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# The influence of fire frequency on arbuscular mycorrhizal colonization in the shrub *Dillwynia retorta* (Wendland) Druce (Fabaceae)

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**Abstract** Fire regimes have three inter-related components that can affect population dynamics: frequency, intensity and season. However, there has been little effort to study the effects of any of these components on arbuscular mycorrhizas (AM). In order to examine the long-term effects of fire frequency on AM colonization, the roots of *Dillwynia retorta* were examined at 32 sites supporting Hawkesbury Sandstone vegetation in the Sydney region of southeastern Australia. These sites were representative of the broad-scale variability in fire frequencies with respect to the length and timing of inter-fire intervals found in the Sydney region during the previous 30 years. The length of the shortest inter-fire interval was significantly correlated with total AM colonization, and the length of the longest inter-fire interval was related to the arbuscular colonization. The length of the most-recent inter-fire interval and the time since the shortest inter-fire interval were not related to AM colonization in *D. retorta*. Furthermore, AM colonization was directly related to the local abundance of the host plant, indicating that the effects of fire frequency on AM colonization are likely to occur indirectly via direct effects on the host plant. Canonical correspondence analysis demonstrated that the presence and abundance of alternate potential hosts had no influence on mycotrophy in *D. retorta*. Thus, the impact of fire on *D. retorta* was probably the main factor influencing its mycorrhizal status in relation to fire history.

**Key words** Glomalean · Arbuscule · Inter-fire interval · Wildfire

## Introduction

It has previously been shown that arbuscular mycorrhizas (AM) have a critical influence on the regrowth of plants in disturbed areas (eg. Brockhoff and Allaway 1989; Khan 1978; Miller 1979; Reeves et al. 1979). The mechanisms of post-fire plant regrowth are well described (Bond and van Wilgen 1996; Whelan 1995), but the impact of burning upon mycorrhizas, especially in the longer term, has received inadequate study. This paper describes an investigation into the influence of variation in the length of the shortest and longest inter-fire intervals (IFIs), the most recent IFI and the time since the shortest IFI on AM colonization of a single, susceptible host species. Knowledge of the responses of mycorrhizas to fire is of intrinsic interest, as well as being essential for the scientific management of plant communities.

Fire regimes are usually considered to have three inter-related components that can affect plant population dynamics: fire frequency, fire intensity, and season of burning (Whelan 1995). Plant population changes at short and long intervals are often determined by fire frequency, while changes at intermediate intervals are influenced more by season and intensity (Bond and van Wilgen 1996). The effects of fire frequency, which is the number of fires per unit of time, can be further subdivided into those resulting from at least three variables (Morrison et al. 1995): (1) the length of the IFIs, (2) the variability of the length of the IFIs, and (3) the time since the most recent fire. These variables are inter-related, since as the fire frequency changes so does the average length of the IFIs in any one period and the time-since-fire (Morrison et al. 1995).

The effects of complex fire-frequency interactions have received previous study in plant communities by Bradfield (1981), Cary and Morrison (1995), Morrison et al. (1995), and Nieuwenhuis (1987). Morrison et al. (1995) found that the variability of distribution of plant

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species whose adults can survive fires increases with increasing time-since-fire, whilst shorter IFIs increase the distribution variability of fire-sensitive species. They also found that the effect of IFI was not purely related to the length of the shortest interval, but also the length of previous intervals. Morrison et al. (1995) concluded that variability in IFI with time is one factor contributing to the large plant species diversity present in dry-sclerophyll communities of Australia.

There has been little concerted effort to study the effects of fire regimes on AM. Several workers observed reductions in AM host colonization and/or rhizosphere spore numbers as a result of burning (Allsopp and Stock 1994; Bellgard et al. 1994; Dhillion et al. 1988; Rashid et al. 1997; Vilariño and Arines 1991; Wicklow-Howard 1989). It has been suggested that the impact of burning results from soil heating (Klopatek et al. 1988; Rashid et al. 1997), host plant responses (Dhillion et al. 1988), chemical changes to the solum (Vilariño and Arines 1992), or loss of vegetation and topsoil due to post-fire erosion (Rashid et al. 1997). Opinions on the longer-term effects of fire vary. Estimates of the time taken for burned areas to recover to control levels of host colonization or spore counts vary from one season (Dhillion et al. 1988), to the time required for wash-out of aqueous soluble residues (Vilariño and Arines 1992), to two growing seasons (Allsopp and Stock 1994), to 6–8 growing seasons (Wicklow-Howard 1989). Gibson and Hetrick (1988) considered that fire frequency, along with topography, was a major influence on arbuscular mycorrhizal fungi (AMF) species diversity. Variation in host flora and soil types may confound direct comparison between any of these studies.

