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Impact of severe forest dieback caused by *Phytophthora cinnamomi* on macrofungal diversity in the northern jarrah forest of Western Australia

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ABSTRACT

The relative diversity and abundance of different functional groups of macrofungi were investigated in the northern jarrah forest, a mediterranean climate sclerophyllous forest dominated by eucalyptus trees in Western Australia. We sampled paired sites that were either severely affected by dieback, a disease caused by *Phytophthora cinnamomi* which causes selective plant mortality, or unaffected by this type of forest decline. Macrofungi were sampled 3 times during the growing season along six 100 m × 2 m transects in these sites. Dieback-unaffected sites were found to have significantly different macrofungal floras than unaffected sites. Macrofungal abundance and diversity were approximately 1.5 times and 1.8 times greater respectively in dieback-unaffected sites than in severely affected sites. Dieback-affected sites had a similar diversity of saprotrophic and ectomycorrhizal fungi, whereas more fungal taxa on dieback-unaffected sites were mycorrhizal (>60%). Dung fungi were the most common saprophytes, especially in dieback-affected sites, but abundance data greatly overestimated the importance of these relatively small fungi. We concluded that vegetation changes linked to dieback had a negative effect on fungal community structure and biodiversity in the northern jarrah forest, in a similar manner to other forms of severe disturbance. Conversely, high tree mortality increased the abundance of wood decay fungi, at least in the short term. We expect that reductions in macrofungal species richness were indirectly linked to impacts on mycorrhizal host plants and saprotrophic substrates. Our data show that changes in vegetation composition had the greatest effect on ectomycorrhizal fungi, presumably due to their obligate symbiotic associations.

1. Introduction

Jarrah forest is dominated by jarrah (*Eucalyptus marginata* Donn ex Sm.) and mari (*Corymbia calophylla* Lindl.), which are eucalypt trees. This ecosystem covers about 4.5 million ha in southwestern Australia (Environmental Protection Authority, 2007). A type of severe forest decline (dieback), caused by *Phytophthora cinnamomi* Rands, is a major environmental problem that has severe impacts on the health of jarrah forest, woodlands and coastal heath in this region. *P. cinnamomi* is an exotic soil borne pathogen that kills plants by rotting the root system and lower stem tissues which restricts the plant's ability to uptake water and nutrients (Shearer et al., 2004; D'Souza et al., 2005). Plants native to southwest Western Australia (WA) did not evolve with *P. cinnamomi* and many are highly susceptible to infection. Dieback of vegetation linked to *Phytophthora* is considered to be one of the major threats to biodiversity in this region (McDougall et al., 2002; D'Souza et al., 2005; Hardham, 2005). It is estimated that 15–20% of the jarrah forest is infested with *P. cinnamomi*, with the most severe impacts occurring in highest rainfall areas (Department of Environment and Conservation, 2006).

Substantial knowledge has been obtained by research on the effect of dieback on vegetation structure and species composition in the jarrah forest (Shearer and Dillon, 1996; McDougall et al., 2002; Hardham, 2005; Department of Environment and Conservation, 2007) and there is some data on indirect impacts on animals (Garkaklis et al., 2004). In the northern jarrah forest, 33% of the flora is susceptible to *P. cinnamomi* and dieback causes major changes in floral community structure and composition due to loss of prevalent species such as jarrah and *Banksia grandis* Willd. (McDougall et al., 2005; Department of Environment and Conservation, 2006). McDougall et al. (2005) observed that the dominant overstorey species are killed by dieback leaving scattered marri (*C. calophylla*) with a sparse herbaceous understorey, resulting in a massive reduction in primary productivity. McDougall et al. (2002) suggest that death of susceptible canopy species may affect understorey plants that are not susceptible to *P. cinnamomi* infection but are reliant on canopy cover of the dominants.

It is estimated that over 12,000 species of larger fungi (macrofungi) occur in Australia, but only about 25% of these have

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been named (Chapman, 2005). Macrofungi play major roles in decomposition and nutrient cycling, contribute to soil structure and health and fruit bodies provide a food resource for native fauna, such as potoroos and woylies (Fitter and Garbaye, 1993; Claridge and May, 1994; Maser et al., 2008). Mycorrhizas enhance water and nutrient uptake (especially phosphorus, zinc and copper) for the majority of plants and in return fungi gain energy from the plants, but can also protect roots in adverse soil conditions such as low pH and high soil temperature (Smith and Read, 1997; Brundrett, 2004). The majority of jarrah forest plants rely on mycorrhizal associations with fungi for survival, but carnivorous plants, parasitic plants and those with non-mycorrhizal cluster roots are also very important in the nutrient poor soils of Western Australia (Lamont, 1982; Brundrett and Abbott, 1991; Lambers et al., 2006; Brundrett, 2009). The diversity of fungi in jarrah forest sites has been investigated in rehabilitated areas following bauxite mining (Gardner and Malajczuk, 1988; Glen et al., 2008) and in a broader context by the Forestcheck monitoring program (Department of Environment and Conservation, 2003–2007). Despite their high ecological significance in jarrah forest ecosystems, there have been no prior studies on the impacts that forest decline caused by dieback disease may have on fungal communities.

We postulate that there are likely to be substantial indirect impacts of dieback disease on the diversity and abundance of jarrah forest macrofungi, particularly on those species that form mycorrhizal associations with susceptible plant species. Conversely, fungi that decompose the remains of dead plants may benefit from dieback, at least in the short term. The aim of this project was to compare the diversity and composition of macrofungi on severely dieback affected and adjacent unaffected sites in order to investigate the impact that jarrah forest dieback caused by *P. cinnamomi* may have on macrofungal communities in the northern jarrah forest. Paired dieback-affected and -unaffected areas were studied by measuring: (i) macrofungal abundance and biodiversity on transects, (ii) relative dominance of mycorrhizal and saprotrophic fungi fruiting on different substrates, (iii) changes to vegetation structure and composition and the relative dominance of plants with mycorrhizal associations and those without, (iv) interrelationships between fungal and plant diversity and (v) litter cover and soil chemistry.

2. Materials and methods

2.1. Study sites

Three sites located in similar vegetation within 5 km of each other were established in Myara forest block which is approximately 60 km southeast of Perth (Fig. 1). These locations were identified in previous studies of the impacts of *P. cinnamomi* on vegetation in the jarrah forest by McDougall et al. (2002, 2005) who confirmed the presence of dieback disease using baiting techniques. Myara Rd, Berkeley Rd and North Rd sites were chosen for wet season accessibility to adjacent dieback-affected and -unaffected jarrah forest (referred to as paired sites here). Dieback-unaffected forest was defined as areas without visible impacts on vegetation structure or composition (i.e. totally symptom free) (Fig. 1). GPS coordinates for each site were as follows: North Rd 32°29′13″S and 116°5′23″E, Berkeley Rd 32°28′23″S and 116°28′23″S, Myara Rd 32°27′58″S and 116°3′1″E.

