

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

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7
8 **Abstract**

9
10 Jarrah dieback was the name given to the sudden death of *Eucalyptus marginata* in
11 the southwest of Western Australia, a serious economic problem. Although deaths were
12 attributed to *Phytophthora cinnamomi* in the 1960s, the supporting evidence was weak;
13 these deficiencies were not realised until 1980. Renewed interest in jarrah pathology
14 showed that the incidence and severity of root lesions caused by *P. cinnamomi* in live trees
15 was low, but in recent deaths it could be isolated from the root collar and large roots of
16 some, but not all trees. Jarrah deaths result from hydraulic failure, implying extensive
17 sapwood damage. This is unlikely to result from *P. cinnamomi* infection, which
18 preferentially invades phloem, but could result from waterlogging, which causes tyloses to
19 form in xylem vessels so they no longer conduct water. Tylosed root sapwood has been
20 reported from investigations into jarrah deaths. An interpretation of past deaths based on
21 stress factors better fits where and when deaths occur. This is within 3 years of
22 exceptionally heavy rainfall, an inciting factor. Predisposing conditions are sites with
23 some form of poor drainage, such as water-gaining sites, or those with impeded sub-soil

24 drainage. Recent logging further increases site wetness. *Phytophthora cinnamomi* should
25 be seen as a contributing factor, which is normally compartmentalised by the host, but can
26 spread extensively in dying trees.

27

28 **Keywords:** perched water tables, Phytophthora dieback, selective reporting, tolerant hosts,
29 tree excavations

30

31

Introduction

32

33 Jarrah, *Eucalyptus marginata*, is the most important timber tree in the southwest of
34 Western Australia. By the mid-20th century it was also the most important timber exported
35 from Australia (Davison 2015). These exports were threatened by the decline and death of
36 jarrah trees, a problem known as jarrah dieback, which occurred mainly between the mid-
37 1940s and mid-1960s. These deaths were jointly investigated by the Western Australian
38 Forests Department and the Forestry and Timber Bureau in Canberra (FTB). In 1965,
39 Frank Podger (Research Officer, FTB) advised the Forests Department that jarrah dieback
40 was caused by the introduced, soil-borne oomycete *Phytophthora cinnamomi* (Podger
41 1968, 1972). His explanation was accepted in good faith by the Forests Department which
42 immediately initiated a research and management programme to control this pathogen
43 (Forests Department 1967). By the 1970s, phytophthora control dominated forest
44 management in Western Australia.

45 In 1979 I was appointed to a position as mycologist/plant pathologist in the Western
46 Australian Department of Conservation and Environment (~~DCE~~), to provide back-up to

47 local researchers working on jarrah dieback. This position was located at Murdoch
48 University. In 1980 as part of my review of previous work, I found that Podger's
49 unpublished results did not support his conclusion that *P. cinnamomi* killed jarrah trees.
50 Local researchers and forest managers were unaware of this. Consequently, the Forests
51 Department's control measures may not have been as well targeted as they believed,
52 because an accurate diagnosis is essential for formulating appropriate measures for disease
53 management.

54 A review of how *P. cinnamomi* became associated with the death of jarrah trees has
55 been recently published (Davison 2015). In this paper I briefly summarise the earliest
56 work, review the management of *P. cinnamomi* in the jarrah forest during the 1970s, and
57 comment on the renewed interest in jarrah pathology that occurred between 1980 and
58 1997. [Knowing the history of any investigation is important because the standards of](#)
59 [proof and reporting that is required now may be different from what was acceptable in the](#)
60 [past.](#) I also present an interpretation of these observations based on the decline hypotheses
61 of Manion (1981) and Houston (1987) which better fit the data, and allow predictions of
62 where and when deaths are likely to occur.

63

64 **Background**

65

66 The jarrah forest in the southwest of Western Australia covers an area of about 15
67 000 km² (Abbott and Loneragan 1986). The climate in its habitat is Mediterranean, with
68 cool wet winters and hot dry summers; about 90 % of the annual rainfall occurs between
69 April and October. Jarrah trees reach a height of at least 27 m on the best quality sites,

70 which are those with deep gravel soils on upper and mid slopes in the subdued landscape
71 of the western part of the Darling Range. It is a phreatophyte, accessing water in summer
72 from moist soil at depth through an extensive vertical root system. Jarrah grows in
73 association with marri (*Corymbia calophylla*), and is replaced by *E. megacarpa*, *E. patens*
74 and *E. rudis* on wetter sites. In the drier, eastern forest it also grows in association with *E.*
75 *wandoo*.