The consensus is that burning causes a reduction in AM root colonization and soil propagule levels, especially in the short term. The longer-term impact of fire on mycorrhizal relationships, however, has received insufficient study, as both mycorrhizal status and fire are known to have significant influences on plant communities. One hypothesis is that more frequent burning could increase AMF abundance through increases in relative population sizes of AM host species, such as grasses, at the expense of nonmycorrhizal plants. Alternatively, the physical impact of repeated fires could reduce soil inocula to a level from which recovery would be slow, thus causing an overall reduction in the hypogeous AMF population density. Repeated burning could also reduce AMF abundance by destroying host plants.

In this paper, we present an initial step towards clarifying the long-term inter-relationship between fire frequency and AM ecology in Australian dry-sclerophyll plant communities. Specifically, we aimed to determine whether there are longer-term influences on AM colonization of a susceptible host from variation in the lengths of the shortest and longest IFIs, the most recent IFI, and the time since the shortest IFI.

## Methods and materials

The work was carried out in dry-sclerophyll communities in three coastal national parks in the Sydney region, following a sampling strategy similar to that of Morrison et al. (1995). Samples were collected in July 1996 from the area between Staples Lookout and Kariong in Brisbane Water National Park (33°27'S, 151°17'W; 5 sites), on the Lambert Peninsula in Ku-ring-gai Chase National Park (33°37'S, 151°16'W; 15 sites), and in Royal National Park between Loftus Heights and Wattamolla (34°07'S, 151°05'W; 12 sites). These areas were representative of the variability in fire frequency in the parks with respect to combinations of IFIs and time-since burning (see Table 1 for details).

Samples were taken from plateaus and ridge-tops over Hawkesbury Sandstone at approximately 150 m a.s.l. The soil in this area is composed of grey-brown and yellow-grey medium- and coarse-grained sands, with smaller quantities of fine sandy loam and yellow podsols. There is no profile development apart from a slight organic matter accumulation at the surface, the profile passing directly into undifferentiated mineral solum (Walker 1958). Underlying the soil are discontinuous layers of highly cross-bedded quartz sandstone with an argillaceous content (Bryan et al. 1966). The vegetation type on the sites was closed scrub and low to low-open woodland (Benson and Faulding 1981; Thomas and Benson 1985), which is the most widespread natural vegetation type remaining in the Sydney region (Benson and Howell 1990).

Each sampled site met the following criteria:

1. It was burnt by a wildfire in the period between 1964–1968, to provide a standardized first known fire (records are inadequate prior to this time).
2. The most recent fire was 2 years previous to sampling, to avoid problems with identifying small seedlings and with sampling

**Table 1** Fire histories of the National Park study sites. All sites were exposed to a January 1994 wildfire

| Site number | Location | Inter-fire intervals |
|---|---|---|
| 1 | Royal | 11 15 |
| 2 | | 8 18 |
| 3 | | 8 3 15 |
| 4 | | 8 18 |
| 5 | | 8 4 14 |
| 6 | | 2 8 4 12 |
| 7 | | 4 6 3 13 |
| 8 | | 3 20 6 |
| 9 | | 20 6 |
| 10 | | 8 12 6 |
| 11 | | 6 2 12 6 |
| 12 | | 11 8 7 |
| 13 | Brisbane Water | 26 |
| 14 | | 3 8 1 11 6 |
| 15 | | 15 14 |
| 16 | | 11 9 6 |
| 17 | | 20 6 |
| 18 | Ku-ring-gai Chase | 8 5 11 5 |
| 19 | | 13 16 |
| 20 | | 27 2 |
| 21 | | 18 11 |
| 22 | | 18 5 6 |
| 23 | | 23 6 |
| 24 | | 22 1 6 |
| 25 | | 18 10 1 |
| 26 | | 7 8 14 |
| 27 | | 20 1 8 |
| 28 | | 8 16 5 |
| 29 | | 15 14 |
| 30 | | 20 1 8 |
| 31 | | 8 4 17 |
| 32 | | 29 |

