

Original papers

The impact of wildfire on vesicular-arbuscular mycorrhizal fungi and their potential to influence the re-establishment of post-fire plant communities

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Abstract. Wildfires are a typical event in many Australian plant communities. Vesicular-arbuscular mycorrhizal (VAM) fungi are important for plant growth in many communities, especially on infertile soils, yet few studies have examined the impact of wildfire on the infectivity of VAM fungi. This study took the opportunity offered by a wildfire to compare the infectivity and abundance of spores of VAM fungi from: (i) pre-fire and post-fire sites, and (ii) post-fire burned and unburned sites. Pre-fire samples had been taken in May 1990 and mid-December 1990 as part of another study. A wildfire of moderate intensity burned the site in late December 1990. Post-fire samples were taken from burned and unburned areas immediately after the fire and 6 months after the fire. A bioassay was used to examine the infectivity of VAM fungi. The post-fire soil produced significantly less VAM infection than the pre-fire soil. However, no difference was observed between colonization of plant roots by VAM fungi in soil taken from post-fire burned and adjacent unburned plots. Soil samples taken 6 months after the fire produced significantly more VAM than corresponding soil samples taken one year earlier. Spore numbers were quantified by wet-sieving and decanting of 100-g, air-dried soil subsamples and microscopic examination. For the most abundant spore type, spore numbers were significantly lower immediately post-fire. However, no significant difference in spore numbers was observed between post-fire burned and unburned plots. Six months after the fire, spore numbers were the same as the corresponding samples taken 1 year earlier. All plants appearing in the burned site resprouted from underground organs. All post-fire plant species recorded to have mycorrhizal associations before the fire had the same associations after the fire, except for species of *Conospermum* (Proteaceae), which lacked internal vesicles in cortical cells in the post-fire samples.

Key words: Wildfire – Vesicular-arbuscular mycorrhizal (VAM) fungi – Spores – Post-fire plant community

Introduction

Fire is considered a natural environmental variable over most of the vegetation of Australia (Gill 1975, 1981a). There has been considerable interest over recent years in the effects of fire on native ecosystems, largely because of the increasing use of prescribed burning in the management of native plant communities closely adjacent to major population centers (Bissett and Parkinson 1980; Whelan and Muston 1991). Many plants in the Australian flora are associated with mycorrhizal fungi (Warcup 1980), but few Australian studies have examined the impact of fire on mycorrhizal fungi. Furthermore, it is not known if the observed responses of plants to fire are related in any way to possible fire-induced changes in the populations of mycorrhizal fungi. Plants colonized by mycorrhizal fungi have higher tissue levels of some inorganic nutrients, greater biomass yield, and more rapid uptake of water, and they are often more tolerant of various forms of stress than nonmycorrhizal plants of the same species (Harley and Smith 1983). Consequently, the impacts of fire on the mycorrhizal association could potentially play a critical role in plant community change after fire.

Plants of the Australian biota possess adaptations which enable them to regenerate after fire, such as sprouting from buds located in underground organs and fire-stimulated seed germination (e.g., Gill 1981b; Noble and Slatyer 1981; Bell et al. 1984). Studies on the effects of fire on vegetation in eastern Australia have shown that most of the species regenerate after fire by sprouting (e.g. heaths: Specht et al. 1958; Russels and Parsons 1978; forest: Purdie 1977a, b). In these studies, the species that lacked the ability to resprout, i.e., obligate seeders, regenerated either by fire-stimu-

lated germination of seed stored in the soil or by dispersal of seeds held in woody fruits which had been stimulated to open by fire.

The manner in which plant communities respond to fire is dependent upon the individual regeneration strategies of the various plant species, and the conditions of the fire. For example, high-intensity fires may kill underground organs (e.g. Biswell 1974; Naveh 1974), and soil-stored seed (Naveh 1974; Purdie 1977b). In comparison, a fire of low intensity may fail to stimulate germination of seed with enforced dormancy (McArthur and Cheney 1966).

The penetration of heat through the soil during a fire is an important factor in determining post-fire plant regeneration. Klopatek et al. (1988) found that high soil temperatures resulting from a fire were correlated with reductions in subsequent formation of vesicular-arbuscular mycorrhizae in the roots of bioassay plants. Similar findings were reported by Wicklow-Howard (1989): infection by vesicular-arbuscular mycorrhizal (VAM) fungi was 50% lower in bioassay plants grown in soil from a burnt site than an unburnt site. Dhillon et al. (1988) found that fire in a prairie community significantly affected subsequent colonization of roots by VAM fungi, sporulation of VAM fungi, plant above-ground production, and tissue inorganic nutrient concentrations.

