CALMScience Supplement 4: 151-158 (1995)

Interdependence of woody plants, higher fungi and small marsupials in the context of fire

B. B. LAMONT[1]

[1] School of Environmental Biology, Curtin University of Technology, GPO Box U1987, Perth 6001, Western Australia.

ABSTRACT

As a 'fire weed', the gastrolobiums and other mycorrhizal peas form dense thickets after intense fires: these serve as essential shelters and nesting sites for the woylie, *Bettongia penicillata*. This marsupial is the major consumer of the underground sporocarps of at least 18 species of higher fungi in eucalypt forest in Western Australia. When fresh faecal pellets from captured animals were applied to seedlings of *Gastrolobium bilobum* (Fabaceae) and *Eucalyptus calophylla* (Myrtaceae) in autoclaved soil they formed far more ectomycorrhizal rootlets than the controls in non-autoclaved soil. Application of fresh spores of two hypogeous species to the seedlings produced neither mycorrhizas nor growth responses. The most likely explanation is that digestion by the marsupial facilitates germination of the spores. More recent work on the *Gastrolobium* has shown the pellets are likely to increase the numbers and frequency of mycorrhizal types from one or two to five in soils varying in fire history. Restoration of these fungi after fire appears vital for re-establishment of species such as the *Gastrolobium* as it is killed by fire. Not only does consumption of sporocarps escalate after fire but the woylie may travel up to 3 km overnight and moves from one burnt patch to another. This gives it the capacity to be an effective dispersal and restoration agent, but the extent to which the soil is sterilized by fire remains uncertain.

INTRODUCTION

Fires have direct and indirect effects on the ecosystem. My aim here is to highlight one of the intriguing indirect effects, that of the relationships between major woody plants, higher fungi and certain moderately small marsupials. While the full details are still under study or remain unexplored, it is already clear that this triangular trophic relationship is a prime example of the 'balance of nature'. The starting point for any species conservation or habitat management program is to understand the repercussions of any change in status of one component on other components of the ecosystem. I focus on the southern dry sclerophyll forest in Western Australia as the system I know best, referring to work in eastern Australia where this helps amplify points. I examine the interacting components in turn with fire as the starting point for restoration of the ecosystem. I concentrate on fungi which form sheathing (ecto) mycorrhizas with the rootlets of many plants in Australian forests (Fig. 1, Warcup 1980a).

RESPONSES TO FIRE

Effect of Fire on Mycorrhizal Fungi

The effect of fire on mycorrhizal fungi depends on where the mycelium and mycorrhizas are located in relation to the intensity of the fire. Mycorrhizal fungi live saprophytically in litter or on rootlets in decaying litter or the organically rich surface soil (Malajczuk and Hingston 1981; Reddell and Malajczuk 1984). Intense fires will burn off the litter and heat the soil to a depth of 100 mm or more. Malajczuk and Hingston (1981) showed the density of mycorrhizal rootlets was lower after an intense fire than the controls in *Eucalyptus marginata* (jarrah) forest. A decrease in rootlet numbers could have contributed to these results and no counts were made before the fire. Subsequent work (Reddell and Malajczuk 1984) showed that prescribed burning reduced by 90 per cent the numbers of white and brown ectomycorrhizas in *E. marginata* but not the deeper located black mycorrhizas. Warcup (1981) noted that a steam treatment of 55°C for 5 minutes was sufficient to reduce fungal numbers markedly. While all *E. regnans* seedlings grown in soils heated at 55-82°C for 5 to 30 minutes were mycorrhizal, several ectomycorrhizal types formed by basidiomycetes present in the controls were absent.

In contrast to the above, there are many instances of the stimulation of sporulation by fire. This is most obvious for the epigeous (toadstool-type) fungi (Christensen 1980), many of which are