individuals that could prove to be unsuccessful in establishment after the fire. Poor establishment after burning is potentially related to mycorrhizal development. We considered that 2 years was sufficient to eliminate effects due to this factor. All of the sites were burnt by wildfires in January 1994.

3. All fires in the recorded history covered an area of a least 5 ha, to avoid effects related to small spot fires.
4. Boundaries between areas with different fire histories were clearly defined, to ensure accurate sample placement.
5. The composition of the plant communities was apparently consistent with the recorded fire histories, and was completely burnt by at least the most recent fire, to ensure accuracy of the recorded fire regime.

Fire histories were determined from the records of the NSW National Parks and Wildlife Service. From these data it was possible to locate suitable replicate sampling areas with respect to vegetation type and fire history.

The sampling design assumed that the fire histories of all of the areas were similar or at least randomized prior to the recording of fire regimes in the early 1960 s. This assumption is reasonable, based on the fact that fires in the Sydney region before this period were mainly wildfires covering very large areas (Kodela and Dodson 1989). The sampling protocol also assumes that intensity, season and wild or prescribed fire effects were randomized across areas.

Two data sets were collected at each of the 32 sites: floristic composition, and %AM root colonization. For the floristic data, we estimated the abundance of each of the 214 vascular plant species encountered at each site using the importance-score technique of Outhred (1984), each sample consisting of a pair of 100 $m^2$ quadrats. This technique produces abundance scores functionally equivalent to frequencies and thus directly related to plant density. The abundance data from the replicate quadrats were pooled for analysis. All species nomenclature follows Beadle et al. (1982).

For AM quantification, five complete root systems from seedlings of *Dillwynia retorta* (Wendland) Druce ssp. *retorta* were sampled from each of the sites. A single plant species was sampled at all sites, to avoid any confounding influence resulting from the use of different hosts with variable demands on the mycorrhizal symbiosis. *D. retorta* was one of the species present at all sites examined. Microtopographical variation may have led to differences in symbioses, but we assumed that this was randomized throughout the samples. Only seedlings were sampled (plants which were growing from seed); resprouting plants identified by the presence of well-developed, woody rootstocks were avoided. Seedlings were chosen as we wished to sample roots which could only have become infected by contact with soil-borne propagules or extraradical hyphae, rather than by hyphal extension through attachment to a surviving host infected pre-fire. At least 150 mm of fine feeder root was collected from each plant by excavation of the entire phytomass. The plants sampled were of similar size due to the 1994 fire at all sites. Note that plants were collected in the vicinity of the quadrats described above, but no attempt was made to place them in exactly the same place. Nevertheless, the floristic composition data are a good indication of the relative densities of plant species (potential alternate AM hosts) at each of the sites.

The roots were fixed in absolute ethanol immediately on collection in the field. In the laboratory, root systems were rinsed to remove adhering soil and residual ethanol, before clearing, bleaching and staining with trypan blue in acidic glycerol using the method of Koske and Gemma (1989). Arbuscular, vesicular and total AM colonization (comprising arbuscules, vesicles, intraradical hyphae and intracellular hyphal coiling, but not extraradical structures) were determined for fine lateral roots using the gridline-intercept method of McGonigle et al. (1990) and an Olympus BX50 microscope with Nomarski differential interference contrast optics.

To determine the relationship between fire frequency characteristics of a site (shortest IFI, longest IFI, most recent IFI, time since the shortest IFI) and the AM colonization levels in *D. retorta* roots, the percent colonization data were arcsin transformed, and then analysed using non-linear least-squares curve fitting (Wilkinson 1991) with a maxima-function model of the form: $y=c+[a_* x_* e^{(b^* x)}]$ (Keen and Spain 1992). The shortest IFI was 1–29 years and the longest IFI was 11–29 years. Pearson correlation analyses (Wilkinson 1991) were used to determine whether AM colonization was related to *D. retorta* abundance.