The study sites have a mediterranean climate, characterized by cool, wet winters and hot, dry summers (Fig. 2). The mean annual rainfall for this area is 1170 mm, with the majority of rainfall occurring from April to October (Fig. 2), but during this study the study sites received below average rainfall (Bureau of Meteorology, 2007). The maximum rainfall during the study period occurred from June to July, when the majority of macrofungi fruit in WA (Fig. 2).

Fig. 1. Contrasting appearance of dieback-unaffected (A) and -affected (B) transects at the Myara Rd site.

All three sites were on gravelly sandy loam over lateritic duricrust and were level or had gentle slopes (<10°). The dieback-unaffected transect at the Berkeley Rd site had a dominant jarrah overstorey with a dense understorey including *Macrozamia riedei* Gaudich., *Xanthorrhoea preissii* Endl., *Bossiaea aquifolium* Benth., *Thomasia triphylla* Labill. and *Clematis pubescens* Endl. The adjacent dieback-affected transect was lower in the landscape, and parallel with a seasonal creek line. A sparse overstorey was dominated by marri with an open herbaceous understorey including *B. aquifolium*, *Phyllanthus calycinus* Labill., *Hypocalymma angustifolium* Endl. and *Trymalium ledifolium* Fenzl.

The dieback-unaffected transect at the North Rd site was dominated by jarrah and *B. grandis* with a dense understorey of *B. aquifolium* and other shrubs and herbs. The adjacent dieback-affected transect was on a gravelly slope and had a sparse

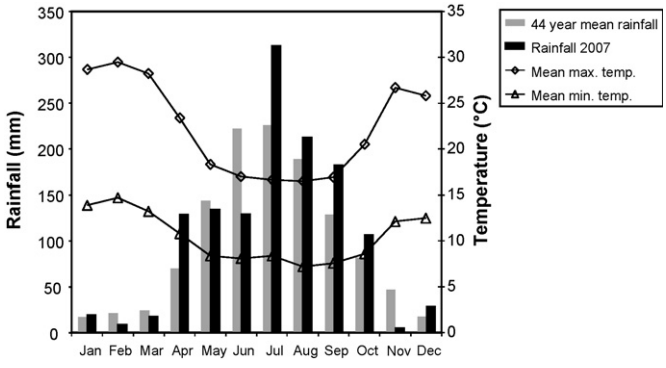

Fig. 2. Temperature and rainfall data for the year when sampling occurred (2007) and the 44-year average rainfall at the Myara Forest Block. Observations from Karnet Rehabilitation Center, approximately 4 km north of the study site (www.bom.gov.au).

overstorey of marri and an open herbaceous understorey including *Conostylis* sp., *B. aquifolium*, *Banksia dallanneyi* (formerly *Dryandra lindleyana*) and *H. angustifolium*.

The dieback-unaffected transect at the Myara Rd site had a mixed dominant overstorey of jarrah, *Xylomelum occidentale* R. Br. and *B. grandis* Willd. and an open understorey (Fig. 1) including *Conostylis* sp., *Adenanthos barbiger* Lindl., *Lomandra* sp., *Hibbertia diamesogenos* Steud., *Gompholobium* sp. and *X. preissii*. The adjacent dieback-affected transect was on an exposed gravelly hillside with a sparse overstorey of marri and an open understorey dominated by *B. dallanneyi*, *Conostylis* sp., *H. diamesogenos* and *Lepidosperma* sp. (Fig. 1). All plant names are consistent with Florabase (florabase.calm.wa.gov.au, accessed February 2009).

2.2. Sampling design

At Myara Rd, North Rd and Berkeley Rd sites paired 100 m × 2 m transects were established in areas with severe forest decline symptoms and adjacent symptomless areas. These paired transects are referred to as dieback-affected and unaffected here. Dieback-affected transects were located near the centre of patches where dieback has been slowly spreading for many years and which displayed prominent tree and understorey death, as established by the detailed studies of McDougall et al. (2005). Unaffected transects were positioned well in advance of the disease front, which was visible due to recent jarrah and *Banksia* deaths and other susceptible plants showing symptoms of disease adjacent to healthy vegetation. All of the sites were sampled 3 times, approximately every fortnight for two months in the early winter (22/6/07, 10/7/07 and 25/7/07). On each of the six transects, all visible fresh fungal fruit bodies were counted and photographed *in situ*. The transect positions and abundance of each macrofungus category was recorded. Where possible taxa were identified in the field, but some fungal categories could not be identified immediately, so were sampled for examination in the laboratory to determine their identity (see below).

2.3. Vegetation surveys

For each transect, 1 m^2 quadrats at 10 m intervals were used to estimate overstorey cover, understorey cover, coarse woody debris, litter depth and litter cover. Overstorey cover was also estimated to the nearest 10% for every 10 m × 1 m block then averaged for each transect. Percentage cover of individual species were identified and recorded for each transect and further categorized into mycorrhizal and non-mycorrhizal plants by referring to Brundrett and Abbott (1991) and the lists of Australian host plants at mycorrhizas.info (Brundrett, 2008). Root samples were also collected to assess the mycorrhizal status of some additional plants and confirmed using a standard clearing and staining protocol with 10% KOH and Trypan blue in lacto-glycerol followed by microscopic assessment (Brundrett et al., 1996).

2.4. Identification of macrofungi

Macrofungi were selected as the focus for this study as they produce readily visible fruit bodies (mushrooms, puffballs, coral, bracket fungi, etc.) that can be relatively easily counted and collected. Hypogeal macrofungi were only opportunistically sampled to avoid major disturbance to transects. Macrofungi were assigned to species where possible, and otherwise assigned to morphotypes within genera. Morphotypes were defined by a short description (e.g. *Cortinarius* sp. 'chestnut') and species groups (e.g. *Cortinarius* spp. 7 – 'small brown'). Many of the taxa encountered were unnamed but familiar from other studies on jarrah forest fungi (R. Robinson, pers. comm.). A list of fungal names and corresponding herbarium voucher specimen numbers for many of these fungi are provided by Robinson and Tunsell (2007) and reports from other monitoring within jarrah forest (Department of Environment and Conservation, 2003–2007). Voucher collections for some of the less-common species encountered during this survey were also lodged at the Perth Herbarium. Saprophytic fungi were assigned to ecological categories based on their substrate and ectomycorrhizal fungi were assigned based on the list of families and genera of these fungi at mycorrhizas.info (Brundrett, 2008).

The average diameter of fruit bodies was measured for each species to compensate for the relative size of fungi, since some fungi had numerous small fruit bodies while others produced a few larger fruit bodies. This "fruiting effort" data was used as a scaling factor for abundance data to provide more representative values.