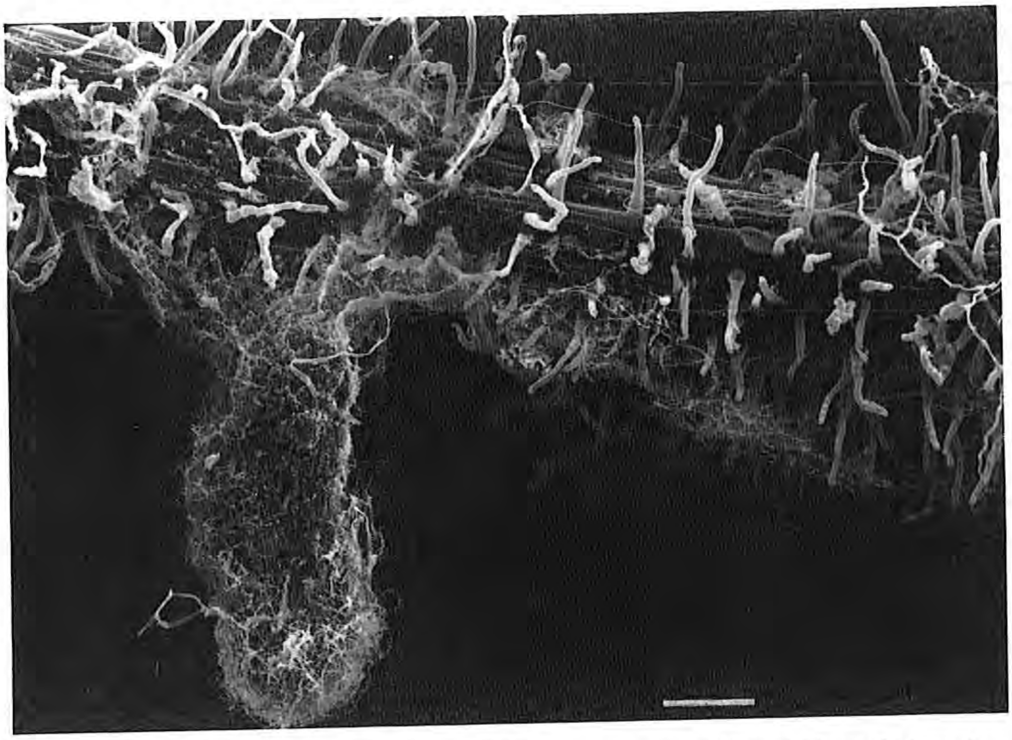

Figure 1. Scanning electron micrograph of mycorrhiza rootlet (simple, tan type) on Gastrolobium calycinum *from Dryandra State Forest. Scale = 0.1 mm.*

ectomycorrhizal, in the autumn after fire. The hypogeous (underground puffball-type) sporocarps are much more difficult to observe (Fig. 2). After a wildfire, most hypogeous discomycetes only sporulated in the first year, nine of which formed ectomycorrhizas with *Eucalyptus obliqua* or *Melaleuca uncinata* (Warcup 1990). In lighter burnt areas, hyphae grew up from the non-heated part of the surface soil and produced abundant hypogeous basidiocarps in the second winter-spring.

Johnson (in Taylor 1992a) claims that sporulation may be much quicker than this - at least in Tasmania: sporocarps were more common a week after a burn than in the controls, rising to six times greater eventually. This appears to be a specific enhancement of the hypogeous genus *Mesophellia* (Taylor 1991), a major ectomycorrhizal fungus in Australia because of its association with eucalypts (Ashton 1976; Malajczuk *et al.* 1987; Dell *et al.* 1990). Johnson's research was in response to suggestions that increase in sporulation was more apparent than real, as it is easier to locate *Mesophellia* sporocarps after fire and they are more likely to survive than other groups (Christensen 1980; Warcup 1990; Claridge 1992), but it has yet to be fully reported. The formation of discomycete mycorrhizas on several eucalypts was stimulated by steam heating soil at 55-82°C for up to 30 minutes (Warcup 1981) - presumably germination of the spores was stimulated by the heat.

Effect of Fire on Mycophagous Marsupials

The woylie *(Bettongia penicillata)* is the main consumer of fungi (mycophagy) in Western Australia (Christensen 1980). The short-nosed bandicoot *(Isoodon obesulus)* and the southern bush rat *(Rattus fuscipes)* occasionally dig up and consume sporocarps. Within six days of a prescribed burn, there were more excavations per unit area in burnt patches than in the controls (Table 1). Most (73 per cent) of the holes in burnt areas were surrounded by *Mesophellia* remnants, while there was no evidence of fungi for 97 per cent of holes in the unburnt areas: either a different (softer) type of sporocarp which is more edible predominates in the unburnt sites (Claridge *et al.* 1993) or many diggings yielded no sporocarps. The latter is less likely as the animals rely on the odour of sporocarps to locate them. Over a two-year period since fire, there were 10 ± 9 (sd) woylie holes per 100 m^2 in the burnt patches and 3 ± 2 in the unburnt (Lamont *et al.* 1985). A similar pattern has been noted for *Bettongia gaimardi* in Tasmania (Taylor 1991) and the potoroos (*Potorous longipes* and *P. tridactylus*) in south-eastern Australia (Guiler 1971; Bennett and Henry in Claridge 1992).