To examine the relationship between mycorrhizal colonization in *D. retorta* and abundance of the vascular plant species, canonical correspondence analysis (ter Braak 1988) was performed on the arcsin-transformed colonization data and the frequency data from the 214 plant species. This is a multivariate analysis technique based on correspondence analysis which, in a joint analysis of two data sets (e.g. floristic and AM colonization in *D. retorta*), assesses the degree to which they show co-variation (ter Braak and Prentice 1989). Thus, patterns among the samples that occur in both data sets are recorded, while patterns unique to either one of the data sets are ignored. The canonical correspondence analysis produces two inter-related ordination diagrams, one for each of the two data sets, which can be displayed simultaneously in a biplot. The floristic variation associated with the AM variables displayed by the biplot can be assessed from the percentage variation shared between the two data sets. A Monte Carlo permutation test was used to assess the statistical significance of the association found.

## Results

In contrast to the findings of Bellgard (1991) that *D. retorta* harboured no AM colonization in soils similar to ours, this species was found to be consistently AM. A total of 17.8% of 152 plants examined had arbuscules, 65.1% harboured vesicles, and 99.3% contained at least one AM structure including AM intraradical hyphae. Mean arbuscular infection was low, at 0.44%, whilst mean vesicular colonisation was 1.84% and total infection was 23.13% (all data untransformed). Root-length infection was 0–69% (untransformed). According to the scheme of Brundrett et al. (1996), *D. retorta* would be classified as facultatively mycorrhizal (low infection levels, fine root system), but also has features of obligate mycorrhization (consistently colonized, short root hairs).

The regression analyses of the arcsin-transformed colonization data for *D. retorta* with the various fire characteristics (Table 2) indicate significant ($P<0.05$) relationships between total AM colonization and the length of the shortest IFI and between arbuscular colonization and the length of the longest IFI. No relationships were detected between arbuscular colonization and shortest IFI, or vesicular/total colonization and longest IFI, or between colonization type and time since the most recent fire or time since the shortest IFI. For total colonization and shortest IFI (Fig. 1), total AM colonization was maximal (ca. 55% arcsin transformed) when the shortest IFI was ca. 6 years, decreasing exponentially with increasing or decreasing duration of the shortest IFI. For arbuscular colonization and longest IFI (Fig. 2), there was an exponential decrease in arbuscular colonization with longest IFI increasing from 10 to 13 years, with an asymptote at greater IFI

**Table 2** Results of the least-squares non-linear regression analyses of the arcsin-transformed arbuscular mycorrhizal (AM) colonization data for *Dillwynia retorta A* arbuscular colonization, *Total* AM colonization including A, V and intraradical hyphal infection, *V* vesicular colonization

| Fire characteristic | | $r^2$ | *F* | *P* |
|---|---|---|---|---|
| Shortest inter-fire interval | A | 0.078 | 1.227 | 0.255 |
| | V | 0.088 | 1.393 | 0.224 |
| | Total | 0.298 | 6.142 | 0.006 |
| Longest inter-fire interval | A | 0.264 | 5.211 | 0.012 |
| | V | 0.013 | 0.194 | 0.563 |
| | Total | 0.137 | 2.307 | 0.111 |
| Most recent inter-fire interval | A | 0.091 | 1.444 | 0.216 |
| | V | 0.023 | 0.348 | 0.500 |
| | Total | 0.079 | 1.239 | 0.253 |
| Time since shortest inter-fire interval | A | 0.084 | 1.327 | 0.236 |
| | V | 0.005 | 0.071 | 0.619 |
| | Total | 0.003 | 0.039 | 0.634 |

