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REVIEW

Relative importance of site, weather and *Phytophthora cinnamomi* in the decline and death of *Eucalyptus marginata* – jarrah dieback investigations in the 1970s to 1990s

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Abstract

Jarrah dieback was the name given to the sudden death of *Eucalyptus marginata* in the southwest of Western Australia, a serious economic problem. Although deaths were attributed to *Phytophthora cinnamomi* in the 1960s, the supporting evidence was weak; these deficiencies were not realised until 1980. Renewed interest in jarrah pathology showed that the incidence and severity of root lesions caused by *P. cinnamomi* in live trees was low, but in recent deaths it could be isolated from the root collar and large roots of some, but not all trees. Jarrah deaths result from hydraulic failure, implying extensive sapwood damage. This is unlikely to result from *P. cinnamomi* infection, which preferentially invades phloem, but could result from waterlogging, which causes tyloses to form in xylem vessels so they no longer conduct water. Tylosed root sapwood has been reported from investigations into jarrah deaths. An interpretation of past deaths based on stress factors better fits where and when deaths occur. This is within 3 years of exceptionally heavy rainfall, an inciting factor. Predisposing conditions are sites with some form of poor drainage, such as water-gaining sites, or those with impeded sub-soil drainage. Recent logging further increases site wetness. *Phytophthora cinnamomi* should be seen as a contributing factor, which is normally compartmentalised by the host, but can spread extensively in dying trees.

Keywords Perched water tables · Phytophthora dieback · Selective reporting · Tolerant hosts · Tree excavations

Introduction

Jarrah, *Eucalyptus marginata*, is the most important timber tree in the southwest of Western Australia. By the mid-twentieth century it was also the most important timber exported from Australia (Davison 2015). These exports were threatened by the decline and death of jarrah trees, a problem known as jarrah dieback, which occurred mainly between the mid-1940s and mid-1960s. These deaths were jointly investigated by the Western Australian Forests Department and the Forestry and Timber Bureau in Canberra (FTB). In 1965, Frank Podger (Research Officer, FTB) advised the Forests Department that jarrah dieback was caused by the introduced, soil-borne oomycete *Phytophthora cinnamomi* (Podger 1968, 1972). His explanation was accepted in good faith by the Forests Department which immediately initiated a research and management programme to control this pathogen (Forests Department 1967). By the 1970s, phytophthora control dominated forest management in Western Australia.

In 1979 I was appointed to a position as mycologist/plant pathologist in the Western Australian Department of Conservation and Environment, to provide back-up to local researchers working on jarrah dieback. This position was located at Murdoch University. In 1980 as part of my review of previous work, I found that Podger's unpublished results did not support his conclusion that *P. cinnamomi* killed jarrah trees. Local researchers and forest managers were unaware of this. Consequently, the Forests Department's control measures may not have been as well targeted as they believed, because an accurate diagnosis is essential for formulating appropriate measures for disease management.

A review of how *P. cinnamomi* became associated with the death of jarrah trees has been recently published (Davison 2015). In this paper I briefly summarise the earliest work, review the management of *P. cinnamomi* in the jarrah forest during the 1970s, and comment on the renewed interest in

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jarrah pathology that occurred between 1980 and 1997. Knowing the history of any investigation is important because the standards of proof and reporting that are required now may be different from what was acceptable in the past. I also present an interpretation of these observations based on the decline hypotheses of Manion (1981) and Houston (1987) which better fit the data, and allow predictions of where and when deaths are likely to occur.

Background

The jarrah forest in the southwest of Western Australia covers an area of about 15,000 km^2 (Abbott and Loneragan 1986). The climate in its habitat is Mediterranean, with cool wet winters and hot dry summers; about 90% of the annual rainfall occurs between April and October. Jarrah trees reach a height of at least 27 m on the best quality sites, which are those with deep gravel soils on upper and mid slopes in the subdued landscape of the western part of the Darling Range. It is a phreatophyte, accessing water in summer from moist soil at depth through an extensive vertical root system. Jarrah grows in association with marri (*Corymbia calophylla*), and is replaced by *E. megacarpa*, *E. patens* and *E. rudis* on wetter sites. In the drier, eastern forest it also grows in association with *E. wandoo*.

Jarrah timber has been commercially exploited since the European settlement of Western Australia in 1829, and was an important source of export revenue for the developing state (Abbott and Loneragan 1986). Logging was unregulated until the formation of the Forests Department in 1918, by which time almost all of the high quality jarrah stands in the northern jarrah forest had been logged (Davison 2015). In these harvested areas the forest canopy had been reduced by almost 50%, there were rising water tables in winter, and jarrah crowns had declined, a condition known as crown deterioration (Fig. 1).

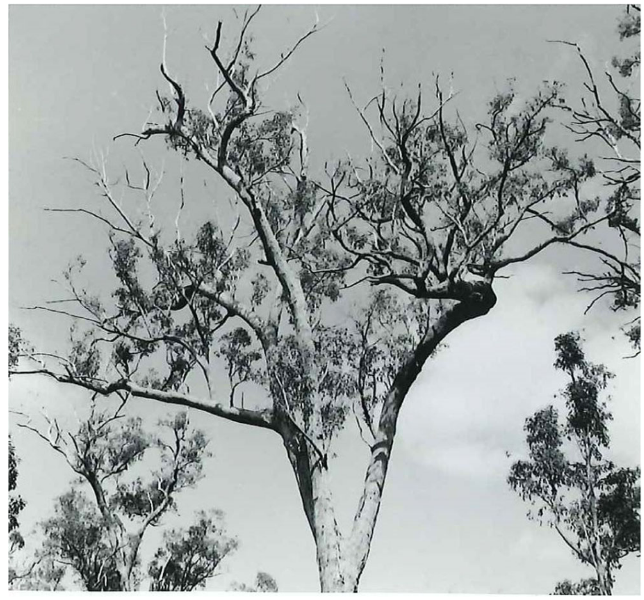

Fig. 1 Plate 4 from Podger (1959). The caption reads: 'Banksiadale Compartment 6. Stagheaded condition in a jarrah tree … The crown is almost entirely composed of secondary epicormics growth. This is typical of the nature of veteran and tree crowns in many places. Where this condition is not associated with dieback it would be described as "crown deterioration" by Western Australian foresters.' © Copyright CSIRO Australia

