# Author's personal copy

Forest Ecology and Management 257 (2009) 1063-1069

Contents lists available at ScienceDirect



Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

## Full length article

# Do fungi have a role as soil stabilizers and remediators after forest fire?

Andrew W. Claridge a,b,\*, James M. Trappe c,d, Karen Hansen<sup>e</sup>

<sup>a</sup>*Department of Environment and Climate Change, Parks and Wildlife Group, Planning and Performance Unit, Southern Branch, P.O. Box* 733, *Queanbeyan, New South Wales 2620, Australia* 

<sup>b</sup>*School of Physical, Environmental and Mathematical Sciences, University of New South Wales, Australian Defence Force Academy, Northcott Drive, Canberra, Australian Capital Territory 2600, Australia* 

<sup>C</sup>*Department of Forest Science, Oregon State University,* Corvallis, *OR* 97331-5752, *United States* 

*dCSIRO Sustainable Ecosystems, P.O. Box* 284, *Canberra, Australian Capital Territory 2601, Australia* 

<sup>e</sup>*Fungal Herbarium, The Swedish Museum of Natural History, Box 50007, Stockholm* 104 OS, *Sweden* 

#### ARTICLE INFO ABSTRACT

*Article history:*  Received 22 September 2008 Received in revised form 6 November 2008 Accepted 11 November 2008

*Keywords:*  Postfire recovery Erosion control Soil aggregation *Anthracobia* 

The functional roles of fungi in recovery of forest ecosystems after fire remain poorly documented. We observed macrofungi soon after fire at two widely separated sites, one in the Pacific Northwest United States and the other in southeastern mainland Australia. The range of species on-site was compared against macrofungi reported after the volcanic eruption at Mount St. Helens, also in the Pacific Northwest. Each of the three sites shared species, particularly representatives of the genus Anthracobia. Soon after disturbance, we noted extensive mycelial mats and masses of fruit-bodies of this genus, particularly at heavily impacted microsites. The mycelial mats appeared to play an important functional role on-site, possibly aggregating soil particles in otherwise highly erodable landscapes. We hypothesise that fungi such as Anthracobia are pivotal species in early system recovery after disturbance, helping minimize the movement of soil in the absence of plant roots. As plant root systems recover, the im portance of these fungi in soil stabilization may diminish. Other functional roles of early postfire fungi might include nutrient acquisition, leading to the reestablishment of vegetation. These potential roles need to be experimentally tested and relevant findings incorporated into programs aimed at restoring forest ecosystems after disturbance.

© 2008 Elsevier B.V. All rights reserved.

net Pandara

#### 1. Introduction

Forest ecosystems around the Pacific are variously shaped by wildfire, particularly in North America and southeastern Australia, which are characterized by hot, dry summers and associated lightning events that serve as excellent ignition sources (Agee, 1993; Pyne, 2001, 2006). The postfire recovery of these systems has been relatively well documented in the scientific literature, particularly for better-known organisms within the animal and plant kingdoms (see Cary et aI., 2003 ). In contrast, much remains to be learned about the response of fungi to disturbances such as wildfire, in part because few scientists per capita work on this significant component of biodiversity. Moreover, despite a general understanding of the types of roles of fungi in ecosystem functioning, including nutrient acquisition, water transfer and carbon and nutrient cycling, the precise ecological roles of many species after fire remain undetermined.

Cairney and Bastias (2007) in Australia and Hart et ai. (2005) in the western United States have extensively reviewed literature relating to the many and varied effects of fire on fungi, including studies that have documented recovery of these organisms several years after disturbance, saving us the need to do that here. The consensus of these studies to date is that fire, particularly of high intensity, is detrimental to the majority of fungal species at least in the short-term and sometimes in the long-term (i.e. Claridge and Trappe, 2004; Vernes et aI., 2004; Hart et aI., 2005; Cairney and Bastias, 2007; Jimenez Esquilin et aI., 2007 ). In this brief paper, we focus on fungi that appear to benefit from disturbance, combining our field observations in southeastern mainland Australia and Pacific Northwestern America with review of selected literature relevant to the first 6 months after wildfire. Although the immediate postfire activities of such fungi are transient (Hart et aI., 2005), our observations indicate they may be important in stabilizing soils and setting the stage for subsequent, longer-term forest recovery processes. For that reason, we consider it useful to integrate the literature with our own field observations as a

<sup>\*</sup> Corresponding author at: Department of Environment and Climate Change, Parks and Wildlife Group, Planning and Performance Unit, Southern Branch, P.O. Box 733, Queanbeyan, New South Wales 2620, Australia. Tel.: +61 2 6229 7041. *E-mail* address: andrew.cJaridge@environment.nsw.gov.au (A.W. Claridge).

*<sup>0378-1127/\$</sup>* - see front matter © 2008 Elsevier B.V. All rights reserved. doi: 10.1016/j.foreco.2008.11.011

baseline for fire ecologists to test hypotheses on fungal roles in the immediate aftermath of fire, especially because we can report that postfire fungal phenomenon occur similarly halfway around the world in forest types as dissimilar as Pacific Northwestern conifers and southeastern Australian eucalypts.