2.5. Soil analysis

Soil samples were taken at the beginning and then every 20 m along each transect. Percent moisture (wet soil weight–dry weight) was determined. Labile inorganic nitrogen was extracted using the method of Rayment and Higginson (1992). Nitrate (NO_3^-) and ammonium (NH_4^+) were analysed using auto analyzer techniques (Technicon, 1977) after extraction in 1 M KCl. Inorganic phosphorus was extracted by adding a dilute acid-fluoride solution to approximately 2.85 g of air dry soil, shaking by hand for 45 s and then filtering immediately (Bray and Kurtz, 1945). The filtrate was then analysed for inorganic P using the Murphy and Riley method by measuring absorbance of the extractant and added reagents (Kuo, 1996). For total percentage of soil C and N, air dried samples were ground to a fine powder in a ball mill and 19–21 mg used to determine total nitrogen and carbon using mass spectrometry techniques (Roboprep-Tracermass Spectrometer, Europa, UK) at the Western Australia Biochemistry Centre (WABC), University of Western Australia.

2.6. Data analysis

Differences in fungal community composition and abundance, vegetation structure and environmental data between sites were analysed using multivariate statistics in Primer 6 with Permanova using Multidimensional Scaling (MDS) and Principal Coordinate Analysis (PCO) using square root transformed data (Clarke and Gorley, 2006). Canonical Discrimination Analysis (CAP) in Primer with was also used to test hypotheses about macrofungal diversity (Ratkowsky, 2007). The StatView 5 statistical package was used for analysis of variance (www.sas.com).

3. Results

3.1. Vegetation, litter and soil properties

There were substantial differences in the understorey and overstorey structure and litter cover between dieback-affected and -unaffected sites (Fig. 3 and Table 1). Overstorey and litter cover were significantly different among the three locations (Table 1). Litter and coarse woody debris differed significantly between sites, but only the former was correlated with dieback (Table 1). Soil chemical data are not presented here as the measured parameters were variable across sites within treatments and only nitrate was significantly different between the dieback-affected and -unaffected sites (Table 1).

As shown in Fig. 3, plants with ectomycorrhizal (EM) and non-mycorrhizal (NM) roots are co-dominant in the overstorey of the unaffected sites. In affected sites, there is an almost total loss of NM trees (*B. grandis*), as well as major reductions in EM canopy trees (eucalypts) and some reduction in NM and EM understorey plants.

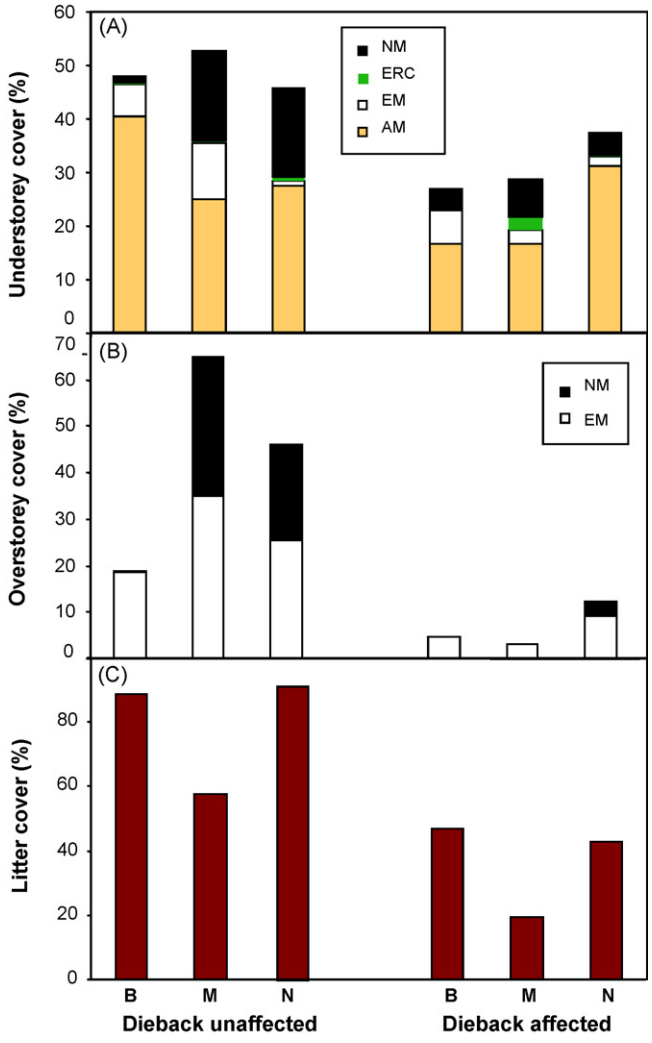

Fig. 3. Understorey, overstorey and litter cover in dieback-affected and dieback-unaffected sites, averaged across sampling times. NM = non-mycorrhizal, EM = ectomycorrhizal, ERC = ericoid mycorrhiza, AM = arbuscular mycorrhiza, B = Berkeley Rd, M = Myara Rd, N = North Rd.

The PCO plot in Fig. 4 illustrates strong trends in vegetation structure attributed to dieback in addition to a high degree in natural heterogeneity in vegetation. These data suggest the greatest impacts of dieback were on the trees *E. marginata*, *C. calophylla* and *B. grandis*. Fig. 4 also shows that vegetation at the North Rd site is less severely affected that the other two sites.

3.2. Macrofungal diversity and abundance

Overall, 149 putative species of macrofungi were recorded, of which 64 could be identified to species. The most dominant genera were *Cortinarius* (32 spp.), *Galerina* (9), *Collybia* (8), *Russula* (6) and *Boletus* (6). Many species were only encountered once and only 30 species (20% of total) were recorded in both dieback-affected and -unaffected transects. Overall, unaffected transects had almost twice the macrofungal diversity of dieback-affected transects and 84 species (57% of total) were exclusive to unaffected transects, but only 34 (23% of total) were exclusive to dieback-affected transects (Fig. 5). Mycorrhizal fungi were significantly more diverse in unaffected transects, but there was no significant difference in the diversity of saprotrophic fungi across sites (Figs. 5 and 6, Table 1).

When comparing sampling sites, the Berkeley Rd site had the highest total macrofungal diversity (120 spp.) and abundance (869) and North Rd had the lowest diversity (112 spp.) and abundance (426). The average diversity was significantly higher in all the unaffected transects than the dieback-affected transects, with Berkeley Rd and North Rd having the highest average

Table 1
Two-way ANOVAs contrasting the effects of dieback, site and their interactions on (A) vegetation and litter, (B) soils and (C) fungi.