Groups of dying jarrah trees started to occur in the mid-1940s (Figs. 2 and 3) (Davison 2015). These deaths were site-specific, on poorer quality, previously-logged, water-gaining sites, which were often waterlogged in winter. Jarrah, but not marri, was the only large tree species affected. There were other vegetation changes on affected sites, such as the death of the mid-storey trees *Banksia grandis* and *Allocasuarina fraseriana*, and changes in understorey composition to plants better adapted to wet sites.

The jarrah deaths were not associated with pests (because there were no consistent signs of insect attack), pathogens (because there were no consistent lesions) or soil properties (Davison 2015). The only unusual feature was that there were more tyloses in the roots of affected trees. Tyloses are ingrowths into xylem vessels in the sapwood that indicate that these capillaries no longer conduct water; a symptom now known to be caused by waterlogging (Davison and Tay 1985). Tyloses also form locally as one of a host's response to drought, damage and wounding (Zimmermann 1983), for example in the sapwood adjacent to *P. cinnamomi* lesions in jarrah phloem (Tippett et al. 1983).

In 1959, Podger, a forester from the Forests Department was appointed by the FTB to investigate jarrah dieback (Davison 2015). He started by investigating some of the site changes that would have occurred following heavy logging, and showed that jarrah was less tolerant of waterlogging than other forest eucalypts (Podger 1967). However, in 1963 his research changed to actively looking for a *Phytophthora* as the cause of jarrah dieback. In 1964, with the assistance of Ralph Doepel (Western Australian Department of Agriculture) and George Zentmyer (University of California, Riverside Campus), *P. cinnamomi* was isolated from soil. Pathogenicity tests showed that it could infect and kill jarrah and *B. grandis* seedlings, but not marri (Podger et al. 1965). It was isolated by soil baiting from sites where jarrah trees had died, but not from unaffected areas, and by using phytophthora-selective agar, could be isolated from the roots of jarrah and many other forest species (Podger 1968). He deliberately infested a forest site with *P. cinnamomi* and one jarrah tree and many mid- and understorey species died over a number of years (Podger 1972).

Podger's advice to the Forests Department in 1965 was premature; it was based on his initial observation that jarrah deaths were associated with infested sites. Between 1965 and

1968 he attempted to establish the first of Koch's postulates in order to show that there was a constant association between infection of jarrah and death of these trees. However, he was only able to isolate *P. cinnamomi* from 5% of 100 sampled jarrah trees (Davison 2015). He failed to mention this low recovery rate to either the Forests Department or the FTB. His work also failed to satisfy the fourth of Koch's postulates because he only showed that the site where he conducted his field pathogenicity test became infested, not that the plants that died there were infected. Podger presented his work as showing that *P. cinnamomi* killed jarrah trees as well as many mid- and understorey species, and extended the definition of jarrah dieback to all species that died on infested sites. As jarrah appeared to have no resistance to *P. cinnamomi* (Podger 1972) he asserted that commercial forestry would decline. All the early work was forgotten, and phytophthora control dominated forest management.

Research and control, 1965–1979

The Forests Department accepted Podger's explanation that jarrah deaths were caused by *P. cinnamomi*, even though Eric Björkman (Royal College of Forestry, Stockholm), who reviewed Podger's work for the FTB, was sceptical about some of his claims (Björkman 1966). The Forests Department appointed new staff and constructed or upgraded their research facilities. By 1972, there was a comprehensive research programme in progress (Batini and Hopkins 1972). This tackled the immediate problems of mapping the extent of infestations, determining the environmental limits on sporulation and survival of *P. cinnamomi* throughout the jarrah forest, and investigating how it spread between sites. Salvage logging was important to minimise the economic loss to the sawmilling industry and the most impacted areas were heavily logged. Uninfested, high-quality forest areas were intensively managed for future timber production and alternative timber species were evaluated for rehabilitating infested sites. In addition, the Forests Department funded research scholarships at the University of Western Australia and the Australian National University. There was also a public education programme targeting government departments, shires, the army, the mining industry, professional societies and public interest groups. Its approach was widely applauded by plant pathologists and foresters (Newhook 1968; Zentmyer 1968; Marks and Idczak 1973).

There were concerns in eastern Australia about the implications of site infestation by *P. cinnamomi* on timber production and conservation (Newhook and Podger 1972; Weste 1974; Incoll and Fagg 1975). Within the research community there was considerable interest and investigation of why some eucalypts, such as jarrah and *E. sieberi* were susceptible to *P. cinnamomi*, whilst others, such as marri and *E. maculata* were field resistant (e.g. Malajczuk et al. 1977; Halsall 1978; Grant and Byrt 1984), but no consensus emerged of why this was so.

