



Post-fire vegetative dynamics as drivers of microbial community structure and function in forest soils

Stephen C. Hart^{a,*}, Thomas H. DeLuca^b, Gregory S. Newman^a,
M. Derek MacKenzie^b, Sarah I. Boyle^a

^a School of Forestry and Merriam-Powell Center for Environmental Research, POB 15018,
Northern Arizona University, Flagstaff, AZ 86011-5018, USA

^b Department of Ecosystem and Conservation Sciences, The University of Montana, Missoula, MT 59812, USA

Abstract

Soil microorganisms have numerous functional roles in forest ecosystems, including: serving as sources and sinks of key nutrients and catalysts of nutrient transformations; acting as engineers and maintainers of soil structure; and forming mutualistic relationships with roots that improve plant fitness. Although both prescribed and wildland fires are common in temperate forests of North America, few studies have addressed the long-term influence of such disturbances on the soil microflora in these ecosystems. Fire alters the soil microbial community structure in the short-term primarily through heat-induced microbial mortality. Over the long-term, fire may modify soil communities by altering plant community composition via plant-induced changes in the soil environment. In this review, we summarize and synthesize the various studies that have assessed the effects of fire on forest soil microorganisms, emphasizing the mechanisms by which fire impacts these vital ecosystem engineers. The examples used in this paper are derived primarily from studies of ponderosa pine-dominated forests of the Inland West of the USA; these forests have some of the shortest historical fire-return intervals of any forest type, and thus the evolutionary role of fire in shaping these forests is likely the strongest. We argue that the short-term effects of fire on soil microflora and the processes they catalyze are transient, and suggest that more research be devoted to linking long-term plant community responses with those of the mutually dependent soil microflora.

© 2005 Elsevier B.V. All rights reserved.

Keywords: Fire; Microbial ecology; Nutrient cycling; Soils; Substrate quality; Vegetation

1. Introduction

Fire has been an important part of the evolutionary history of most forest ecosystems in Inland

West of North America (Covington et al., 1994). Within the semi-arid areas of this region, ponderosa pine (*Pinus ponderosa*) dominated forests abound. The natural fire-return intervals in these forests range from as few as two to as many as 40 years (Table 1; Covington et al., 1994). Historically, these forests were characterized by relatively open, park-like stands with a vigorous herbaceous and shrub

* Corresponding author. Tel.: +1 928 523 6637;
fax: +1 928 523 1080.

E-mail address: steve.hart@nau.edu (S.C. Hart).

Table 1
Historical (pre-Euro-American settlement) fire regimes of forests and woodlands of the Inland West, USA

Potential climax vegetation	Presettlement fire frequency (year)
Piñon pine and/or juniper	7–90
Ponderosa pine	2–38
Douglas-fir	20–60
Mixed Conifer	6–150
Cedar-hemlock	60–>400
Lodgepole pine	25–500
Subalpine-fir and/or spruce	50–350

Data from Covington et al. (1994).

understory that was maintained, in part, by frequent, reoccurring fire.

After a century or more of fire exclusion from most of these forests, the unmanaged forest of today is characterized by very high tree densities and an understory almost devoid of vegetation (Covington and Moore, 1994). Where ponderosa pine occurs in mixed-conifer stands, less fire-resistant and more shade-tolerant tree species such as Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) have become dominant (Arno et al., 1995). These contemporary forests contain extremely high fuel loads that are likely to support high-intensity, stand-replacing wild-fires, and are increasingly susceptible to large-scale pathogen outbreaks (Covington and Moore, 1994).

The significance of fire as a shaper of vegetation composition and structure is well known. Individual plant species within a forest are susceptible to mortality following a fire of a given intensity based largely on their carbon (C) reserves, presence of fire adaptive traits, and the fire regimes to which the plant is exposed. Furthermore, fire selectively influences plant regeneration in forests, thus altering the species composition of plant recruitment following fire. Finally, forest structure is also altered in that trees of a given species with greater diameter (and thus usually taller) are generally more resistant to fire than smaller diameter trees (DeBano et al., 1998).

Despite the substantial body of research that has been conducted on vegetation dynamics following fire, as well as immediate post-fire changes in the physical and chemical properties of soils, fewer studies have assessed the impacts of fire on soil microorganisms. Soil microorganisms (primarily bacteria and fungi)

have numerous functional roles in forest ecosystems, including: serving as sources and sinks of key nutrients and catalysts of nutrient transformations; acting as engineers and maintainers of soil structure; and forming mutualistic relationships with roots that improve plant fitness (Paul and Clark, 1996). Hence, understanding both the short- and long-term impacts of fire on these organisms is important for elucidating the role of fire in forest ecosystems.