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

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

90 The jarrah deaths were not associated with pests ([because there were no consistent](#)
91 [signs of insect attack](#)), pathogens ([because there were no consistent lesions](#)) or soil
92 properties (Davison 2015). The only unusual feature was that there were more tyloses in
93 the roots of affected trees. Tyloses are ingrowths into xylem vessels in the sapwood that

94 indicate that these capillaries no longer conduct water; a symptom now known to be
95 caused by waterlogging (Davison and Tay 1985). Tyloses also form locally as one of a
96 host's response to [drought](#), damage and wounding (Zimmerman 1983), for example in the
97 sapwood adjacent to *P. cinnamomi* lesions in jarrah phloem (Tippett *et al.* 1983).

98 In 1959, Podger, a forester from the Forests Department was appointed by the FTB
99 to investigate jarrah dieback (Davison 2015). He started by investigating ~~at~~ some of the
100 site changes that would have occurred following heavy logging, and showed that jarrah
101 was less tolerant of waterlogging than other forest eucalypts (Podger 1967). However, in
102 1963 his research changed to actively looking for a *Phytophthora* as the cause of jarrah
103 dieback. In 1964, with the assistance of Ralph Doepel (Western Australian Department of
104 Agriculture) and George Zentmyer (University of California, Riverside Campus), *P.*
105 *cinnamomi* was isolated from soil. Pathogenicity tests showed that it could infect and kill
106 jarrah and *B. grandis* seedlings, but not marri (Podger *et al.* 1965). It was isolated by soil
107 baiting from sites where jarrah trees had died, but not from unaffected areas, and by using
108 phytophthora-selective agar, could be isolated from the roots of jarrah and many other
109 forest species (Podger 1968). He deliberately infested a forest site with *P. cinnamomi* and
110 one jarrah tree and many mid- and understorey species died over a number of years
111 (Podger 1972).

112 Podger's advice to the Forests Department in 1965 was premature; it was based on
113 his initial observation that jarrah deaths were associated with infested sites. Between 1965
114 and 1968 he attempted to establish the first of Koch's postulates in order to show that there
115 was a constant association between infection of jarrah and death of these trees. However,
116 he was only able to isolate *P. cinnamomi* from 5 % of 100 sampled jarrah trees (Davison
117 2015). He failed to mention this low recovery rate to either the Forests Department or the
118 FTB. His work also failed to satisfy the fourth of Koch's postulates because he only

119 showed that the site where he conducted his field pathogenicity test became infested, not
120 that the plants that died there were infected. Podger presented his work as showing that *P.*
121 *cinnamomi* killed jarrah trees as well as many mid- and understorey species, and extended
122 the definition of jarrah dieback to all species that died on infested sites. As jarrah appeared
123 to have no resistance to *P. cinnamomi* (Podger 1972) he asserted that commercial forestry
124 would decline. All the early work was forgotten, and phytophthora control dominated
125 forest management.

126

127 **Research and control, 1965 – 1979**

128

129 The Forests Department accepted Podger's explanation that jarrah deaths were
130 caused by *P. cinnamomi*, even though Eric Björkman (Royal College of Forestry,
131 Stockholm), who reviewed Podger's work for the FTB, was sceptical about some of his
132 claims (Björkman 1966). The Forests Department appointed new staff and constructed or
133 upgraded their research facilities. By 1972, there was a comprehensive research
134 programme in progress (Batini and Hopkins 1972). This tackled the immediate problems
135 of mapping the extent of infestations, determining the environmental limits on sporulation
136 and survival of *P. cinnamomi* throughout the jarrah forest, and investigating how it spread
137 between sites. Salvage logging was important to minimise the economic loss to the
138 sawmilling industry and the most impacted areas were heavily logged. Uninfested, high-
139 quality forest areas were intensively managed for future timber production and alternative
140 timber species were evaluated for rehabilitating infested sites. In addition, the Forests
141 Department funded research scholarships at the University of Western Australia and the
142 Australian National University. There was also a public education programme targeting

143 government departments, shires, the army, the mining industry, professional societies and
144 public interest groups. Its approach was widely applauded by plant pathologists and
145 foresters (Newhook 1968; Zentmyer 1968; Marks and Idczak 1973).