Hygiene and the imposition of quarantine

It was very quickly realised that the most important way that *P. cinnamomi* was spread was through infested soil adhering to machinery, and infested gravel used for building roads (Batini and Hopkins 1972). The Forests Department found that hygiene measures such as the removal of soil from the underside of vehicles were very effective in minimising spread through soil movement, and this was implemented (Underwood and Murch 1984). However, although the Forests Department could control what was done by their staff, they were not able to impose strict hygiene measures on other forest users, including the general public.

The Forests Department considered that infestation by *P. cinnamomi* resulted in four main threats to: forest productivity; the state's flora reserves such as National Parks; the survival of some indigenous plant species, and; water quality. At that time most of the infested areas were in the western part of the forest, but if *P. cinnamomi* was introduced into the eastern forest, the death of jarrah and other vegetation would result in rising water tables. This would result in increased salinity in streams feeding the reservoirs supplying Perth and the southwest by mobilising salt stored in the soil profile (Forests Department 1974).

Hygiene measures would only be effective if the distribution of *P. cinnamomi* was known. Research had shown that there was a time lag of 6 to 18 months between the time a site became infested and the development of field symptoms, so the Forests Department realised that they needed sufficient time for symptoms to develop before they could map infested areas. One way to achieve this was by restricting access to the forest by the imposition of quarantine. They consulted widely with other forest users, and this approach was supported. The Western Australian cabinet approved the imposition of quarantine; the Forests Act was appropriately amended, and Forest Disease Risk areas in the northern forest proclaimed in 1976 and in the southern forest in 1977 (Forests Department 1975, 1976, 1977). There was a public education campaign to explain why such measures were essential to protect Perth's water supply, the timber industry, and the conservation values of the jarrah forest (Shea 1975a). These measures were widely supported by forest users and the general public.

Bauxite mining

The lateritic soils of the Darling Range are rich in bauxite. It occurs in small pockets and has been mined through an open cut process since 1963 (Alcoa of Australia 1979). Mining started in state forest close to Jarrahdale, and by 1978 bauxite was also being mined north west of Dwellingup (Fig. 2).


PERTH
FREMANTLE
COLLIER
SOMERVILLE
ARMADALE
MUNDARING WEIR
YORK
BEVERLEY
BERAKING
MT DALE
GLENEAGLE
JARRAHDALE
PINJARRA
DWELLINGUP
MURRAY
RIVER
DWARDA
DRYANDRA
NARROGIN
WILLIAMS
HAMEL
Mc LARTY
HARVEY
HARVEY WEIR
MYALUP
BUNBURY
COLLIE
BOWELLING
WAGIN
STIRLING
COOLILUP
BUSSELTON
DONNYBROOK
J.C. WILLCOCK
KIRUP
GRIMWADE (E. KIRUP)
KATANNING
METRICUP
BOYUP BROOK
KEENAN
MARGARET RIVER
NANNUP
BRIDGETOWN
BLACKWOOD
JALBARRACUP
RIVER
BORANUP
MANJIMUP
DONNELLY
CRANBROOK
WARREN R.
FRANKLAND
AUGUSTA
PEMBERTON
NORTHCLIFFE
PARDELUP
MT BARK
DEEP R.
NORNALUP
ALBANY
Major Developement
Other Occurences
JARRAH DIE BACK.
To illustrate main occurence and spread
(not complete nor precise.)

◀ **Fig. 2** Map from Podger (1959). The caption reads 'JARRAH DIEBACK. To illustrate main occurrence and spread (not complete or precise)'. The legend on the left reads 'Jarrah Dieback Major Development [coloured red], Other Occurrences [red spots], Patch Deaths Wandoo [green spots]'. (NB this map is too large to be copied on an A3 scanner, which is why some of the text is missing.) This map was probably drawn from a survey conducted by Hamilton (1951), however all of Hamilton's notes, field books and maps appear to have been destroyed in the 1961 Dwellingup fire (J. B. Sclater, pers. comm. 7 April 2015). © Copyright CSIRO Australia

Mining involves clearing the native forest, mining the bauxite, and then restoring the land back to forest. Much of Alcoa's operations were in areas infested with *P. cinnamomi*. The research programme that the Forests Department had undertaken for mapping the distribution of *P. cinnamomi*, minimising its spread, and rehabilitating infested areas, were directly applicable to Alcoa's operations. These two organisations worked collaboratively, using the experience of the Forests Department, with funding from Alcoa, to minimise the impact of *P. cinnamomi* in all aspects of bauxite mining. Alcoa estimated that for every 1 million tonnes of alumina it refined, 75 ha of forest were cleared, mined and then restored; rehabilitation costs were about \$10,000 ha^{-1} (Alcoa of Australia 1979). In 1979, Alcoa gave the Western Australian government a total of \$500,000 over three years, to establish a Dieback Foundation to co-ordinate research funding for the control or eradication of this disease.

