disease but generally there is a progression of disease beginning with the most susceptible understorey species, then the younger eucalypts, and eventually the more mature eucalypts. Mortality occurs in eucalypts ranging from newly emerging seedlings to specimens more than 45 m in height and at least 150 yr of age.

Within the eucalypt group, members of the subgenus *Monocalyptus** appear to be most affected by disease. Species in the subgenera *Blakella*, *Corymbia*, *Eudesmia*, *Idiogenes*, and *Symphyomyrtus* generally appear resistant or tolerant but can be seriously affected in immature stages or where they occur in heavily diseased stands of *Monocalyptus*, or where there are other predisposing stress factors such as simultaneous insect attack.

The major economic timber species affected by disease include *E. regnans*, *E. obliqua*, *E. pilularis*, and *E. sieberi* in eastern and southern Australia and *E. marginata* in Western Australia. Field observation throughout Australia indicates *Eucalyptus* spp. can be broadly classified in relation to disease as shown in Table 3.

IV. DISCUSSION

(a) Recovery by Baiting

Previously some workers have recovered *P. cinnamomi* from soil by direct plating (Hendrix and Kuhlman 1965), and by baiting with pineapple leaves (Anderson 1951), apples (Tucker 1931; Campbell 1949), lupins (Chee and Newhook 1965), and avocados (Zentmyer *et al.* 1967).

In the current program, where large numbers of samples have to be processed, lupins have been used satisfactorily for recovery of *P. cinnamomi* and have the advantages of low cost, ready availability, and ease of germination and handling.

Direct microscopic identification of *P. cinnamomi* sporangia on roots with lesions is a rapid and reliable technique (Pratt and Heather 1972) and greatly increases the rate of sample assay. Previous workers have declined to use sporangial characters alone for the identification of *P. cinnamomi* because of the variability of the size and shape of the sporangium. This difficulty is largely overcome where the fruit body is produced on the living roots, instead of on agar, and where baiting conditions are standardized.

* Based on "A Classification of the Eucalypts" by L. D. Pryor and L. A. S. Johnson, Australian National University, 1971.

Nevertheless, the baiting technique has certain limitations depending on release of zoospores from infested roots and soil and migration of these to lupin root tips where infection occurs (Zentmyer 1961). Production of sporangia can be influenced strongly by soil bacteria (Zentmyer 1965; Chee and Newhook 1966; Manning and Crossan 1966) and other factors (Shirley *et al.* 1971).

TABLE 3

FIELD RESISTANCE OF *EUCALYPTUS* SPP. TO THE DISEASE ASSOCIATED WITH
P. CINNAMOMI

Resistant: no disease evident; tolerant: disease rare, usually limited to scattered individuals, particularly young plants; susceptible: plants of all ages diseased, usually in small groups; highly susceptible: severe disease widespread in community

Category	Species and subgenus*
Resistant	E. (S.) alba Reinw. ex Blume, E. (C.) citriodora Hook, E. (S.) cypellocarpa Johnson, E. (S.) diversicolor, E. (S.) grandis, E. (C.) maculata, E. (S.) mannifera, E. (S.) melliodora A. Cunn. ex Schau., E. (S.) ovata Labill, E. (S.) pellita F. Muell., E. (S.) polyanthemos Schau., E. (S.) smithii B. T. Bak., E. (S.) wandoo Blakely
Tolerant	E. (C.) calophylla, E. (S.) globulus, E. (C.) gummifera, E. (S.) punctata DC., E. (S.) rubida Dean & Maiden, E. (S.) saligna, E. (S.) sideroxylon A. Cunn. ex Wools., E. (S.) viminalis
Susceptible	E. (M.) acmenoides, E. (M.) agglomerata Maiden, E. (M.) delegatensis R. T. Bak., E. (M.) eugenioides, E. (M.) globoidea, E. (M.) muellerana Howitt, E. (M.) pilularis, E. (M.) piperita, E. (M.) radiata
Highly susceptible	E. (M.) amygdalina, E. (M.) baxteri, E. (M.) dives, E. (M.) macrorhyncha, E. (M.) marginata, E. (M.) obliqua, E. (M.) regnans, E. (M.) rossii, E. (M.) sieberi

* C, *Corymbia; M, Monocalyptus; S, Symphyomyrtus.*

While stimulatory bacteria are known to be common in Australian soils (Pratt and Heather, unpublished data), it is not known if sufficient stimulation occurs in all samples at all times. Unfortunately there is little knowledge of the levels of population or activity of *P. cinnamomi* needed for its detection by lupin baiting, and there is insufficient knowledge of the interactions between the fungus and other soil organisms to determine whether there is inhibition of infection of lupin root tips.

