Fungi and fire in Australian ecosystems: a review of current knowledge, management implications and research gaps and solutions

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Abstract

Despite their importance, fungi are generally poorly studied and understood. Fungi are essential components of all ecosystems. Their various roles include acting as symbiotic partners, decomposers, nutrient cyclers and as sources of food for vertebrates and invertebrates. Management of fire in Australia is based mainly on knowledge of the effect of fire on vegetation. Studies of fungal communities in Australian vegetation types show that the effects of fire are highly variable and depend on factors such as soil and vegetation type and variation in fire intensity and history, including the length of time between burns. Fire changes the environment in which the fungi function: including affects on soil structure, nutrient availability, organic and inorganic substrates and other biotic components including plants and animals with which fungi interact, particularly their interdependent vertebrate vectors. Many saprotrophic fungi grow only on specific substrates (i.e. litter, woody debris, burnt soil). Modification or loss of a substrate due to fire will impact on all components of the fungal environment.

In this review, differences in research methodologies and gaps in current knowledge are discussed. The functional roles of fungi in ecosystems and the effects and interactions of fire on these roles are explained and discussed. Responses of fungi to fire are reviewed in general and for each fungal trophic group. Fungal trophic groups are highlighted as being identifiable and potentially useful targets in effective management of functional ecosystems. This review aims to help managers make informed decisions on best practice with respect to fire regimes in parks and reserves. Recommendations are made to include monitoring of fungi, particularly macrofungi, in fire management plans.

1. INTRODUCTION

The fungal kingdom is megadiverse, with a range of vital ecological roles and a high degree of interdependency with other organisms. Fire is an integral part of Australian ecosystems and controlled or prescribed burning is a process that is increasingly under active management. Fire affects fungi in various ways. However, knowledge of fungal diversity and ecology in Australian native ecosystems is generally poor, which retards management of fungi in respect of factors such as fire. Other organisms that rely on fungi may also be compromised by knowledge deficiencies about their fungal partners.

The understanding of fire regimes and their effects on Australian vegetation has developed rapidly from a generally science-based endeavour, when 'Fire and the Australian Biota' (Gill *et al.* 1981) was current, to a much more management-, consequence- and biodiversity-orientated approach (see papers in (Bradstock *et al.* 2002). More recently still and, as a consequence of extensive fires which have occurred on most continents, new frameworks and theories are being applied to develop strategies which will support effective ecosystem functioning in the face of changing climates (Williams and Bradstock 2008).

Although most current fire management policies are supposed to aim to maximise biodiversity, generally the data collected are predominantly concerned with vegetation, fuel quantifies and conditions and the likely locations of recognised threatened species. Fungi do not fit well into these management frameworks. Our supposition is that although the roles of fungi are similar in Australia and other global ecosystems, their relative importance in most Australian ecosystems is enhanced due, in part, to particularly old and nutrient-poor soils. Australian vegetation is also significantly different in origins due to the isolation from most other land masses for long periods of time. Many fungi have strong associations with specific plant species or the substrates they create. Although research from other vegetation systems might be indicative of ecological trends, it is likely that the roles of fungi in Australian systems are considerably different. (Cairney and Bastias 2007) have recently reviewed how fire influences forest soil fungi, particularly ectomycorrhizal fungi, but only 10% of studies reviewed were Australian.

Recently, concern has been expressed that management of fire for vegetation may not provide the best outcomes for other biota (Clarke 2008). The purpose of this review is to summarise current knowledge of how fire affects fungi in Australian ecosystems, particularly from a management perspective, and to identify gaps and suggest steps by which fungi and fire may be better understood and managed.

As there is a poor general awareness of fungal biology and ecology, these aspects are first summarised below to provide background to a discussion of the effect of fire on fungi. Further sections deal with fungal trophic groups and substrate to highlight the functional roles of fungi and to suggest a context to help managers integrate fungi into ecosystem management.

2. BASIC FUNGAL BIOLOGY AND ECOLOGY

2.1. Classification and diversity

Fungi are classified as a separate kingdom of the natural world, distinguished by the production of spores, heterotrophic (non-photosynthetic) nutrition and the presence of chitin in cell walls. A few organisms traditionally included in Fungi belong in other kingdoms—slime moulds in Protozoa and Oomycetes (e.g. *Phytophthora*) in Chromista. The main phyla of true Fungi are Ascomycota, Basidiomycota, Chytridiomycota and Glomeromycota. Lichenised fungi (lichens) occur mainly within the Ascomycota; they form a symbiotic relationship with a photosynthetic photobiont (cyanobacteria or green algae).

The terms 'macrofungi' and 'microfungi' are used for convenience to distinguish fungi with readily visible fruit-bodies from those without. Familiar examples of macrofungi include agarics (mushrooms), puffballs, coral fungi, bracket fungi and cup fungi. Australia is rich in truffle-like fungi that produce fruit-bodies belowground or in leaf litter and, unlike aboveground fungi, their spore producing tissues remain enclosed (sequestrate). Sequestrate fungi have evolved in a number of different lineages within the Ascomycota, Basidiomycota and Glomeromycota. Microfungi include mildews, moulds and rust and smut fungi. Microfungi are often only visible in the field when their hosts develop symptoms such as wounds, lesions, leaf spots and cankers.

Some 11,846 described species of fungi are known from Australia, of which 3,495 are lichens (Chapman 2009). There are likely to be at least 10,000 macrofungi (about twice as many as currently known) and estimates for Australian fungi as a whole range from 50,000 to 250,000 species (Chapman 2009). Not only are there many species awaiting formal description, but the biology and ecology of named species is often poorly known. Three taxonomic volumes of the *Fungi of Australia* series have been produced, but otherwise species descriptions are scattered in technical literature. For all groups of fungi, identification usually requires use of microscopic characters. However, there are some readily recognisable macrofungi, illustrated in field guides such as (Fuhrer 2005) and (Grey and Grey 2005).

Very few fungi are formally listed on state or national conservation schedules (May 1997; May 2003). Fungi are usually not or only incidentally considered in biodiversity policy documents and management plans for conservation reserves and other areas. Most Australian state and national conservation and management agencies do not have mycologists on staff, the only exception being Western Australia. The low number of mycologists in Australian herbaria compounds the problem: essential taxonomic work and production of identification tools is limited compared to the number of botanists working on the Australian flora. However, there is increasing attention and involvement of community groups, such as Fungimap and various state fungi interest groups, in monitoring and recording fungi.

2.2 Life cycle and biology

Fungal spores are generally microscopic and germinate to form thread-like structures, hyphae (singular hypha) that develop into a network of mycelium. The mycelium is the vegetative stage of the fungus and grows within or on the host substrate (i.e. soil, dung, wood, leaves etc.). The mycelium is not usually visible but sometimes aggregates into discernible cord or cobweb-like structures, particularly in the leaf litter layer. Fruit-bodies are dense aggregations of hyphae that produce and liberate spores. Fruit-bodies of fleshy fungi such as mushrooms or truffles are relatively short-lived, but the underlying mycelium may persist for one or more years. Sexual reproduction usually involves fusion of two compatible parent hyphae. Asexual reproduction is common. Drought resistant resting stages include thick-walled chlamydospores and sclerotia (dense aggregations of hyphae) or pseudosclerotia (soil particles bound together with hyphae).

Spore dispersal may be by wind, water or animal movement including mycophagy. Details of life histories of most fungi in their natural environment are unknown. Thus, there is little information on spore dispersal distance, the rate of establishment of new individuals and the lifespan of fungal individuals. Fruit-bodies indicate the presence of underlying mycelia, but they do not always develop throughout the whole, often extensive, network of hyphae nor in every fruiting season. Individual mycelia can occupy areas of up to several hectares or more but, conversely, a number of individual mycelia from the same or several species can occur within a single piece of wood. For example, as many as eight different species of mycorrhizal fungi have been found in 4 cm^3 of soil (Gebhardt *et al.* 2009).

2.3 Trophic modes and interactions

Fungi are heterotrophic, and thus must gain carbon nutrition from external sources. A variety of nutritional strategies are employed including saprotrophism, parasitism and the formation of mutualistic partnerships such as mycorrhizas and lichens (May and Simpson 1997).

Saprotrophic or decomposer fungi grow in soil (Bridge and Spooner 2001) or directly on litter and wood (Rayner and Boddy 1988). They are particularly important in the degradation of dung, plant litter and woody debris due to their ability to break down complex compounds such as cellulose and lignin. Decomposer fungi are essential components of carbon, nitrogen, phosphorus and other nutrient cycles in ecosystems (Berg and Laskowski 2006). Consumption of fruit-bodies and mycelium of many fungi by mycophagous animals, particularly invertebrates, also contributes to nutrient cycling.

One reason for the massive biodiversity of fungi is that most species fill specific niches, with many decomposer fungi having substrate preferences that are often more explicit than simply a preference for dung, wood, litter or organic matter in soil. For example, wood-decay fungi may prefer substrates of a particular size or stage of decay, and can also be host specific, although some have wide host ranges. There can be a succession of fungi on substrates as the process of decay and decomposition develops. Saprotrophic fungi are ecologically important for the creation of nesting hollows and as habitat and food for invertebrates. In addition, the results of decomposition may be canopy gaps that promote small scale diversity in plant communities.

The majority of parasitic fungi are microfungi; these live on or in plant, animal and even fungal hosts. Many parasitic fungi are highly host specific at the host species, genus or family level, but some have wide host ranges. In agricultural and silvicultural systems, parasitic fungi can cause extensive damage, but in natural ecosystems parasitic fungi are an integral part of the interactions between organisms (as are predatory animals). Parasitic fungi of *Eucalyptus* plantations in Australia and overseas are well-studied, but knowledge of plant parasitic fungi of native plants in native Australian ecosystems is particularly limited. Many plants contain endophytic fungi that live in healthy plant tissue without causing symptoms. Some endophytes are potential parasites or may become saprotrophs once plant material dies and falls. For example, among Australasian Rhytismatales, some species are generalists, but most are endemic and are host-specialised, interacting as endophytes within the living tissue of their hosts (Johnston 2001). Secondarily these are putative decomposers with the fruit-bodies then continuing to develop on fallen, dead or dying leaves.