Renewed interest in jarrah deaths, 1980–1996

Most of the work undertaken on jarrah dieback between 1965 and 1979 focussed on *P. cinnamomi* in the belief that jarrah trees would die out on infested sites. In early 1980, following my review of the early work on jarrah dieback, I concluded that

Fig. 3 Jarrah (*Eucalyptus marginata*) deaths, 1968. Photograph H653, F.D. 5374 © Library of the Department of Biodiversity, Conservation and Attractions

Podger had reported his work more enthusiastically than it warranted. These conclusions were discussed with colleagues and I was advised to make them public (J. F. Loneragan, Professor of Plant Biology, Murdoch University, pers. comm. March 1980). This needed to be done with care, as firstly, it would reduce confidence in the Forests Department's competence, and secondly, there was no alternative explanation of past jarrah deaths. My doubts about the interpretation of Podger's work were raised at a national meeting at the University of Western Australia (Summary of the Phytophthora workshop, 15-16 May 1980). My concerns were not well received (Havel 1980a). The Forests Department conceded that the recovery of *P. cinnamomi* from only 5% of sampled jarrah trees was a cause for concern (Havel 1980b). Based on past observations and previous work, there were two possible causes of jarrah deaths. Waterlogging could not be discounted, because trees had died on wet sites (Podger et al. 1965), and Podger had shown jarrah to be sensitive to waterlogging (Podger 1967). It was conceded by the Forests Department that waterlogging might cause jarrah deaths in valleys, but would not account for deaths on upland sites, which were believed to be well drained. The other explanation, which was more acceptable to both the Forests Department and Alcoa, was that jarrah deaths were caused by *P. cinnamomi*, even though Podger had been unable to convincingly demonstrate this. The Forests Department indicated that work was already underway by Syd Shea (Senior District Forest Officer, Forests Department) and John Gardner (Environmental Scientist, Alcoa) to again investigate jarrah deaths (Havel 1980b).

Jarrah's sensitivity to waterlogging

When soil is saturated with water, the dissolved oxygen in the soil solution is rapidly used by plant roots and microorganisms. As oxygen diffuses 10^4 times more slowly through water than through air, it is used more rapidly than it is replaced, and the soil initially becomes hypoxic and then anoxic; the rate at which this happens depends on the soil temperature (Kozlowski 1986; Drew 1992). Most plants, including jarrah, are intolerant of anoxic soil. Glasshouse experiments showed that when jarrah seedlings are waterlogged, the xylem vessels in the tap roots become blocked by tyloses, and this happens within a few days. Water deficits build up because the seedlings continue to transpire, even though conduction is reduced; consequently, the seedlings wilt and die, especially during hot weather (Davison and Tay 1985). If mature jarrah trees behave in the same way as seedlings, tylosed sapwood would be an indication of past waterlogging damage.

Excavation of jarrah trees

Between 1980 and 1983, about 90 jarrah trees were excavated, and their roots and root collars intensively sampled for

P. cinnamomi by using phytophthora-selective agar. All of the trees were on infested sites. Most of the work was done near Dwellingup (Fig. 2) by the Forests Department, and most was funded by the Dieback Foundation. In 1980, recently-dead trees were sampled, and *P. cinnamomi* was isolated from the bark and wood at the root collar, large and small roots from some of these trees (Dell and Wallace 1981; Shearer et al. 1981). Both groups concluded that their work showed that *P. cinnamomi* was able to invade the root collar and large roots of jarrah, but could not determine whether this invasion occurred before or after tree death. Some of the trees may have been affected by waterlogging (Shearer et al. 1981), or by runoff from a nearby road (Dell and Wallace 1981). Dell and Wallace (1981) noted that infected roots had tylosed sapwood.

A further 41 jarrah trees from seven sites near Dwellingup were sampled in 1981 and 1982; most of these trees had died suddenly (Shea et al. 1982). Excavations showed that these deaths were on sites with an impeding layer of concreted laterite 5 to 75 cm below the soil surface, and most of the sites were upland, not valley sites. On three sites, major disturbances upslope would have caused excessive runoff into the areas where jarrah trees had died. *Phytophthora cinnamomi* was isolated from 39 trees. It was isolated from the root collars and lateral roots; Shea et al. (1982) also stated that it was consistently isolated from vertical roots. Shea et al. (1982) suggested that infection of vertical roots where they penetrated through potholes in the impeding layer, caused reduced conduction of water from deep water tables, and this resulted in severe water deficiency and tree death. Subsequent work showed that, under appropriate conditions, *P. cinnamomi* could sporulate in soil from above the impeding layer deep in the soil profile, and zoospores could be dispersed laterally in seepage water as well as vertically during soil drainage (Shea et al. 1984; Kinal et al. 1993). These sites were seen as areas where abundant zoospore production would occur in wet weather, where dispersal would be facilitated by internal soil drainage and seepage, with massive root infection and tree death being the inevitable consequence.

The work by Shea et al. (1982) was very important, because it explained how jarrah deaths were related to certain site characteristics, and were not an inevitable consequence of site infestation, as had been suggested by Podger (1972). The impact of *P. cinnamomi* on jarrah appeared to differ on different site types; these site types being defined by the composition of understorey species (Havel 1975a, 1975b). Joe Havel (Superintendent (Research), Forests Department) believed that this impact would be related to the amount of root damage. He directed Bryan Shearer and Joanna Tippett (Research Officers, Forest Department) to study root infection on a range of site types, including some in the lower rainfall, eastern forest (Havel 1983). Over the next 4 years, Shearer and Tippett conducted very through excavations of 26 apparently healthy jarrah trees from a number of infested sites. Lesions were present on the large roots of 16 of these trees; 4.7% of all large roots were infected, with most lesions being less than 12 cm long (Shearer and Tippett 1989). Havel's expectations were not met; there did not appear to be a relationship between the amount of root infection and perceived impact on jarrah. Davison and Tay (1995a), in a smaller study, found similar results, only 3.4% of large surface roots of jarrah had *P. cinnamomi* lesions on them, and the mean lesion length was 17.5 cm. In other words, in live trees, the incidence and severity of infection of jarrah roots is low. Jarrah appears to be a tolerant host.