Thus whilst successful baitings are positive demonstrations of the presence of *P. cinnamomi* in soil, non-successful baitings cannot be taken to indicate absence of the fungus.

(b) *Distribution of* P. cinnamomi

P. cinnamomi obviously is widespread in Australian coastal native plant communities and occurs in a wide range of environments. Possibly it exists wherever environmental conditions are favourable. The fungus can be associated with the roots of plants of many species, but does not necessarily induce disease in these plants

under all field conditions. Thus it probably occurs unnoticed in many areas and more detailed surveys are required to determine the exact distribution of the organism.

Assuming this widely distributed fungus constitutes a potential for disease development, a very large proportion of Australia's productive hardwood forests must be kept under critical observation for disease occurrence. Future development of disease will depend on the correct conjunction of susceptible host plants and a suitable environment in the upper soil layers where the fungus is present.

(c) Origin of P. cinnamomi

The widespread occurrence of the fungus raises the obvious question of its origin. Crandall and Gravatt (1967), after an exhaustive investigation, suggested *P. cinnamomi* probably developed in south-east Asia and was distributed to other countries by European man. Introduction to many countries was thought to have occurred during the 15th Century and to Australia at some later date. However, this was not examined in detail prior to the present study and the work of Pratt *et al.* (1973) which indicated that *P. cinnamomi* could be indigenous to south-eastern Australia.

A major difficulty in determining the origins of *P. cinnamomi* is that the present forest environments are largely those resulting from up to 175 years of man-made disturbance which could have altered both the floral and microbial characters of the communities. Thus it is particularly important to study remote, relatively undisturbed forest communities where vegetational and microbial patterns are likely to be more representative of original types.

In eastern Australia, *P. cinnamomi* is found to be a common component of the soil microflora in both disturbed and non-disturbed areas throughout a wide range of different geographic and topographic areas, suggesting the organism has been present for an exceedingly long time and has adapted to these sites.

If the organism is indigenous then variant types of the fungus could be expected. A_1 and A_2 mating types have been isolated with other possibly more complex mating types (Pratt *et al.* 1972). Further, isolates show considerable variation in growth rate on specific agars and in sporangial producing ability (Shepherd *et al.* 1971*a*, 1971*b*). These features are currently being investigated by the authors.

Finally, an expected consequence of a long period of association of a pathogen with vegetation would be disease resistance in the vegetation developing in the habitat occupied by the pathogen. In eastern Australia this pattern is obvious, and indeed the fungus may have been partly instrumental in determining the present distribution of eucalypts and other sensitive plant species. For example, in natural, undisturbed environments in eastern Australia, eucalypt and understorey species along drainage lines and other moist sites tend to be resistant to *P. cinnamomi* disease while those on drier sites tend to be susceptible.

Past disease in some of these eastern and southern areas may not have been apparent in the form in which it is currently obvious. Thus sensitive plants which invaded *P. cinnamomi* sites may have become diseased and died when environmental conditions became favourable for fungal activity or unfavourable to the plant. The intervals between upsurges in disease would depend largely on the relative frequency of these favourable disease conditions. In areas with a high frequency of the fungus

it is likely that the boundaries between communities of sensitive and non-sensitive species would become sharply defined. With a lower frequency, invading species might develop for a considerable time before being removed by disease. This "advance and retreat" of particular species is an obvious feature of many eastern areas examined during the survey, and is more pronounced amongst understorey than overstorey species. Similar patterns of disease development have been noted in native plant communities in southern Queensland by Pegg and Alcorn (1972).

Certain circumstantial evidence suggests *P. cinnamomi* first entered Australia with elements of the Indo-Malayan flora from south-east Asia. For example, the Indo-Malayan flora appears field-resistant to *P. cinnamomi* disease, and there is greater field resistance to disease in eucalypts in north-eastern Australia than in southern Australia.