146 There were concerns in eastern Australia about the implications of site infestation by
147 *P. cinnamomi* on timber production and conservation (Newhook and Podger 1972; Weste
148 1974; Incoll and Fagg 1975). Within the research community there was considerable
149 interest and investigation of why some eucalypts, such as jarrah and *E. sieberi* were
150 susceptible to *P. cinnamomi*, whilst others, such as marri and *E. maculata* were field
151 resistant (e.g. Malajczuk *et al.* 1977; Halsall 1978; Grant and Byrt 1984), but no consensus
152 emerged of why this was so.

153

154 *Hygiene and the imposition of quarantine*

155

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

164 The Forests Department considered that infestation by *P. cinnamomi* resulted in four
165 main threats to: forest productivity; the state's flora reserves such as National Parks; the

166 survival of some indigenous plant species, and; water quality. At that time most of the
167 infested areas were in the western part of the forest, but if *P. cinnamomi* was introduced
168 into the eastern forest, the death of jarrah and other vegetation would result in rising water
169 tables. This would result in increased salinity in streams feeding the reservoirs supplying
170 Perth and the southwest by mobilising salt stored in the soil profile (Forests Department
171 1974).

172 Hygiene measures would only be effective if the distribution of *P. cinnamomi* was
173 known. Research had shown that there was a time lag of 6 to 18 months between the time
174 a site became infested and the development of field symptoms, so the Forests Department
175 realised that they needed sufficient time for symptoms to develop before they could map
176 infested areas. One way to achieve this was by restricting access to the forest by the
177 imposition of quarantine. They consulted widely with other forest users, and this approach
178 was supported. The Western Australian cabinet approved the imposition of quarantine; the
179 Forests Act was appropriately amended, and Forest Disease Risk areas in the northern
180 forest proclaimed in 1976 and in the southern forest in 1977 (Forests Department 1975,
181 1976, 1977). There was a public education campaign to explain why such measures were
182 essential to protect Perth's water supply, the timber industry, and the conservation values
183 of the jarrah forest (Shea 1975a). These measures were widely supported by forest users
184 and the general public.

185

186

Bauxite mining

187

188 The lateritic soils of the Darling Range are rich in bauxite. It occurs in small pockets
189 and has been mined through an open cut process since 1963 (Alcoa of Australia 1979).
190 Mining started in state forest close to Jarrahdale, and by 1978 bauxite was also being
191 mined north west of Dwellingup (Fig. 2). Mining involves clearing the native forest,
192 mining the bauxite, and then restoring the land back to forest. Much of Alcoa's operations
193 were in areas infested with *P. cinnamomi*. The research programme that the Forests
194 Department had undertaken for mapping the distribution of *P. cinnamomi*, minimising its
195 spread, and rehabilitating infested areas, were directly applicable to Alcoa's operations.
196 These two organisations worked collaboratively, using the experience of the Forests
197 Department, with funding from Alcoa, to minimise the impact of *P. cinnamomi* in all
198 aspects of bauxite mining. Alcoa estimated that for every 1 million tonnes of alumina it
199 refined, 75 ha of forest were cleared, mined and then restored; rehabilitation costs were
200 about \$10 000 ha⁻¹ (Alcoa of Australia 1979). In 1979, Alcoa gave the Western Australian
201 government a total of \$500 000 over three years, to establish a Dieback Foundation to co-
202 ordinate research funding for the control or eradication of this disease.

203

204 **Renewed interest in jarrah deaths, 1980-1996**

205

206 Most of the work undertaken on jarrah dieback between 1965 and 1979 focussed on
207 *P. cinnamomi* in the belief that jarrah trees would die out on infested sites. In early 1980,
208 following my review of the early work on jarrah dieback, I concluded that Podger had
209 reported his work more enthusiastically than it warranted. These conclusions were
210 discussed with colleagues and I was advised to make them public (J. F. Loneragan,
211 Professor of Plant Biology, Murdoch University, pers. comm. March 1980). This needed