The current study took advantage of the recent occurrence of a wildfire at a site in which mycorrhizal associations had been studied for over 2 years. A considerable amount of information had already been accumulated for the site, including the compilation of a comprehensive list of plant species showing mycorrhizal associations (Bellgard 1991), the seasonal variation in the infectivity of VAM fungi and VAM spore types and abundance (Bellgard 1993), and an assessment of the propagules responsible for perpetuating VAM infectivity in disturbed soils (Bellgard 1992). In late December of 1990, a wildfire burned the site. The co-occurrence of the wildfire and the well-studied site provided a good opportunity to examine the effects of fire on VAM fungi. By comparing pre-fire estimates of the infectivity of VAM fungi and spore abundance with samples taken from both burned and unburned locations in the site, we aimed to investigate the following: (i) how fire affects the ability of VAM fungi to colonize plant roots, and (ii) how fire affects VAM spore densities in soil. We also sampled roots from seedlings and resprouting plants appearing after the fire, and classified them according to our knowledge of whether the species were mycorrhizal or nonmycorrhizal based on samples taken prior to the fire.

Materials and methods

Description of the study site and fire history

The southern part of the Hawkesbury Sandstone plateau, located 90 km south of Sydney and to the west of the Wollongong, Australia, covers approximately 1200 km². The average annual precipi-

itation in this region is 1420 mm, with a slight summer predominance. The 5-ha study site was located within the O'Hares catchment (34°14'S, 150°53'E). The site supported an open, sclerophyllous shrubland dominated by *Angophora hispida* (Sm.) Blaxell (Myrtaceae) associated with species of *Acacia*, *Leptospermum*, *Banksia*, *Conospermum*, *Grevillea* and *Persoonia*. The soil at the site was a loose shallow sand, about 30 cm deep, with abundant ironstone overlying the sandstone surface [Lateritic-Podzolic Soils (Dy3.61)] (Hazelton and Tille 1990). For a more detailed description of the soil at the study site, please refer to Bellgard (1993).

The previous fire at the site was a hazard reduction fire carried out during 1982 (Anon. 1983). A wildfire burned the site between 23 and 28 December 1990. The fire was of moderate intensity with a scorch height of approximately 3 m. Although the fire was fairly uniform in intensity across the site, some patches of vegetation remained unburned. These patches of unburned vegetation provided an opportunity for a comparison of mycorrhizae in burned and unburned soil.

Pre-fire sampling

In May 1990 and mid-December 1990, intact soil blocks (20 × 20 × 15 cm) were removed from 16 random locations from within the site and placed in square, 6-l plastic containers. Seeds of *Acacia linifolia* (Vent.) Willd. (Mimosaceae), a local plant species known to form vesicular-arbuscular mycorrhizae (Bellgard 1991), were immersed in boiling water to break enforced dormancy (Cavanagh 1987). The seeds were germinated on damp filter paper prior to sowing. Fifteen seedlings were sown into each container of soil. All pots were tap-watered daily, and no nutrients added. The containers were placed in a naturally lit glasshouse in which the temperatures ranged between 14.9°C and 23.5°C for the May (1990) bioassay, and between 21.0°C and 30.7°C for the December (1990) bioassay (see Bellgard 1993).

To monitor potential aerial contamination of VAM fungi in the glasshouse, 16 containers of river sand, each sown with 15 seedlings of *Acacia linifolia*, were used as controls. Eight and 12 weeks after sowing, five randomly selected seedlings were extracted from each container. The roots of each seedling were washed gently in a 0.4% sodium hexametaphosphate solution to remove any adhering soil. The roots were excised and fixed in 50% ethanol, cleared with a 10% KOH solution and stained with 0.01% acid fuchsin-lactic acid-glycerol solution (Kormanick et al. 1980), and the total root length and root length colonized by VAM fungi quantified (Ambler and Young 1977). The length of root colonized by VAM fungi (i.e. VAM length) is a composite index: the sum of the length of root colonized by vesicles, arbuscules and internal hyphae (%VAM = VAM length/total root length × 100).

Spores of VAM fungi were obtained from soil samples also taken in May and mid-December 1990. Soil samples (10 × 10 × 15 cm) were collected at 25 randomly chosen locations from within the site. Soil samples were mixed thoroughly with tap water. The slurry was then washed through a tier of four sieves: (i) 1 mm, (ii) 250 µm, (iii) 106 µm, and (iv) 75 µm. The material caught on the 75 µm sieve was then examined. Turgid spores filled with oil droplets were considered viable (McGee 1989) and counted microscopically.