Effect of Fire on Woody Plants

Some plant species survive fire (resprouters) while others are usually killed (non-sprouters). Most trees in dry sclerophyll forest recover but their non-lignotuberous seedlings are killed (Abbott and Loneragan 1984). More important is the diverse array of sclerophyllous shrubs in the understorey. Although many of these are killed, germination of their seeds is stimulated by fire heat - either directly through

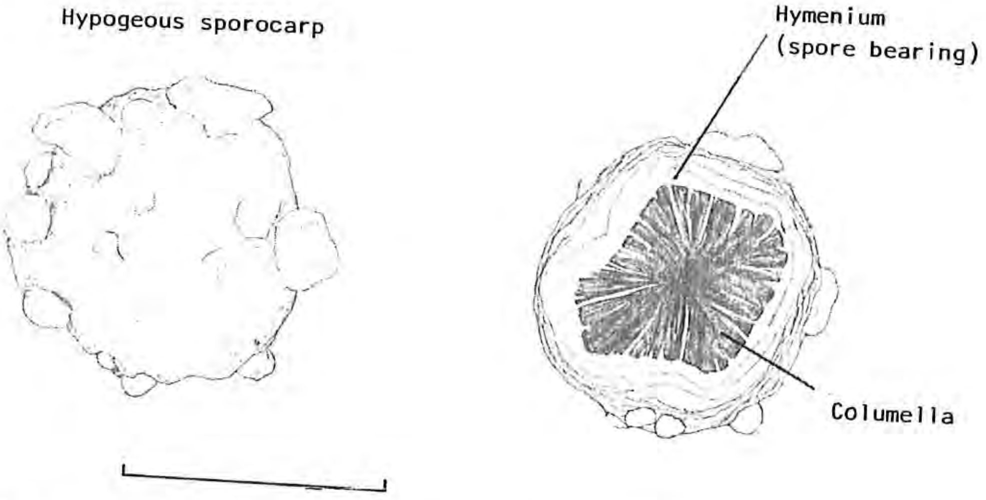

Figure 2. One of the two most abundant types of underground (hypogeous) sporocarp in gully vegetation at Perup forest. Note the lateritic pebbles, charcoal and sand embedded in the outer peridium on the left, and the cutaway on the right showing the nutritious central columella surrounded by the spore-bearing hymenium. This is a member of the Mesophelliaceae which formed simple, tan-coloured mycorrhizas with potted Gastrolobium bilobum *(N. Malajczuk, pers. comm.). Scale = 20 mm. Drawn by C. Ralph.*

increasing water permeability of their hard soil-stored seeds (Christensen 1980; Warcup 1980b) or indirectly through promoting the release of canopy-stored seeds (Lamont *et al.* 1991). In addition, many of these are ectomycorrhizal (Table 2). Some species are major thicket-formers after fire and contribute greatly to nitrogen fixation (Shea and Kitt 1976) and thus nutrient cycling in the ecosystem (Lamont 1992). There is no doubt that their rapid post-fire growth is largely due to the presence of ectomycorrhizas (Warcup 1980a; Lamont *et al.* 1985).

INTERACTIONS

Relationship between Marsupials and Fungi

Christensen (1980) showed that hypogeous sporocarps are a major part of the diet of the woylie. The nitrogen content of the *Mesophellia* columella (Fig. 2), favoured by mycophagous animals, is comparable to that in green leaves and contains high levels of lipids as well (Kinnear *et al.* 1979). The columella cannot be consumed without ingesting thousands of spores. The number of spore types per monthly batch of woylie faecal pellets was 3-10 (Christensen 1980). Of the 17 spore types identified in faeces, at least 10 belonged to ectomycorrhizal fungal groups (Lamont *et al.* 1985). *Mesophellia* was by far the best represented, especially over summer and after fire, with an average 565 ± 329 (sd) spores per mg pellet. Hypogeous fungi, especially *Mesophellia*, were also the main food of the Tasmanian Bettong, with 8-22 spore types per batch and 49 altogether (Taylor 1992b). Similar sporocarps are important in the diet of the Long-nosed Bandicoot, especially in autumn-winter and after fire (Guiler 1971; Bennett and Baxter 1989). Claridge *et al.* (1992) identified 27 ectomycorrhizal spore types in the scats of this animal.