Mycorrhizal fungi associate with roots (or other underground structures) and form distinct structures which facilitate exchange of carbohydrates to the fungus and nitrogen and phosphorus to the plant (van der Heijden and Sanders 2002; Brundrett 2004; Cairney 2005). Mycorrhizal fungi thus contribute to nutrient cycling (Tommerup and Bougher 2000) and can also protect plants against some pathogens and increase tolerance to environmental stress such as drought. Several different types of mycorrhizas are known including ectomycorrhizas (ECM), vesicular arbuscular mycorrhizas (VAM), ericoid mycorrhizas and orchid mycorrhizas, each association formed by a particular group of fungi and plants, and each with a characteristic structure. For example, ECM are formed mainly by Ascomycota and Basidiomycota which create a visible sheath of fungal hyphae around roots of woody plants in the Casuarinaceae, Mimosaceae, Myrtaceae, Nothofagaceae and Rhamnaceae. Vesicular arbuscular mycorrhizas are mostly formed by Glomeromycota (Schwarzott *et al.* 2001; Brundrett 2004) which produce microscopic vesicles or arbuscules within plant root tissue of many groups of terrestrial plants. Ericoid mycorrhizas are associated with Ericaceae (Perotto *et al*. 2002), while orchid mycorrhizal fungi are vital for seed germination and adult plant nutrition (Rasmussen 1995; Brundrett 2006). Some plants form more than one type of mycorrhiza, such as ECM and VAM, often at different life stages. Mycorrhizal fungi, particularly ECM, are often difficult or impossible to grow in pure culture.

Apart from a few families, notably the Proteaceae, most vascular plants and some liverworts form mycorrhizas of one sort or another. Surveys of a variety of Australian ecosystems with *Eucalyptus* or *Angophora* overstoreys have found mycorrhizas in 66-96% of the plant species present with VAM the most common type of mycorrhizal association formed (Brundrett *et al.* 1996a); papers summarised in (May and Simpson 1997).

In addition to the roles of fungi directly related to their trophic mode, (Christensen 1989) identified a number of other ecosystem functions where fungi have critical roles. Fungi influence soil structure as they affect soil permeability, ionic exchange and promote aggregation of soil particles. Fungal mycelia can increase the carbon content, water holding capacity and infiltration of water into soil (Bastias *et al.* 2006a; Claridge *et al.* 2009).

Fungi are food for many invertebrates and vertebrates. In particular, fungi form a substantial proportion of the diet of many native animals, including potoroos and bettongs which have evolved specialised digestive tracts to assist in breakdown of fungal tissue (Vernes 2009). These animals consume mainly sequestrate (truffle-like) macrofungi all year round. The fungi rely on mycophagous mammals for dispersal of the spores which remain viable after passage through the animal. There is a three-way mutualistic partnership between sequestrate fungi (most of which are ectomycorrhizal), their plant hosts and mycophagous animals.

2.4 Distribution

Fungi occur in all terrestrial ecosystems and in freshwater and marine environments. As well as occurring in association with all parts of living plants, they are extremely common in soil, on all types of dead organic matter and on other sources of carbohydrates and nutrients such as animal droppings, nectar and sap flows.

Most ectomycorrhizal and saprotrophic macrofungi are very widely distributed in Australia, both geographically and in a variety of ecosystems (May 2002; Grey and Grey 2005). However, there are no studies on the degree of genetic differentiation across such wide distributions which often include greatly separated areas such as across the Nullarbor Plain or Bass Strait. Narrow host ranges potentially limit the distribution of parasitic microfungi but comprehensive data for Australian species are lacking.

3. CURRENT AND EMERGING TECHNIQUES FOR STUDYING FUNGI IN ECOSYSTEMS

3.1 Fruit-body surveys

Macrofungal communities have traditionally been studied by surveying the presence of fruit-bodies, which is the simplest and least expensive method and causes minimal interference (Watling 1995; Peter *et al.* 2001). However, only species that produce fruit-bodies at the time of survey are recorded and even these species may not fruit every year. Most studies are only conducted for one or two years, but long-term surveys (5-10 years) over relatively large areas are required for an estimation of overall fungal diversity (Rossman *et al.* 1998; Mueller *et al.* 2004a). The majority of fruit-bodies only last for a relatively short time so fortnightly and even weekly surveys conducted during peak growing periods can still miss significant amounts of diversity (Lodge *et al.* 2004). For these reasons, fungal fruit-body diversity should not be assumed to represent the relative importance and abundance of the full suite of species present in an environment.

Fruit-bodies are traditionally identified by morphology. Some species can be recognised in the field, others need detailed examination of microscopic features for identification. For most genera of Australian fungi there are no up-to-date monographs and an estimated 60-75% of species are undescribed (Chapman 2009). Even where recent monographs are available such as for *Mycena*, many collections can not be identified with confidence to known species and ‘tag’ or ‘field’ names have to be used (Robinson and Tunsell 2007). While field names are consistent within a particular study, there has been no attempt to match them up across studies in different ecosystems.

The trophic mode of particular fungi is established from a combination of field observations of substrate, investigations of enzymatic capability, stable isotope data (indicative of the carbon source) and *in vitro* experiments involving synthesis of mycorrhizal associations of the fungus and the plant host. Observations of substrate alone may not be sufficient as saprotrophs and ECM can fruit on the ground and on wood. Trophic status is highly correlated with phylogeny, and is generally uniform within genera but can vary considerably within families (Tedersoo *et al.* 2009b).

3.2. Sampling of ectomycorrhizas

Ectomycorrhizal fungal associations can be determined from soil cores by sieving and washing of root tips. There is variation in the overall morphology of mycorrhizas formed by different types of fungi, but macro-morphological characters rarely allow identification to species (Anderson and Cairney 2007). Microscopic characters of the mantle, the hyphal network formed around roots, allow identification of most species involved in ECM, but microscopy is time-consuming and requires sectioning of the fungal sheath (Brundrett *et al.* 1996d). Some aspects of morphology may vary depending on the particular host+fungus combination. The morphology of ECM roots can be compared against a databank of morphological characteristics of mycorrhizas formed by known combinations of fungi and hosts, such as those formed from *in vitro* synthesis (Agerer 1987-2002). Among published descriptions of ECM associations, only a few are available for mycorrhizas formed by Australian fungi.

3.3 Culturing

Fungi that grow in substrates such as soil or decaying wood can be isolated into pure culture for identification. Identification traditionally relies on culture, hyphae and spore morphology (Stalpers 1978), but some cultures do not produce spores. Some fungi (especially ECM) will not grow in culture (Liesack and Stackebrandt 1992) and the diversity and abundance of the suite of fungi isolated into pure culture may differ from that in nature due to differential survival and growth under artificial conditions .

3.4. Fungal biomass

3.4.1 Direct quantification

The biomass of fungal mycelia in soil has traditionally been estimated directly by microscopic examination of the length of hyphae emanating from root tips (Sharma *et al.* 1977; Wallander 2006). Microscopic quantification of hyphae in soil is difficult and time-consuming particularly when differentiating fungal hyphae from mineral soil particles and in separating living from dead fungal tissues. Such results have been criticised to both over- and under estimate fungal biomass.

3.4.2 Fungal biomass - chemical methods

Several fungal-specific molecules, such as chitin, ergosterol and phospholipid fatty acids (PLFAs), can be measured in soil to give an indication of fungal biomass (Wallander *et al.* 2001). Biochemical markers have advantages over more traditional morphological techniques, including less observer associated variability (Stahl and Parkin 1996) and increased efficiency in quantification (Ruzicka *et al.* 2000).

Ergosterol is the dominant sterol in fungal cell membranes (Peacock and Goosey 1989). It is characteristic of higher fungi and is not found in significant quantities in bacteria or higher plants. Ergosterol is easy to measure using high pressure liquid chromatography and is readily distinguishable from major sterols of other organisms. Ergosterol has been shown to be a more sensitive and reliable indicator of fungal biomass than other biochemical markers such as chitin (Davis and Lamar 1992). Unlike chitin, it rapidly degrades upon cell death and hence is a potential marker of viable biomass. Phospholipid fatty acid (PLFA) is another fungal marker frequently used as an indicator of change in soil fungal biomass. There does not appear to be any significant difference between the measures of PLFA or ergosterol with several studies finding good correlation between both marker molecules (Klamer and Bååth 2004; van der Wal *et al.* 2006).

3.4. Molecular methods for identification of fungi

Development of molecular methods in recent years has moved fungal taxonomy and ecology into a new phase of research. Molecular methods are relatively quick and easy to learn and generate highly reproducible results (Horton and Bruns 2001). Sequencing of small sections of DNA (Deoxyribonucleic Acid) can be achieved by amplification with the polymerase chain reaction (PCR), using primers specific for the region. Restriction fragment length polymorphism (RFLP) is another simple method for assaying specific amplified DNA segments.

DNA can be isolated from pure cultures as well as various parts of a fungus such as fruit-bodies, spores or the sheath of mycorrhizal root tips. In addition, techniques such as Terminal RFLP (TRFLP) can be used to profile the community of organisms in bulk samples of soil or wood. Such methods dispense with the need to isolate individual fungi and include substrates that are difficult to sample such as hyphae emanating from ECM (Anderson and Cairney 2007; Martin 2007). Thus molecular tools not only offer the promise of rapid identification of fungi but also provide novel techniques for sampling fungal communities.

There are two impediments to the wider application of molecular methods. The first is that the isolation and sequencing costs have been relatively expensive. However, the cost per sample is rapidly diminishing and new high-throughput techniques such as 454 pyrosequencing can generate many thousands of samples (Hibbett *et al.* 2009). The second and more problematic impediment is that identification of fungi using DNA sequence data relies on two things (1) a region that is species-specific – the so-called barcode region, and (2) a databank of sequences from the barcode region for known and accurately named fungi. The internal transcribed spacer (ITS) region of the ribosomal DNA is a very promising barcode region for fungi although it does not appear to discriminate for all species (Nilsson *et al.* 2008). The main problem in identifying sequences is that there are relatively few sequences for named species against which to compare those from environmental samples. This is especially so for studies on Australian fungal communities, where many sequences do not match well with any named sequences in International Nucleotide Sequence Databases (INSD) such as Genbank, although they may match other environmental sequences from Australian forests. Sequences, whether from fruit-bodies or environmental samples, can be identified against those in INSD by either matching on overall similarity (such as a BLAST search) or by including the unknown sequences within a phylogenetic analysis including other related sequences. Reliability of identification will improve as each study adds to the number of sequences available for analysis.