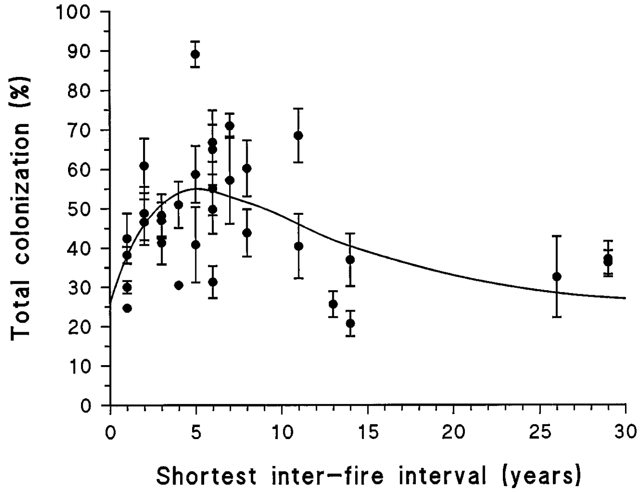

**Fig. 1** Relationship between total arbuscular mycorrhizal (AM) colonization, including arbuscular, vesicular and intraradical hyphal infection, of *Dillwynia retorta* and the shortest time between fires

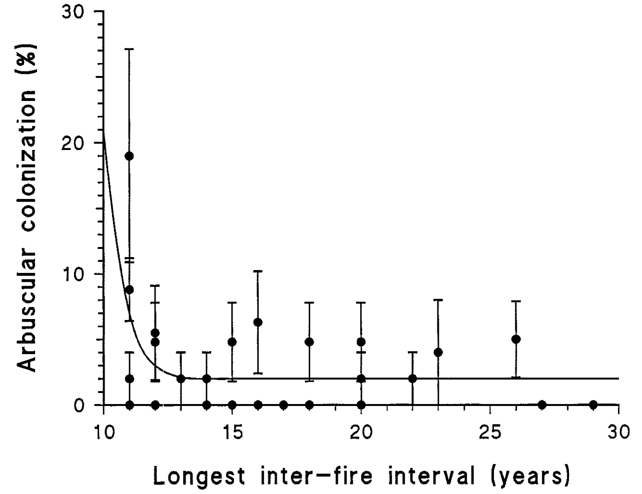

**Fig. 2** Relationship between arbuscular colonization in *D. retorta* and the longest time between fires

lengths, representing a stable and minimal level of arbuscular colonization at ca. 2.2% (arcsin transformed).

The Pearson correlations between the arcsin-transformed *D. retorta* mycorrhizal colonization and the abundance of the host plant were carried out in an attempt to detect influences on AM colonization related to host abundance. Pearson correlations were significant ($P<0.05$) and positive for both arbuscular and total colonization (Table 3), indicating increasing AM infection levels with increasing abundance of *D. retorta*. Vesicular colonization and host abundance were not significantly correlated.

Due to the significant correlation between arbuscular and total colonization with the abundance of the host plant, canonical correspondence analysis was applied to determine whether AM colonization of *D. retorta* demonstrated trends consistent with the presence or absence, and relative abundances of other plants in the immediate area.

For the canonical correspondence analysis, the sum of the eigenvalues for the unconstrained analysis was 1.788, with a total of 0.220 for the constrained analysis. Thus, only 12.3% of the overall variation in abundance among the plant species was related to the intensity of AM colonization in *D. retorta* (i.e. the joint variation is 12.3% of the variation in the abundance of the vascular plant species). The association between the floristic data and AM colonization is thus weak, the statistical test indicating $P=0.077$, based on 1000 Monte Carlo permutations and the total eigenvalues.

**Table 3** Pearson correlations between arcsin-transformed proportions of *D. retorta* AM colonization and its abundance (*A* arbuscular colonization, *Total* AM colonization, including A, V and intraradical hyphal infection, *V* vesicular colonization)

| AM colonization | *r* | *P* |
|---|---|---|
| A | 0.358 | 0.044 |
| V | 0.248 | 0.171 |
| Total | 0.387 | 0.029 |