212 to be done with care, as firstly, it would reduce confidence in the Forests Department's
213 competence, and secondly, there was no alternative explanation of past jarrah deaths. My
214 doubts about the interpretation of Podger's work were raised at a national meeting at the
215 University of Western Australia (Summary of the Phytophthora workshop, 15-16 May,
216 1980). My concerns were not well received (Havel 1980a). The Forests Department
217 conceded that the recovery of *P. cinnamomi* from only 5 % of sampled jarrah trees was a
218 cause for concern (Havel 1980b). Based on past observations and previous work, there
219 were two possible causes of jarrah deaths. Waterlogging could not be discounted, because
220 trees had died on wet sites (Podger *et al.* 1965), and Podger had shown jarrah to be
221 sensitive to waterlogging (Podger 1967). It was conceded by the Forests Department that
222 waterlogging might cause jarrah deaths in valleys, but would not account for deaths on
223 upland sites, which were believed to be well drained. The other explanation, which was
224 more acceptable to both the Forests Department and Alcoa, was that jarrah deaths were
225 caused by *P. cinnamomi*, even though Podger had been unable to convincingly
226 demonstrate this. The Forests Department indicated that work was already underway by
227 Syd Shea (Senior District Forest Officer, Forests Department) and John Gardner
228 (Environmental Scientist, Alcoa) to again investigate jarrah deaths (Havel 1980b).

229

230 *Jarrah's sensitivity to waterlogging*

231

232 When soil is saturated with water, the dissolved oxygen in the soil solution is rapidly
233 used by plant roots and microorganisms. As oxygen diffuses 10^4 times more slowly
234 through water than through air, it is used more rapidly than it is replaced, and the soil
235 initially becomes hypoxic and then anoxic; the rate at which this happens depends on the

236 soil temperature (Kozlowski 1986; Drew 1992). Most plants, including jarrah, are
237 intolerant of anoxic soil. Glasshouse experiments showed that when jarrah seedlings are
238 waterlogged, the xylem vessels in the tap roots become blocked by tyloses, [and this](#)
239 [happens within a few days](#). Water deficits build up because the seedlings continue to
240 transpire, even though conduction is reduced; consequently, the seedlings wilt and die,
241 especially during hot weather (Davison and Tay 1985). If mature jarrah trees behave in
242 the same way as seedlings, tylosed sapwood would be an indication of past waterlogging
243 damage.

244

245 *Excavation of jarrah trees*

246

247 Between 1980 and 1983, about 90 jarrah trees were excavated, and their roots and
248 root collars intensively sampled for *P. cinnamomi* by using phytophthora-selective agar.
249 All of the trees were on infested sites. Most of the work was done near Dwellingup (Fig.
250 2) by the Forests Department, and most was funded by the Dieback Foundation. In 1980,
251 recently-dead trees were sampled, and *P. cinnamomi* was isolated from the bark and wood
252 at the root collar, large and small roots from some of these trees (Dell and Wallace 1981;
253 Shearer *et al.* 1981). Both groups concluded that their work showed that *P. cinnamomi*
254 was able to invade the root collar and large roots of jarrah, but could not determine
255 whether this invasion occurred before or after tree death. Some of the trees may have been
256 affected by waterlogging (Shearer *et al.* 1981), or by runoff from a nearby road (Dell and
257 Wallace 1981). Dell and Wallace (1981) noted that infected roots had tylosed sapwood.

258 A further 41 jarrah trees from seven sites near Dwellingup were sampled in 1981 and
259 1982; most of these trees had died suddenly (Shea *et al.* 1982). Excavations showed that
260 these deaths were on sites with an impeding layer of concreted laterite 5 to 75 cm below
261 the soil surface, and most of the sites were upland, not valley sites. On three sites, major
262 disturbances upslope would have caused excessive runoff into the areas where jarrah trees
263 had died. *Phytophthora cinnamomi* was isolated from 39 trees. It was isolated from the
264 root collars and lateral roots; Shea *et al.* (1982) also stated that it was consistently isolated
265 from vertical roots. Shea *et al.* (1982) suggested that infection of vertical roots where they
266 penetrated through potholes in the impeding layer, caused reduced conduction of water
267 from deep water tables, and this resulted in severe water deficiency and tree death.
268 Subsequent work showed that, under appropriate conditions, *P. cinnamomi* could sporulate
269 in soil from above the impeding layer deep in the soil profile, and zoospores could be
270 dispersed laterally in seepage water as well as vertically during soil drainage (Shea *et al.*
271 1984; Kinal *et al.* 1993). These sites were seen as areas where abundant zoospore
272 production would occur in wet weather, where dispersal would be facilitated by internal
273 soil drainage and seepage, with massive root infection and tree death being the inevitable
274 consequence.