Post-fire sampling

Ten intact soil blocks were extracted from randomly chosen burned and adjacent unburned sites from within the O'Hares site in mid-January 1991 and May 1991. The soil blocks were placed in square plastic containers and taken to the glasshouse. Control containers of washed river sand were set up to monitor for poten-

tial aerial contamination in the glasshouse. Fifteen seedlings of *Acacia linifolia* were sown in each container of soil. All pots were tap-watered daily, and no additional nutrients added. Four and 12 weeks after sowing, five randomly selected seedlings were extracted from each container and the roots were treated in a manner similar to that described for the pre-fire sampling. The containers were placed in a naturally lit glasshouse in which the temperatures ranged between 21.0°C and 30.7°C for the January (1991) bioassay, and between 16.4°C and 25.4°C for the May (1991) bioassay.

Soil samples (10 × 10 × 15 cm) were taken from 25 random locations from within burned and adjacent unburned plots in mid-January 1991 and May 1991. Spores of VAM fungi were obtained using a protocol similar to that described for the pre-fire sampling.

Mycorrhizal status of post-fire plant species

Six months after the fire, five patches of burned regeneration approximately 50 × 50 m were selected within the site. Line transects (20 m long) were set up in each of the areas. The first five representatives of each post-fire plant species encountered on the transect were sampled. If five representatives were not discovered on the first transect, subsequent transects were laid out till five representatives of each plant species were obtained from within the chosen burned area.

The post-fire regeneration strategy of plants (i.e., obligate seeders versus resprouters) was recorded in each of the chosen areas. Plants regenerating from seed initially have only one single erect stem and cotyledons. These seedlings were easily differentiated from the sprouting species, which tend to have many stems arising from a common underground organ. At least 20 cm of fine feeder root was obtained from each post-fire plant. The roots were fixed in 50% ethanol, cleared and stained (Kormanick et al. 1980), and the mycorrhizal association recorded according to the nomenclature of Bellgard (1991).

Statistical analysis

Comparisons were made between vesicular-arbuscular mycorrhizae formation before and after the fire, and between burned and unburned patches after the fire. For the spores, only the data for the most abundant spore type were analyzed, and similar pre- and post-fire comparisons were carried out. Both the VAM and spore data were analyzed using *t*-tests. Because the sample sizes for each data set were large (i.e., $n \geq 25$), the resultant *t*-values were compared to normal tables (Zar 1984). The following comparisons were made:

- A. Pre-fire versus post-fire:
 - (a) VAM formation after 12 weeks
 - (i) May 1990 versus May 1991
 - (ii) Dec. 1990 versus Jan. 1991
 - (b) Type I spore numbers
 - (i) May 1990 versus May 1991
 - (ii) Dec. 1990 versus Jan. 1991
- B. Post-fire burned versus unburned:
 - (a) VAM formation after 4 and 12 weeks
 - (i) Burned Jan. 1991 versus unburned Jan. 1991
 - (ii) Burned May 1991 versus unburned May 1991
 - (b) Type I spore numbers
 - (i) Burned Jan. 1991 versus unburned Jan. 1991
 - (ii) Burned May 1991 versus unburned May 1991

Results

Root growth and VAM formation

No VAM fungi were found on the roots of any of the bioassay seedlings grown in the control containers, so there was no aerial contamination in the glasshouse. The total length of roots of bioassay seedlings was not different between burned and unburned soil blocks. Consequently, the trends observed in the lengths of root colonized by VAM fungi (i.e., VAM length) and the proportion of root length colonized by VAM fungi (i.e., %VAM) were identical. Therefore, only the %VAM data are reported here.

For bioassay seedlings grown in the soil blocks extracted just prior to the wildfire (15 December 1990), the %VAM was significantly higher than that observed in both the burned and unburned samples taken immediately after the fire (Fig. 1; Table 1). However, for bioassay seedlings growing in the soil blocks extracted 8 months before the fire (15 May 1990), the %VAM was significantly lower than that observed in seedlings growing in soil blocks extracted from post-fire burned and unburned plots sampled 6 months after the fire (Fig. 1; Table 1).

No difference was observed between the %VAM for bioassay plants grown in post-fire burned and unburned soil blocks (Fig. 1; Table 1). A similar result was observed for the soil blocks extracted 6 months after the fire from post-fire burned and unburned plots (Fig. 1; Table 1). However, the levels of colonization were less than those observed in the soil blocks extracted in January 1991 (Fig. 1).