We have specific experience with postfire fungi following large scale intensive wildfires in southeastern mainland Australia in 2003, and a smaller scale though locally intensive wildfire in Washington State, USA, during 2006. One of us (Trappe) collected fungi within a month after the explosive eruption of Mount St. Helens in Washington State in 1980. The parallels between the fires in these far removed and markedly different forests were striking, as was the similar mycological aftermath of the Mount St. Helens eruption (Carpenter et al., 1987). In this paper we compare some of the fungal activity observed soon after these events and discuss their possible broader ecological meaning.

### 2. **Definition of postfire fungi**

The term "postfire fungi" as we use it here refers specifically to species that fruit as a result of fire or eruption effects (e.g. heat, ashing of organic matter), but generally not to fire survivors, (i.e. fungi that were active in the prefire habitat and escaped fire effects by being deep in soil or in patches of unburnt habitat). Some postfire fungi are carbonicolous, fruiting on charcoal or partially burned organic debris; others are terrestrial, fruiting on ash or heated soil; still others appear to be mycorrhizal symbionts with or pathogens on tree roots (Egger and Paden, 1986). Whereas some species produce only microscopic fruiting structures, others form fruit-bodies visible to the naked eye. Most postfire fungi are ascomycetes, but basidiomycetes and zygomycetes are also represented (Petersen, 1970; Warcup, 1990; Dahlberg, 2002 ).

Postfire fungi normally fruit during the first significant rain event following disturbance and are not the product of spores dispersed during that season, because the same species fruiting elsewhere have yet to produce spores or have only begun to. Their source is usually the spore bank in the soil built up over time since previous fire. Spore longevity in the soil is known for only a few species, but spores of terrestrial fungi in general retain viability for many years. Some fungal spores are strongly dormant and require heat treatment to germinate (Jalaluddin, 1967; El-Abyed and Webster, 1968; Wicklow and Zak, 1979; Izzo et aI., 2006). Repeatedly deposited on the soil, the spores are carried over time to various depths in upper soil profiles by infiltrating water. When a site burns, the heat from the fire may kill spores near the surface, but at some depth the soil temperature will climb to the range that, rather than killing spores, breaks their dormancy.

We are aware of only two recent studies on effects of fire on fungal activity in the soil during the first year following fire. Hart et al. (2005) reported that the variation of functional diversity of bacteria in the top 5 cm of soil in a New Mexican *Pinus ponderosa*  pine stand was greater than that of fungi. A severe wildfire subsequently burned the site, 1 month after which the soil was resampled. At that time, the variation of bacterial functional diversity had decreased while fungal functional diversity increased. These data reinforce that fungi can be particularly active soon after wildfire and are potentially important to postfire recovery of forests.

In the Rocky Mountains of Colorado, Jiménez Esquilin et al. (2007) sampled soils for microbial populations and activities at different time intervals after burns of slash piles following logging. Lethal temperatures in the top 5 cm of soil under the middle of piles were reached within an hour after ignition and maintained for more than 24 h. Soil fungal biovolume and respiration in the top 5 cm of soil were significantly reduced compared to nonburned

control samples up to at least 15 months. At 15 cm depth under piles, fungal biovolume did not differ from nonburned controls, although fungal respiration was reduced over a similar timeframe. While these observations are relevant to understanding postfire responses of fungi *per se,* they are not directly comparable to the present study since the authors did not record fungal fruiting activities.

#### 3. **Functions of postfire fungi**

Postfire fungi have many potential functions with either positive or negative importance to stabilization of soils, restoration of habitat, recovery of damaged plants or replacement of dead vegetation. They decompose organic matter, including woody debris (Egger, 1986), thereby incorporating it into the soil and releasing organically bound nutrients. Mycelial networks bind soil particles into aggregates, thereby improving aeration and water infiltration (Bond and Harris, 1964; Tisdale and Oades, 1982; Hallett, 2007). Simultaneously, however, mycelium near or on the surface may increase water repellency, either or both by production of hydrophobic substances or a hyphal network dense enough that the surface tension of water may prevent quick infiltration. Fungal-induced repellency may increase surface runoff and thereby risk of erosion.

Other factors may also play a key role in increasing repellency. For example, Mataix-Solera and Doerr (2004) reported that fireincreased soil hydrophobicity was accompanied by improved soil aggregation. They attributed this to heating and distillation of plant litter, which subsequently condensed in the organic and mineral soil profile. Moreover, as pointed out by Hallett (2007), seasonal water repellency may switch off during soil water recharge in autumn and winter but return in surface soils during dry months. At that time, the repellent layer could act as a barrier minimising evaporative water loss. In Australia, fire-adapted hypogeous fungi may survive fire to be dug up by mammal mycophagists (Claridge et aI., 2001; Claridge and Trappe, 2004). The resulting excavations break through the repellent layer and act as catchments of surface runoff that then infiltrates to the fungal colony and its associated host root system (Garkaklis et al., 1998).