The southernmost extension of Indo-Malayan flora in eastern Australia is not clearly defined, but the area most commonly suggested for one group is approximately the border between New South Wales and Victoria. Coincidentally, it is south of this border that *P. cinnamomi* shows increasingly less evidence of being indigenous. Possibly the fungus is still in a period of active adjustment to the environment of this zone, and disease expression generally is most intense in areas where invasion has been most recent. Thus severe disease has developed in Victoria, Tasmania, and Western Australia. To understand disease development in these areas, however, we need to know more of the effect of environmental factors on development of eucalypts of the different subgenera and the rate of increase in *P. cinnamomi* disease in different plant communities.

Probably it can never be determined unequivocally whether *P. cinnamomi* is an indigenous or introduced organism on the Australian continent. Nevertheless, this question is of more than academic interest, for acceptance of one or other of these viewpoints may have an important bearing on the practical measures adopted to control or contain the disease. Weste and Taylor (1971) and Marks *et al.* (1972) have concluded that the organism was introduced following a study of a small area in which there was pronounced disease affecting a small number of plant species indigenous to that area. However, there are many examples of disease or pest organism affecting or killing other organisms occupying the same ecological situation. It appears to us that on balance the weight of the evidence from the study of distribution and ecology of the organism throughout Australia supports the viewpoint that *P. cinnamomi* has been on the eastern part of the Australian continent for an exceedingly long time and can best be regarded as indigenous. Certainly this approach should not be rejected in forest management consideration.

There is less evidence that the fungus is indigenous to other areas of Australia. Western Australia is of particular interest because of the widespread and highly damaging disease which occurred in the *E. marginata* forest, and also because available evidence suggests the fungus is of relatively recent introduction. A large proportion of the plant species appears to be susceptible to the root rot associated with *P. cinnamomi* (Western Australian Forests Department, personal communication) and it is especially significant that these include many relict or primitive angiosperms such as *Stirlingia* and *Adenanthos*. It seems unlikely there could have been simul-

taneous development of these susceptible species with *P. cinnamomi* if they occur on the same restricted sites.

The south-west forest area of Western Australia has been isolated from eastern parts of Australia by oceans from the Cretaceous to late Tertiary period, then by large tracts of arid country since at least the beginning of the Pleistocene era (cf. Atlas of Australian Resources, published by Department of National Development, Canberra, 1966). Natural movement of vegetation and associated fungi such as *P. cinnamomi* from east to west since that time would be unlikely. By contrast, there would have been numerous opportunities during the past 150 years for European man to have transferred the organism in soil or plant material from overseas or from eastern Australia.

The present distribution of disease in Western Australia presupposes an ability by *P. cinnamomi* to invade and colonize soil–plant root habitats throughout an exceptionally large forest area. While this is not strictly in accord with established thinking on soil-borne pathogens there are several exceptional circumstances in Western Australia. Firstly there is a virtual monoculture of susceptible *E. marginata* in the overstorey, and high concentrations of susceptible plant species in the understorey. Secondly, the accidental but widespread use of gravel from old *P. cinnamomi*-disease sites for construction of roads throughout the forest in relatively recent years has provided remarkable opportunities for spread of inoculum. This latter practice, incidentally, has been controlled since 1966 and forbidden since 1969. Finally, the pattern of heavy rain in midwinter, followed by excessive drying could be conducive to heavy zoospore infection of fine roots followed by intense development of disease when the plants are under severe transpirational stress.

In addition to natural spread of *P. cinnamomi* through soil by growth along roots or in waterborne zoospores it can be transferred in infested soil on machinery and vehicles, particularly crawler type vehicles, on roots of nursery plants, and in soil and gravel used in roadmaking. This could account for the presence of *P. cinnamomi* in areas in which it is not indigenous.

Many areas shown to be positive for *P. cinnamomi* during the survey are relatively close to areas previously suspected to carry the fungus, such as orchards, home gardens, Botanical Gardens, conifer nurseries, plantations, and windbreaks, and some had common drainage lines or would have been traversed by vehicles with adhering soil. This type of spread and interchange could be of particular importance if different pathogenic strains of *P. cinnamomi* have developed in different floristic communities.

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