The idea that these animals act as dispersal agents for these fungi has merit, for how else would spores be dispersed any distance from these underground sporocarps? Mycophagy at least frees the (uneaten) spores from the sporocarps but wind dispersal from the fragments would appear ineffective. The alternative is that most spores are dispersed in the faeces. Although there has been no work on Australian mammals, Cork and Kenagy (1989) showed that hypogeous fungal spores were retained for up to 80 hours, the concentration in faeces peaking at 20 hours, in the squirrel (*Spermophilus saturatus*). Woylies complete a circuit, in and out of burnt areas, up to a distance of 3 km overnight (Christensen 1980). Since sporocarps are highly clumped (Taylor 1992c) and different species (sporocarp types) are associated with different parts of the landscape (Claridge *et al.* 1993), this capacity for extensive transport of spores may be important in ensuring all potential host plants have access to suitable inocula.

The above arguments assume that the spores pass through mammal guts unharmed. Lamont *et al.* (1985) were the first to show this for Australian organisms. Suspensions of macerated faecal pellets collected from caged woylies applied to heat-sterilized Perup soil resulted in the production of five

TABLE 1

Total number of small holes with *hypogeous sporocarp* remains along five transects six days after fire in Perup Forest (from Christensen 1980).

	MESOPHELLIA TYPE	OTHER TYPES	No. SPOROCARPS	TOTAL
Burnt patches	263	19	78	360
Unburnt patches	8	1	285	294

TABLE 2

Selection of sclerophyll shrub species in dry eucalypt forests, most of which are killed by fire, their seed germination is promoted by fire heat and which are also ectomycorrhizal. Collated from Specht *et al.* (1958), Warcup (1980a,b), Ralph (1984), Brundrett and Abbott (1991), D. Bell, J. Warcup and B. Lamont (personal observations).

+ = yes, - = no, ? = uncertain

SPECIES	KILLED BY FIRE	GERMINATION ENHANCED BY FIRE	ECTOMYCORRHIZAL
Acacia myrtifolia	+	+	+
Acacia pycnantha	+	+	+
Bossiaea ornata	-	+	+
Bossiaea prostrata	?	+	+
Chorizema cordatum	+?	+	+
Cryptandra arbutiflora	+?	+?	+
Cryptandra tomentosa	+	+	+
Gastrolobium bilobum	+	+	+
Gastrolobium calycinum	+	+	+
Gastrolobium oxylobiodes	+	+	+?
Gastrolobium spinosum	+	+	+?
Gompholobium marginatum	+	+	+
Gompholobium tomentosum	+	+	+
Gompholobium venustum	+	+	+
Kennedia prostrata	+	+	+
Melaleuca decussata	+?	+	+
Melaleuca unicinata	+?	+	+
Melaleuca viminea	+	+	+?
Mirbelia dilatata	+	+	+
Opercularia varia	+?	+	+
Oxylobium capitatum	-	+	+
Oxylobium lanceolatum	+	+	+
Oxylobium linearifolium	+?	+	+
Pericalymma ellipticum	+	+	+
Platysace heterophylla	-?	+	+
Pultenaea ericifolia	+?	+	+?
Pultenaea scabra	+?	+	+
Pultenaea trinervis	+	+	+
Spyridium cordatum	+	+	+?
Spyridium parvifolium	+?	+	+
Trymalium floribundum	+	+	+
Trymalium ledifolium	+	+	+?

ectomycorrhizal types by six-month-old *Eucalyptus calophylla* and five by *Gastrolobium bilobum*, seven altogether. Plants in heat-sterilized soil receiving sterilized pellets produced no mycorrhizas and grew poorly by comparison (Table 3).

Further, spores removed from the two most common sporocarp types at the site and applied in a similar way yielded no mycorrhizas and even poorer growth. One interpretation is that these fungal species do not form mycorrhizas with these plants. However, one of the inoculated *G. bilobum* plants produced a sporocarp which proved to be the same species as used for inoculation and responsible for one of the mycorrhizal types (simple tan) routinely produced on its root system (Fig. 1). Both plant species had white, pyramidal-type mycorrhizas like those in other eucalypts after inoculation with spores or mycelium of *Mesophellia* spp. (Ashton 1976; Malajczuk *et al.* 1987).