Factor	*P*-value		
	Dieback	Site	Dieback × site
(A) Vegetation and litter			
Total understorey cover (%)	<0.0001*	0.8694	0.0122*
Total overstorey cover (%)	<0.0001*	0.0245*	0.5605
Total litter cover (%)	<0.0001*	<0.0001*	0.6559
Non-mycorrhizal plant cover (%)	0.0418*	0.0137*	0.0019*
Mycorrhizal plant cover (%)	0.0004*	0.0175*	0.3924
Cover of coarse woody debris (%)	0.7405	0.0124*	0.2567
(B) Soils			
NO_3^- (ppm)	<0.0001*	<0.0001*	<0.0001*
NH_4^+ (ppm)	0.5455	<0.0001*	0.2604
Soil moisture (%)	0.8443	<0.0001*	0.0802*
Pi (μg/g dry weight soil)	0.8029	<0.0001*	0.4030
Total C (%)	0.4399	0.0075*	0.1261
Total N (%)	0.7714	0.1077	0.1172
(C) Fungi			
Total fungal species diversity	<0.0001*	0.0415*	0.1253
Species diversity of mycorrhizal fungi	<0.0001*	0.0002*	0.0127*
Species diversity of saprotrophic fungi	0.0148*	0.4421	0.5715
Average fungal abundance	0.0490*	0.0952	0.5164
Abundance of saprotrophic fungi (%)	0.1103	0.0179*	0.0528
Abundance of mycorrhizal fungi (%)	0.0072*	0.0025*	0.0051*

* indicates a significant difference, $P < 0.05$.

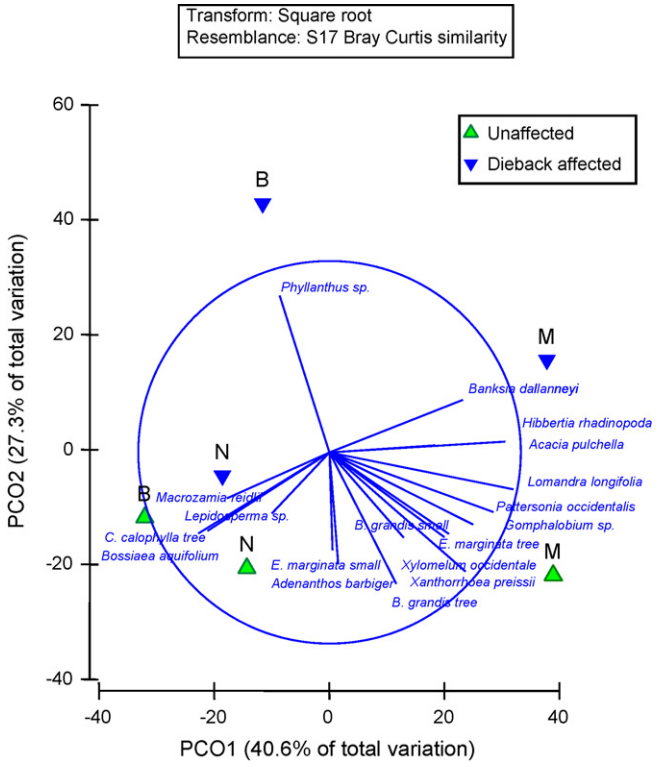

Fig. 4. Principal Coordinate Analysis plot showing the relative dissimilarity in vegetation cover between sites. Vectors of the relative cover of common plant species are overlain on the plot (longer vectors have represent higher correlation and the circle represents 100% correlation, trees and saplings are separated). B = Berkeley Rd, M = Myara Rd, and N = North Rd.

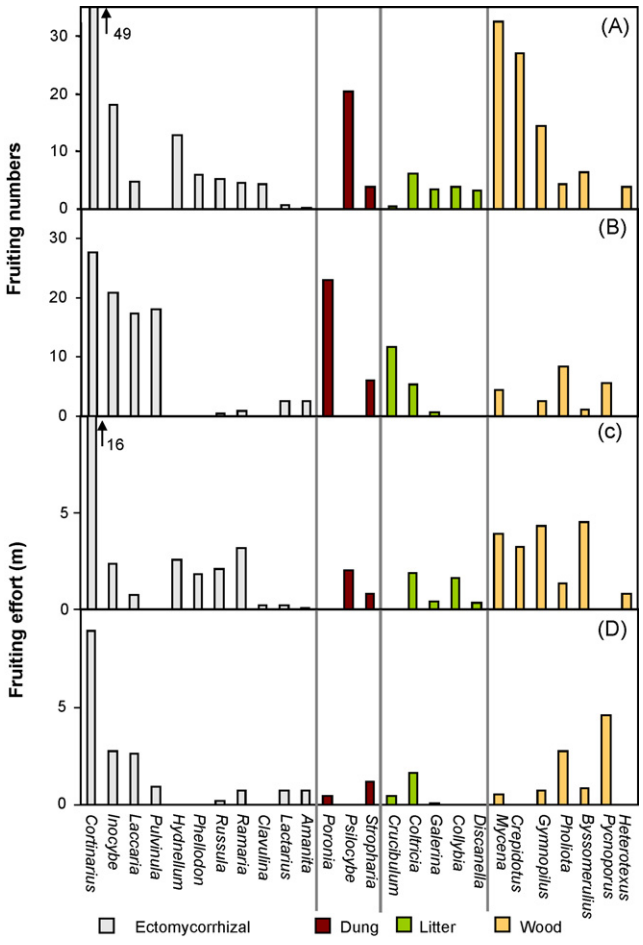

Fig. 5. Average abundance (A and B) and fruiting effort (C and D) for mycorrhizal and saprophytic fungi separated by substrate type for the most abundant genera of fungi in unaffected (A and C) and dieback affected (B and D) sites.