Some fire-surviving fungi also act as postfire fungi, because they fruit only after fire, even though they may have formed mycorrhizae with surviving trees prior to fire (Egger and Paden, 1986; Vrålstad et al., 1998; Dahlberg, 2002). These fungi importantly facilitate regrowth of trees requiring mycorrhiza formation to survive (e.g. eucalypts and pines). Finally, a few postfire fungi are pathogenic on plant roots (Egger and Paden, 1986).

One overlooked function of fungi soon after fire would be sequestration of nitrogen. Nitrogen is lost through combustion, the loss generally being proportional to quantity of forest litter and upper soil organic layer consumed (Little and Ohmann, 1988; Wan et al., 2001). However, when combustion is incomplete, soil NH<sub>4</sub><sup>+</sup> may increase substantially and  $NO<sub>3</sub>$  may increase somewhat through pyrolysis of organic matter (Wan et al., 2001 ). As nonpareil scavengers, fungi undoubtedly capture much of those newly released, highly leachable nitrogen ions plus any newly biologically fixed and released nitrogen and convert them to organic compounds needed for continued growth and fruiting. As fungal hyphae and fruit -bodies die the nitrogen released through decomposition becomes available to other organisms. That turnover can be rapid: fruit-bodies may begin to decompose within weeks of their formation. It is this activity that we had in mind when suggesting above that fungi 'set the stage' for further recovery of a site following fire. The importance of restoring nitrogen and organic compounds to an impoverished substrate

was dramatically illustrated by an observation made by one of us (I.M. Trappe) a year after the Mount St. Helens eruption. Fluids from the decaying remains of a horse killed by the eruption had seeped down slope. The seepage zone was a lush garden of bryophytes and fungal fruiting bodies set amidst the gray, nonvegetated tephra otherwise blanketing that site.

#### **4. Postfire fungi in southeastern Australia and Pacific Northwestern USA**

Having defined what postfire fungi are, and discussing their potential ecological roles, we now describe our observations of such organisms immediately following wildfires at two geographically well-separated sites, hereafter referred to as Byadbo (Australia) and Flick Creek (Pacific Northwest United States). These observations are also contrasted against observations of fungi immediately following the aftermath of the Mount St. Helens volcanic eruption, again in the Pacific Northwest.

#### 4.1. Study sites

Byadbo, New South Wales, 2003. The summer of 2002-2003 was a difficult and prolonged wildfire season in southeastern mainland Australia, with more than 1.6 million ha of forest burned in eastern Victoria and adjacent southern New South Wales (Gill, 2005; Kanowski et al., 2005; Taylor and Webb, 2005 ). Much of the affected area burnt at severe to high intensity, but significant areas of either lightly burnt or nonburnt areas remained within overall fire perimeters.

The study area we discuss here occurred within the jacobs River and Ingebirah Creek catchments in the Byadbo Wilderness Area of Kosciuszko National Park, approximately 40 km south of the township of jindabyne, southern New South Wales. The area is highly dissected with locally common cliff-faces and outcrops of large granite boulders. The climate is dry, with less than 600 mm rainfall per annum. Predominant vegetation reflects this low rainfall, with a dry White Box (Eucalyptus albens) and White Cypress Pine (Callitris glaucophylla]. Thompson & L.AS. johnson) community dominating below 650 m with riparian strips of Ribbon Gum (Eucalyptus viminalis Labill.). Above 650 m a grassy or shrubby Yellow Box (Eucalyptus melliodora A. Cunn.) woodland occurs, grading through Long-leaved Box [Eucalyptus nortonii (Blakely) L.AS. johnson] woodland to Mountain Gum (Eucalyptus dalrympleana Maiden) open forest with increasing elevation (Pulsford, 1991).

At Byadbo the intensity of wildfire during the summer of 2002-2003 was mostly severe, with almost total canopy scorch of eucalypt trees and complete removal of understorey vegetation (Fig. 1). In places, the intensity of fire was so great that non-living structures such as granite tors were fractured by heat from the flames, while stags and large fallen trees were completely combusted leaving ash beds. As a consequence of complete removal of canopy and understorey vegetation, and other components of the forest such as the leaf litter layer, the existing friable granitic topsoil was made highly erodable. A few weeks after fire had passed, the study site received substantial rainfall: much topsoil moved down slope into lower parts of the watershed, resulting in significant changes to the sediment load of the jacobs River and Ingebirah Creek in particular.

Postfire recovery of the vegetation and wildlife at Byadbo has been detailed by Maser et al. (2008) and will not be discussed further here, other than to say that reemergence of plants and animals commenced within weeks after the fire, and the area generally began a rapid recovery.

Flick Creek, Washington USA, 2006. In the Pacific Northwestern United States, the summer of 2006 was unusually hot and dry.