The anticipated impact of *P. cinnamomi* on jarrah was based on the sampling results of Shea et al. (1982), but this work is difficult to interpret because the recoveries of *P. cinnamomi* were not clearly presented. Re-examination of the raw data (Forests Department, Dwellingup Research Local Experiment files 395 and 402) shows that between October 1981 and May 1983, 70 jarrah trees were excavated; all were on infested sites. Sufficient details of attempted isolations of *P. cinnamomi* and other pathogens were given for 62 of these trees (Table 1). The excavated trees were live (green) trees, recent and old deaths, and some whose health status was not specified. *Phytophthora cinnamomi* was isolated from some, but not all trees, and where it was isolated, it was not isolated consistently from the root collar or a particular root type. It was not isolated consistently from the vertical roots, because it was only isolated from 29 out of 40 trees in which the vertical roots were sampled, even though Shea et al. (1982) stated that this had been the case. The way that these results were presented obscured the important conclusion that *P. cinnamomi* was not present consistently from particular root types or from the root collar.

January 1982 at Dwellingup was notable because it was the wettest on record, with about 200 mm, almost 20% of the annual rainfall, occurring over 4 days (Table 2). Shea et al. (1982) mention that the jarrah deaths they investigated followed 2 years of average rainfall. Havel, however, was convinced that this heavy rainfall contributed to jarrah deaths on one site, which, he concluded from the suite of understorey plants that occurred there, had impeded subsoil drainage and would be seasonally waterlogged (Havel 1982). The soil on such sites would have been saturated with water following the heavy rainfall, and would have rapidly become anoxic because the soil was warm. There is no evidence of extensive examination of jarrah roots for tylosed sapwood; however, tyloses were mentioned in vertical roots in two trees (Forests Department, Dwellingup Research Local Experiment files 395 and 402). Waterlogging does not appear to have been considered as contributing to jarrah deaths on these sites in the contemporary publications, however, the coincidence of exceptionally heavy rainfall (which was not mentioned) and impeded subsoil drainage, indicate that it cannot be discounted.

Table 1 Number of jarrah trees on infested areas sampled between October 1981 and May 1983, from which *Phytophthora cinnamomi* was isolated from the root collar, lateral roots and vertical roots. Not all root collars, lateral and vertical roots were sampled in all trees. [Data from Forests Department, Dwellingup Research Local Experiment files 395 and 402.] Reproduced with permission

Health status	Sample size	Trees with +ve isolations	Root collar		Lateral roots		Vertical roots	
			+ve	-ve	+ve	-ve	+ve	-ve
Dead	19	16	6	6	13	6	4	6
Live	24	19	3	5	14	9	13	3
Not specified	19	15	1	3	11	3	12	2
Total	62	50	10	14	38	18	29	11

The next occurrence of dying jarrah trees was in January 1993 (Davison 1997). Deaths occurred on an infested site, close to a rehabilitated bauxite pit. Several jarrah trees were excavated by Giles Hardy (Lecturer, Murdoch University), Ian Colquhoun (Environmental Scientist, Alcoa) and me. The site had concreted laterite in the profile, the deaths were upslope of a dolerite dyke and additional water would have drained into the site from a drain failure upslope. There were no visible lesions at the root collars, lateral or vertical roots, but the root sapwood was tylosed, and weather records showed that there had been exceptionally heavy rainfall the previous February, March and November (Table 2). The observations of absence of lesions on large roots, evidence of water flows into this site, and symptoms consistent with waterlogging damage in the root sapwood of the excavated jarrah trees, were presented to the Western Australian Dieback Review Panel (S. H. James, P. M. Jones, M. J. Mulcahy, F. D. Podger (chairman)) and others (I. J. Colquhoun, G. E. StJ. Hardy, J. F. Loneragan) on 8 April 1994, they all concluded that these jarrah deaths could not be attributed to *P. cinnamomi,* and that waterlogging damage could not be discounted as a cause. This site became waterlogged in August 1996.

Discussion

Jarrah deaths have been attributed to *P. cinnamomi* for over 50 years, and it is conceptually difficult to consider any other explanation. There are serious deficiencies with this explanation, however, that became apparent in 1980 when it was realised that Podger's work failed to provide conclusive proof that this was the case (Davison 2015).

Shortcomings of the explanation that jarrah deaths are caused by Phytophthora cinnamomi

Observations indicate that jarrah deaths result from hydraulic failure. Firstly, the dieback and sudden wilting of the crown are symptoms of extreme water deficiency. Secondly, Shea et al. (1982) showed that dying trees on an infested site had much lower xylem pressure potentials than trees on a similar uninfested site. Thirdly, dendrometer band measurements showed that the stems of trees shrink excessively for several weeks or months before the foliage died, indicating that trees dried out from the roots upwards (Crombie and Tippett 1990; Davison and Tay 1995b). All of these observations indicate a shortage of water that could be caused either by reduced water uptake by fine roots, or reduced conduction through the sapwood, or excessive transpiration, or all of these, ultimately leading to dehydration and death.

Zentmyer (1968) suggested that the low recovery of *P. cinnamomi* from jarrah was because it caused a fine root necrosis. This explanation was accepted without question by the Forests Department (Batini and Hopkins 1972), even though extensive fine root necrosis had not been demonstrated in jarrah roots from the field (Shea et al. 1980; Shea and Dell 1981). Although *P. cinnamomi* can be isolated from fine roots and soil samples by soil baiting, this does not mean that jarrah roots are infected.