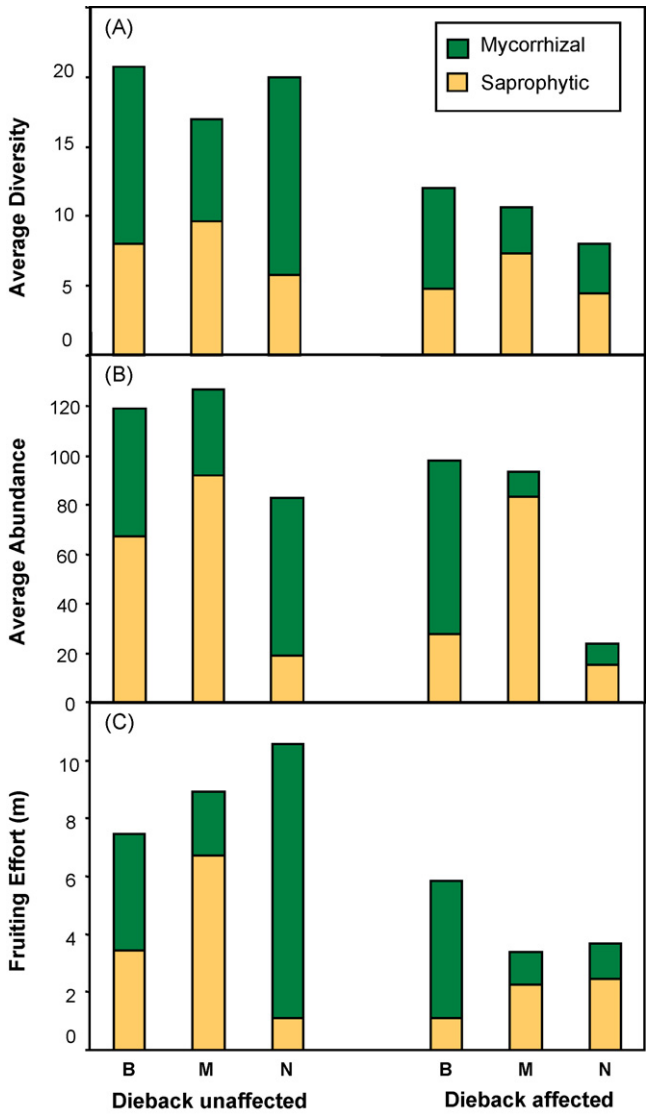

Fig. 6. (A) Diversity of mycorrhizal and saprotrophic fungi per transect, averaged across sampling times. (B) Abundance of mycorrhizal and saprotrophic fungi per transect, averaged across sampling times. (C) Fungi fruiting effort (average abundance × average size in m), of mycorrhizal and saprotrophic fungi per transect averaged across sampling times. B = Berkeley Rd, M = Myara Rd, N = North Rd.

diversity, of which over 60% were mycorrhizal species (Fig. 6 and Table 1). The overall diversity of saprotrophic fungi was significantly higher in dieback-affected transects but their relative abundance did not vary significantly (Table 1), presumably because many dung fungi occurred in all sites.

During the sampling period 1957 individual fruit bodies were recorded. The most abundant genera were *Cortinarius* (348 individuals), *Mycena* (171), *Inocybe* (171), *Crepidotus* (113), *Laccaria* (94), *Poronia* (92), *Psilocybe* (88) and *Gymnopilus* (88). *Cortinarius* species were by far the most important mycorrhizal fungi, followed by *Inocybe*, *Laccaria*, *Pulvinula* and *Hydnellum*. The saprophytic mycota were dominated by wood decay fungi such as *Mycena*, *Crepidotus* and *Gymnopilus*, followed by dung (coprophilous) fungi, including *Poronia* and *Psilocybe*, and litter fungi including *Crucibulum* and *Coltricia*. Coprophilous fungi were especially common in dieback-affected sites on dung of macropods (kangaroos and wallabies).

Dieback-unaffected transects had a significantly greater total fruit body abundance than affected transects (Table 1). The average abundance of fruit bodies was more variable than species richness with only Myara Rd and North Rd showing a large decrease in average abundance between unaffected and affected transects, especially for mycorrhizal species (Fig. 6). The overall diversity of saprotrophic species did not differ significantly between affected and unaffected transects (Table 1).

Abundance data were not necessarily indicative of relative dominance, as some abundant species, such as *Crepidotus* sp. and *Poronia ericii*, were smaller than 1 cm in diameter. Consequently we also calculated a weighted abundance scale using the average size of fruit bodies (referred to here as fruiting effort) to provide a better indication of the relative dominance of macrofungi. Fig. 6C shows a significant difference in fruiting effort between all unaffected and dieback-affected transects, with the North Rd unaffected transect having the most mycorrhizal fungus fruit bodies. When comparing average abundance with fruiting effort (Fig. 5), the relative importance of small saprotrophic fungi (especially dung and litter fungi) is greatly reduced in the latter.

The multivariate ordination (MDS) plot (Fig. 7) illustrates a strong shift in community composition between each pair of unaffected and dieback-affected transects and also shows shifts in the macrofungal community over time at each site. The temporal shifts are due to turnover of earlier versus later fruiting fungi, but may also have been influenced by atypically low rainfall early in winter (Fig. 2). The PCO plot of fungal assemblages also shows correlations between multivariate fungal community patterns and ecological categories of fungi (Fig. 8). These correlations further support the hypothesis that mycorrhizal fungi were most affected

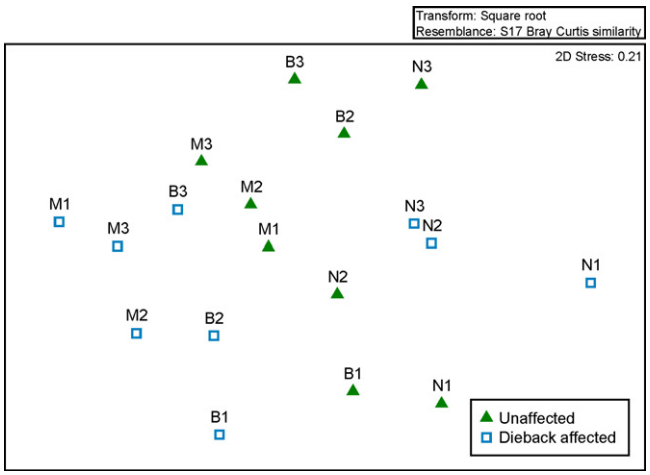

Fig. 7. Multidimensional Scaling plot summarising variations in fungal diversity between jarrah forest dieback-affected and -unaffected sites at different sampling times. B = Berkeley Rd, M = Myara Rd, and N = North Rd.

by dieback associated vegetation changes at these sites. Fungi parasitic on other fungi were also observed most often in dieback-affected sites, but were relatively uncommon (Fig. 8).

3.3. Comparison of fungal communities to plant communities

A Canonical Correlation Analysis (CAP) contrasting fungal community composition and vegetation structure is presented in Fig. 9. This analysis illustrates both the gradient between unaffected transects (positive scores on Axis 2) and the dieback-affected transects (negative scores on Axis 2), but also strongly demonstrates the uniqueness of the North Rd site (separated by Axis 1). The North Rd site had the lowest fungal species diversity and abundance, but had a higher tree cover than the other dieback-affected sites (Figs. 3 and 6). Cross validation and permutation tests from the CAP analysis confirmed there was a significant relationship between vegetation and macrofungal assemblages (cross validation test: 15/18 (83.333%), permutation test: $P = 0.0001$).

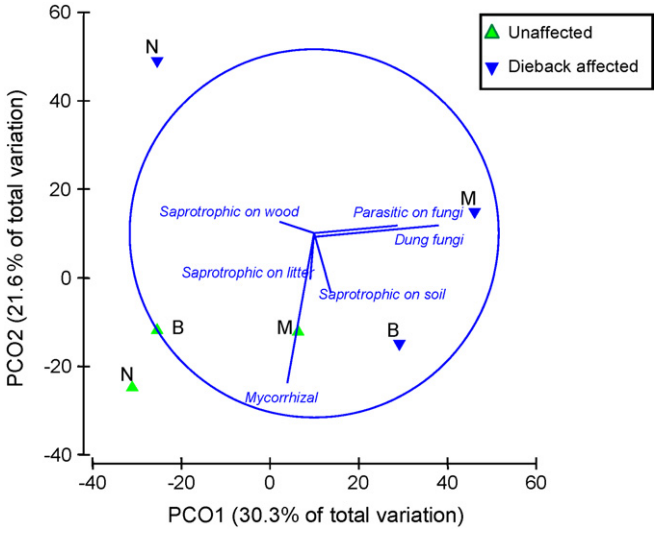

Fig. 8. Principal Coordinate Analysis plot of macrofungal species abundance data between sites averaged over sampling times. Correlation vectors show the relative abundance of different functional groups of fungi. B = Berkeley Rd, M = Myara Rd, and N = North Rd.