Fig. 1. Burned eucalypt woodland after the forest fire of 2003 in Byadbo Wilderness, Kosciuszko National Park, New South Wales, Australia.

Thunderstorms raged over the Cascade Mountains and lightningcaused fires taxed fire fighting resources throughout the West. The Flick Creek Fire in the North Cascade Mountains of Washington State, USA, was started not by lightning but by a careless camper in early summer, 2006, and burned into autumn. Covering only about 3200 ha, it was minor compared to the 2003 fires in southeastern mainland Australia, but threatened the village of Stehekin producing a mosaic of burn intensities. Severely burned areas were abundant, but individually they covered only 1-10 ha. The forest canopy was primarily of non-resprouting conifers, so tree mortality in severe burns was complete. Light autumn rains dampened the fire until heavy snow in November extinguished it. Cold weather and the snow cover minimized runoff until snowmelt in spring; because the spring was cool. melting was gradual and relatively little erosion occurred before fungi became active at the soil surface.

Flick Creek is in the Lake Chelan National Recreation Area, part of the North Cascades National Park Complex in the North Cascades Range of Washington State. It empties into the fjord-like Lake Chelan at 550 m elevation. The entire range experienced heavy Pleistocene glaciation. The top of the catchment culminates in ridges and peaks 2000-2200 m in elevation. Annual precipitation at the lower end of the catchment is about 500 mm. The forests in which we collected the fungi are dominated by ponderosa pine (P. ponderosa Dougl.), Douglas fir [Pseudotsuga menziesii (Mirb.) Franco] and grand fir (Abies grandis Dougl.). With increases of elevation the forest composition transitions to subalpine fir [Abies lasiocarpa (Hook.) Nutt.], lodgepole pine (Pinus contorta Dougl.) and Engelmann spruce (Picea engelmannii Parry). At the highest elevations the treeline is dominated by subalpine larch (Larix lyallii Parl.) and whitebark pine (Pinus albicaulis Engelm.).

Mount St. Helens, Washington USA, 1980. We include mycological observations following the eruption of Mount St. Helens in Washington State on 18 May 1980, because the early fungal recovery was strikingly similar to that of the 2003 Byadbo and 2006 Flick Creek burns. Accordingly, some general principles can be drawn beyond the two fires that we observed. Fungi need an organic source of nutrition, and such is scarce or lacking in newly deposited tephra. However, the explosive force of the eruption produced superheated winds that ripped vegetation and soils from slopes facing the volcano, mixed them with hot tephra, and deposited them several kilometers to the north. It was on these heated mixtures of organic debris and tephra that posteruption fungal phenomena were subsequently observed (Carpenter et al., 1987; Allen et al., 2005).

The part of the Mount St. Helens devastation zone in which postfire fungi were collected was north of the crater and consisted of thousands of hectares of heat-treated debris mixed with soil and fine-grained tephra on gentle to steep topography. Subsequent minor eruptions deposited additional tephra to varying depths. Because heat, rather than fire, was the "treatment", parallels between Mount St. Helens and the two burnt sites can be ascribed to heating effects rather than the chemical effects induced by burning (e.g. conversion of organically bound minerals to ash).

#### *4.2. Methods of fungal collection and identification*

Byadbo was repeatedly visited from early May to mid-July 2003. Subsequent visits in 2004-2005 produced none of the postfire fungi we report on here (Table 1). Flick Creek was visited only once in spring, April 2007; collecting focused on the lower elevations of the burn (550-900 m), because the snow pack had not melted off higher up. Travel distance to the site was too far to schedule additional visits, but a good diversity of fungi was found in the one survey conducted. The Mount St. Helens fungi were collected in spring 1980, from June through October. The snowpack at time of eruption was unusually deep and the ensuing spring and summer were relatively damp, so fungi fruited throughout the summer.

On each visit at any of the three study sites we opportunistically surveyed for macrofungi on burned sites by sight searches while walking through the landscape. Where aboveground fruiting fungi were observed, we collected a subset of the total available fruitbodies of each species. Fresh colour, size, texture and odor were recorded for each collection. Representative specimens of each species were photographed while fruit-bodies were still freshly collected. All collections were subsequently dried in an electric, forced-air food dehydrator (35 °C for 12 h), then placed in glassine (wax paper) bags for storage.

At the laboratory spores and other microscopic structures from dried specimens were described and measured by use of a compound light microscope. Species were identified by standard taxonomic works dealing with postfire fungi (e.g. Rifai. 1968: Smith et al., 1981; Hansen et al., 2001; Fuhrer, 2005) as well as recent monographs. Because postfire morphological species tend to be cosmopolitan, the Australian taxa could be identified by use of monographs and mycological treatises developed mostly for northern hemisphere fungi. Future molecular studies, however, may well reveal that some of the northern names are incorrectly applied to Australian taxa. In the northern hemisphere different authors disagree somewhat on species limits in the genus *Anthracobia,* prominent after fire in Australia and the northern hemisphere alike. Our identifications of *Anthracobia* spp. are thus provisional, pending complete revision of that genus.