Shea et al. (1982) suggested that extensive infection of jarrah's vertical roots would lead to reduced conduction, implying that infection results in extensive invasion and dysfunction of the sapwood. However, their wound inoculation experiments did not support this explanation, because these showed that *P. cinnamomi* invades the bark, not the sapwood (Tippett et al. 1983). There is some sapwood invasion, but it only results in a very narrow, inapparent infection internal to phloem lesions (Davison et al. 1994). It is also difficult to reconcile dysfunction of the sapwood that is of sufficient magnitude to cause death, with the low incidence and severity of root infection in live jarrah trees (Shearer and Tippett 1989; Davison and Tay 1995a). Something appears to be missing.

To date, the only damage that would reduce conduction in the sapwood sufficiently to cause death is that resulting from waterlogging (Davison and Tay 1985; Davison 1997). Symptoms of tylosed sapwood were observed in the earliest investigations, but it was not known whether they were the cause, or consequence, of death (Davison 2015). Tylosed sapwood is not necessarily discoloured, but is apparent when longitudinal sections are examined microscopically. It would not be detected in roots plated out for fungal isolation. As this symptom has been known since 1985, all subsequent investigations into jarrah deaths on infested sites need to include examination of sapwood, in addition to fungal isolations, to determine whether or not waterlogging has contributed to the deaths. Failure to do this is a failure to consider all of the potential stress factors that may have contributed to jarrah deaths.

Stress factors and tree decline hypotheses

Tree declines and death are different from diseases and disorders of annual agricultural crops, because they can occur over many years, even decades. Also, the large size of trees makes them much more difficult to sample than annual plants. Manion (1981) presents one approach that is valuable when trying to determine the cause(s) of tree decline. He suggests that there are three levels of stress factors that should be considered. First, there are predisposing factors that are long-term static or non-changing factors, such as climate, site, or soil moisture which weaken a plant growing in the wrong location. Second, there are short-term inciting factors such as frost, insect defoliation or mechanical injury that produce a drastic injury. Third, there are contributing factors such as insect pests or fungal pathogens that are long-term, persistent, and when abundant, indicators of a weakened host. Houston (1987) similarly proposed that diebacks and declines are initiated by predisposing factors, with facultative pests and pathogens being able to attack and invade hosts that would normally be able to contain infection. Direct and indirect effects of these environmental stresses are on photosynthesis, the uptake of water and minerals, and movement and storage of carbohydrates. A consequence is the reduced ability of the host to compartmentalise damaged tissue (Shigo 1984), leading to increased damage by pests and pathogens. Extensive invasion by pests and pathogens is therefore considered to be a consequence, not a cause of tree decline.

Jarrah deaths are sporadic and occur within 3 years of exceptionally heavy rainfall (Table 2). Most deaths occurred between the mid-1940s and mid-1960s, a period that was exceptionally wet. At Dwellingup, for example, the June rainfall in 1945 was 719.2 mm, the July rainfall in 1946 was 573 mm, and the February rainfall in 1955 was 269.1 mm; all are the highest on record. In Manion's terminology (Manion 1981), exceptional rainfall is an inciting factor.

Heavy rainfall will be most damaging on sites that are poorly drained or water-gaining, the predisposing factors of Manion (1981) and Houston (1987). Sites where jarrah trees died were described as waterlogged, or with impeded subsoil drainage, or likely to have had water draining into them (Hamilton 1951; Waring 1950; Loneragan 1961; Dell and Wallace 1981; Shearer et al. 1981; Shea et al. 1982; Davison 1997). The earliest reports of jarrah deaths also mention a further disturbance, because they were on recently-logged sites. As these were also described as poor-quality sites, it is likely that these sites had not been previously logged. Such sites would be wetter than unlogged areas, because of reduced interception of rainfall and reduced evapotranspiration (Christensen 1975; Shea 1975b). The salvage logging that was conducted in the 1970s on the most heavily impacted sites reduced the economic impact of jarrah deaths on the sawmilling industry (Batini and Hopkins 1972), but would have further increased the frequency and duration of soil saturation.

Houston (1987) recognised that environmental stresses alone can cause tree death. As many of the poorly drained sites in the jarrah forest are infested by *P. cinnamomi*, it is not possible to determine the cause of death without examination of the roots. Some jarrah deaths in the mid-1940s to mid-1960s may have been on uninfested sites; Podger (1968) gives one example. Reports of tree excavations at that time mention tylosed sapwood; they do not mention extensive and consistent lesions (Davison 2015).

Zoospores are believed to be the most important infective propagule of *P. cinnamomi* in the jarrah forest. Sporangia are produced in soil at matric potentials close to zero (Gisi et al. 1980), when soil temperature is above 15 °C (Shea et al. 1980). However, sporulation also requires good aeration which is reduced under hypoxic and anoxic conditions (Mitchell and Zentmyer 1971; Davison and Tay 1986). Therefore, in soils that are waterlogged, or where perched water tables develop over an impeding layer, sporulation will occur in the moist soil above the water table, but not within the saturated soil where aeration is inadequate. Zoospores liberated from mature sporangia will be passively dispersed in drainage and seepage water (Shea et al. 1984; Kinal et al. 1993). Experiments under controlled conditions show that more or longer lesions are formed on roots in saturated soil or under hypoxic or anoxic conditions (Allen and Newhook 1973; Davison and Tay 1987; Burgess et al. 1998); however, there is no field evidence that supports this observation (Shearer and Tippett 1989; Davison and Tay 1995a).

According to both Houston's (1987) and Manion's (1981) hypotheses, *P. cinnamomi* would be considered a contributing factor, a pathogen that is normally contained by the host's responses to damage (Tippett et al. 1983; Davison et al. 1994). Uncontained lesions are only formed when the host is affected by inciting factors. This is what has been observed in jarrah, where the extensive invasion of root collars, lateral and vertical roots has only been recorded in some, but not all, dying or dead trees (Dell and Wallace 1981; Shearer et al. 1981; Shea et al. 1982; Hardy et al. 1996).