4. STUDIES ON THE FUNGAL COMMUNITY AND FIRE

The effects of fire are often complex and dependant on a combination site characteristics and histories. The generalities of fire complexity from a management framework are discussed in section *7.1. The complex fire regime*. Furthermore specific fungal issues on fire frequency are discussed in sections *7.2 Fire frequency and fungi* and *7.3. Fungi that require long unburnt forest*. Although responses of biotic and abiotic ecosystem elements may be complex due to the combination and circumstance of each fire, some generalisations about the usual consequences of heat from fire on soil are summarised in section *4.1 Biogeochemical effects of fire on soil fungi*.

One of the difficulties in generalising the effects of fire on fungi is that fungi belong to a diverse range of phylogenetic groups which have developed different roles in ecosystems based on their trophic needs. These fungal trophic groups and their ecological niches are discussed separately in section *5. The effect of fire on different trophic groups of fungi*. There are also difficulties in interpreting fungal responses to fire which arise from the use and interpretation of techniques used to study different fungal groups, the common limitations are discussed in section *4.2 Methodological limitations of fire and fungal studies*. Generalisations and a summary of the results from studies of the effects of fire on fungi in Australian ecosystems are reviewed in section *4.3 Fungal communities and fire* and the phenomenom of post fire macrofungal fruiting in section *4.4 Pyrophilous macrofungi*.

4.1 Biogeochemical effects of fire on soil fungi

The effects of fire on the biogeochemical cycles of soil are complex and result from interactions of site, fire and vegetation. The general effects, both direct and indirect, and their variability are generally well understood and are summarised in this section.

Direct effects of fire on soil include heating, with ensuing sterilisation of upper soil layers, and loss of nutrients and carbon through volatilisation and combustion of litter and soil organic matter (Certini 2005). Most soil organisms and nutrients are concentrated in the upper 20-30 cm of soil and any heating or combustion in this layer can have repercussions on post-fire recovery of vegetation. For most fires, radiative heat provides enough heat to kill soil organisms including fungi within the upper soil layer (Raison *et al*. 1985). Heating to as little as 60 ºC is enough to kill living tissue, particularly unprotected fungal mycelia (Schenck *et al.* 1975; Klopatek *et al.* 1988). Temperatures sufficient to decrease soil biota are often reached during fires (Humphreys and Lambert 1965; Bradstock *et al.* 1992; Pattinson *et al.* 1999).

Indirect effects of fire on soil include loss of nutrients through erosion and leaching, change in water repellence and greater absorption of heat by blackened surfaces and loss of the shading cover of vegetation (Gochenaur 1981). These indirect effects will in turn affect recolonisation by soil fungi.

Loss of nitrogen from the system can have subsequent impacts on recovery of vegetation and nutrient balances (Neary *et al.* 1999; Howell *et al.* 2006; Neary *et al.* 2008) and presumably, fungal populations. Despite the direct loss of nitrogen from soil, nitrogen availability in soil can increase as a result of fire (Raison 1979). Total soil nitrogen may increase if soil temperatures are in the range of 100-300 °C but at higher temperatures nitrogen availability decreases rapidly. In *Eucalyptus regnans* forest trials (Launonen *et al.* 1999), seedlings with ECM were shown to grow better in the cooler burnt black soils than the hot burnt red soils and these differences were attributed to nitrogen availability. In a similar manner to nitrogen, availability of phosphorus can change with different types of fires. In a cool burn (200 °C), total available phosphorus does not change appreciably but a hot burn (>400 °C) will release greater amounts of phosphorus (Raison *et al.* 1985; Gray and Dighton 2006). Fungi are directly and indirectly reliant on soil nutrients so this is an important consideration for post-fire recolonisation. Fire can significantly alter fungal populations that affect soil processes such as decomposition. Disruption to such processes can alter the carbon:nitrogen ratio in the soil and mineralisation rates and will ultimately affect plant growth and productivity (Neary *et al.* 1999; Bastias *et al.* 2006a; Neary *et al.* 2008).

4.2 Methodological limitations of fire and fungal studies

Broad findings about the effects of fire on fungi for Australian studies are hard to compare due to different research approaches and the limited number of studies conducted in Australia. Similar difficulties were encountered by (Cairney and Bastias 2007) in their review of global forest soil fungi and the effects of fire. The few rigorous studies of the effect of fire on fungal communities which have directly monitored the response to fire are listed in Table 1. Some of these studies are unreplicated or, while there is replication of sites within treatments, surveys were limited to collection of data at different times after a single fire. Replication of sampling tends to occur with planned experimental studies (Theodorou and Bowen 1982; Warcup 1983; Bellgard *et al.* 1994; Launonen *et al.* 1999; McGee *et al.* 2006) compared to descriptive studies. The latter type of study merely provide a list of the fungi present in vegetation of known time since the last fire. For example, a great diversity of macrofungi has been reported from Mt Wellington in Tasmania (Ratkowsky and Gates 2002; Gates and Ratkowsky 2004; Gates and Ratkowsky 2005; Trappe *et al.* 2008) which was burnt in 1967. These reports provide a valuable data set on the inventory of fungi from wet forest, gully vegetation and dry forests for 27-38 years since fire. Such studies could add to an understanding of the effect of fire but at present there are too few to make meaningful comparisons.

Various survey methods for detecting fungi have been used in studies of the effects of fire on fungi. The most common is surveying for epigeous macrofungi, often for their fruit-bodies only (Table 1). Surveys for macrofungi are labour- and time-intensive and thus are limited by the frequency with which surveying is carried out . Even with repeated surveys, a number of species will always be missed (Mueller *et al.* 2004b; Cairney and Bastias 2007). Some studies dealing with macrofungi have focused on whole community data only (McMullan-Fisher *et al.* 2002; Packham *et al.* 2002), while others have also considered trophic fungal assemblages (Tommerup *et al.* 2000; Gates *et al.* 2005; Robinson *et al.* 2008).

Table 1. Studies on the fungal community in Australian ecosystems of known fire history (years) by vegetation type (* repeated fire frequency). State, trophic groups (TG), morphological groups (MG), data collection technique (Data) and fungal identification method (ID) of the cited studies (Bolded references replicated sites for all age classes, = replicated samples for single fire events for age classes).

Vegetation type (dominant tree species)	Fire <12 months	Fire 1-10 yrs	Mature	Long unburnt	TG	MG	Data	ID	State	Literature
Alpine woodland (*Eucalyptus pauciflora*, *E. dalrympleana* and *E. stellulata);* Tall wet sclerophyll forest (*E. regnans*, *E. fastigata* and/or *E. dalrympleana)*; Dry sclerophyll forest (*E. mannifera* and *E. macrorhyncha)*;	X	X (1–10)	X (11–20; 21–30)	X (>30)	M	S	FBS	MO	Vic & NSW	**(Claridge and Barry 2000; Claridge *et al.* 2000a; Claridge *et al.* 2000b; Claridge and Trappe 2004)**
Tropical *Allocasuarina* Forest, *Eucalyptus* woodland and tropical rainforest	X	X (4-5)*			M	S	FBS	MO, BM, SSA	QLD	(Vernes *et al.* 2001; Vernes and Haydon 2001; Vernes *et al.* 2004)
Dry sclerophyll woodland (*E. rossii* and *E. macrorhyncha*	X	X (4)	X (21)		All	S, EM	FBS	MO	ACT	**(Trappe et al. 2006)**
Woodland *(E. albens* and *Callitris glaucophylla*); Riparian strips (*E. viminalis*), grassy or shrubby woodland (*E. melliodora*), Woodland (*E. nortonii*) grading to open forest (*E. dalrympleana*)	X	X			All	EM	FBS	MO	NSW	(Claridge et al. 2009)
Alpine heath			X (39)	X (56)	All	EM	FBS	MO	Tas	**(McMullan-Fisher et al. 2003)**
Wet sclerophyll forest *(E. regnans)*	X	X (2, 4, 7)	X (57)		All	EM	FBS	MO	Tas	**(McMullan-Fisher et al. 2002)**

Wet sclerophyll forest *(E. obliqua* and/or *E. delegatensis)*			X (25–30)	X	All	EM	FBS	MO	Tas	**(Packham et al. 2002)**
Wet forest *(E. obliqua)*				X (73, 109,200-300)	All	EM	FBS	MO	Tas	(Ratkowsky and Gates 2008)
Wet sclerophyll forest *(E. obliqua)*	X	X (2-3)			All	EM	FBS	MO	Tas	(Ratkowsky and Gates In Press)
Wet sclerophyll forest *(E. obliqua)*		X (2-3)	X (70)		All	EM	FBS	MO	Tas	(Gates *et al.* 2005; Ratkowsky 2007; Gates *et al.* In Press)
Sclerophyll woodland (*Eucalyptus cladocalyx*, *E. baxteri*)	X				All	S, EM	FBS	MO	SA	(George 2008; Catcheside 2009; Robinson 2009)
Sclerophyll forest *(E. marginata)*		X (2-4)*	X (28-30)		All	EM	FBS, BM	MO	WA	(Tommerup et al. 2000)
Regrowth forest *(*E. *diversicolor)*	X	X	X (17-25)		All	EM	FBS	MO	SA	**(Robinson 2003; Robinson et al. 2008)**
Sclerophyll forest *(E. marginata)*		X*	X		All	EM	FBS	MO	WA	**(Hilton et al. 1989)**
Sclerophyll forest *(E. marginata* & *Corymybia calophylla*)		X (6-7)*	X (66)		M	S, EM & ECM	FBS & MA (PCR RFLP)	MO & DB	WA	(Glen et al. 2001)
Tropical Savannas	X	X*			M	ECM & VAM	Bio	MO	NT	**(Brundrett *et al.* 1996a; Brundrett *et al.* 1996b)**
Wet sclerophyll forest *(E. regnans)*	X (2 mths)	X (14 & 25 mths)			M	ECM	Bio	Bio, ERG	Vic	(Launonen et al. 1999)
Sclerophyll forest *(E. marginata)*	1	6	45		M	ECM	SC	MO	WA	(Malajczuk and Hingston 1981)