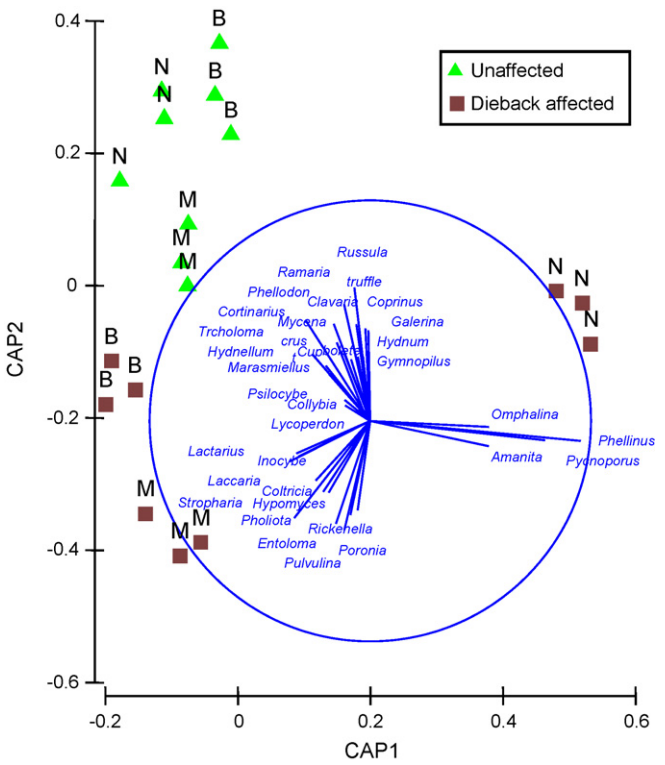

Fig. 9. The first two axes of a Canonical Correlation analysis showing the relationship between macrofungal assemblages and vegetation structure for transects in dieback-affected and -unaffected jarrah forest. Multiple letters with the same treatment denote different sampling times. Correlation vectors show the relative abundance of fungal genera. B = Berkeley Rd, M = Myara Rd, and N = North Rd.

4. Discussion

Our findings were consistent with previous observations of the major impacts of dieback on the jarrah forest (Podger, 1972; Shearer and Dillon, 1996; McDougall et al., 2002, 2005). In particular, overstorey cover, understorey cover and litter were all significantly lower in dieback-affected sites, which were relatively open and exposed. This study is one of relatively few that include data on the relative dominance of mycorrhizal and non-mycorrhizal plants. Results for the jarrah forest presented here are similar to those from the study of a site 20 km further northeast by Brundrett and Abbott (1994), except that NM plants were less dominant, even in the absence of dieback impacts. Indeed the relative dominance of AM, EM and NM plants varied considerably between sites due to natural variations in relative plant dominance in the jarrah forest, even before major impacts of dieback, which are patchy due to localized disease fronts, as well as the impacts of past logging practices and fires.

Many of the fungi observed in this study were identified using designated field names, which are consistent with broader jarrah forest area surveys (Department of Environment and Conservation, 2003–2007). Improved taxonomic knowledge of fungi in the jarrah forest and the use of molecular techniques to identify fungi in the plant roots in the absence of their fruiting bodies will allow for a more comprehensive dataset of fungal diversity. However, issues with the detection and identification of fungi were less important to this study which compared paired sample sites with similar vegetation composition, over the same sampling period.

Our results suggest that dramatic changes to vegetation structure and composition resulting from *Phytophthora* dieback have a major impact on the diversity and abundance of macrofungi,

especially ectomycorrhizal fungi. This is not surprising since EM fungi are considered to be highly dependent on host plants for energy (Smith and Read, 1997; Brundrett, 2004). At each site, the overstorey and litter cover appeared to be closely related to the macrofungal diversity and abundance, especially for mycorrhizal fungi, presumably because both are linked to tree cover. Other disturbances which have substantially altered vegetation cover in forests, such as fire and logging, can also reduce the diversity and abundance of some macrofungi in the short term (Byrd et al., 2000; Dahlberg et al., 2001; Robinson and Bougher, 2003; Robinson et al., 2008).

This study provides fungal fruiting abundance and fruiting effort data (corrected for size differences in fungi) that indicates the productivity of fungi in this ecosystem. However, species diversity and abundance measures from each site may be underestimated, as hypogeal and microfungi were excluded from sampling, and some taxa not yet formally named but referred to by field names may include multiple species. Additionally, macrofungi which fruited between sampling times or outside the duration of the study have also been missed. Other studies have shown that above-ground fruiting bodies do not fully reflect the below-ground diversity, especially in regard to ectomycorrhizal fungi (Dahlberg and Stenlid, 1995; Gardes and Bruns, 1996; Peter et al., 2001; Yamada and Katsuya, 2001; Glen et al., 2008). Because all fungi do not fruit every year (Tyler, 1992), an extended study covering several years and a variety of sampling methods is required to gain better estimates of species diversity and abundance.

Difference in fruit body abundance between affected and unaffected transects was less dramatic than differences in species diversity but were still significant and were consistent with trends in both litter cover and overstorey cover. The relative size of the most abundant fruit bodies in the dieback-affected areas was considerably smaller than that of the unaffected areas, e.g. fruit bodies of *P. ericii*, *Pulvinula tetraspora*, *Laccaria fraterna* and *Crucibulum laeve* are an order of magnitude smaller than most other species observed in this study. Consequently, the relative importance of these species was better represented by fruiting effort data. This index provides a correction for major differences in fungal size, but would be less accurate than biomass data. However, biomass sampling requires destructive harvesting which is not always appropriate or feasible.

Our results suggest mycorrhizal fungi are generally more dominant in the jarrah forest than saprotrophic fungi, especially under relatively healthy trees. These results are consistent with the findings of Brundrett and Abbott (1991), Gardner and Malajczuk (1988), Hilton et al. (1989) and Glen et al. (2008) that show that the two most dominant forest trees *E. marginata* and *C. calophylla*, have mycorrhizal associations. In contrast, the abundance of saprotrophic fungi did not decrease substantially in dieback-affected transects. This is not surprising since saprotrophic fungi will feed on dead or dying vegetation remains and some litter would blow in from adjacent healthy forest. Also, saprotrophic fungi may tend to fruit more abundantly when their substrates become depleted. The amount of organic materials available to support the formation of sporocarps would vary across sites because of varying times since *P. cinnamomi* infection and the impact of fire on fallen wood. In the long term, the quantity of infected dead trees and wood debris can be expected to decline as woody debris is decayed by saprotrophic fungi or burnt by fire. Therefore, forest dieback should also eventually have a negative impact on saprotrophic fungi.