It is difficult to visualise how the different stresses interact because some, such as exceptionally heavy rainfall, are

Table 2 Rainfall in the three years prior to the death of groups of jarrah trees. Monthly rainfall is shown in parentheses. Data from http://www.bom.gov.au/climate/data/, viewed March 2014

Approximate date deaths noted	Location	Closest weather station (number)	Year	Rainfall (mm)				Reference
				Annual	Significant monthly rainfall			
					Highest ever recorded	>95th percentile	>90th percentile	
1921	Karragullen	Mundaring (9031)	1919	904.8				Weston, pers. com in Wallace and Hatch (1953)
			1920	1229.7		Jun (360), Aug (326.7)		
			1921	1179.7			May (243.2), Oct (120.6)	
About 1928/1929	Near Myara Hill	Jarrahdale (9023)	1926	1729.2 (>95th %ile)	Apr (221.6)	Mar (85.4)	Jul (402.6)	Wallace pers. com in Waring (1950)
			1927	1254.6		Jan (53.1)		
			1928	1486.4 (>90th %ile)		Aug (309.4)	Jul (395.7), Sep (211.3)	
1948	Mundaring Division	Mundaring (9031)	1945	1419.5 (>90th %ile)	Jun (566.9)	Aug (329.3)		Hamilton (1951)
			1946	1542.2 (>95th %ile)	Jul (542.1), Nov (151.9)		May (250)	
			1947	1146.4			Apr (110.7), Jun (335.1), Oct (115.1)	
1948	Gleneagle District	Gleneagle (9019)	1945	1657.5 (>95th %ile)	Jun (654.9)	Aug (370.6)		Hamilton (1951)
			1946	1620.2	Nov (132.4)	May (298.2), Jul (583.8)		
			1947	1318.5		Apr (157.4)		
1948	Kirup Division	Nannup[a] (9585)	1945	1143.1		Aug (238.6)	Jun (274.6)	Hamilton (1951)
			1946	1013.5	Jul (337.7)	Nov (93)		
			1947	1205.9 (>95th %ile)		Apr (122.2), May (248.6), Jun (348)		
Summer 1947/1948	Teesdale	Dwellingup (9538)	1945	1887.1 (>95th %ile)	Jun (719.2)	Aug (405.8)		Hamilton (1951)
			1946	1572.8 (>90th %ile)	Jul (573), Nov (150.8)			
			1947	1308.6			May (265.2)	
Sometime between Jan 1954 and Aug 1959	Teesdale	Dwellingup (9538)	1954	1010.3				Unpublished file Kelsmcott WA7 L.T. 7.16[d]
			1955	1977.3 (highest ever)	Feb (269.1), Aug (554.1), Oct (237.5)			
			1956	1352.3		May (310.3)		
			1957	1366.1		Jun (479.4)	Apr (127)	
			1958	1122.3		Jul (477.2)		
			1959	1078.3		Dec (69.4)		
1963/4 summer	Teesdale regeneration transect	Dwellingup (9538)	1961	b				Unpublished file Kelsmcott WA7 L.T. 7.16[d]
			1962	1226.7			Nov (97.9)	
			1963	1701.2			May (291.9), Jun (406.4), Aug (306)	
	Karnet	Jarrahdale[c] (9023)	1962	1226.7			Nov (97.9)	Podger (1968)

Table 2 (continued)

Approximate date deaths noted	Location	Closest weather station (number)	Year	Rainfall (mm)				Reference
				Annual	Significant monthly rainfall			
					Highest ever recorded	>95th percentile	>90th percentile	
Sometime between Dec 1962-Aug 1967			1963	1701.2 (>95th %ile)			May (291.9), Jun (406.4), Aug (306)	
			1964	1828.6 (>95th %ile)		Jun (598.8), Jul (495.3),	Aug (302.6), Dec (51.6)	
			1965	1449.8		Oct (212.8)	May (251.1), Dec (46.9)	
			1966	1177.8			Jul (353.4)	
			1967	1413.1			Jun (370.5)	
1982–1984	Northern jarrah forest	Dwellingup (9538)	1979	991.9				Shearer and Tippett (1989)
			1980	1283.5		Dec (59.1)	Feb (49.2), Apr (132.9)	
			1981	1317.8				
			1982	1158.8	Jan (237.4)			
			1983	1315		Feb (112.6)	Aug (304.6)	
			1984	1323.6	May (325.3)	Nov (119.1),	Apr (127.5)	
Jan 1993	Admiral Road	Jarrahdale (9023)	1990	1157		Jan (57.4), Feb (70), Mar (85.6)	Apr (139)	Davison (1997)
			1991	1373			Feb (44.8), Nov (87)	
			1992	1312.2		Feb (127.2), Nov (96.8),	Mar (76.4)	