Spore types and abundance

Three types of spores were found in the soil sampled. Descriptions of the diagnostic characters of the spore

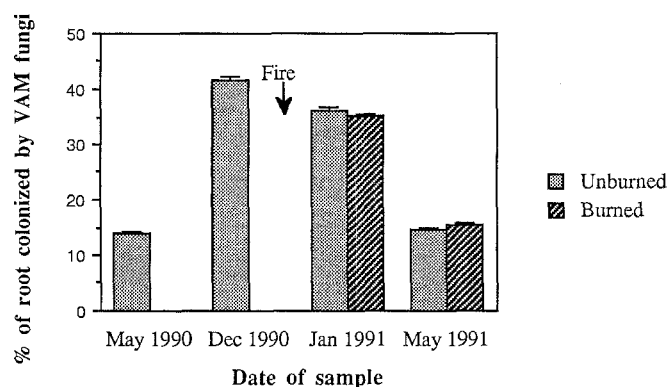


Fig. 1. Proportion of root length colonized by vesicular-arbuscular mycorrhizal fungi in 12-week-old seedlings grown in intact soil blocks taken from unburned and burned plots from the O'Hares study site in southeastern Australia. Arrow indicates the occurrence of the fire. Pre-fire bars represent the mean (\pm SEM) of five seedlings extracted from each of 16 replicates, and post-fire bars represent the mean (\pm SEM) of five seedlings extracted from each of 10 replicates

Table 1. Summary of statistical comparisons for pre- and post-fire % vesicular-arbuscular mycorrhizal (VAM) and type I spore data from unburned and burned plots in a burned sclerophyllous shrubland in southeastern Australia. S, Significant; NS, nonsignificant

Comparison	Date of sample	Result
% VAM		
Pre-fire versus post-fire	15. 5. 90–17. 7. 90 versus 12. 5. 91–17. 7. 91 15. 12. 90–18. 2. 91 versus 14. 1. 91–17. 3. 91	S ($Z \leq 0.05$) S ($Z \leq 0.05$)
Post-fire (i) burned versus unburned (4 weeks)	14. 1. 91–17. 3. 91 12. 5. 91–17. 7. 91	NS ($Z \leq 0.05$) NS ($Z \leq 0.05$)
(ii) burned versus unburned (12 weeks)	14. 1. 91–17. 3. 91 12. 5. 91–17. 7. 91	NS ($Z \leq 0.05$) NS ($Z \leq 0.05$)
Type I spores		
Pre-fire versus post-fire	May 1990 versus May 1991 Dec. 1990 versus Jan. 1991	NS ($Z \leq 0.01$) S ($Z \leq 0.01$)
Post-fire (i) burned versus unburned	Jan. 1991	NS ($Z \leq 0.01$)
(ii) burned versus unburned	May 1991	NS ($Z \leq 0.01$)

types can be found in Bellgard (1993). For the most abundant spore type (i.e., type I), significantly more spores were recovered from soil just prior to the fire than after the fire (Tables 1, 2). However, there was no significant difference between the number of spores recovered from the soil extracted in May 1990 (i.e., pre-fire) and May 1991 (i.e., post-fire). No difference was observed between the number of spores in the post-fire samples taken in burned and unburned plots (Tables 1, 2).

Post-fire mycorrhizal status of recolonizing plant species

For the five burned plots examined, 43 of the 47 plant species at the site overall were recorded after the fire (Table 3). All the plant species regenerated from underground organs. Twenty eight of the 43 resprouting plant species (i.e., 65%) possessed mycorrhizal associa-

tions. The majority of the mycorrhizal plant species that regenerated after the fire acquired the same mycorrhizal associations as that of pre-fire representatives of these species (Table 3). The only minor exceptions were the two species of *Conospermum* (Proteaceae). These two plant species consistently failed to develop internal vesicles in cortical cells after the fire. Before the fire, both species possessed typical VAM associations (Table 3).

Discussion

The use of fire in the management of plant communities in Australia has been, and continues to be, controversial. The introduction of burning for hazard reduction and regeneration has been justified on the grounds that in many Australian plant communities the alternatives, periodic wildfire and inadequate regeneration, are untenable and that fire was a natural factor in plant communities prior to European colonization (Shea et al. 1981). Although the advantages of using prescribed burning for hazard reduction and regeneration have been clearly demonstrated in some situations (Whelan and Muston 1991), because the potential ecological effects of changed fire regimes are very complex, the choice of the imposed fire regime should be tailored to the individual plant community under consideration.