Sclerophyll shrubland (*Angophora hispida)*	X	X (8)		X (unburnt)	M	VAM	Bio & SSS	MO	NSW	(Bellgard et al. 1994)
Plantation (*E. maculata*)					M	ECM	Bio	MO	SA	(Warcup 1983)
Dry open sclerophyll forests (*E. gummifera*, *Syncarpia glomulifera; Eucalyptus* spp.; and *E. squamosa*, *E. resinifera*, *E. haemastoma*, *E. bauerana*, *Allocasuarina littoralis*, *Angophora hispida*, *Leptospermum attenuatum)*	X (2 wks)	X (8, 10)	X (25)		All	ECM & SF	MA SA (PCR RFLP)	DB	NSW	(Chen and Cairney 2002)
Wet forest (*E. pillularis*)		X (2*, 4*)			M	ECM & SF	BM, POA, PLFA SA, MA, HIB (PCR, RFLP, ITS, T-RFLP)	DB & DGGE	QLD	(Bastias *et al.* 2006a; Bastias *et al.* 2006b; Anderson *et al.* 2007; Artz *et al.* 2009)
Open forest (*E. pillularis*)	X (48 hrs)			X (unburnt)	S	MI (Tric)	C	MO	NSW	(McGee et al. 2006)
Low Open Dry Sclerophyll Woodland (*E. baxteri, E. obliqua*)	X (1, 2, 7 mths)	X (12 & 20 mths)			S	MI	SA, C	MO	SA	(Theodorou and Bowen 1982)
Wet forest *(E. obliqua)*	X	X (3)		X (65-101)	L	L	FBS	MO	Tas	**(Kantvilas and Jarman 2006)**

Mallee (*Callitris preissii* subsp *verrucosa*)	X (1)	X (3, 4, 7)	X (13, 16, 18)	X (35, 100)	L	CSC	FBS	MO	NSW	(Eldridge and Bradstock 1994)
Temperate grassland (*Themeda australis–Poa sieberiana)*		(2, 4, 8)*		X (unburnt)	L	CSC	FBS	MO	NSW	**(O'Bryan *et al.* 2009)**

Trophic Groups: M = mycorrhizal, S = saprotrophic, P = parasitic, L = lichenised and All = all trophic groups except Lichens;

Morphological Groups: S = sequestrate fungi, EM = epigeous macrofungi, SF = soil fungi, ECM = ectomycorrhiza, VAM = vesicular arbuscular mycorrhiza, MI = microfungi, Tric = Trichocomaceae, L = lichens, CSC = cryptogamic soil crusts;

Data Collection Technique: FBS = Fruit-body survey, BM = biomass, SSA = spore scat analysis, Bio = Bioassays, SSS = soil spore survey, ERG = ergosterol analysis, POA = phenol oxidase activity, PLFA = Phospholipid-derived fatty acids SC = soil core root analysis MA = molecular analysis, SA = soil analysis, HIB = hyphal ingrowth bags;

Molecular analysis abbreviations: PCR = polymerase chain reaction, RFLP = Restriction fragment length polymorphism, ITS = internal transcribed Spacer, T-RFLP = terminal restriction fragment length polymorphism;

Fungal Identification method: MO = morphology, C = cultured, and DB = genetic database matching, GLD = genetic laccase diversity;

Sequestrate fungi are both a morphological and trophic groups, since nearly all are ectomycorrhizal. Some studies have used both fruit-body survey and the analysis of type and number of fungal spores in animal scats (Vernes *et al.* 2001; Vernes *et al.* 2004). Generally spore/scat analyses shows an increased species richness of fungi when compared to fruit-body surveys, probably due to the difficulties of collecting belowground fruit-bodies. However, spores can often only be identified to genera or broad groups of species (Vernes *et al.* 2004).

Some studies focus on fungi in a particular trophic group, for example most studies are of mycorrhizas (Table 1). Older studies of ECM used morphological root tip analyses both from bioassays (Warcup 1983; Bellgard *et al.* 1994; Brundrett *et al.* 1996a; Brundrett *et al.* 1996b; Launonen *et al.* 1999) and soil cores (Malajczak and Hingston 1981). One limitation of morphological root tip analyses is that, before molecular techniques, it was very difficult and time-consuming to match fruit-bodies and root-tips (Anderson and Cairney 2007), so most studies were limited to morphological categories for root tips. Some of these studies also used supplementary data from soil analyses and soil spore counts.

Many of the more recent studies of mycorrhizal fungi use molecular techniques alone (Table 1). A related study which focused on ECM used both molecular root-tip and fruit-body surveys (Glen *et al.* 2008), although this study looked at rehabilitation after mining as the disturbance rather than fire. Although their study was unreplicated, (Chen and Cairney 2002) revealed significant differences in soil fungal communities before and after fire using molecular RFLP profiles. In this case, trophic groups were attributed using information from current genetic databases. However, these databases are still limited and have a bias towards northern hemisphere fungi. Ideally, in future studies, a well-referenced set of genetic data for local fungi which is based on documented, identified and vouchered morphological specimens would allow matching to at least generic level.

4.3 Fungal communities and fire

The common thread in all of the fire and fungi studies is that fire changes the fungal community in someway (Table 1). The effects fire effects may be short term, for example soil communities returned to pre-fire levels within 20 months (Theodorou and Bowen 1982). Other studies show long term differences between sites of different fire histories. For example, in wet sclerophyll *E. obliqua* forest differences in site history are reflected by the fungal community more than 75 years after fire (Ratkowsky and Gates 2008). The findings of (Osborn 2007) are unusual in that there were no long term effects on the forest soil fungi by repeated low intensity fires. This contrasts strongly with other studies on repeated burning which show a simplification of fungal communities, a loss of fungal community stratification in the soil profile and reduced soil mineralization rates where sites were burnt at two yearly intervals (Bastias *et al.* 2006a; Bastias *et al.* 2006b; Anderson *et al.* 2007; Artz *et al.* 2009).

For the macrofungi, a post-fire flush of pyrophilous macrofungi is commonly reported (see section 4.4). For the period between 3-10 years after fire a number of studies from wet forests have noted a decreased macrofungal species richness (McMullan-Fisher *et al.* 2002; Gates *et al.* 2005). As well as a decrease in macrofungal species richness some authors have found that the species common in the regenerating forests have been the widespread, ubiquitous decomposer species (Gates *et al.* 2005; Ratkowsky 2007; Ratkowsky and Gates 2008). There may be a trend for decomposer fungi dominating the post-fire sites or more frequently burnt sites (Tommerup *et al.* 2000; Gates *et al.* In Press).

Studies on fire and fungi are restricted to a small range of vegetation types (Table 1). Studies are particularly lacking in grasslands, arid areas and woodlands. Knowledge of alpine fungi is limited, but one exploratory study in Tasmania showed no evidence of differences in macrofungal communities on sites burnt 39 and 56 years previously, despite clear differences in vegetation composition and structure resulting from the different fire histories (McMullan-Fisher *et al*. 2003). This information is somewhat restricted for wider application to other plant communities as alpine vegetation rarely burns and takes a long time to recover after fire (Kirkpatrick *et al*. 2002; Williams *et al*. 2008).

4.4 Pyrophilous macrofungi

There is a suite of macrofungi, mostly in the Ascomycota and Basidiomycota, that produce fruit-bodies on recently burnt substrates (typically the first and second years after fire) such as burnt soil and charcoal. These are often called pyrophilous ('fire-loving') fungi. They range from the strictly pyrophilous, that are totally dependent on fire for stimulation of spore germination and mycelial growth, to those that tolerate both burnt and unburnt sites. Agaricoid (mushroom-like) fungi fruiting in the first year after fire include decomposer fungi in *Pholiota*, *Psathyrella* and *Coprinus* (Gates *et al.* 2005; Robinson and Tunsell 2007; Catcheside *et al.* 2008; Robinson *et al.* 2008; Claridge *et al.* 2009). There are also fungi that are unable to grow on recently burnt sites.

The first and most conspicuous fungi observed after fire are those that produce fruit-bodies from subterranean storage organs, sclerotia or pseudosclerotia (McMullan-Fisher *et al.* 2002; George 2008; Robinson *et al.* 2008; Robinson 2009). The pyrophilous basidiomycetes *Neolentinus dactyloides, Laccocephalum mylittae* and *L. tumulosum* are common in both wet and dry eucalypt forests across southern Australia. These species are well adapted to fire and large fruit-bodies develop from the underground organs as early as two days after bushfires. Their mycelia decay large fallen logs and the subterranean sclerotia or pseudosclerotia develop under or adjacent to the host logs (Wills 1983). There is no information on how long it takes for these fungi to re-colonise logs following fire or how long sclerotia take to mature to the stage where fruit-body development can occur. Although these species are stimulated to reproduce by fire, repeated frequent burns may have a negative impact because of the requirement for the large logs characteristic of longer unburnt sites (Grove and Meggs 2003).

Australian studies report the abundance of ascomycetes on recently burnt sites (Warcup 1981; Warcup 1990; Gates *et al.* 2005; Robinson *et al.* 2008; Catcheside *et al.* 2009; Catcheside 2009). This post-fire flush of ascomycetes is a global phenomenon (Zak 1992; Cairney and Bastias 2007). The causes have been widely debated (Cairney and Bastias 2007), and include post-fire gap-filling possibly due to decreased competition, tolerance to post-fire conditions such as altered pH, and post-fire activation of germination of spores. It is likely that, depending on the condition of the site, all or some of these reasons may be important. Whatever the reasons, pyrophilous ascomycetes appear to be fulfilling multiple functional roles including decomposition, soil stabilization (Claridge *et al.* 2009) and in forming biotrophic associations. Some typically mycorrhizal species may survive the post-fire period as saprotrophs (Cairney and Bastias 2007).

5. THE EFFECT OF FIRE ON DIFFERENT TROPHIC GROUPS OF FUNGI

Differences in species richness and fungal assemblages in Australian forests when compared with time since fire have been linked to the distributions of available substrates (Tommerup *et al.* 2000; McMullan-Fisher *et al.* 2002; Packham *et al.* 2002; Gates *et al.* 2005; Robinson *et al.* 2008). Preferred substrates for a number of macrofungi from wet forests from Tasmania have been reported (Gates *et al*. 2005) and such requirements could be used to help guide the management of substrate in these forests. In the northern hemisphere, a link has been demonstrated between species rarity and uncommon substrates (Berg *et al.* 1994; Jonsson *et al.* 2005; Raphael and Molina 2007), thus the retention and maintenance of a diverse range of substrates within the landscape has been highlighted as important for the conservation of fungi (Grove and Meggs 2003). The differing physiology and ecological roles of the various trophic groups of fungi merit separate consideration of such groups when considering the effects of fire. Research into the specific functional roles and interactions of fire on fungi is still in its infancy (Cairney and Bastias 2007), but even the use of a functional ecology framework may advance our understanding of fungi.