Another possibility is that digestion is required as a pretreatment before germination will occur. This is consistent with the usual failure of ectomycorrhizal fungal spores to germinate in culture or the requirements for special treatments to induce germination (references in Lamont *et al.* 1985). Perhaps reports of success with *Mesophellia* spores actually included active mycelium? The pretreatment hypothesis was supported seven years later by the parallel experiments of Claridge *et al.* (1992). They showed application of spores of the most common species in south-eastern Australian forests, *M. pachythrix*, to two eucalypt species in heat-sterilized soil failed to produce mycorrhizas. They considered that this fungus was responsible for the white, pyramidal-type ectomycorrhizas induced on *E. sieberi* in the presence of scats from the Long-nosed Potoroo, especially as it accounted for 16 per cent of the spores in the scats, as well as non-sterilized soil.

Relationship between Marsupials and Shrubs after Fire

It is possible that the passage of time is sufficient to precondition the spores for germination or that mycelial regrowth after fire is enough for inoculation of new roots of surviving plants or new seedlings. In unpublished work, we examined the effect of scats on mycorrhizal production by *G. bilobum* in Perup soil collected four days after fire (prescribed burn) and from sites burnt 18 months and >10 years earlier. All were fine loams from *G. bilobum* dominated gullies to a depth of 50 mm after brushing away any coarse organic matter. Since woylies began digging within a day of the April 1986 fire, samples were taken away from sites already visited by these animals. By giving the results on a per pot basis, we have an index of how well distributed was each fungal type in each soil as well as its occurrence at all.

By six months growth, scats had contributed three ectomycorrhizal types and increased the frequency of two others, while a sixth was already present in all pots of the three soils (Table 4). The most notable effects were the addition of two mycorrhizal types to the 4-day burnt soil and two to the 18 month burnt soil. Even in the >10-year burnt soil, inoculation increased the incidence of four ectomycorrhizal types by 16-66 per cent. While the change in mycorrhizal status due to the fresh scats had no effect on plant growth (unpublished), the extra fungal types resulted in a significant increase in the proportion of root tips that were mycorrhizal in the 4-day burnt soil (Table 5). This indicates that scats increase the inoculation capacity of the soil at the level of the individual root system of establishing plants.

In a similar way, Claridge *et al.* (1992) found that scats of the potoroo increased the number of ectomycorrhizal types from five to seven in *E. sieberi*, but the results are less useful as there were no unsterilized soils to which fresh or sterilized scats had been added and the interval since the last fire is not stated. Bougher *et al.* (1990) showed that some isolates and species of ectomycorrhizal fungi are far more effective than others at enhancing growth and P content of *E. diversicolor* at low soil P. By supplementing the range of ectomycorrhizal fungi available at any time the marsupial scats increase the likelihood of the presence of the nutritionally most efficient and the plant can take full advantage of the different metabolic and environmental optima of the various species associated with its root system.

Rapid restoration of the shrub layer is also important for the marsupials. The woylie shelters from predators, nests, feeds, mates and rears its young under the protection of a moderately dense understorey (Christensen 1980; Christensen and Leftwich 1980). It gathers litter to line its nest among branches arising from the ground; and quickly makes other nests nearby after fire. The woylie also collects *G. bilobum* seeds, and occasionally pulls out and consumes young seedlings arising from the caches after fire. While it is one of the most monofluoroacetate-resistant animals known, and *G. bilobum* one of the most toxic (Oliver *et al.* 1977), the poison peas appear to contribute little to the woylie's diet compared with the fungi.

DISCUSSION

There is a remarkable reciprocal relationship between certain small marsupials, shrubs (especially legumes) and ectomycorrhizal fungi (Fig. 3). The partners are different, but the relationships are the same, in eucalypt forests in mainland south-eastern Australia and south-western Tasmania. This partnership is jeopardized by fire; animals scatter or die, plants lose their foliage or die, fungi in the litter or humus are incinerated or heat-killed. However, a series of events is triggered off which soon restores the relationships. The animals return to the burnt sites almost immediately and start searching for the hypogeous sporocarps of ectomycorrhizal fungi, now, if not before, a preferred

TABLE 3

Ectomycorrhizal status and growth of *Eucalyptus calophylla* and *Gastrolobium bilobum* in heat-sterilized soil from their natural habitat (Perup) inoculated with fresh or sterilized woylie scats (faecal pellets) or spores of *Mesophellia trabalis* or *M.* sp. (summarized from Lamont *et al.* 1985).