Burning radically changes the physical, chemical, and biological properties of soils, e.g., the temperature and moisture conditions, the pH, the solubility of plant nutrients, and the microbial and animal life (Hatch 1960; Mikola et al. 1963; Well 1971; Warcup 1981, 1983). A number of studies have suggested that fire alters soil microbial populations in various ways, depending upon area, soil type, fire intensity, and a range of other factors (Ahlgren and Ahlgren 1965; Bissett and Parkinson 1980). Post-fire increases in microorganisms were noted by Cohen (1950) and Ahlgren (1974), decreases were reported by Jorgensen and

Table 2. Pre- and post-fire comparison of VAM spore densities in the topsoil (0–15 cm) of an open sclerophyllous shrubland in southeastern Australia. All entries represent means (\pm SEM) of 25 random samples taken at each sampling occasion

Sample	Spore type		
	Type I	Type II	Type III
Pre-fire			
May 1990	6.6 (0.3)	1.0 (0.1)	0.04 (0.03)
Dec. 1990	9.2 (0.5)	2.0 (0.1)	0.12 (0.05)
Post-fire			
Unburned			
Jan. 1991	4.5 (0.6)	1.0 (0.1)	0.2 (0.08)
May 1991	6.2 (0.4)	2.2 (0.4)	0.00 (0.00)
Burned			
Jan. 1991	4.2 (0.5)	1.4 (0.2)	0.12 (0.07)
May 1991	7.2 (0.5)	2.0 (0.3)	0.00 (0.00)

Table 3. Mycorrhizal associations of pre- and post-fire plants sampled from five burned areas (6 months after the fire) from a dry sclerophyllous shrubland community on Hawkesbury Sandstone soil within the O'Hares Catchment (southeastern Australia).

The numbers represent the number of root samples out of five possessing a mycorrhizal association (S/Re, Seedling/resprouting from root stock; Ecto, ectomycorrhizae; Ih, internal hyphae; V, vesicles; A, arbuscules; Cc, Cortical coils)