5.1 Saprotrophic fungi

Saprotrophic fungi decay a wide variety of substrates, including the non-living heart wood of standing live trees and all the parts of trees and other plants once they are dead. The Australian literature on the effects of fire on saprotrophic fungi is discussed in the following substrate categories.

5.1.1 Standing trees

High intensity fires cause scars on living standing trees that act as entry points for fungi that decay the non-living heart wood and for pathogenic fungi (Parmenter 1977; Abbott and Loneragan 1983; McCaw 1983). Some decay fungi are important in the development of habitat for other organisms, including invertebrates and small reptiles and for generating nesting hollows for birds and animals (Kile and Johnson 2000; Hopkins *et al.* 2005). Alternatively, trees may become stressed or weakened, making them more susceptible to attack from root and canker pathogens (Parmenter 1977) or they may be killed, creating new habitat for wood decay fungi (Penttilä and Kotiranta 1996) either as standing dead trees (stags) or fallen logs and branch material.

5.1.2 Coarse woody debris

Coarse woody debris (CWD) is the woody debris from branches and whole trees lying on the ground. The importance of CWD in forest management has recently been recognised for its role in long-term nutrient cycling, biodiversity, carbon storage, moisture retention, tree health, structure and habitat for fauna and fungi (Grove *et al*. 2002). Saprotrophic fungi are important in CWD decomposition (Grove and Meggs 2003; Mackensen *et al.* 2003) and this substrate supports a succession of fungal species (Dix and Webster 1995; Boddy 2001). The size range of CWD is dependent on vegetation age, composition and disturbance history. Many saprotrophic fungi have preferences for size of CWD, wood type, decomposition stage or moisture level (Johnston 2001; McMullan-Fisher *et al.* 2002; Grove and Meggs 2003; Berg and Laskowski 2006).

Fire may reduce the total amount of CWD and alter its characteristics (Robinson 2003). Overall, fire may increase heterogeneity of CWD by having patchy effects on decay processes, by altering microclimates and by increasing the diversity of species which contribute to the woody debris pool (Grove *et al*. 2002). Fire is also one of the key cyclic disturbances which can produce CWD in forest systems. For example, stags are often initialled during fire events and contribute to types and quantities of CWD present. In timber production forests, removal of wood for timber and firewood reduces the amount of CWD and has profound negative implications for species dependent on CWD (Huston 1996). In these forests, the degree of utilisation and the length of rotations of tree stand have an impact on CWD (Grove *et al*. 2002; Jonsson *et al*. 2005). (Grove and Meggs 2003) have highlighted the importance of CWD for the survival of a range of saproxylic (wood-inhabiting) organisms including invertebrates and fungi.

Intense fires reduce the amount of CWD on the forest floor, thus they impact significantly on the species of fungi that colonise and decay dead wood (Penttilä and Kotiranta 1996; Robinson *et al.* 2008). In regrowth karri forest in Western Australia, the number of species recorded fruiting on wood was shown to be significantly lower for three years following an intense wildfire, but after five years species richness had increased and was higher on comparable unburnt sites (Robinson *et al*. 2008). Other studies have shown similarly decreased species richness of wood-inhabiting macrofungi on more recently (2-5 years) burnt sites (McMullan-Fisher *et al.* 2002; Gates *et al.* 2005). A possible explanation is that regenerating sites are more exposed to wind, rain and temperature variation and may be unfavourable for fungal fruiting, hence the reduced numbers of reproductive structures (McMullan-Fisher *et al.* 2002; Gates *et al.* 2005). In comparison, and despite this seemingly low diversity of wood-inhabiting macrofungi, a post-fire (3-5 years) increase in the fruiting of semi-parasitic ascomycetes such as *Daldinia* spp. and *Hypoxylon* spp. has been demonstrated (Gates *et al*. 2005; Robinson *et al*. 2008). These fungi live within the wood of healthy understorey trees and shrubs and rapidly spread and fruit after the host plant has been weakened or killed by fire (Robinson *et al*. 2008).

5.1.3 Litter

Litter is composed of dead leaves and fine woody material from plants. The time since last fire is particularly relevant to fungal studies as the leaf litter layer is generally removed and post-fire conditions are not conducive to fungal growth. At some time after a fire, the litter layer will return to pre-fire levels and vegetation cover will have re-established. The rate of fuel accumulation (living and dead) is particularly relevant from the point of view of fire management and fire risk. Fungal populations studied immediately after fire therefore likely to differ considerably from those surveyed several years after fire.

Succession of litter-decomposing fungi has been reported in non-Australian ecosystems (Berg and Laskowski 2006) and there is some evidence for a litter succession in Australian systems. For example, in *Eucalyptus marginata* and *E. diversicolor* forests in Western Australia, litter-dwelling fungi such as *Mycena* and *Marasmius* appeared as soon as two years after fire, while other genera did not appear until an organic layer had formed below the litter layer (Robinson *et al*. 2008). Rates of litter deposition vary across plant communities. In Jarrah forests the litter layer continues to accumulate in sites which have not been burnt (McCaw *et al.* 2002) and some of this accumulation is attributed to the senescence of the understorey. In mixed eucalypt foothills forest in Victoria, the fuel load remains at a relatively steady state of 16 t ha^{-1} with rates of accumulation more or less equalling decomposition (Department of Sustainability and Environment 2003a).

After fire in wetter eucalypt forests, the litter layer may take longer to develop and provide conditions that favour the production of fruit-bodies. For example, McMullan-Fisher *et al*. (2002) noted that litter-dependent fungi in *Eucalyptus regnans* forest did not appear until after the canopy had closed, seven years after fire. *Eucalyptus regnans* forests in Victoria have higher litter fall than other forests, reaching a maximum at about 40-50 years (Ashton 1975). Production of fruit-bodies will be influenced by microclimates within sites and conditions will change with season, canopy development, tree health and other factors. Fires reset or interrupt the succession of litter-decomposing fungi. Studies from a range of eucalypt forests (McMullan-Fisher *et al.* 2002; Gates *et al.* 2005; Robinson *et al.* 2008) suggest that it takes 5-10 years for litter-dwelling macrofungi to recover sufficiently from fire to develop reproductive structures.

Distribution of macrofungal species associated with litter reflects differences in substrate condition such as found in burnt compared to mature forest sites and also in differences in vegetation types. For example, in alpine vegetation in Tasmania, one unidentified discomycete was restricted to the litter produced by the dominant plant *Orites acicularis* which was abundant on older sites (McMullan-Fisher *et al*. 2003). Thus, distributions of individual macrofungal species may be influenced by fire due to restricted associations with specific litter substrates.

5.2. Parasitic fungi

There is little information on how fire interacts with parasitic fungi, although fire has been investigated as a tool to control some root disease pathogens. High intensity fire was successfully trialled in jarrah forest in Western Australia to promote a resistant leguminous understorey in an attempt to control dieback disease caused by *Phytophthora cinnamomii* (Shea *et al*. 1979). High intensity fire may also be detrimental to the root rot pathogen *Armillaria luteobubalina* as fire has the potential to destroy the outer sapwood of stumps and to burn tree buttress and lateral roots on which the fungus would normally survive (Kile 1980; Kile 1981). In the southern United States and Finland, stump infection by *Heterobasidion* *annosum* was reduced following fire (Parmenter 1977). Ironically, the increased accumulation of fuel caused by parasitic fungi may promote fire (Robinson and Bougher 2003). There is no information available about the effect of fire on the numerous parasitic leaf-spot fungi found on native plants in Australia.

5.3. Mycorrhizal fungi

Several different types of mycorrhizas are known, each with a characteristic structure and each predominantly formed by particular groups of fungi and plants. The main groups of ectomycorrhizas are discussed below. The case of sequestrate fungi, which are predominantly mycorrhizal, is further discussed in section *6.2. Fungi-vertebrate interactions*.

5.3.1 Vesicular arbuscular mycorrhizas

Vesicular arbuscular mycorrhizas (VAM) are probably the most widespread mycorrhizas globally. Their responses to fire have been shown to be quite variable but fire usually impacts negatively (Hart *et al.* 2005; Cairney and Bastias 2007). Similarly, studies in Australian ecosystems have shown variable but usually negative effects of fire on VAM. As an example, fire had an immediate detrimental effect on VAM in open sclerophyll shrubland, however the fire event had no long-term effect on infectivity and spore abundance (Bellgard *et al*. 1994). There is evidence that fire reduces the inoculum potential of VAM from topsoil in eucalypt woodlands in northern Australia (Brundrett 1991; Brundrett *et al.* 1996a; Brundrett *et al.* 1996b). Experiments using VAM (Bellgard *et al*. 1994; Pattinson *et al*. 1999) show that heat similar to that from a moderate intensity fire decreased inoculum and the mycelial network was lost where soil temperatures were greater than 80 °C. Pattinson *et al*. (1999) argue that it is the loss of the mycelial network after fire rather than modifications to inoculum potential which drives the post-fire reductions in VAM. Given that early seedling development, particularly of small seeded plants, may well depend on VAM (Adjoud-Sadadou and Halli-Hargas 2000), such decreases in inoculum may be important. Survival of VAM after fire may therefore have a direct effect on the development of the subsequent plant community (Bellgard *et al*. 1994; Pattinson *et al*. 1999). Responses of vegetation post-fire may be further complicated by the interaction of vertebrates (Gehring *et al*. 2002). This increased dispersal VAM fungal inoculum and abundance by vertebrates has been linked to a corresponding increased diversity of these mycorrhizas .

5.3.2 Orchid mycorrhizas

Orchids are particularly dependent on their fungal symbionts for survival (Rasmussen 1995; Smith and Read 2002; Dearnaley and Le Brocque 2006). Fire stimulates the flowering of some terrestrial orchids such that declining populations may need regular disturbance by fire. For other terrestrial orchids, fires that occur too frequently have a negative impact on populations, presumably due to the effect of fire on fungal symbionts as well as on the host plants (Brundrett 2007). High fire frequency has been shown to reduce the number of epiphytic orchids in tropical savannah, partly due to the decreased numbers of host trees on burnt sites, but also by the direct impact of fire (Cook 1991). Many orchid species are threatened and altered fire regimes are considered to be one of the threatening processes. An understanding of the ecology of the fungal symbionts of orchids has an important role in promoting their orchid conservation (Brundrett 2006).