## *4.3. Postfire fungi compared between the study sites*

Because we undertook opportunistic rather than systematic sampling for fungi, it is not possible to strictly compare species composition and diversity across each of the three study sites. Nevertheless, a few commonalities and inferences can be drawn. For example, representatives of 4 ofthe 17 genera collected in total were common to each of the three study sites (Table 1): *Anthracobia, Peziza, Pholiota* and *Psathyrella,* with the first genus particularly prevalent.

At Byadbo, fruit-bodies from a total of seven macrofungal species were collected in the first autumn following wildfire, including four species of Ascomycota and three Basidiomycota (Table 1). A clear pattern was evident regarding microsites at which particular macrofungi were observed fruiting. For the three species of *Anthracobia,* most fruit-bodies occurred where the fire effect had been most intense, in and adjacent to burnt out stumps of once-standing trees and along ash beds from combusted fallen trees. These microsites were the most erodable parts of the landscape, where the litter layer had been completely removed and lateral plant root systems destroyed. At time of first observation, approximately 3 months after the fire, fruit-bodies of *Anthracobia*  were arising from large masses of white mycelium (Fig. 2), which covered the soil surface and seemingly bound surface soil particles for up to a meter radiating out from any given microsite. That surface mycelium became inconspicuous after a few weeks, but it

#### **Table 1**

First year postfire/posteruption fungal fruiting in the Byadbo Wilderness. New South Wales. Australia; Flick Creek. Washington, USA; and Mount St. Helens Volcano. Washington. USA.

Trophic type	Class	<b>Species</b>	Locality		
			Byadbo	<b>Flick Creek</b>	St. Helens
Saprobe	Ascomycota	Anthracobia macrocystis (Cooke) Boud.	×	$\propto$	
		Anthracobia melaloma (Alb. & Schwein.) Arnould		$\propto$	$\mathbf{\times}$
		Anthracobia tristis (Bomm., Rouss. & Sacc.) Boud.	×		
		Ascobolus carbonarius P. Karst.			$\mathbb{X}$
		Gelasinospora reticulospora (Greis & Greis-Dengler)			$\infty$
		C. Moreau & M. Moreau			
		Morchella elata Fr.			×
		Octospora axilaris (Nees) M. Moser			×
		Peziza petersii Berk.			×
		Peziza praetervisa Bres.		$\times$	
		Peziza pseudoviolacea Donadini		×	×
		Peziza tenacella W. Phillips	×		
		Plicaria endocarpoides (Berk.) Rifai		$\times$	×
		Pulvinula archeri (Berk.) Rifai			$\times$
		Pyronema confluens (Bull.) Fuckel		×	
		Strattonia carbonaria (W. Phillips & Plowr.) N. Lundq.			×
	Basidiomycota	Myxomphalia maura (Fr.) Hora		×	
		Neolentinus dactyloides (Cleland) Redhead & Ginns			
		Pholiota highlandensis (Peck) A.H. Sm. & Singer	×	×	×
		Psathyrella sp.			
		Psathyrella carbonicola A.H. Sm.		×	×
Mycorrhizal	Ascomycota	Geopyxis carbonaria (A. & S.) Sacc.		×	
Pathogenic	Ascomycota	Rhizina undulata Fr.			×

A.W. Claridge et al./Forest Ecology and Management 257 (2009) 1063-1069



Fig. 2. Web of mycelium of Anthracobia sp. on severely burned soil surface 1 month after the forest fire of 2003 in Byadbo Wilderness, Kosciuszko National Park, New South Wales, Australia.



Fig. 3. Fruit-bodies of Anthracobia melaloma, a cosmopolitan postfire ascomycete.

remained intermixed with the soil. Colonies of Anthracobia were prevalent across the Byadbo study site during that first postfire autumn. They produced masses of minute fruit-bodies (Fig. 3): sample counts indicated 400 to 1000+ fruit-bodies in individual colonies. A conservatively estimated 10 colonies per 1000  $m<sup>2</sup>$  in a hard-burned area could then produce 40,000 to 100,000 fruitbodies per ha. These, in turn would produce many billions of spores to be added to the soil spore bank. Populations of fruit-bodies varied markedly from one place to another, depending on severity of burn and availability of ash from burned-out stumps or coarse woody debris. The other, less abundant but still widely distributed species (Figs. 4-6), are presented in Table 1. When collected, all these, like Anthracobia, held considerable ash and charcoal to the fruit -body base by mycelium. Though not as conspicuous as that of Anthracobia, this mycelium near or at the soil surface may playa role in stabilizing soil.