Family	Recolonizing plant species	Pre-fire mycorrhizal status	S/Re	Post-fire mycorrhizal status					
				Ecto	Ih	V	A	Cc	
Site 1									
Cyperaceae	<i>Ptilantheium deustem</i> (R. Br.) Kükenth	V	Re	0	5	4	0	0	
Dilleniaceae	<i>Hibbertia serpyllifolia</i> R. Br. ex DC.	VA	Re	0	5	5	5	3	
Eparidaceae	<i>Brachyloma daphnoides</i> (Sm.) Benth.	VA	Re	0	5	5	5	3	
Fabaceae	<i>Leucopogon juniperinus</i> R. Br.	VA	Re	0	5	5	5	4	
	<i>Mirbelia rubiifolia</i> (Andr.) G. Don.	Ecto + VA	Re	5	5	5	5	3	
	<i>Pultenaea elliptica</i> Sm.	Ecto + VA	Re	5	5	5	5	4	
Goodeniaceae	<i>Dampiera stricta</i> (Sm.) R. Br.	Ecto + VA	Re	5	5	5	5	5	
Iridaceae	<i>Patersonia sericea</i> R. Br.	nil	Re	0	0	0	0	0	
Mimosaceae	<i>Acacia suaveolens</i> (Sm.) Willd.	Ecto + VA	Re	5	5	5	5	5	
Myrtaceae	<i>Angophora hispida</i> (Sm.) Blaxell	Ecto	Re	5	0	0	0	0	
	<i>Eucalyptus haemastoma</i> Sm.	Ecto	Re	5	0	0	0	0	
	<i>E. stricta</i> Sieb. ex Spreng.	Ecto	Re	5	0	0	0	0	
	<i>Kunzea capitata</i> Reichb.	Ecto	Re	5	0	0	0	0	
	<i>Leptospermum juniperinum</i> Sm.	Ecto	Re	5	0	0	0	0	
	<i>Banksia paludosa</i> R. Br.	nil	Re	0	0	0	0	0	
	<i>B. serrata</i> L. f.	nil	Re	0	0	0	0	0	
Proteaceae	<i>B. spinulosa</i> Sm.	nil	Re	0	0	0	0	0	
	<i>Conospermum longifolium</i> Sm.	VA	Re	0	5	0	5	4	
	<i>C. taxifolium</i> Sm.	VA	Re	0	5	1	5	3	
	<i>Grevillea oleoides</i> Sieb. ex Schult et f.	V	Re	0	5	5	0	2	
	<i>Hakea dactyloides</i> (Gaertn.) Cav.	V	Re	0	5	5	0	2	
	<i>Isopogon anemonifolius</i> (Salisb.) Knight	nil	Re	0	0	0	0	0	
	<i>Lambertia formosa</i> Sm.	nil	Re	0	0	0	0	0	
	Xanthorrhoeaceae	<i>Lomandra confertifolia</i> (F.M. Bailey) Fahn	nil	Re	0	0	0	0	0
		<i>L. glauca</i> (R. Br.) Ewart	nil	Re	0	0	0	0	0
		<i>L. obliqua</i> (Thunb.) MacBride	nil	Re	0	0	0	0	0
Site 2									
Cyperaceae	<i>Caustis flexuosa</i> R. Br.	VA	Re	0	5	4	3	2	
	<i>Ptilantheium deustem</i> (R. Br.) Kükenth	V	Re	0	5	5	0	2	
Dilleniaceae	<i>Hibbertia serpyllifolia</i> R. Br. ex DC.	VA	Re	0	5	5	5	3	
Droseraceae	<i>Drosera pygmaea</i> DC.	nil	Re	0	0	0	0	0	
Epacridaceae	<i>Brachyloma daphnoides</i> (Sm.) Benth.	VA	Re	0	5	4	5	2	
	<i>Epacris microphylla</i> R. Br.	VA	Re	0	5	5	5	2	
	<i>Leucopogon juniperinus</i> R. Br.	VA	Re	0	4	5	5	3	
Fabaceae	<i>Daviesia corymbosa</i> Sm.	VA	Re	0	5	5	5	3	
	<i>Mirbelia rubiifolia</i> (Andr.) G. Don.	Ecto + VA	Re	5	5	5	5	2	
	<i>Pultenaea elliptica</i> Sm.	Ecto + VA	Re	5	5	5	5	2	
Goodeniaceae	<i>Dampiera stricta</i> (Sm.) R. Br.	Ecto + VA	Re	5	5	4	5	0	
Iridaceae	<i>Patersonia sericea</i> R. Br.	nil	Re	0	0	0	0	0	
Mimosaceae	<i>Acacia myrtifolia</i> (Sm.) Willd.	Ecto + VA	Re	5	5	5	5	5	
Myrtaceae	<i>Angophora hispida</i> (Sm.) Blaxell	Ecto	Re	5	0	0	0	0	
	<i>Kunzea capitata</i> Reichb.	Ecto	Re	5	0	0	0	0	
	<i>Leptospermum juniperinum</i> Sm.	Ecto	Re	5	0	0	0	0	
	<i>L. lanigerum</i> (Ait.) Sm.	Ecto	Re	5	0	0	0	0	
	Proteaceae	<i>Banksia ericifolia</i> L. f.	nil	Re	0	0	0	0	0
		<i>B. paludosa</i> R. Br.	nil	Re	0	0	0	0	0
		<i>B. spinulosa</i> Sm.	nil	Re	0	0	0	0	0
<i>Conospermum longifolium</i> Sm.		VA	Re	0	5	0	5	3	
<i>C. taxifolium</i> Sm.		VA	Re	0	5	0	5	3	
<i>Grevillea oleoides</i> Sieb. ex Schult et f.		V	Re	0	5	5	0	3	
<i>Hakea dactyloides</i> (Gaertn.) Cav.		V	Re	0	5	5	0	2	
Rutaceae	<i>Isopogon anemonifolius</i> (Salisb.) Knight	nil	Re	0	0	0	0	0	
	<i>Lomatia silaifolia</i> (Sm.) R. Br.	nil	Re	0	0	0	0	0	
	<i>Petrophile pulchella</i> (Schrad.) R. Br.	nil	Re	0	0	0	0	0	
	<i>Eriostemon australasius</i> Pers.	VA	Re	0	5	5	5	5	
	Xanthorrhoeaceae	<i>Lomandra confertifolia</i> (F.M. Bailey) Fahn	nil	Re	0	0	0	0	0
<i>L. glauca</i> (R. Br.) Ewart		nil	Re	0	0	0	0	0	
<i>L. obliqua</i> (Thunb.) MacBride		nil	Re	0	0	0	0	0	

Table 3 (continued)