Multidimensional Scaling, Principal Component Analysis and Canonical Correlation were found to be valuable tools for visualising differences in plant and fungal diversity across sites (see Ratkowsky, 2007). The latter also allowed correlation vectors to be overlain that show dominant trends in fungal and plant distribution across sites. These ordination methods showed that the variation in fungal communities between the different dieback-affected sites was a lot greater than variation between different unaffected sites, which may be attributed to variations in the impacts if dieback on tree cover, perhaps due to the time since *P. cinnamomi* infection, as well as difference in original vegetation composition.

Fungal communities can respond to changes in soil nutrient status (Grierson and Adams, 2000; Packham et al., 2002; Robinson and Bougher, 2003; Kranabetter et al., 2009). In our study, nitrate, ammonium, soil moisture and total soil carbon all varied significantly between sites, possibly helping to explain the observed differences in macrofungal communities between sites. However, only nitrate showed a significant difference between affected and unaffected transects, with proportions higher in dieback-affected transects. Mycorrhizal fungi influence the acquisition of nitrogen and phosphorus for plants (Hobbie et al., 1998; Smith and Read, 1997), therefore, the greater plant available nitrate in affected transects may be due to less competition from plants and mycorrhizal fungi for available nutrients.

This study provided valuable new insight into the impacts of jarrah forest dieback on fungal communities, especially concerning the relative abundance of saprophytic and mycorrhizal fungi. Future studies would benefit from the investigation of host and substrate specificity to better understand successional dynamics of fungi as plant communities change due to major disturbances such as dieback. Fire and logging also have impacts on the relative dominance and abundance of trees and understorey vegetation, and potential interactions of these with dieback are worthy of further investigations.

In addition to the impacts of dieback on plant communities we observed substantial changes in the relative dominance of many genera and functional groups of fungi. Our data show that severe dieback on the jarrah forest plants is linked to major impact on fungal diversity, as is the case with other types of disturbance to ectomycorrhizal tree dominated ecosystems. In this study, particular mycorrhizal genera including *Lactarius*, *Amanita* and *Entoloma* were observed to be more common in dieback-affected areas than unaffected areas, in contrast to other genera including *Russula*, *Ramaria* and *Cortinarius* that were largely absent from affected areas. Fungi such as *Laccaria* are well known as early colonists of jarrah forest following bauxite mining (Gardner and Malajczuk, 1988; Glen et al., 2008) as well as young eucalypt plantations in Western Australia (Lu et al., 1999). The reverse is true of *Russula* and *Cortinarius* which are typically absent from disturbed habitats. Thus, despite greatly reduced tree cover, dieback-affected forest stands still contain mycorrhizal fungi, but these tend to be relatively disturbance tolerant species. Our results suggest that dieback is impacting fungal communities in a similar way to other forms of severe disturbance, perhaps because trees affected by dieback are less able to support the most specialised mycorrhizal fungi. However, reduced soil quality and litter cover are also likely to contribute to these trends.

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References

Bray, R., Kurtz, L., 1945. Determination of total, organic and available forms of phosphorus in soils. Soil Sci. 59, 39–45.

Brundrett, M.C., 2004. Diversity and classification of mycorrhizal associations. Biol. Rev. 79, 473–495.

Brundrett, M.C., 2008. Mycorrhizal Associations: The Web Resource. www.mycorrhizas.info.

Brundrett, M.C., 2009. Mycorrhizal associations and other means of nutrition of vascular plants: understanding the global diversity of host plants by resolving conflict information and developing reliable means of diagnosis. Plant Soil 320, 37–77.

Brundrett, M.C., Abbott, L.K., 1991. Roots of jarrah forest plants. I. Mycorrhizal associations of shrubs and herbaceous plants. Aust. J. Bot. 39, 445–457.

Brundrett, M.C., Abbott, L.K., 1994. Mycorrhizal fungus propagules in the jarrah forest. I. Seasonal study of inoculum levels. New Phytol. 127, 539–546.

Brundrett, M.C., Bougher, N., Dell, B., Grove, T., Malajczuk, N., 1996. Working with Mycorrhizas in Forestry and Agriculture. ACIAR Monograph 32. Australian Centre for International Agricultural Research, Canberra.

Bureau of Meteorology, 2007. Climate Statistics for Western Australia. www.bom.gov.au.

Byrd, K., Parker, T., Vogler, D., Cullings, K., 2000. The influence of clear-cutting on ectomycorrhizal fungus diversity in a lodgepole pine (*Pinus contorta*) stand, Yellowstone National Park, Wyoming, and Gallatin National Forest, Montana. Can. J. Bot. 78, 149–156.

Chapman, A.D., 2005. Numbers of living species in Australia and the world. Australian Biodiversity Information Services, Toowoomba, Australia. A report for the Department of the Environment and Heritage, September 2005.

Claridge, A.W., May, T.W., 1994. Mycophagy among Australian mammals. Aust. J. Ecol. 19, 251–257.

Clarke, K., Gorley, R., 2006. PRIMER v6. User Manual/Tutorial. PRIMER-E Ltd., Plymouth.

D'Souza, N.K., Colquhoun, I.J., Shearer, B.L., Hardey, G.E.S.J., 2005. Assessing the potential for biological control of *Phytophthora cinnamomi* by fifteen native Western Australian jarrah-forest legume species. Australasian Plant Pathol. 34, 533–540.

Dahlberg, A., Schimmel, J., Taylor, A., Johannesson, H., 2001. Post-fire legacy of ectomycorrhizal fungal communities in the Swedish boreal forest in relation to fire severity and logging intensity. Biol. Conserv. 100, 151–161.

Dahlberg, A., Stenlid, J., 1995. Spatiotemporal patterns in ectomycorrhizal populations. Can. J. Bot. 73, 1222–1230.

Department of Environment and Conservation, 2006. Phytophthora Dieback Atlas from the Bush to Your Back Fence: What You Need to Know. Kensington, WA.

Department of Environment and Conservation, 2003–2007. Forestcheck: Reports of Progress. http://www.naturebase.net/content/view/2388/482.

Department of Environment and Conservation, 2007. Managing Dieback – Impacts in WA. http://www.dec.wa.gov.au/diebackatlas/impacts-in-wa.html.

Environmental Protection Authority, 2007. State of the Environment Report: Western Australia 2007. http://www.dec.wa.gov.au/content/view/5605/2290/.

Fitter, A.H., Garbaye, J., 1993. Interactions between mycorrhizal fungi and other soil organisms. Plant Soil 159, 123–132.

Gardes, M., Bruns, T., 1996. Community structure of ectomycorrhizal fungi in a *Pinus muricata* forest: above- and below-ground views. Can. J. Bot. 74, 1572–1583.