At Flick Creek our opportunistic sampling following the fire yielded a few more postfire species than at Byadbo, including seven species of Ascomycota and three species of Basidiomycota (Table 1 and Figs. 3-6). The mycelial growth of Anthracobia was much the same as at Byadbo. Localized colonies of Anthracobia were again most prevalent at microsites where fire intensity had been greatest. In contrast, the mycorrhizal Geopyxis carbonaria (Fig. 5), which also fruited prolifically, typically was recorded in the relatively light burn sites where many trees survived. This or a



Fig. 4. Fruit-bodies of Peziza pseudoviolacea, a cosmopolitan postfire ascomycete.



Fig. 5. Fruit-bodies of Geopyxis carbonaria, a cosmopolitan mycorrhizal postfire basidiomycete.

closely related species has been reported from Australia (Warcup, 1990; Fuhrer, 2005).

Mount St. Helens produced the most species of the three sites, including 10 species of Basidiomycota and three species of Ascomycota (Table 1). Snowmelt and a relatively cool, moist



Fig. 6. Fruit-bodies of Pholiota highlandensis, a cosmopolitan postfire basidiomycete.

spring and summer plus opportunity for several collecting trips likely account for this apparent increased diversity.

A striking feature of postfire fungi at Mount St. Helens and Flick Creek was growth of bryophytes and algae on and near fruit-bodies of postfire fungi. Nutrients such as nitrogen were apparently concentrated by the fungi and quickly made available to the photosynthesizing pioneers (Carpenter et ai., 1987). We did not observe this phenomenon at Byadbo, but it did occur at intensely burnt forest sites following 2003 wildfires in the Brindabella Range west of Canberra, Australian Capital Territory (J.M. Trappe, personal observations).

#### 5. **Postfire fungi and forest recovery after fire**

Cairney and Bastias (2007, p. 213) concluded from an extensive literature review that "at present it is impossible to assign any level of functional significance to fire-mediated changes in soil fungal communities," due to variations in such factors as study design and approach, timeframe, and fire intensity. Still, our observations of early postfire fungi at both sides of the Pacific show similarities. Most striking is the rapid response of Anthracobia spp. early after fire at Byadbo, Flick Creek and Mount St. Helens. In each case, microsites where their fruit-bodies occurred were highly disturbed by intense heat. Past studies of the genus associate it with burned sites: indeed, Australian Anthracobia collections from the late 1800s and again more recently have been noted from burned sites (Rifai, 1968; Warcup, 1990).

The masses of Anthracobia fruit-bodies associated with thick mats of white mycelium on and within the soil at such microsites suggest that after fire these structures and accompanying algae and bryophytes perform a key role in helping bind the soil in the absence or near absence of plant rootlets, humus and leaf litter. In North America Hart et al. (2005) recorded increases of fungal functional diversity in burned soils 1 month after fire, and O'Dea (2007) reported that fungal activity in the topsoil strongly mitigated the postfire erodability of local landscapes, such that sites with greatest fungal activity were the least erosive. In the three sites we observed, mycelial mats of Anthracobia and other postfire fungi were intermixed with soil in the absence of vegetation in the months following severe wildfire or volcanism, when soils are otherwise highly vulnerable to erosion. Despite the seeming fragility of fungal hyphae, Bond and Harris (1964) reported that they persist in well aggregated soils. We hypothesise that proliferation of hyphae in ash by postfire fungi initiates soil aggregation and captures and concentrates nutrients to then be gradually replaced by other fungi as well as root systems of recovering vegetation. This hypothesis requires experimental testing by comparative trials where surface runoff, soil aggregate stability and nutrient loads are compared at sites with and without these mycelial mats.

The generally overlooked phenomenon of decaying fruit-bodies of postfire fungi facilitating establishment of photosynthesizing plants on burned soils, as we observed for bryophytes both in Australia and Pacific Northwestern USA, may be more common and more important than is now realised. Mycologist Larry Evans reported that pits in senescent fruit-bodies of morels (Morchella spp.), common postfire fungi in the northern hemisphere, catch Populus seeds, which germinate there and send roots into the soil amidst the nutrients released by the decaying fruit-bodies (Maser et aI., 2008). The role of these fungi may be transient, but nonetheless pivotal in jump-starting initial postfire vegetation succession.

The role of fungi in postfire recovery of forest ecosystems needs to be better understood, especially because commonly used and expensive erosion control programs such as grass seeding are often ineffective (Amaranthus et aI., 1993; Robichaud et aI., 2000). It may

be that in many circumstances fungi already assist. For example, Shakesby et al. (2007) conclude that in southeastern mainland Australia postfire erosion of soil is generally of relatively minor, long-term geomorphological importance. While making no mention of fungi as mitigating factors in their paper, our observations and those of others (e.g. Warcup, 1990) indicate that early postfire fungal activity abounds. If action to stabilize and remediate soil after forest fire is deemed desirable, methods to enhance postfire fungal activity merit attention. Toward this end, several research needs and approaches come to mind. Recently developed techniques can greatly expedite study of postfire fungal ecology and roles in stabilizing soil, for example quantification of mycelial content of soils by biochemical analysis of the soil content of fungus-specific compounds or direct DNA extraction from soil to characterize fungal communities (Anderson and Cairney, 2007). Postfire fungal growth and function needs to be assessed from soon after fire to establishment of plant communities, as done by Jimenez Esquilin et al. (2007). Broad-scale, careful observations of visible fungal activity after fire can add much to our understanding of its facilitation of plant establishment and on what kinds of substrates that and soil stabilization occur.