275 The work by Shea *et al.* (1982) was very important, because it explained how jarrah
276 deaths were related to certain site characteristics, and were not an inevitable consequence
277 of site infestation, as had been suggested by Podger (1972). The impact of *P. cinnamomi*
278 on jarrah appeared to differ on different site types; these site types being defined by the
279 composition of understorey species (Havel 1975a; 1975b). Joe Havel (Superintendent
280 (Research), Forests Department) believed that this impact would be related to the amount
281 of root damage. He directed Bryan Shearer and Joanna Tippett (Research Officers, Forest
282 Department) to study root infection on a range of site types, including some in the lower

283 rainfall, eastern forest (Havel 1983). Over the next 4 years, Shearer and Tippett conducted
284 very through excavations of 26 apparently healthy jarrah trees from a number of infested
285 sites. Lesions were present on the large roots of 16 of these trees; 4.7 % of all large roots
286 were infected, with most lesions being less than 12 cm long (Shearer and Tippett 1989).
287 Havel's expectations were not met; there did not appear to be a relationship between the
288 amount of root infection and perceived impact on jarrah. Davison and Tay (1995a), in a
289 smaller study, found similar results, only 3.4 % of large surface roots of jarrah had *P.*
290 *cinnamomi* lesions on them, and the mean lesion length was 17.5 cm. In other words, in
291 live trees, the incidence and severity of infection of jarrah roots is low. Jarrah appears to
292 be a tolerant host.

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

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

321 ~~In 1983, there was a change of government in Western Australia, followed by~~
322 ~~reorganisation of the public service. The Forests Department, together with other agencies~~
323 ~~that managed public lands were amalgamated into the Department of Conservation and~~
324 ~~Land Management (CALM) in 1985; Shea was appointed as Executive Director. My~~
325 ~~position at DCE was moved to CALM.~~

326 The next occurrence of dying jarrah trees was in January 1993 (Davison 1997).
327 Deaths occurred on an infested site, close to a rehabilitated bauxite pit. Several jarrah trees
328 were excavated by Giles Hardy (Lecturer, Murdoch University), Ian Colquhoun
329 (Environmental Scientist, Alcoa) and me. The site had concreted laterite in the profile, the
330 deaths were upslope of a dolerite dyke and additional water would have drained into the
331 site from a drain failure upslope. There were no visible lesions at the root collars, lateral

332 or vertical roots, but the root sapwood was tylosed, and weather records showed that there
333 had been exceptionally heavy rainfall the previous February, March and November (Table
334 2). The observations of absence of lesions on large roots, evidence of water flows into this
335 site, and symptoms consistent with waterlogging damage in the root sapwood of the
336 excavated jarrah trees, were presented to the Western Australian Dieback Review Panel (S.
337 H. James, P. M. Jones, M. J. Mulcahy, F. D. Podger (chairman)) and others (I. J.
338 Colquhoun, G. E. StJ. Hardy, J. F. Loneragan) on 8 April 1994, they all concluded that
339 these jarrah deaths could not be attributed to *P. cinnamomi*, and that waterlogging damage
340 could not be discounted as a cause. This site became waterlogged in August 1996.

341 ~~A few weeks after the preliminary results were known, I was accused of professional~~
342 ~~misconduct by Jim Armstrong (Director, Science and Information Division, CALM); these~~
343 ~~accusations were later shown to be without foundation (George 1994).~~

344

345 **Discussion**

346

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

351

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

354

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

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

371 Shea *et al.* (1982) suggested that extensive infection of jarrah's vertical roots would
372 lead to reduced conduction, implying that infection results in extensive invasion and
373 dysfunction of the sapwood. However, their wound inoculation experiments did not
374 support this explanation, because these showed that *P. cinnamomi* invades the bark, not the
375 sapwood (Tippett *et al.* 1983). There is some sapwood invasion, but it only results in a
376 very narrow, inapparent infection internal to phloem lesions (Davison *et al.* 1994). It is
377 also difficult to reconcile dysfunction of the sapwood that is of sufficient magnitude to

378 cause death, with the low incidence and severity of root infection in live jarrah trees
379 (Shearer and Tippett 1989; Davison and Tay 1995a). Something appears to be missing.

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

391

392 *Stress factors and tree decline hypotheses*

393

394 Tree declines and death are different from diseases and disorders of annual
395 agricultural crops, because they can occur over many years, even decades. Also, the large
396 size of trees makes them much more difficult to sample than annual plants. Manion (1981)
397 presents one approach that is valuable when trying to determine the cause(s) of tree
398 decline. He suggests that there are three levels of stress factors that should be considered.
399 First, there are predisposing factors that are long-term static or non-changing factors, such
400 as climate, site, or soil moisture which weaken a plant growing in the wrong location.