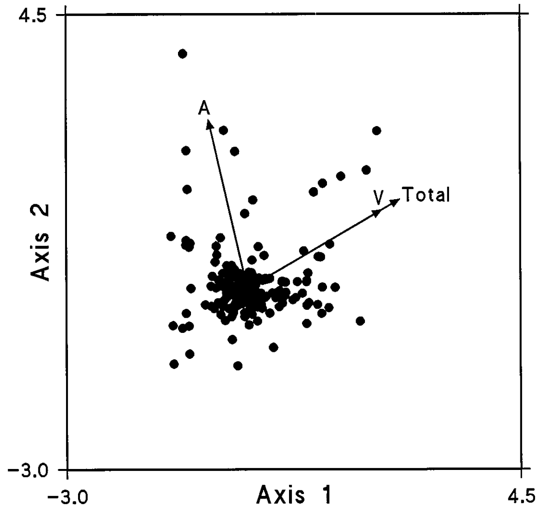

**Fig. 3** Multivariate analysis of the effects of varying AM colonization on the floristic composition of dry-sclerophyll plant communities in the Sydney region. Canonical correspondence analysis of arcsin-transformed AM colonization data for *D. retorta* and the abundance of 214 vascular plant species. Each symbol represents one plant species, and their proximity indicates how similar they are in terms of their overall distribution among the 42 sample sites. The directions and lengths of the arrows indicate the relationship with each of the AM colonization characteristics (*A* arbuscular colonization, *Total* AM colonization, including A, V and intraradical hyphal infection, *V* vesicular colonization)

The first two axes of the biplot from the analysis are shown in Fig. 3, these axes accounting for 73% of the total variation of the constrained ordination. The similarities among the species are indicated by the spatial relationship of the points on the ordination – points near each other show more similarity among themselves (based on their overall distribution among the sample sites) than they do to points further away. The relationship with each of the AM colonization characteristics is indicated by the direction and length of the arrows – longer arrows indicate a more influential variable and orthogonal arrows indicate unrelated variables.

F-tests were not performed on the axes in the CCA due to the low level of variability described by the constrained ordination (i.e. 12%). The significance or otherwise of such tests would have no value as we are claiming that interactions between floristic species abundance and AM colonization in *D. retorta* are likely to have no biological significance.

A relationship between AM colonization in *D. retorta* and plant species distribution in proximity would appear in the biplot as a concentration of points representing plants positively influencing mycorrhizal colonization in *D. retorta* in parts of the diagram representing increasing AM colonization. Plant species negatively influencing mycorrhizal colonization would group in opposite parts of the diagram. Neither pattern emerged from this analysis (Table 4).

## Discussion

Our work further elucidates the AM status of plants in Australian sandstone soils. Virtually all root samples of *D. retorta* were AM colonized, although neither arbuscular nor vesicular colonization was intense. The proportion of root length colonized was lower than previously found for Fabaceae. For example, Allsopp and Stock (1994) found South African species, including plants in burnt areas, with 28–31% root infection with AMF. This difference may be due to a seasonal effect, as our samples were taken outside of the season of maximal arbuscule production (Brundrett et al. 1996). Ectomycorrhizal infection, which was reported to be the dominant mycorrhiza of *D. retorta* by Bellgard (1991), was recorded in 3 of 152 sample, in all cases coexisting with AM.

Analyses of the relationship between the colonization data and the fire characteristics indicate that only IFI (longest or shortest) had an effect on AM colonization. It is noteworthy that the duration of the most recent IFI had no significant effect on colonization, whilst earlier inter-fire intervals did. This is evidence of a long-term effect of burning on AM colonization, which has not been detected in previous work.

The relationships detected are likely to reflect the response to fire of the host plant. So, very short IFIs tend to reduce the population density of *D. retorta* by killing plants before they mature and produce seed, whilst longer IFIs lower abundance through a decrease in recruitment by fire-induced germination from the soil seed bank, as well as through plant death from old age (Purdie 1977a). A balance between the two effects occurs with a shortest IFI of ca. 6 years, which coincides with maximal AM colonization levels. We detected similar effects of reduced recruitment and age-related plant death: population density declined through age-related plant death with longest IFIs of more than 10 years. Therefore, change in AMF colonization of *D. retorta* roots parallels change in plant abundance in response to variation in IFI.