#### **Acknowledgements**

Hansen participated in these studies while a post-doctoral fellow at The Farlow Herbarium, Harvard University, Cambridge, Massachusetts. Trappe's participation was supported in part by the U.S. Forest Service, Pacific Northwest Research Station, Corvallis, Oregon; CSIRO Sustainable Ecosystems, Canberra; and a grant from the North Coast and Cascades Research Learning Network. Personnel of Kosciuszko National Park in Australia and North Cascades National Park and Gifford Pinchot National Forest in the USA generously facilitated our studies.

#### **References**

Agee,J.K., 1993. Fire Ecology of Pacific Northwest Forests. Island Press, Washington, **USA** 

- Allen, M.F., Crisafulli, e.M., Morris, S.J., Egerton-Warburton, L.M., MacMahon, J.A., Trappe, J.M., 2005. Mycorrhizae and Mount St. Helens: story of a symbiosis. In:<br>Dale, V., Swanson, F., Crisafulli, C. (Eds.), Ecological Responses to the 1980 Eruption of Mount St. Helens. Springer, New York, pp.221-231.
- Amaranthus, M.P., Trappe,J.M., Perry, D.A., 1993. Soil moisture, native revegetation, and Pinus lambertiana seedling survival, growth, and mycorrhiza formation
- following wildfire and grass seeding. Restor. Ecol. 188-195. Anderson, I.e., Cairney, J.W.G., 2007. Ectomycorrhizal fungi: exploring the mycelial frontier. FEMS Microbiol. Rev. 2007, 1-19.
- Bond, R.D., Harris,J.R., 1964. The influence of the microflora on physical properties of soils. I. Effects associated with filamentous algae and fungi. Aust.J. Soil Res. 2, 111-122.
- Cairney, J.W.G., Bastias, B.A., 2007. Influences of fire on forest soil fungal communities. Can. J. For. Res. 37, 207-215.
- Carpenter, S.E., Trappe,J.M., Ammiratijr.,].. 1987. Observations of fungal succession in the Mount St. Helens devastation zone, 1980-1983. Can.J. Bot. 65, 716-728.
- Cary, G., Lindenmayer, D.B., Dovers, S. (Eds.), 2003. Australia Burning: Fire Ecology, Policy and Management Issues. CSIRO Publishing. Melbourne. Australia.
- Claridge. A.W .• Trappe, J.M .• 2004. Managing habitat for mycophagous (fungus-feeding) mammals: a burning issue? In: Lunney, D. (Ed.), Conservation of Australia's Forest Fauna 2nd edition. Royal Zoological Society of New South Wales, Mosman. pp. 936-946.
- Claridge. A.W., Trappe, J.M., Claridge. D.L., 2001. Mycophagy by the swamp wallaby (Wallabia bicolor). Wildl. Res. 28, 643-645.
- Dahlberg, A., 2002. Effects of fire on ectomycorrhizal fungi in Fennoscandian boreal forests. Silva Fennica 36, 69-80.
- Egger, K.N., 1986. Substrate hydrolysis patterns of postfire ascomycetes. Mycologia 78, 771-780.
- Egger, K.N., Paden, J.W., 1986. Biotrophic associations between lodgepole pine seedlings and postfire ascomycetes (Pezizales) in monoxenic culture. Can. J. Bot. 64, 2719-2725.
- EI-Abyed, M.S.H., Webster,J., 1968. Studies on pyrophilous discomycetes. Trans. Br.
- Mycol. Soc. 51, 353-367. Fuhrer, B., 2005. A Field Guide to Australian Fungi. Bloomings Books. Melbourne, Australia.