[a] Kirup is closer, but there are no rainfall records between 1944 and 1974

[b] no total annual rainfall because some values missing

[c] no complete rainfall records for Karnet (9111) before 1965

[d] this file was destroyed when the CSIRO Division of Forest Research, Kelmscott, was closed in the mid-1980s

unpredictable. Davison and Tay (1989) compared jarrah phenology in adjacent infested and uninfested areas on three sites, Churchmans, Karnet and Ross. These sites differed in drainage: Churchmans was better drained than the other two, and a perched water table developed more frequently at Ross than at Karnet. Trees in the adjacent infested and uninfested areas at each site showed similar growth patterns, but phenology differed between sites. The Churchmans and Karnet sites were being measured in January 1982, and although the rainfall was not as heavy as that recorded for Dwellingup (Table 2), it resulted in differences between the sites, not between the infested and uninfested areas of each site (Fig. 4). At Churchmans, following this rain, the proportion of trees producing new leaves (the normal summer pattern) decreased, and the vascular cambium became active, with the trees putting on about a third of their annual increment in a 2 week period; 2 weeks later the cambium was inactive and new leaves were again produced. At Karnet, the vascular cambium did not become active, even though there was more rain than at Churchmans; no observations were being made of leaf production at Karnet. The most important factors affecting phenology were the site characteristics, followed by the weather; there was no detectable effect of *P. cinnamomi.* This is what would be expected from the hierarchy of stress factors, with site and weather being more important than pests and pathogens (Manion 1981; Houston 1987).

Deaths of mid-and understorey plants

The southwest of Western Australia is a Global Biodiversity Hotspot, botanically diverse with a high degree of endemism (Myers et al. 2000; Hopper and Gioia 2004; Lambers 2014). Much of the present concern about site infestation by *P. cinnamomi* focusses on its effects on the conservation value of natural ecosystems (Cahill et al. 2008; Lambers et al. 2013), rather than its effects on timber production, and in order to emphasise this, the name has been changed to Phytophthora dieback.

Awareness of the association of *P. cinnamomi* with the death of mid- and understorey species was raised by Podger (1968, 1972), who concluded that *P. cinnamomi* was a threat to the whole ecosystem, not just to jarrah. Podger's work was between 1959 and 1968, a period of exceptionally heavy rainfall (Table 2). His main focus, together with the FTB and the Western Australian Forests Department, was on jarrah. However, as discussed, the conclusion that jarrah is killed by *P. cinnamomi* is not based on solid arguments, and jarrah deaths can be better explained by considering its sensitivity to waterlogging following exceptionally heavy rainfall, on poorly drained sites. Mid-storey and understorey species too will be affected by site and weather conditions, and the subtleties of soil moisture and aeration that are important for jarrah trees will also affect the health and distribution of other

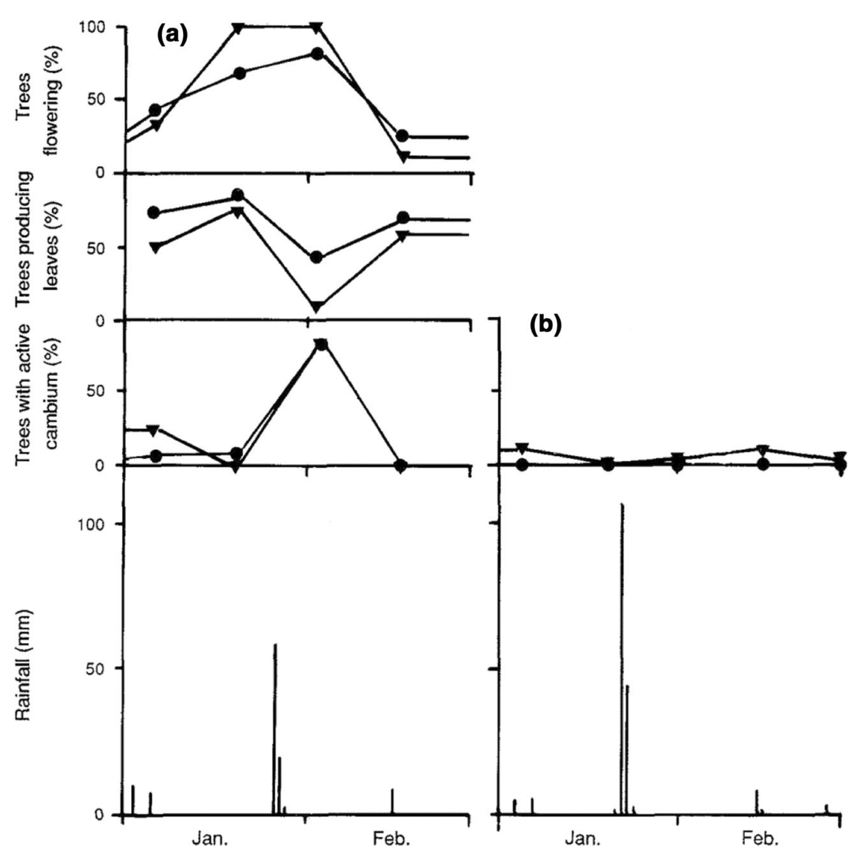

Fig. 4 Flowering, leaf production and cambial activity of jarrah (*Eucalyptus marginata*) trees at (*a*) Churchmans and cambial activity of trees at (*b*) Karnet during January and February 1982. Rainfall data is from Jarrahdale meteorological station (Churchmans) and Karnet meteorological station (Karnet). ● trees on part of the site infested with *Phytophthora cinnamomi*; ▼ trees on uninfested part of the site. Modified from Davison and Tay (1989), reproduce with permission from CSIRO Publishing

species. Describing native species as susceptible or resistant based on their survival on infested sites is an oversimplification. Some species may be susceptible, some may be tolerant hosts (Crone et al. 2013), while changes in the abundance of others may be because of changes to edaphic conditions, rather than their susceptibility to *P. cinnamomi* (Weste 2003; Shearer et al. 2009). A better understanding of how *P. cinnamomi* infects mid-storey and understorey species in the field, together with improved knowledge of their ecophysiology, may provide additional options for the revegetation of infested areas.

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