The Pearson correlation analyses revealed further relationships between plant and fungal behaviour, including a significant positive correlation between colonization variables and host abundance. This may confound interspecific extrapolation of findings from fire research when performed on mycorrhizal plants in the field. Certainly, the major impact of fire on AM colonization in *D. retorta* in our study was via effects on the plant rather than directly on the hypogeous partner. This is in line with the results of Dhillion et al. (1988) and suggestions by Gibson and Hetrick (1988) but in contrast to data from Vilariño and Arines (1991); the latter results may have been influenced by floristic differences.

The lack of a significant correlation between vesicular colonization and host abundance is somewhat anomalous. This may be related to the sampling season,

**Table 4** Vascular plant species associations with AM colonization data for *D. retorta*, as indicated by canonical correspondence analysis

| AM colonization | | Family |
|---|---|---|
| Arbuscular/vesicular/total colonization, positive relationship | *Caustis pentandra* | Cyperaceae |
| | *Xanthorrhoea arborea* | Xanthorrhoeaceae |
| | *Eucalyptus eximia* | Myrtaceae |
| | *Eucalyptus piperita* | Myrtaceae |
| | *Angophora costata* | Myrtaceae |
| Arbuscular colonization, positive relationship | *Dianella revoluta* | Liliaceae |
| | *Pterostylis* sp. | Orchidaceae |
| | *Lepidosperma filiforme* | Cyperaceae |
| | *Xyris gracilis* | Xyridaceae |
| | *Acacia oxycedrus* | Mimosaceae |
| | *Acacia longifolia* | Mimosaceae |
| | *Viminaria juncea* | Fabaceae |
| | *Indigophora australis* | Fabaceae |
| | *Callistemon linearis* | Myrtaceae |
| | *Zieria laevigata* | Rutaceae |
| | *Bauera rubioides* | Baueraceae |
| | *Actinotus helianthi* | Apiaceae |
| | *Tetratheca thymifolia* | Tremandraceae |
| | *Hibbertia cistiflora* | Dilleniaceae |
| Vesicular/total colonization, positive relationship | *Lomandra longifolia* | Xanthorrhoeaceae |
| | *Restio dimorphus* | Restionaceae |
| | *Hardenbergia violacea* | Fabaceae |
| | *Kunzea ambigua* | Myrtaceae |
| | *Eriostemon australasius* | Rutaceae |
| | *Dichondra repens* | Convolvulaceae |
| | *Chloanthes stoechadis* | Verbenaceae |
| | *Ricinocarpos pinifolius* | Euphorbiaceae |
| | *Pteridium esculentum* | fern |
| Arbuscular colonization, negative relationship | *Phyllanthus thymoides* | Euphorbiaceae |
| | *Eucalyptus capitata* | Myrtaceae |
| Vesicular/total colonization, negative relationship | *Sprengelia incarnata* | Epacridaceae |
| | *Persoonia lanceolata* | Proteaceae |
| | *Leptospermum flavescens* | Myrtaceae |
| | *Lomandra multiflora* | Xanthorrhoeaceae |
| Arbuscular/vesicular/total colonization, negative relationship | *Restio tetraphyllus* | Restionaceae |
| | *Anisopogon avenaceus* | Poaceae |

during which all individual mycorrhizas produced large and relatively similar numbers of vesicles in reaction to the prevailing period of low root growth. AMF species distribution was not formally quantified, but we observed several AMF genera (*Acaulospora*, *Glomus* spp. and a fine endophyte). It is not known whether the fire responses of AMF taxa differ.

Canonical correspondence analysis is a general multivariate technique and is more suited to descriptive than hypothesis-testing procedures (Tabachnick and Fidell 1989). We used it to assess the degree of relationship between AM colonization in *D. retorta* and abundance of the other 214 vascular species present in the area. We aimed to determine whether local abundance of potential hosts affected mycotrophy in the particular plant species examined. This analysis would also detect trends in colonization data related to topographical or soil variation, assuming that such variation is reflected in the floristic composition of the sites. The nature of any patterns detected could suggest more specific types of analysis for clarification of the responses. Canonical correspondence analysis was appropriate for this data as limitations due to interpretability, tendency of the canonical algorithm to maximize linearity and sensitivity of the analysis to changes in one set of variables (Tabachnick and Fidell 1989) were not of major consequence due to the nature of the data set.