	EUCALYPTUS CALOPHYLLA		*GASTROLOBIUM BILOBUM*	
TREATMENT	DRY WEIGHT (mg)	MYCORRHIZAL TIPS (%)	DRY WEIGHT (mg)	MYCORRHIZAL TIPS (%)
Fresh scats	1359	56	759	89
Heat-sterilized scats	951	0	81	0
Spores	675	0	50	0

TABLE 4

Percentage of six-month-old plants of *Gastrolobium bilobum* (n = 12-15) bearing each of six ectomycorrhizal types in the presence of fresh or heat sterilized scats of the woylie in three soils of different fire histories. All soils were collected six days after the April 1986 fire (B. Lamont and L. Stewart, unpubl.).

		ECTOMYCORRHIZAL TYPE[a]					
DATE OF LAST FIRE	CONDITION OF APPLIED SCATS	S,W	S,T	S,B	P,T	P,B	C,B
April 1986	fresh	67	100	67	100	0	33
	sterilized	62	100	0	85	0	0
October 1984	fresh	100	100	0	92	58	33
	sterilized	67	100	0	75	0	0
<1976	fresh	83	100	83	92	0	67
	sterilized	67	100	17	67	0	8

[a] S = simple, W = white, T = tan-coloured, B = black, P = pyramidal, C = coralloid

TABLE 5

Growth and ectomycorrhizal status of *Gastrolobium bilobum* grown in April 1986 burn soil. *T* = results of *t* - test.

	WOYLIE SCATS		
	FRESH	STERILIZED	*T*
Shoot weight (mg)	420±133	402±142	$p > 0.25$
Root tips mycorrhizal (%)	64.9±7.0	57.9±8.3	$p = 0.0001$

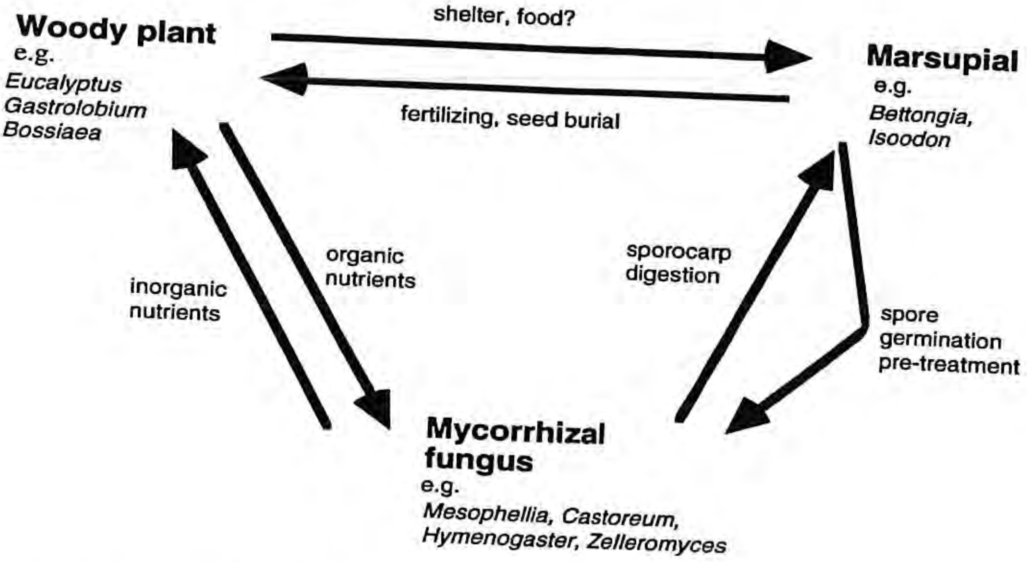

Figure 3. Food web between woody plants (producers), mycorrhizal fungi (heterotrophs), and Bettongia penicillata *and other mycophagous mammals - all relationships are mutualistic and stimulated by fire (modified from Lamont 1994).*

food source. There is some evidence, yet to be fully documented or corroborated, that sporocarp production of the major genus, *Mesophellia*, is stimulated within days of the fire. The marsupials range in and outside the burnt patches redistributing the spores from tight mono-specific clumps to other parts of the landscape.