5.3.3 Ericoid mycorrhizas

Ericoid mycorrhizas are common in Australian forest and heathlands, the latter ecosystem being characterised by low nutrient soils and highly seasonal drought conditions (Bell and Pate 1996b; Cairney and Burke 1998; Chambers *et al.* 2008). In European heathland ecosystems, it is thought that this type of mycorrhizal association allows the Ericaceae to be important colonizer plants in disturbed, low nutrient or toxic environments (May and Simpson 1997; Perotto *et al.* 2002). The effect of fire on Australian ericoid mycorrhizas has not been studied however; seedlings of species of Australian Ericaceae recruited after fire were found to accumulate substantial fractions of nutrients (nitrogen and phosphorus) and dry matter during hot, dry summer months when infected mycorrhizal roots were absent (Bell and Pate 1996a).

5.3.4 Ectomycorrhizas

Ectomycorrhizal fungi (ECM) are common in woody vegetation types such as forests and woodlands (Dell 2002). These fungi predominate in the top 10-20 cm of soil and in leaf litter (Bastias *et al.* 2006a). There is evidence that fire reduces the inoculum potential of topsoil from eucalypt woodlands in northern Australia (Brundrett *et al.* 1996a; Brundrett *et al.* 1996b). Several studies have noted a predominance of ectomycorrhizal fungi in mature forest compared with recently burnt (2-3 years) sites (Glen 2002; Gates *et al.* 2005). Once forests have matured, the diversity of ECM fungi is similar in forests of different ages, although individual fungal species may favour vegetation stands of a particular age (Packham *et al.* 2002).

Preferences of ectomycorrhizal fungi for their plant host may affect the plant community: host generalist ECM fungi facilitate seedling establishment in late succession forests (Tedersoo et al. 2008). Tedersoo *et al*. (2008) suggest that fire-dependent tree species such as *Pomaderris* *apetala* and *Eucalyptus regnans* may competitively exclude each other through the low compatibility of their respective ectomycorrhizal fungi.

Most ECM fungi grow and produce their fruit-bodies in soil. However, large fallen logs may house a range of ECM fungal mycelia, associated with seedlings of trees such as *Nothofagus cunninghamii* (Tedersoo *et al.* 2009a). In addition, some ECM fungi in the Thelephoraceae are unusual in producing fruit-bodies on CWD (Tedersoo et al. 2003) and eighteen species of this family were isolated from ECM root tips in wet forests in Tasmania (Tedersoo et al. 2008). These ECM fungi which produce fruiting-bodies on CWD may be particularly sensitive to the changes and loss of CWD after fire.

5.4 Lichens

Like many fungi, lichens often have strong associations with particular substrates and habitats (Brodo 1973; Brodo *et al*. 2001). Where fires modify microclimatic and substrate conditions, lichen communities are often greatly altered, particularly as few lichens survive fire and are slow to recover (Stevens 1997). Lichens are so sensitive to changes in vegetation occurring over time since fire that, in central Brazil, they have been used as bio-indicators for the age of *cerrado* vegetation (Jayalaxshmi 1998). However, where distribution data are limited, care needs to be taken when assigning indicator species. Two lichens which previously had been thought to be indicators of old growth sites in Tasmanian wet forests (Kantvilas and Jarman 2004), have since been found to be common on burnt sites (Kantvilas and Jarman 2006). Post-fire communities of wood- and tree-dwelling lichens in these forests were dominated by common species and drier climate specialists and species changes were attributed to differences microclimate and structural characteristics after fire (Kantvilas and Jarman 2006). There are a number of rare lichens limited to rainforests (Kantvilas and Jarman 1993; Rogers 1995; Kantvilas 2000; Morley and Gibson 2004) which have not been burnt for long periods of time (100-500 years).

Soil lichens are a component of the biological soil crusts that are particularly important in dryland ecosystems (Eldridge 2003). These crusts tend to be damaged by extreme disturbances such as high intensity fires (Eldridge and Bradstock 1994; Eldridge 1996; Eldridge and Tozer 1997), while local species richness may be maintained if there are lower impact disturbances (Eldridge *et al.* 2000; Eldridge *et al.* 2006; O'Bryan *et al.* 2009). In mallee, soil crusts with different dominant groups formed after different fire frequencies (Eldridge and Bradstock 1994) and greatest diversity of lichens was achieved by fire intervals of 13-35 years

6. FIRE AND FUNGAL-FAUNAL INTERACTIONS

Fire can impact indirectly on fungi through their interactions with animals and invertebrates, which are themselves influenced directly and indirectly by fire.

6.1. Fungi-invertebrate interactions

Studies on the interactions between VAM and invertebrates do not deal specifically with the effects of fire (Wardle *et al.* 2004). While there is some knowledge about the aboveground interactions of invertebrates with fungi (Wardle *et al*. 2004), there is little specific information about the effect of fire on the relationships formed. This is surprising considering the prevalence of larvae and adult stages of many invertebrates using fruit-bodies of macrofungi as a food source and habitat. Frequent fire has recently been shown to disrupt the nature of fungal/invertebrate interactions in the leaf litter leading to substantial changes in decomposition rates (Brennan *et al*. 2009).

Belowground, larger soil organisms such as earthworms, mites and collembola are likely to be involved in long-distance transport of spores (Brown 1995; Dighton *et al.* 1997; Dighton 2003; Dromph 2003). Fire is known to impact upon the abundance of these and other soil- and litter-dwelling invertebrates (Neumann 1991; Neumann and Tolhurst 1991; Collett *et al.* 1993; York 1999). Grazing of soil mycelia by invertebrates such as collembolans, mites and nematodes exerts an influence on fungal biomass and community composition, such as through preferential grazing. This could have flow-on effects on leaf litter decomposition and the efficiency of mycorrhizas to facillitate nutrient uptake of host plants (Hanski 1989; Shaw 1992; Brennan *et al.* 2009). Preferential grazing by collembola can affect interactions between VAM and saprotrophic fungi (Tiunov and Scheu 2005). Even a single low intensity fire can alter the abundance and composition of collembolan communities (Greenslade 1997) and repeated burning can reduce collembolan numbers by more than half (York 1999).

Because of these complex associations and interactions, changes in plant community structure resulting from altered fire regimes could have dramatic effects on soil invertebrates and fungi, their activities and the interactions among them. These will feed back to the plant community by altering nutrient availability and rates of processes such as synthesis and growth.

6.2. Fungi-vertebrate interactions

The interactions of fire, fungi and mycophagous animals are complex, affecting both above- and belowground components. Fungal fruit-bodies, particularly sequestrate or truffle-like fruit-bodies, are a staple food for many native Australian animals that unearth, ingest and subsequently disperse the spores in a concentrated ‘spore packet’ that is deposited some distance away; the spores germinate and form mycorrhizas with trees or shrubs (Claridge and May 1994; Blaney 1996; Johnson 1996; Vernes 2009; Vernes and Dunn 2009). In digging for truffle fruit-bodies in the leaf litter and top 5-20 cm of soil, animals increase soil aeration and water incursion (Garkaklis *et al.* 2000; Garkaklis *et al.* 2003), and create small-scale surface topography aiding seed settlement and establishment. The loss of the mycophagous animals from an ecosystem is likely to have a deleterious impact upon the long-term health, viability and diversity of truffle-like fungi, soil structure and nutrient cycling and, eventually the mycorrhizal plant communities.

(Claridge and Barry 2000) point out that time since fire is just one of the many factors which influence the distribution of mycophagous animals, other factors such as vegetation cover and abundance of predators are also important. The focus of much of the relevant research has been on mitigating the effects of fire on mycophagous animals, but there are still large gaps in the understanding of the interactions among fungi, fire events and vegetation development. Only one comprehensive longitudinal study has been done (Claridge *et al.* 2000a; Claridge *et al.* 2000b), but it has shown that diversity of truffle-like fungi is influenced by many factors including the time since fire, climatic variables such as temperature and moisture levels, topographic position, geology, soil fertility, depth of litter and diversity of mycorrhizal hosts.

Investigation of the foraging habits of mycophagous animals before and after fire has found they foraged preferentially on burnt ground and frequently moved from burnt to adjacent unburnt habitat during foraging (Johnson 1994; Johnson 1996; Vernes and Haydon 2001; Vernes and Trappe 2007). Exclusion of small animals from plots within different vegetation types has shown a general trend of lower rates of seedling colonization and altered community composition in rainforest with VAM (Gehring *et al.* 2002) and for ECM. Not only rare mycophagist specialists (e.g. bettongs, potoroos) but also many of the more common macropods and rodents may be critical for maintenance of fungal communities and dispersal into disturbed habitats or across mosaics of vegetation types and ages that exist in many Australian forests (Vernes and Trappe 2007; Vernes and Dunn 2009; Vernes and McGrath 2009).

Comparison and interpretation of existing studies on fire and sequestrate fungi should be undertaken carefully as survey methods often differ (i.e. overall diversity studies, evidence of animal diggings, select fungal groups) and fungal communities should not be assumed to be similar in different ecosystems (Claridge and Trappe 2004; Trappe *et al.* 2005; Trappe *et al.* 2006). For example, studies in the ACT (Trappe *et al*. 2006) and NSW (Claridge *et al.* 2000a) found that prescribed burning decreased the overall diversity and abundance of truffle-like fungi. Conversely, several Tasmanian and Queensland studies suggest that prescribed burning may stimulate the fruiting of some species of truffle-like fungi (Taylor 1992; Johnson 1994; Johnson 1997; Vernes *et al.* 2004).

7. FIRE REGIMES AND MANAGEMENT FOR FUNGI

Differences in macrofungal communities have been attributed to links among vegetation composition, structural elements (substrates) and environmental factors (McMullan-Fisher *et al.* 2002; Packham *et al.* 2002; Gates *et al.* 2005; McMullan-Fisher 2008; Ratkowsky and Gates 2008; Robinson *et al.* 2008). For eucalypt forests, stand structure and vegetation composition is related to time since fire and fire frequency (Burrows 2008). Prescribed fire and management strategies for conservation of biodiversity are currently being developed in Victoria (e.g. (Fire Ecology Working Group 2004; Tolsma *et al.* 2007) and Western Australia (Burrows 2006; Burrows 2008). In this scheme, fire intervals are based on 'vital attributes' (i.e. life history characteristics) of different plant species and habitat preferences for (endangered) animals (Fire Ecology Working Group 1999; Burrows 2008). There is some knowledge of the seral stages favoured by different fungal species (McMullan-Fisher *et al.* 2002; Ratkowsky 2007; Robinson *et al.* 2008), but there is poor understanding of the biology governing these preferences and distributions.