Family	Recolonizing plant species	Pre-fire mycorrhizal status	S/Re	Post-fire mycorrhizal status				
				Ecto	Ih	V	A	Cc
Site 3								
Cyperaceae	<i>Caustis flexuosa</i> R. Br.	VA	Re	0	5	5	5	0
	<i>Ptilantheium deustum</i> (R. Br.) Kükenth	V	Re	0	5	5	0	0
Epacridaceae	<i>Epacris microphylla</i> R. Br.	VA	Re	0	5	5	5	2
	<i>Leucopogon juniperinus</i> R. Br.	VA	Re	0	5	5	5	1
Fabaceae	<i>Dillwynia retorta</i> (Wendl.) Druce	Ecto	Re	4	0	0	0	0
Goodeniaceae	<i>Dampiera stricta</i> (Sm.) R. Br.	Ecto+VA	Re	5	5	5	5	2
Iridaceae	<i>Patersonia sericea</i> R. Br.	nil	Re	0	0	0	0	0
Myrtaceae	<i>Angophora hispida</i> (Sm.) Blaxell	Ecto	Re	5	0	0	0	0
	<i>Kunzea capitata</i> Reichb.	Ecto	Re	5	0	0	0	0
Xanthorrhoeaceae	<i>Lomandra confertifolia</i> (F.M. Bailey) Fahn	nil	Re	0	0	0	0	0
	<i>L. glauca</i> (R. Br.) Ewart	nil	Re	0	0	0	0	0
	<i>L. obliqua</i> (Thunb.) MacBride	nil	Re	0	0	0	0	0
Site 4								
Cyperaceae	<i>Caustis flexuosa</i> R. Br.	VA	Re	0	5	5	4	2
	<i>Ptilantheium deustum</i> (R. Br.) Kükenth	V	Re	0	5	4	0	0
Dilleniaceae	<i>Hibbertia serpyllifolia</i> R. Br. ex DC.	VA	Re	0	5	5	5	0
Epacridaceae	<i>Leucopogon juniperinus</i> R. Br.	VA	Re	0	5	5	5	1
Goodeniaceae	<i>Dampiera stricta</i> (Sm.) R. Br.	Ecto+VA	Re	5	5	5	5	1
Iridaceae	<i>Patersonia sericea</i> R. Br.	nil	Re	0	0	0	0	0
Myrtaceae	<i>Angophora hispida</i> (Sm.) Blaxell	Ecto	Re	5	0	0	0	0
	<i>Kunzea capitata</i> Reichb.	Ecto	Re	5	0	0	0	0
Proteaceae	<i>Banksia spinulosa</i> Sm.	nil	Re	0	0	0	0	0
	<i>Conospermum longifolium</i> Sm.	VA	Re	0	5	0	5	1
	<i>C. taxifolium</i> Sm.	VA	Re	0	5	0	5	1
	<i>Lambertia formosa</i> Sm.	nil	Re	0	0	0	0	0
Xanthorrhoeaceae	<i>Lomandra confertifolia</i> (F.M. Bailey) Fahn	nil	Re	0	0	0	0	0
	<i>L. glauca</i> (R. Br.) Ewart	nil	Re	0	0	0	0	0
	<i>L. obliqua</i> (Thunb.) MacBride	nil	Re	0	0	0	0	0
Site 5								
Cyperaceae	<i>Ptilantheium deustum</i> (R. Br.) Kükenth	V	Re	0	5	4	0	5
Dilleniaceae	<i>Hibbertia serpyllifolia</i> R. Br. ex DC.	VA	Re	0	5	5	5	5
Epacridaceae	<i>Brachyloma daphnoides</i> (Sm.) Benth.	VA	Re	0	5	4	5	5
	<i>Epacris microphylla</i> R. Br.	VA	Re	0	5	5	4	5
	<i>Leucopogon juniperinus</i> R. Br.	VA	Re	0	4	5	5	5
Fabaceae	<i>Daviesia corymbosa</i> Sm.	VA	Re	0	5	5	5	5
	<i>Mirbelia rubiifolia</i> (Andr.) G. Don.	Ecto+VA	Re	5	5	5	5	5
Goodeniaceae	<i>Dampiera stricta</i> (Sm.) R. Br.	Ecto+VA	Re	5	5	5	5	5
Iridaceae	<i>Patersonia sericea</i> R. Br.	nil	Re	0	0	0	0	0
Mimosaceae	<i>Acacia myrtifolia</i> (Sm.) Willd.	Ecto+VA	Re	5	5	5	5	5
Myrtaceae	<i>Eucalyptus stricta</i> Sieb. ex Spreng.	Ecto	Re	5	0	0	0	0
	<i>Leptospermum juniperinum</i> Sm.	Ecto	Re	5	0	0	0	0
Olacaceae	<i>Olax stricta</i> R. Br.	nil	Re	0	0	0	0	0
Proteaceae	<i>Banksia spinulosa</i> Sm.	nil	Re	0	0	0	0	0
	<i>Conospermum longifolium</i> Sm.	VA	Re	0	5	0	5	5
	<i>Grevillea buxifolia</i> (Sm.) R. Br.	V	Re	0	5	5	0	3
	<i>G. oleoides</i> Sieb. ex Schult et f.	V	Re	0	5	3	0	5
	<i>Hakea dactyloides</i> (Gaertn.) Cav.	V	Re	0	5	4	0	5
	<i>H. teretifolia</i> (Salisb.) J. Britten	nil	Re	0	0	0	0	0
	<i>Isopogon anemonifolius</i> (Salisb.) Knight	nil	Re	0	0	0	0	0
	<i>Lambertia formosa</i> Sm.	nil	Re	0	0	0	0	0
	<i>Lomatia silaifolia</i> (Sm.) R. Br.	nil	Re	0	0	0	0	0
	<i>Persoonia levis</i> (Cav.) Domin	V	Re	0	5	5	0	0
	<i>P. pinifolia</i> R. Br.	V	Re	0	5	5	0	2
	<i>P. laurina</i> Pers.	nil	Re	0	0	0	0	0
Xanthorrhoeaceae	<i>Lomandra confertifolia</i> (F.M. Bailey) Fahn	nil	Re	0	0	0	0	0
	<i>L. glauca</i> (R. Br.) Ewart	nil	Re	0	0	0	0	0
	<i>L. obliqua</i> (Thunb.) MacBride	nil	Re	0	0	0	0	0

Hodges (1971), while Bridge Cooke (1970), Jorgensen and Hodges (1970) and Bissett and Parkinson (1980) detected no change in microbial populations.