401 Second, there are short-term inciting factors such as frost, insect defoliation or mechanical
402 injury that produce a drastic injury. Third, there are contributing factors such as insect
403 pests or fungal pathogens that are long-term, persistent, and when abundant, indicators of a
404 weakened host. Houston (1987) similarly proposed that diebacks and declines are initiated
405 by predisposing factors, with facultative pests and pathogens being able to attack and
406 invade hosts that would normally be able to contain infection. Direct and indirect effects
407 of these environmental stresses are on photosynthesis, the uptake of water and minerals,
408 and movement and storage of carbohydrates. A consequence is the reduced ability of the
409 host to compartmentalise damaged tissue (Shigo 1984), leading to increased damage by
410 pests and pathogens. Extensive invasion by pests and pathogens is therefore considered to
411 be a consequence, not a cause of tree decline.

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

418 Heavy rainfall will be most damaging on sites that are poorly drained or water-
419 gaining, the predisposing factors of Manion (1981) and Houston (1987). Sites where
420 jarrah trees died were described as waterlogged, or with impeded subsoil drainage, or
421 likely to have had water draining into them (Hamilton 1951; Waring 1950; Loneragan
422 1961; Dell and Wallace 1981; Shearer *et al.* 1981; Shea *et al.* 1982; Davison 1997). The
423 earliest reports of jarrah deaths also mention a further disturbance, because they were on
424 recently-logged sites. As these were also described as poor-quality sites, it is likely that
425 these sites had not been previously logged. Such sites would be wetter than unlogged

426 areas, because of reduced interception of rainfall and reduced evapotranspiration
427 (Christensen 1975; Shea 1975b). The salvage logging that was conducted in the 1970s on
428 the most heavily impacted sites reduced the economic impact of jarrah deaths on the
429 sawmilling industry (Batini and Hopkins 1972), but would have further increased the
430 frequency and duration of soil saturation.

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

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

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

457 It is difficult to visualise how the different stresses interact because some, such as
458 exceptionally heavy rainfall, are unpredictable. Davison and Tay (1989) compared jarrah
459 phenology in adjacent infested and uninfested areas on three sites, Churchmans, Karnet
460 and Ross. These sites differed in drainage: Churchmans was better drained than the other
461 two, and a perched water table developed more frequently at Ross than at Karnet. Trees in
462 the adjacent infested and uninfested areas at each site showed similar growth patterns, but
463 phenology differed between sites. The Churchmans and Karnet sites were being measured
464 in January 1982, and although the rainfall was not as heavy as that recorded for
465 Dwellingup (Table 2), it resulted in differences between the sites, not between the infested
466 and uninfested areas of each site (Fig. 4). At Churchmans, following this rain, the
467 proportion of trees producing new leaves (the normal summer pattern) decreased, and the
468 vascular cambium became active, with the trees putting on about a third of their annual
469 increment in a 2 week period; 2 weeks later the cambium was inactive and new leaves
470 were again produced. At Karnet, the vascular cambium did not become active, even
471 though there was more rain than at Churchmans; no observations were being made of leaf
472 production at Karnet. The most important factors affecting phenology were the site
473 characteristics, followed by the weather; there was no detectable effect of *P. cinnamomi*.

474 This is what would be expected from the hierarchy of stress factors, with site and weather
475 being more important than pests and pathogens (Manion 1981; Houston 1987).

476

477 *Deaths of mid-and understorey plants*

478

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

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

497 may be susceptible, some may be tolerant hosts (Crone *et al.* 2013), while changes in the
498 abundance of others may be because of changes to edaphic conditions, rather than their
499 susceptibility to *P. cinnamomi* (Weste 2003; Shearer *et al.* 2009). A better understanding
500 of how *P. cinnamomi* infects mid-storey and understorey species in the field, together with
501 improved knowledge of their ecophysiology, may provide additional options for the
502 revegetation of infested areas.