Unlike parallel partnerships reported elsewhere (e.g. Kotter and Farentinos 1984), there is evidence that spore germination is stimulated by passage through the marsupial's gut for the three species examined so far. Application of faecal pellets increases the number and abundance of ectomycorrhizal fungi in surface soil immediately after fire, but even soils from sites not burnt for more than 10 years may benefit from faecal inocula. Fire predisposes the seeds for mass germination in the first winter after the fire. Early ectomycorrhizal formation ensures rapid growth and guarantees establishment of a moderately dense understorey in a few years. In the prolonged absence of fire (>25 years, Christensen 1980), the partnership is again in crisis, as non-sprouting shrubs die, the vegetation becomes very open, and presumably sporocarp production declines.

ACKNOWLEDGEMENTS

Without the high quality research of my colleagues Per Christensen, Catherine Ralph and Lisa Stewart, I would not have had anything worthwhile to contribute on this fascinating topic. The Department of Conservation and Land Management, especially Tom Leftwich, provided logistic support, and, through Per Christensen, met consumable costs. David Bell and Jack Warcup provided data for Table 2, and Christensen, Warcup and another reviewer commented on the manuscript.

REFERENCES

Abbott, I. and Loneragan, O. (1984). Growth rate and long-term population dynamics of jarrah (*Eucalyptus marginata* Donn ex Sm.) regeneration in Western Australian forest. *Australian Journal of Botany* **32**, 353-362.

Ashton, D.H. (1976). Studies on the mycorrhizae of *Eucalyptus regnans* F. Muell. *Australian Journal of Botany* **24**, 723-741.

Bennett, A.F. and Baxter, B.J. (1989). Diet of the long-nosed potoroo, *Potorous tridactylus* (Marsupialia: Potoroideae), in south-western Victoria. *Australian Wildlife Research* **16**, 263-271.

Bougher, N.L., Grove, T.S. and Malajczuk, N. (1990). Growth and phosphorus acquisition of karri (*Eucalyptus diversicolor* F. Muell.) seedlings inoculated with ectomycorrhizal fungi in relation to phosphorus supply. *New Phytologist* **114**, 77-85.

Brundrett, M.C. and Abbott, L.K. (1991). Roots of jarrah forest plants. 1. Mycorrhizal associations of shrubs and herbaceous plants. *Australian Journal of Botany* **39**, 445-457.

Christensen, P. and Leftwich, T. (1980). Observations on the nest-building habits of the brush-tailed rat-kangaroo or woylie *(Bettongia penicillata). Journal of the Royal Society of Western Australia* **63**, 33-38.

Christensen, P.E. (1980). The biology of *Bettongia penicillata* (Gray, 1837), and *Macropus eugenii*

(Desmarest, 1817) in relation to fire. Forests Department of Western Australia, Bulletin 91.

Claridge, A.W. (1992). Is the relationship among mycophagous marsupials, mycorrhizal fungi and plants dependent on fire? *Australian Journal of Ecology* **17**, 223-225.

Claridge, A.W., Robinson, A.P., Tanton, M.T., and Cunningham, R.B. (1993). Seasonal production of hypogeal fungal sporocarps in a mixed-species eucalypt forest stand in south-eastern Australia. *Australian Journal of Botany* **41**, 145-167.

Claridge, A.W., Tanton, M.T., Seebeck, J.H., Cork, S.J. and Cunningham, R.B. (1992). Establishment of ectomycorrhizae on the roots of two species of *Eucalyptus* from fungal spores contained in the faeces of the long-nosed potoroo (*Potorous tridactylus*). *Australian Journal of Ecology* **17**, 207-217.

Cork, S.J. and Kenagy, G.J. (1989). Rates of gut passage and retention of hypogeous fungal spores in two forest-dwelling rodents. *Journal of Mammalogy* **70**, 512-519.

Dell, B., Melajczuk, N., Grove, T.S. and Thomson, G. (1990). Ectomycorrhiza formation in *Eucalyptus* -IV. Ectomycorrhizas in the sporocarps of the hypogeous fungi *Mesophellia* and *Castorium* in eucalypt forests of Western Australia. *New Phytologist* **114**, 449-456.

Guiler, E.R. (1971). Food of the potoroo (Marsupialia, Macropodidae). *Journal of Mammalogy* **52**, 232-234.