VAM fungi are permanent associates of a broad range of both perennial and annual plants, and are probably necessary for the continued growth and survival of plants in nutrient-poor soils subject to water stress. Our study suggests that a wildfire of moderate intensity had no significant impact upon the infectivity of VAM fungi or on the abundance of the spores in the soil. Although there was a decrease in the level of colonization and spore numbers between December 1990 and January 1991 (i.e., before and after the fire), there was no significant difference between the burned and unburned samples. These observations contrast with the recent studies of Dhillion et al. (1987), Klopatek et al. (1988), Wicklow-Howard (1989) and Vilariño and Arines (1990), who all found that burning reduced the infectivity of VAM fungi and spore abundance. Two important questions emerge from the results reported here: (i) What caused the observed variation in the infectivity of VAM fungi and spore numbers over time, and (ii) Why was there no observable difference between the infectivity of VAM fungi in the post-fire burned and unburned plots.

This study emphasizes the importance of having temporal controls in fire ecology experiments. The samples extracted just prior to the wildfire were taken 15 December, and the post-fire samples were extracted only 1 month later, 14 January. Although the post-fire infectivity of VAM fungi and spore numbers were significantly less than the December pre-fire samples, the lack of difference between the post-fire burned and unburned (i.e., the temporal control) plots indicates that the decrease is due to factors other than fire.

From an earlier study (Bellgard 1993), it was suggested that there was a pattern in the infectivity of VAM fungi related to seasonal temperatures. Higher levels of infectivity were associated with spring and summer because these two seasons were characterized by higher diurnal temperature ranges. Although the summer of 1990/1991 was characterized by average temperatures, the rainfall levels were markedly variable. Between 15 November and 16 December 1990 (i.e., during the time of sampling of the pre-fire soil blocks), 21.1 mm of rain was recorded (Anon. 1991). Between 15 December 1990 and 14 January 1991 (i.e., during the sampling of the first post-fire soil blocks), a total of 40.2 mm of rain fell (Anon. 1991). Thus, immediately prior to the fire the soil had been subjected to markedly different soil water regimes than was the case between the fire and the post-fire sampling. Soil water potential has been shown to be an important factor in determining the growth, development and hence infectivity of VAM fungi (e.g., Daniels and Trappe 1980; Daniels and Hetrick 1984; Nelsen 1987; Abbott and Robson 1991). Redhead (1975) demonstrated that the optimal water supply for plant growth is also suitable for mycorrhizal infection. Consequently, differences in the infective potential of VAM fungi resulting from markedly different soil water regimes could explain in

part the decrease in the post-fire infectivity of VAM fungi.

Dhillion et al. (1988) suggested that the response of VAM fungi to fire may be attributed to changes in the host plant and not to any direct effect of the fire. In the current study, all plant species present after the fire were identified as resprouters. The significance of this is that the underground organs of the plants survived the fire (Bell et al. 1984; Dodd et al. 1984). We suggest that because the underground organs survived the fire, their associated VAM fungal symbionts also survived, and retained their infectivity. This would explain why there was no apparent difference between the infectivity of VAM fungi in burned and unburned plots at either of the post-fire sampling dates. The alternative scenario is that in plant communities dominated by obligate seeders (which are killed completely by fire), the fungi would be disadvantaged by the absence of a potential host, and their subsequent post-fire infectivity would be reduced.

The proportion of the post-fire plant species possessing mycorrhizal associations was found to be 65%. An earlier study in this particular plant community (Bellgard 1991) showed that 66% of all the perennial plant species were mycorrhizal. The consistency in the proportion of mycorrhizal plants in both burned and unburned stands of this particular vegetation type may be due to most of the plants possessing a resprouting regeneration strategy. Plants with a resprouting habit are the principal utilizers of environmental resources and, by virtue of their dense spacing, provide only minimal openings for other species (Bell et al. 1984). It would seem that the resprouting habit also perpetuates the survival and infectivity of their mycorrhizal associates, even after a fire of moderate intensity when the plant may have been defoliated.

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