Gardner, J.H., Malajczuk, N., 1988. Recolonisation of rehabilitated bauxite mine sites in Western Australia by mycorrhizal fungi. For. Ecol. Manage. 24, 27–42.

Garkaklis, M.J., Calver, M.C., Wilson, B.A., Hardy, G.E.St.J., 2004. Habitat alteration caused by an introduced plant disease – *Phytophthora cinnamomi*: a potential threat to the conservation of Australian forest fauna. In: Lunney, D. (Ed.), Conservation of Australia's Forest Fauna. 2nd ed. Royal Zoological Society of New South Wales, Sydney, pp. 899–913.

Glen, M., Bougher, N.L., Colquhoun, I.J., Vlahos, S., Loneragan, W.A., O'Brien, P.A., Hardy, G.E.St.J., 2008. Ectomycorrhizal fungal communities of rehabilitated bauxite mines and adjacent, natural jarrah forest in Western Australia. For. Ecol Manage. 255, 214–225.

Grierson, P.F., Adams, M.A., 2000. Plant species affect acid phosphatase, ergosterol and microbial P in a Jarrah (*Eucalyptus marginata* Donn ex Sm.) forest in southwestern Australia. Soil Biol. Biochem. 32, 1817–1827.

Hardham, A.R., 2005. Pathogen profile: *Phytophthora cinnamomi*. Mol. Plant Pathol. 6, 589–604.

Hilton, R., Malajczuk, N., Pearce, M., 1989. Larger fungi of the jarrah forest: an ecological and taxonomic survey. In: Dell, B. (Ed.), The Jarrah Forest. Kluwer Academic Publishers, Dordrecht, pp. 89–109.

Hobbie, E., Macko, S., Shugart, H., 1998. Insights into nitrogen and carbon dynamics of ectomycorrhizal and saprotrophic fungi from isotopic evidence. Oecologia 118, 353–360.

Kranabetter, J.M., Friesen, J., Gamiet, S., Kroeger, P., 2009. Epigeous fruiting bodies of ectomycorrhizal fungi as indicators of soil fertility and associated nitrogen status of boreal forests. Mycorrhiza 19, 535–548.

Kuo, S., 1996. Phosphorus. In: Sparks, D.L. (Ed.), Methods of Soil Analysis. Part 3. Chemical Methods. 3rd ed. Soil Science Society of America, Madison, Wisconsin, pp. 869–920.

Lambers, H., Shane, M.W., Cramer, M.D., Pearse, S.J., Veneklaas, J., 2006. Root structure and functioning for efficient acquisition of phosphorus: matching morphological and physiological traits. Ann. Bot. 98, 693–713.

Lamont, B., 1982. Mechanisms for enhancing nutrient uptake in plants, with particular reference to mediterranean South Africa and Western Australia. Bot. Rev. 48, 597–689.

Lu, X.H., Malajczuk, N., Brundrett, M., Dell, B., 1999. Fruiting of putative ectomycorrhizal fungi under blue gum (*Eucalyptus globulus*) plantations of different ages in Western Australia. Mycorrhiza 8, 255–261.

Maser, C., Claridge, A.W., Trappe, J.M., 2008. Trees, Truffles, and Beasts. Rutgers University Press, New Brunswick.

McDougall, K.L., Hobbs, R.J., Hardy, G.E.S.J., 2002. Vegetation of *Phytophthora cinnamomi*-infested and adjoining uninfested sites in the northern jarrah (*Eucalyptus marginata*) forest of Western Australia. Aust. J. Bot. 50, 277–288.

McDougall, K.L., Hobbs, R.J., Hardy, G.E.S.J., 2005. Distribution of understorey species in forest affected by *Phytophthora cinnamomi* in south-western Western Australia. Aust. J. Bot. 53, 819–831.

Packham, J.M., May, T.W., Brown, M.J., Wardlaw, T.J., Mills, A.K., 2002. Macrofungal diversity and community ecology in mature and regrowth wet eucalypt forest in Tasmania: a multivariate study. Austral. Ecol. 27, 149–161.

Peter, M., Ayer, F., Egli, S., Honegger, R., 2001. Above- and below-ground community structure of ectomycorrhizal fungi in three Norway spruce (*Picea abies*) stands in Switzerland. Can. J. Bot. 79, 1134–1151.

Podger, F.D., 1972. *Phytophthora cinnamomi*, a cause of lethal disease in indigenous plant communities in Western Australia. Phytopathology 62, 972–981.

Ratkowsky, D.A., 2007. Visualising macrofungal species assemblage compositions using canonical discrimination analysis. Australasian Mycol. 26, 75–85.

Rayment, G.E., Higginson, F.R., 1992. Australian Laboratory Handbook of Soil and Water Chemical Analysis Methods. Inkata Press, Sydney.

Robinson, R., Bougher, N., 2003. The response of fungi to fire in Jarrah (*Eucalyptus marginata*) and Karri (*Eucalyptus diversicolour*) forests of south-west Western Australia. In: Abbott, I., Burrows, N. (Eds.), Fire in Ecosystems of South-West Western Australia: Impacts and Management. Backhuys Publishers, Leiden, Netherlands, pp. 269–289.

Robinson, R.M., Tunsell, V.L., 2007. A list of macrofungi recorded in burnt and unburnt *Eucalyptus diversicolor* regrowth forest in the southwest of Western Australia: 1998–2002. Conserv. Sci. West. Aust. 6, 75–96.

Robinson, R.M., Mellican, A.E., Smith, R.H., 2008. Epigeous macrofungal succession in the first five years following a wildfire in karri (*Eucalyptus diversicolor*) regrowth forest in Western Australia. Austral. Ecol. 33, 807–820.

Shearer, B.L., Dillon, M., 1996. Susceptibility of plant species in banksia woodlands on the swan coastal plain, Western Australia, to infection by *Phytophthora cinnamomi*. Aust. J. Bot. 44, 433–445.

Shearer, B.L., Crane, C.E., Cochrane, A., 2004. Quantification of the susceptibility of the native flora of the South West Botanical Province, Western Australia, to *Phytophthora cinnamomi*. Aust. J. Bot. 52, 435–443.

Smith, S.E., Read, D.J., 1997. Mycorrhizal Symbiosis, 2nd ed. Academic Press, London.

Technicon, 1977. Individual/Simultaneous Determination of Nitrogen and/or Phosphorus in BD Acid Digests. Industrial Method No. 329–374 W/B. Technicon Industrial Systems, New York.

Tyler, G., 1992. Tree species affinity of decomposer and ectomycorrhizal macrofungi in beech (*Fagus sylvatica* L.), oak (*Quercus robur* L.) and hornbeam (*Carpinus betulus* L.) forests. For. Ecol. Manage. 47, 269–284.

Yamada, A., Katsuya, K., 2001. The disparity between the number of ectomycorrhizal fungi and those producing fruit bodies in a *Pinus densiflora* stand. Mycol. Res. 105, 957–965.