#### A. W. Claridge et al. / Forest Ecology and Management 257 (2009) 1063-1069 1069

- Garkaklis, M.j., Bradley, j.S., Wooller, R.D., 1998. The effects of woylie (Bettongia penicillata) foraging on soil water repellency and water infiltration in heavy<br>textured soils in southwestern Australia. Aust. J. Ecol. 23, 492–496.
- Gill, A.M., 2005. Landscape fires as social disasters: an overview of 'the bushfire problem'. Environ. Hazards 6, 65-80.
- Hallett, P.O., 2007. Soil water repellency is wonderful-the positive environmental implications. In: Abstracts of the Bouyoucos Conference on the Origin of Water Repellency in Soils, Sanibel Island, Florida, p. 16. Available from URl: http:// geography.swan.ac.uk/bouyocos2oo7.
- Hansen, K., Læssøe, T., Pfister, D.H., 2001. Phylogenetics of the Pezizaceae, with an emphasis on Peziza. Mycologia 93, 958-990.
- Hart, S.c., Deluca, T.H., Newman, G.S., MacKenzie, M.D., Boyle, S.I., 2005. Post-fire vegetative dynamics as drivers of microbial community structure and function
- in forest soils. For. Ecol. Manage. 220,166-184. Izzo, A., Canright, M., Bruns, T.D., 2006. The effects of heat treatments on ectomycorrhizal resistant propagules and their ability to colonize bioassay seedlings. Mycol. Res. 110, 196-202.
- jalaluddin, M., 1967. Studies on Rhizina undulata. I. Mycelial growth and ascospore germination. Trans. Br. Mycol. Soc. 50, 449-459.
- jimenez Esquilin, A.E., Stomberger, M.E., Massman, W.M., Frank,l.M., Shepperd, W.O., 2007. Microbial community structure and activity in a Colorado Rocky Mountain forest soil scarred by slash pile burning. Soil Biol. Biochem. 39, 1111-1120.
- Kanowski, P.J., Whelan, R.J., Ellis, S., 2005. Inquiries following the 2002-2003 Australian bushfires: common themes and future directions for Australian bushfire mitigation and management. Aust. For. 68, 76-86.
- Little, S.M., Ohmann, j.L., 1988. Estimating nitrogen lost from forest floor during prescribed fires in Douglas-fir/western hemlock cIearcuts. For. Sci. 34, 152-164. Maser, c., Claridge, A.W., Trappe, 1.M., 2008. Trees, Truffles and Beasts: How Forests Function. Rutgers University Press, Piscataway, USA
- Mataix-Solera, J., Doerr, S.H., 2004. Hydrophobicity and aggregate stability in calcareous topsoils from fire-affected pine forests in southeastern Spain. Geoderma 118,77-88.
- O'Dea, M.E., 2007. Fungal mitigation of soil erosion following burning in a semi-arid Arizona savannah. Geoderma 138. 79-85.
- Petersen, P.M., 1970. Danish fireplace fungi: an ecological investigation. Dansk Botanisk Arkiv 27,1-97.
- Pulsford, I.F., 1991. History of disturbances in the White Cypress Pine (Callitris glaucophylla) forests of the Lower Snowy River Valley, Kosciuszko National Park. MSc Thesis, The Australian National University, Canberra, Australia.
- Pyne, S.J., 2001. Fire: A Brief History. The British Museum Press, London, England. Pyne, S.l., 2006. The Still-burning Bush. Scribe Short Books, Melbourne, Australia.
- Rifai, M.A., 1968. The Australasian Pezizales in the herbarium of the Royal Botanic Gardens Kew. Verh. Konink. Nederl. Akad. Wetenschap. Natuurk. 57 (3), 1-295. Robichaud, P.R., Beyers, J.L., Neary, D.G., 2000. Evaluating the effectiveness of
- postfire rehabilitation treatments. U.S. Forest Service, Rocky Mountain Research Station General Technical Report RMRS-GTR-63, Fort Collins, Colorado, USA.
- Shakesby, R.A, Wallbrink. P.J., Doerr, S.H., English, P.M., Chafer, C,J., Humphreys, G.S., Blake, W.H., Tomkins, K.M., 2007. Distinctiveness of wildfire effects on soil erosion in south-east Australian eucalypt forests assessed in a global context. For. Ecol. Manage. 238, 347-364.
- Smith, A.H., Smith, H.V., Weber, N.S., 1981. How to Know the Non-gilled Mushrooms, 2nd edition. Wm. C. Brown Company, Dubuque, IA, USA
- Taylor, J., Webb, R.M., 2005. Metereological aspects of the January 2003 southeastern Australia bushfire outbreaks. Aust. For. 68, 94-103.
- Tisdale, J.M., Oades, J.M., 1982. Organic matter and water-stable aggregates in soils. j. Soil Sci. 33,141-163.
- Vernes, K.,johnson, C.N., Castellano, M.A., 2004. Fire-related changes in biomass of hypogeous sporocarps at foraging points used by a tropical mycophagous marsupial. Mycol. Res. 108, 1438-1446.
- Vralstad, T., Holst-jensen, A., Schumacher, T., 1998. The postfire discomycete Geopyxis carbonaria (Ascomycota) is a biotrophic root associate with Norway spruce (Picea abies) in nature. Mol. Ecol. 7, 609- 616.
- Wan, S.Q., Hui, D.F., luo, Y.Q., 2001. Fire effects on nitrogen pools and dynamics in terrestrial ecosystems: a meta-analysis. Ecol. Appl. 11, 1349-1365.
- Warcup, j.H., 1990. Occurrence of ectomycorrhizal and saprophytic discomycetes after a wild fire in a eucalypt forest. Mycol. Res. 94, 1065- 1069.
- Wicklow, D.T., Zak, J.C., 1979. Ascospore germination of carbonicolous ascomycetes in fungistatic soils: an ecological interpretation. Mycologia 71, 238-242.