7.1. The complex fire regime

Fire regimes are a unique property of each ecosystem, generated by the interaction of many factors operating at different spatiotemporal scales. Factors include fire intensity, fire frequency, extent or scale of fire, fire season and time since fire. In managed ecosystems, the type of fire, either unplanned wildfire or prescribed fire (generally for maintenance of biodiversity or fuel reduction purposes) must also be taken into account. Prescribed burns tend to be of lower intensity and generally occur on a smaller scale than wildfires.

Larger fires have different impacts than smaller fires on fungi in terms of resources and re-establishment in the post-fire environment (see (Bradstock 2008). Where ecological or burning for maintenance of biodiveristy is to be undertaken, managers should note that different organisms are likely to have different needs and responses to fire (Abbott and Burrows 2003; Burrows 2008; Clarke 2008). The historical fire regime may determine how ecosystems respond after each fire (Gill and Allan 2008; Williams and Bradstock 2008).

High fire intensity increases the depth of soil sterilisation and removes greater amounts of litter, dead woody material and vegetation, which in turn influences post-fire soil conditions.

Biological activity in soil is affected at fire temperatures of 60-80 ˚C, chemical properties of soil change at 60-300 ˚C and structural or physical properties of soil change at 400-600 ˚C. Higher temperatures may be reached for short periods of time during wildfires and by burning heavy fuels such as logs (Walter *et al.* 1986). As alluded to earlier, litter also takes longer to accumulate following intense fires (McCaw *et al.* 1996).

Wildfires generally occur during the hotter, drier months of summer, while prescribed burning is usually done in autumn or early spring. Autumn burns tend to be hotter than spring burns due to drier fuels resulting from drying during summer. This affects spread of fire and ultimately, the patchiness of resulting burn patterns. Production of fungal fruit-bodies is highly seasonal (Hilton *et al.* 1989; Claridge *et al.* 1993; Johnson 1994; Burns and Conran 1997; Claridge *et al.* 2000b; Vernes *et al.* 2004; Gates *et al.* 2005; Trappe *et al.* 2005; Trappe *et al.* 2006; Ratkowsky 2007; Robinson *et al.* 2008). In southern and mediterranean-like climates, fruiting periods are typically in autumn and spring, but most species produce fruit-bodies in autumn. One Victorian study has suggested that that low-intensity prescribed burning had little long-term effect on the macrofungal fungal community regardless of season of burning (Osborn 2007).

Fires, whether planned or unplanned, are patchy and the effects on soil are equally as irregular. Fire is thought to increase small-scale heterogeneity of fungal populations (Friese *et al.* 1997). Current fire management regimes aim to achieve a landscape mosaic of patches with different fire histories; the complexity derived from such landscape mosaics are thought to maximise biodiversity of flora and fauna. Fire mosaics resulting from cumulative heterogeneity (patchiness) from successive fires may contribute to increased local biodiversity (Grove *et al.* 2002; Bradstock 2008; Burrows 2008), including diversity of macrofungi (Robinson 2006; Robinson *et al.* 2008). For example, some fungi in the family Trichocomaceae that grow on the bark of *Eucalyptus pillularis* in New South Wales have been shown to survive fire (McGee *et al*. 2006). Some species of Trichocomaceae were found only on burnt trees while other species favoured bark from unburnt trees. Patchy distributions of these fungi are likely to eventuate where there is a mosaic of fire histories.

7.2 Fire frequency and fungi

There is limited information on how fungi are affected by repeated burning in Australian ecosystems. This is an important gap in knowledge given the regular use of prescribed burning across Australia. Molecular studies on soil-borne Basidiomycete communities in forests in Queensland dominated by *Eucalyptus pilularis* suggested that repeated prescribed burning at 2 and 4 year intervals (Bastias *et al.* 2006a; Bastias *et al.* 2006b; Anderson *et al.* 2007; Artz *et al.* 2009) does not affect species richness, although 2 year fire interval site have greater species evenness. However, fungal community structure in the upper 10-20 cm of soil become more uniform when compared with unburnt forests. Thus authors recommend 4 year fire intervals over 2 year intervals. In another study conducted in *E. pilularis* forests in New South Wales and mixed eucalypt foothill forests in Victoria, Osborn (2007) investigated the effects of burning at different fire frequencies (long unburnt and 3 and 10 year cycles) and seasons of burning (spring and autumn) on soil fungal communities. Long-term, low-intensity prescribed fire had little effect on the richness and diversity of the fungal communities, nor on diversity of fruit-body morphotypes and trophic groups. Similarly, no significant differences were observed in fungal biomass as indicated by ergosterol concentration in soil (Osborn 2007). Similar results were found for sites with moderate intensity burning in low open dry sclerophyll woodland (Theodorou and Bowen 1982). In this case, it was noted that there was no significant loss of surface organic matter.

Long-term repeated fire at intervals of 2-5 years has been shown to reduce soil organic content (Cairney and Bastias 2007) and carbon and nitrogen concentration in surface soil (Department of Sustainability and Environment 2003b; Bastias *et al.* 2006a), but burning with longer intervals of 10 years result in little change in these nutrients in surface soil (Department of Sustainability and Environment 2003b). It has been suggested however that low nutrient status, high carbon:nitrogen ratio and texture-contrast of topsoil in dry eucalypt forests in Tasmania are the result of long-term frequent fire (McIntosh *et al.* 2005). Thus predicting the long term effects of repeated fire may well require data from specific bioregions, soils and vegetation types.

Fire frequencies of less than ten years alter soil crusts in mallee which include lichens to favour algal-dominated crusts (Eldridge and Bradstock 1994). Lichen composition of soil crusts was highest when the time since fire was between 13 and 35 years. This contrasts with data from studies in temperate grasslands where lichen cover, while relatively low compared to other cryptogams, was highest on sites which were burnt every second year (O'Bryan *et al*. 2009). These crusts, which include lichens, play important roles in preventing soil erosion but their responses to fire may vary with vegetation type.

Vegetation composition has been linked to fire frequency. This is due to the elimination of species that rely on seed production for post-fire recruitment when fire intervals (time between fires) are shorter than the time required for recruitment, maturation and replacement of the seed store prior to the next fire (Ooi *et al.* 2006; Yates *et al.* 2008; Watson *et al.* 2009). Little is known about the corresponding fungal spore banks in soil. There are some data on the longevity of ascomycete spores in soil (Warceup and Baker 1963; Warcup and Baker 1963; El-abyad and Webster 1968; Warcup 1981) but there are no more recent or more general studies on fungal spore banks. Some macrofungi develop underground storage organs that allow fruiting after fire, but we know little about the time they take to develop and mature (Robinson *et al*. 2008). The composition of macrofungal communities in eucalypt forest are different each year after fire and for at least 5 to 7 years (McMullan-Fisher *et al.* 2002; Robinson *et al.* 2008), and there is no knowledge of the consequences of interrupting this succession before communities recover to their pre-fire composition.

7.3. Fungi that require long unburnt forest

In the Northern Hemisphere, there are a number of fungi, many of them included on 'Rarity, Endangerment and Distribution' (RED) lists which are found only in long undisturbed sites (Ing 1993; Berg *et al.* 1994; Odor *et al.* 2006). These fungi are probably not themselves sensitive to fire *per se* but are associated with substrates or microclimate that are most common in areas which have been long unburnt. In Australia, there are few examples of fungi strictly associated with long unburnt sites. The vulnerable Victorian species *Hypocreopsis amplectens* has been found predominantly in long unburnt, over-mature stands of heath tea-tree, *Leptospermum myrsinoides* (Johnston *et al*. 2007). Some rare saprotrophic fungi of the Northern Hemisphere are strictly associated with large, well decayed logs (Berg *et al.* 1994; Odor *et al.* 2006; Robinson *et al.* 2008), a resource more likely to be consumed by both prescribed fire and intense wildfires in dry eucalypt forests (Hollis *et al.* 2008). The rare lichen *Roccellinastrum flavescens* is found exclusively on leaves of *Arthrotaxis cupressoides,* a tree found in long unburnt areas in Central Tasmania (Kantvilas 1990; Kantvilas 2000). It has also been shown that species of the ECM genus *Russula* were found more frequently in long unburnt Jarrah forests than in sites with a prescribed burn frequency of 6-8 years (Hilton *et al.* 1989; Glen *et al.* 1998; Glen *et al.* 2001).

Cool temperate rainforests in Tasmania and Victoria support large and diverse communities of macrofungi, including a number of distinctive ECM fungi strictly associated with the dominant *Nothofagus cunninghamii* (Fuhrer and Robinson 1992). Other species apparently prefer the cooler and moister microclimate generated by closed canopies. By association, many species of macrofungi (TW May, pers. obs.) and lichens (Kantvilas and Jarman 1993; Rogers 1995; Kantvilas 2000; Morley and Gibson 2004) are restricted to cool temperate rainforest and are also likely to be present because there have been no fires for at least 400 years. Mature long unburnt eucalypt forests may also be refugia for fungi, as indicated by the unusually high diversity of macrofungi at sites such as Deep Creek in South Australia (Catcheside and Catcheside 2008). The composition of fungal communities in stands of *E. obliqua* near Geeveston in Tasmania correlated strongly with the vascular plants present and differed from that recorded in younger regrowth forest, suggesting that fire history determined the presence or absence of many macrofungi (Packham *et al.* 2002).

7.4 Fire management and fungi

Fire is a natural phenomenon that can be either adverse or beneficial to biodiversity, depending on the fire regime (Hobbs 2003). Despite being part of the historical regime, large fires are generally perceived as being ecologically disastrous. However, there is evidence showing that large fires vary in intensity, do not result in homogenous landscapes and few plants and animals are eliminated long-term (Bradstock 2008). As a result of large fires causing major loss of life and property, prescribed burning has been practiced within Australia since the 1960 (Department of Sustainability and Environment 2003b; McCaw *et al.* 2003). More recently fuel reduction burning has been conducted in combination with burning to benefit biodiversity. In Wombat Forest in central Victoria, experiments using repeated low-intensity burning showed that variety in time since fire is the most effective regime for the majority of the biota (Department of Sustainability and Environment 2003a). It is now widely recognised that no single optimum fire regime will meet all management objectives (Burrows 2008) and diversity of fire regimes, including long-unburnt patches, across landscapes is now being accepted by land management agencies in adaptive fire management programs.