503

504

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505

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514

515

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- 719

720

721 **Table 1** Number of jarrah trees on infested areas sampled between October 1981 and May
722 1983, from which *Phytophthora cinnamomi* was isolated from the root collar, lateral roots
723 and vertical roots. Not all root collars, lateral and vertical roots were sampled in all trees.
724 [Data from Forests Department, Dwellingup Research Local Experiment files 395 and
725 402.] 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

726

727 **Table 2** Rainfall in the three years prior to the death of groups of jarrah trees. Monthly rainfall is shown in parentheses. Data from

728 <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	>95 th percentile	>90 th 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	Near Myara	Jarrahdale	1926	1729.2 (>95 th)	Apr (221.6)	Mar (85.4)	Jul (402.6)	Wallace pers

1928/1929	Hill	(9023)	%ile)				com in	
				1927	1254.6	Jan (53.1)	Waring (1950)	
				1928	1486.4 (>90 th %ile)	Aug (309.4)	Jul (395.7), Sep (211.3)	
1948	Mundaring Division	Mundaring (9031)		1945	1419.5 (>90 th %ile)	Jun (566.9)	Aug (329.3)	Hamilton (1951)
				1946	1542.2 (>95 th %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 (>95 th %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 ¹ (9585)	1945	1143.1		Aug (238.6)	Jun (274.6)	Hamilton (1951)
			1946	1013.5	Jul (337.7)	Nov (93)		
			1947	1205.9 (>95 th %ile)		Apr (122.2), May (248.6), Jun (348)		

Summer 1947/1948	Teesdale	Dwellingup (9538)	1945	1887.1 (>95 th %ile)	Jun (719.2)	Aug (405.8)	Hamilton (1951)
			1946	1572.8 (>90 th %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 ⁴
			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	Teesdale	Dwellingup	1961	²			Unpublished
summer	regeneration	(9538)	1962	1226.7		Nov (97.9)	file Kelsmcott
	transect						WA7 L.T.
							7.16 ⁴
			1963	1701.2		May (291.9), Jun	
						(406.4), Aug	
						(306)	
Sometime	Karnet	Jarrahdale ³	1962	1226.7		Nov (97.9)	Podger (1968)
between Dec		(9023 ¹)	1963	1701.2 (>95 th		May (291.9), Jun	
1962-Aug				%ile)		(406.4), Aug	
1967						(306)	

			1964	1828.6 (>95 th %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)	

729

730 ¹ Kirup is closer, but there are no rainfall records between 1944 and 1974

731 ² no total annual rainfall because some values missing

732 ³ no complete rainfall records for Karnet (9111) before 1965

733 ⁴this file was destroyed when the CSIRO Division of Forest Research, Kelmscott, was closed in the mid-1980s

734

Figure captions:

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

740

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

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

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

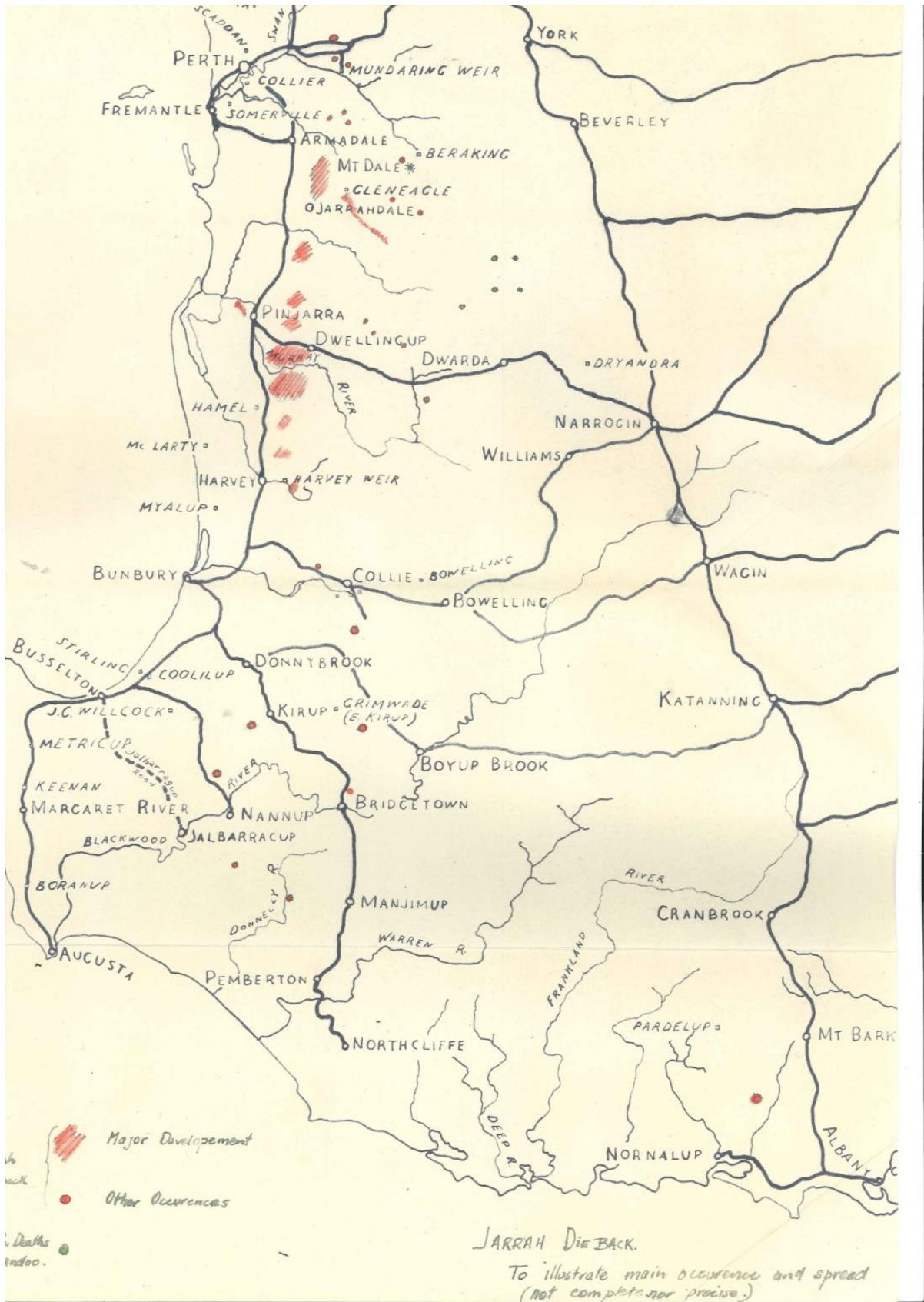
758 Figure 1



759

760

761 Figure 2



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763

764

765 Figure 3

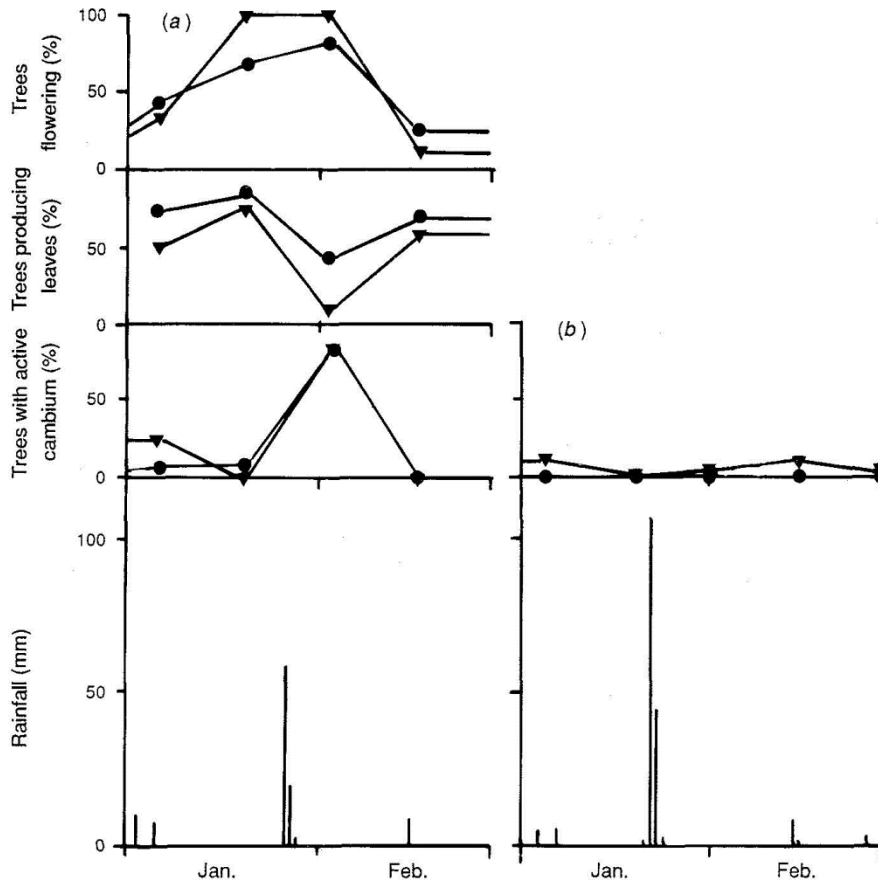


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769 Figure 4



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