The divergence of the axes in the canonical correspondence biplot representing arbuscular versus vesicular and total AM colonization (the latter two forming a common axis due to the linear relationship between them) was unexpected, especially considering the results of the Pearson correlation analysis. This phenomenon indicates that arbuscular colonization behaved in a substantially different manner in response to floristic composition effects than vesicular/total colonization. This is presumably related to the low level of arbuscule production in *D. retorta* at the sites examined.

Weak positive interactions in the correspondence analysis were observed between AM colonization in *D. retorta* and the abundance of *Caustis pentandra* (Cyperaceae), *Xanthorrhoea arborea* (Xanthorrhoeaceae) and three Myrtaceae species. Thus the higher abundances of these species at a site were correlated with higher levels of colonization in *D. retorta*. It is unlikely that any of these plants provided an environment especially favourable for the formation of AM. In fact, these taxa are generally found to be predominantly non-AM (Bellgard 1991; Warcup 1980), although mycorrhization in these species was not quantified in the current investigation. Similarly, the abundance of plants showing negative interactions with AM colonization in this analysis are in no way representative of taxa with putatively low AM dependence. The overall pattern of randomness in the interactions between plant species abundance and AM colonization is evidence that local plant species abundance differences have no influence on the colonization levels in *D. retorta* seedlings after fire. The weakness of the relationship indicated by the canonical biplot axes (12% of the total variation in the data) is further evidence that no biologically significant relationship exists between the relative abundance of plants in an area after burning and the level of colonization in an AM host such as *D. retorta*.

The colonization of post-disturbance ground with predominantly nonmycorrhizal, ruderal plant species has been observed in previous work (Allen and Allen 1984; Brundrett 1991; Khan 1974; Read and Birch 1988; Reeves et al. 1979). This was not a consideration in this investigation due to the general absence of herbaceous, opportunistic plant species in undisturbed Hawkesbury sandstone vegetation. The sites chosen were all undisturbed and showed no evidence of exotic ruderal species.

Morrison et al. (1995) found that differences in floristic species abundance between sites were more releated to fire history than geographical variation between the three areas (ie. Ku-ring-gai Chase, Brisbane Water and Royal National Parks). Although the AM status of species other than *D. retorta* cannot reliably be assumed, the absence of any substantial pattern in the correspondence analysis indicates that effects of fire history on overall plant species density and composition are not reflected in the mycorrhizal status of D. retorta.

A testable hypothesis generated by the current investigation is that the response of the plant dictates the behaviour of the fungal partner and, thus, that burning in Australian sclerophyll plant communities has no influence on AMF independent of the host response. The AMF population in the soil probably follows a fire-response pattern that has evolved in concert with plant behaviour. We have examined this further (manuscript in preparation). Should this be the case, then fire management authorities should base fire protocol designs on plant conservation, simply allowing the AMF population to adjust to the conditions imposed.

Furthermore, the absence of mycorrhizas may be related to the failure of some seedlings to establish after burning, should soil inoculum be eliminated by fire in small areas. Dhillion and Anderson (1993) consider that plant regrowth after burning may be too rapid for the fungal population to keep pace. This could be a further factor causing aborted post-fire establishment, which is generally considered to be related to desiccation, fungal disease and/or insect herbivory (Morrison et al. 1995; Purdie 1977b). Very short and in particular repeated short IFIs would conspire with the above to reduce the population density of all plants using seeds as a fire survival mechanism (Purdie 1977a). Although reductions in *D. retorta* population density in response to short and/or repeated short IFIs are borne out by our findings, it is currently not possible to quantify the effect of mycorrhizal influence on this factor, as plant death due to fire prior to seed-producing age would have a similar effect.

Samples for infectivity bioassay were collected along with the root samples, to determine whether soil propagule levels were affecting the level of colonization in *D. retorta*, and what, if any, were the effects of IFI on infectivity. Unfortunately, a pilot analysis indicated a high degree of variability in the data masking any other interactions and the analysis was curtailed.

Future work will aim to compare the responses of other mycorrhizal plants to burning with those of *D. retorta* and thus to determine whether the patterns detected in the current investigation are limited to one plant taxon or are more general.

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