It is important to include fungi in management decisions regarding prescribed burning. To facilitate this, a number of studies are under way in the south west of Western Australia to investigate the effect fire regimes on the diversity of jarrah forest biota, including fungi (Burrows 2006; Wittkuhn *et al.* 2008). No single fire regime benefits all taxa (Burrows and Wardell-Johnston 2003), but by using an adaptive management framework to manage biodiversity on a landscape scale, a range of fire regimes can be implemented to develop a fine-grained fire mosaic to provide the best option for maintaining biodiversity within that landscape (Burrows 2008). Until more information is available on the response of fungal species and communities to fire and fire regimes, including repeated prescribed burning, it appears that, in order to develop landscapes with mosaics of time since fire (including long unburnt areas), an adaptive management policy involving a range of fire intensities and a variety of burning seasons is the best option. For informed adaptive management decisions to be made, it is necessary to include macrofungi in monitoring and research programs. The close correlation between substrate condition (including quality and quantity) and time since fire suggests that management of substrate diversity in different vegetation types may be an effective interim measure while specific requirements of fungi are being investigated.

8. RESEARCH GAPS AND SOLUTIONS

8.1. Research gaps

Key gaps in research on fire and fungi in Australia include:

- **Ecosystems -** Studies have concentrated on wetter forests in southern Australia. There are little or no data on fungi and fire for many ecosystems such as grasslands, arid, alpine vegetation or northern Australian savannahs.
- **Associations -** We do not know precise host, habitat or substrate range for the majority of fungal species, and nor the fidelity to hosts or vegetation types. Herbarium specimens often lack associated host and habitat information.
- **Taxa -** Current research focuses on macrofungi and mycorrhizal fungi, omitting the highly diverse leaf-inhabiting parasitic microfungi, endophytes and saprotrophic soil microfungi.
- **Life history -** Fungi may have complex breeding systems with different hosts associated with different stages in life cycles. Specifics about reproduction, spore longevity, germination requirements are unknown for most Australian fungi. Reliance on interactions with host species or spore vectors is clearly important but the details of common interactions are still poorly understood.
- **Fire regime complexity -** Time since fire is often the variable tested in relation to the fungal community, often with only one fire age, but a variety of fire regimes (including timing, extent and intensity) has not been investigated.
- **Colonisation after fire** There are no data for Australia on whether post-fire fungi are continuing to grow from pre-existing mycelia, newly germinating from the spore bank or recolonising from spores blown in. It is likely that the immediate post-fire fungi are germinating from spores, but for species that appear later in the succession the source is unknown. Patch size of disturbance may be important in this regard, in that a large patch may make recolonisation from spores more difficult (depending on the distance that spores travel). The age structure of the matrix around a burnt site may be critical, as could be the intensity with which patches burn. All these factors should be tested experimentally.

8.2. Macrofungi in monitoring programs

Further understanding of various aspects of the effect of fire on fungi relies on generation of substantial data sets. Ideally, fungi should be integrated into established monitoring and survey projects. At present, the Department of Environment and Conservation (DEC) in

Western Australia is the only land management agency in Australia that includes macrofungi in permanent monitoring programs. This agency has recognized that macrofungi are a substantial and diverse component of biodiversity in eucalypt forests and the Department has a permanent fungal ecologist on staff with support staff, to undertake monitoring and research in programs and projects including FORESTCHECK (Abbott and Burrows 2004) and the Walpole Fire Mosaic (WFM) project (Burrows 2006).

FORESTCHECK is an integrated, long-term, landscape-scale program devised to record and monitor the status and response of key forest organisms and communities to both forest management activities and natural variation (Abbott and Burrows 2004). FORESTCHECK (see: http://www.dec.wa.gov.au) was initiated in 2001 to satisfy Ministerial conditions contained within the 1994 and current (2004-2013) Forest Management Plans (Lands and Forests Commission 1994; Conservation Commission of Western Australia 2004) regarding monitoring of jarrah silvicultural systems. The WFM project was initiated in 2005 to test the notion that fine-grained mosaics, representing various patches of vegetation at different post-fire seral stages, burnt at varying intensities and different seasons, across a landscape can reduce the severity of wildfires as well as be beneficial to the maintenance of biodiversity (Burrows 2006). Through these projects, knowledge of how macrofungal communities and key species respond to fire in southern eucalypt forests has greatly increased (Robinson 2001; Robinson and Bougher 2003; Robinson 2006; Robinson and Tunsell 2007; Robinson *et al.* 2008). With over 750 species of macrofungi recognized (RM Robinson, pers. obs.), FORESTCHECK and the WFM projects have also provided base-line information on many previously unknown or unrecorded taxa. The ongoing review of survey methods has also provided techniques that allow monitoring of this traditionally difficult group of organisms to be undertaken in a consistent and cost-effective manner. Because these and other biodiversity projects within DEC are included in a State legislative framework they are incorporated within policy relating to sustainable forest management and supported by managers. They provide an important contribution to aid an adaptive management policy within the department with respect to improved fire management and biodiversity outcomes (Burrows 2006).

8.3 Integration and testing of sampling and identification methods

Current studies that aim to characterise the fungal community from fruit-bodies surveys are poorly integrated as far as using a standard taxonomic framework. While some common and readily recognisable species appear in species lists from across Australia, many collections included in inventories are assigned tag or field names or are not identified to species at all. While tag names can be used consistently within surveys, it is currently not possible to match them up across different studies without time-consuming examination of voucher material (where this is available). Improved documentation of the distinctive characters of species to which tag names have been assigned would assist but, in the end, comprehensive taxonomic revisions are the best way to provide reliable names to species encountered in ecological surveys. Molecular characterisation of fruit-bodies would also assist, but requires the same sort of barcode library as for environmental samples.

There is also poor integration between the molecular characterisation of known taxa and the sequences that are being isolated from environmental samples such as ECM root tips or bulk soil samples. The main problem is a lack of sequence data from authoritatively named specimens from Australia. In the long-term, this can only be solved by creation of local, accurate and comprehensive barcode databases backed up by voucher material. In the meantime, at the least, there is a need for a substantial subset of target fungi across phylogenetic and functional groups for which the taxonomy (species limits) is reasonably worked out. A barcode library for these target groups can then be the basis for molecular identification of at least a substantial subset of environmental samples.

At present, no one method precisely characterises the fungal community in soil or other substrates. The choice of sampling and identification methods often comes down to the resources and funding available within the particular organisation. For some management agencies, sampling of fruit-bodies is the most practical choice at present, especially for large-scale monitoring programs such as FORESTCHECK. There is a need for testing of the cost-effectiveness and accuracy of different methods of isolation and identification, so that standard survey techniques and identification protocols can be developed.

There is clearly an advantage in integrating research disciplines (ecology and taxonomy) and data sources (morphological and molecular). Closer co-ordination of research priorities between management agencies and research organisations would assist in this integration.

8.4 Directions for future fungal research

Directions for future fungal research should include:

- **Integration** - Current studies are poorly integrated as far as using a standard taxonomic framework. Differences in results between molecular and fruit-body surveys suggest that both techniques are needed. To be able to successfully compare sites using DNA fingerprinting a local, accurate, comprehensive barcode database is needed. Efficacy of various sample and identification methods need to be tested and new protocols developed which allow better data collection of the different types of fungi.

- **Autecology -** Comprehensive studies of the biology and ecology of dominant Australian fungi across fire sensitivities, taxonomic and trophic groups should be undertaken. If there was information on the range of responses for at least the dominant fungi it would provide useful indications for management purposes.
- **Meta-analysis -** A significant amount of data on fungi and their responses to fire currently reside in unlinked data sets. A meta-analysis of recent studies and data bases such as material held by state management agencies, herbaria, unpublished reports and studies and fungal interest groups would dramatically increase the understanding of fungal distributions, species associations and species responses to fire.
- **Monitoring -** Fungi from all groups (trophic, phylogenetic and morphological) should be included in current monitoring, particularly in adaptive management systems. This data should be widely accessible to facilitate the rapid accumulation of fungal data.

9. CONCLUSIONS

Fire ecology is acknowledged as complex and highly variable, specific responses usually being dependent on site and species characteristics. Not surprisingly, the effects of fire on the numerous fungal components of ecosystems are also complex but are less well understood than for their vascular plant counterparts. This review highlights that effects of fire are multifaceted with biotic and abiotic interactions often mediated by fungal trophic groups. The often heterogeneous effects of fire may include changes in soil structure, water and nutrient availability and cycling, and may impact on biotic elements such as the decomposer and mycorrhizal components. Thus the post-fire vegetation responses are usually highly variable and may be mediated by the response of mycorrhizal communities which in turn may be influenced by vector animals.

Fungal substrates are lost, modified and created by fires, and the degree of change is often dependent on the range of fire intensities and the particular vegetation type and site history. In the short-term there is usually a loss of litter and smaller woody debris, in the longer term some fire events may initiate other structural elements such as standing dead wood and coarse woody debris.

The patchy nature of a single fire at any given site and the preceding history of fire disturbance are widely acknowledged to play a substantial role in biotic and abiotic diversity. This will undoubtedly also affect the local diversity of fungal assemblages and the interactions they promote. The heterogeneity resulting from various fire regimes may play a role in developing landscape diversity which may in turn have its basis in the local diversity of fungal assemblages.

The importance of fungi in ecosystems as symbiotic partners, decomposers, nutrient cyclers and as sources of food for vertebrates and invertebrates cannot be under-estimated. It is clear that an understanding of the functional roles of fungi, of the effects of fire on fungi and of the post-fire interactions between fungi and the biotic and abiotic components of ecosystems will help managers make informed decisions on best management practices.

More research is needed to facilitate better management of fungi across the spectrum of Australian ecosystems. Land managers should include fungi into current monitoring systems for long-term monitoring and adaptive management. Ideally, future fungal research would integrate both traditional and molecular techniques to allow clearer understanding of the complex nature of communities and ecosystems, particularly soil and other important fungal substrates such as litter and coarse woody debris.

Acknowledgements

The review would not have been possible without the generous support of the Victorian National Parks Association to SM-F.

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