Kinnear, J.E., Cockson, A., Christenson, P. and Main, A.R. (1979). The nutritional biology of the ruminants and ruminant-like mammals - a new approach. *Comparative Biochemistry and Physiology* **64A**, 357-365.

Kotter, M.M. and Farentinos, R.C. (1984). Formation of Ponderosa pine ectomycorrhizae after inoculation with faeces of tassel-eared squirrels. *Mycologia* **76**, 758-760.

Lamont, B.B. (1992). Functional interactions within plants - the contribution of keystone and other species to biological diversity. In: R.J. Hobbs (ed.) *Biodiversity of mediterranean ecosystems in Australia*. Surrey Beatty & Sons, Chipping Norton. pp. 95-127.

Lamont, B.B. (1994). Triangular trophic relationships in mediterranean-climate Western Australia. In: Arianoutsou, M. and Groves, R.H. (eds.). *Plant-Animal Interactions in Mediterranean-type Ecosystems*. Kluwer Academic Publishers, Dordrecht. pp. 83-89.

Lamont, B.B., Le Maitre, D.C., Cowling, R.M. and Enright, N.J. (1991). Canopy seed storage in woody plants. *The Botanical Review* **57**, 277-317.

Lamont, B.B., Ralph, C.S. and Christensen, P.E. (1985). Mycophagous marsupials as dispersal agents for ectomycorrhizal fungi on *Eucalyptus calophylla* and *Gastrolobium bilobum*. *New Phytologist* **101**, 651-656.

Malajczuk, N. and Hingston, F.J. (1981). Ectomycorrhizae associated with jarrah. *Australian Journal of Botany* **29**, 453-462.

Malajczuk, N., Trappe, J.M. and Molina, R. (1987). Interrelationships among some ectomycorrhizal trees, hypogeous fungi and small mammals: Western Australian and northwestern American parallels. *Australian Journal of Ecology* **12**, 53-55.

Oliver, A.J., King, D.R. and Mead, R.J. (1977). The evolution of resistance of fluoroacetate intoxication in mammals. *Search* **8**, 130-132.

Ralph, C. (1984). An investigation into the dispersal of ectomycorrhizal fungi by the mycophagy of the woylie *(Bettongia penicillata)*. Third Year Project Report, Curtin University (unpubl.).

Reddell, P. and Malajczuk, N. (1984). Formation of mycorrhizae by jarrah *(Eucalyptus marginata* Donn ex Smith) in litter and soil. *Australian Journal of Botany* **32**, 511-520.

Shea, S.R. and Kitt, R.J. (1976). The capacity of jarrah forest native legumes to fix nitrogen. *Forest Department of Western Australia Research Paper* **21.**

Specht, R.L., Rayson, P. and Jackman, M.E. (1958). Dark Island heath (Ninety-mile Plain, South Australia). VI. Pyric succession: changes in composition, coverage, dry weight and mineral nutrient status. *Australian Journal of Botany* **6**, 58-88.

Taylor, R.L. (1991). Plants, fungi and bettongs: a fire-dependent co-evolutionary relationship. *Australian Journal of Ecology* **6**, 409-411.

Taylor, R.J. (1992a). Fire, mycorrhizal fungi and management of mycophagous marsupials. *Australian Journal of Ecology* **17**, 227-228.

Taylor, R.J. (1992b). Seasonal changes in the diet of the Tasmanian bettong *(Bettongia gaimardi)*, a mycophagous marsupial. *Journal of Mammalogy* **73**, 408-414.

Taylor, R.J. (1992c). Distribution and abundance of fungal sporocarps and diggings of the Tasmanian bettong, *Bettongia gaimardi. Australian Journal of Ecology* **17**, 155-160

Warcup, J.H. (1980a). Ectomycorrhizal associations of Australian indigenous plants. *New Phytologist* **85**, 531-535.

Warcup, J.H. (1980b). Effect of heat treatment of forest soil on germination of buried seed. *Australian Journal of Botany* **28**, 567-571.

Warcup, J.H. (1981). Effect of fire on the soil microflora and other non-vascular plants. In: Gill, A.M., Groves, R.H. and Noble, I.R. (Eds). *Fire and the Australian Biota*. Australian Academy of Science, Canberra. pp. 203-214.

Warcup, J.H. (1990). Occurrence of ectomycorrhizal and saprophytic discomycetes after a wild fire in a eucalypt forest. *Mycological Research* **94**, 1065-1069.