Fire alters the soil microbial community composition and activity directly (in the short-term) through selective heat-induced microbial mortality (DeBano et al., 1998). For instance, bacteria tend to be more resistant to heat induced by fire than fungi; hence, bacteria generally increase in relative abundance compared to fungi immediately following even moderate-intensity fires (Pietikäinen and Fritze, 1995). However, almost no information exists regarding how fire affects soil microorganisms over the long-term, and whether any of the changes in the composition or activity of these organisms feedback to impact the forest plant community. Long-term responses of the soil microflora to fire may be primarily due to alterations in plant community composition and production because of the strong interrelationships between plants and soil microorganisms.

In this paper, we summarize and synthesize the various studies that have assessed the effects of fire on forest soil microorganisms, emphasizing the mechanisms by which fire may impact these vital ecosystem engineers. The scope of this review is generally limited to ponderosa pine-dominated forests of Inland West of the USA, mainly because the high fire-return frequencies historically in these forest types (Table 1) are most likely to lead to strong feedbacks among fire, soil microorganisms, and vegetation. Furthermore, the tone of this synthesis is highly speculative because, as noted above, little information exists on fire–plant–microbe interrelationships.

2. The plant–microorganism connection

The diverse and complex world of plant–microbe interactions cannot possibly be handled in this brief review. However, the major connections at the heart of plant species control on soil microorganisms include the quantity of resources produced (C flow), competi-

tion for nutrients, quality of resources (substrate quality), and mutualisms (Wardle, 2002).

The interaction of plants and the soil microbial community can be viewed as an ecosystem-scale symbiosis, where two groups of living organisms maintain an obligate association with each other. Plants function as a C pump, feeding the primarily heterotrophic soil microbial community with photosynthetically derived organic matter via aboveground litterfall, root exudation and turnover, and sloughed roots and mycorrhizal hyphae (Staddon et al., 2003). In turn, this C stimulates the activities of soil microorganisms that ultimately lead to increased availability of growth-limiting nutrients to plants through the roles of microbes as nutrient sources, sinks, and transformers (Paul and Clark, 1996). Plants release a significant quantity of C into the soil rhizosphere, discharging about 20–40% of total net photosynthetic production into soil via a variety of specific processes (Lynch and Whipps, 1991).

Differences in nutrient uptake strategies of plants and the extent to which plants compete for nutrients with soil microflora potentially influence the soil microbial community (Kaye and Hart, 1997; Wardle, 2002). Plant nutrient foraging strategies differ in the spatial scales at which they acquire nutrients from soil, rates of uptake per unit root length, and rates of increase in nutrient uptake in response to localized patches of high nutrient levels (Wardle, 2002). These conditions lead to varying degrees of competition between plant roots (and their mycorrhizae) and soil microorganisms, and a high degree of spatial heterogeneity in nutrient resource availability.

Different plant species produce litter (leaves, stems, roots) and exudates that vary in their degree of stimulation of soil microorganisms due to differences in the quality of this material for heterotrophic microbial growth. Plant litter with high C:nutrient ratios, high concentrations of secondary metabolites (e.g., condensed tannins), or high levels of structural carbohydrates (particularly lignin) tend to support small microbial populations (Beare et al., 1991; Schweitzer et al., 2004).

Some soil microorganisms also carry out highly specific relationships with higher plants (i.e., symbioses). Generally in these interactions, both partners benefit (i.e., mutualisms) where the plants provide soil microbes with C and the microorganisms provide

plants with increased acquisition of limiting nutrients or water. The most common mutualisms include that of legumes, actinorrhizal plants, and mycorrhizal relationships. Rhizobia and associated genera and actinomycetes (also called actinobacteria) fix atmospheric nitrogen (N), while mycorrhizae increase the uptake of sparingly available nutrients and water.

Dynamic and complex feedback mechanisms likely exist between plant and soil microbial communities. This subject has recently been reviewed in some detail (Bever, 2003). These feedback mechanisms may be positive or negative. In a simplistic sense, plants may be absolutely dependent upon their symbionts as with the case of N fixing symbioses or some mycorrhizal relationships. The ultimate success, or at least the degree of plant success, may be dependent upon the initial presence of the symbiont and the initiation of the symbiotic relationship. Soil borne pathogens may play an important role in plant community dynamics by causing a negative feedback control on plant growth rates and species composition. Bever (2003) cites an example from agroecosystems where the accumulation of species-specific soil pathogens drives the rotation of certain crops in North America (Agrios, 1997). In less managed ecosystems, wild cherry (*Prunus serotina*) trees have been found to maintain the presence of damping off fungi (*Pythium* spp.) in soils under their canopy, thereby reducing competitive pressure from cherry seedling germination (Packer and Clay, 2000). Bever's (2003) feedback model might be adapted to describe post-fire plant and soil community dynamics, where fire provides a disturbance, stress, or stress-relief component in the model that initiates a feedback loop between plants and microbes.

3. Direct effects of fire on microbial communities

Fire is a primary agent of natural disturbance in many ecosystems and has the potential to reshape landscapes and reset biological clocks. Fire is unique as a disturbance in that it causes not only an alteration of the physicochemical and biological environment through heating and oxidation, but also creates new sources of physicochemical and biological inputs into the soil system in the form of charcoal, distillates,

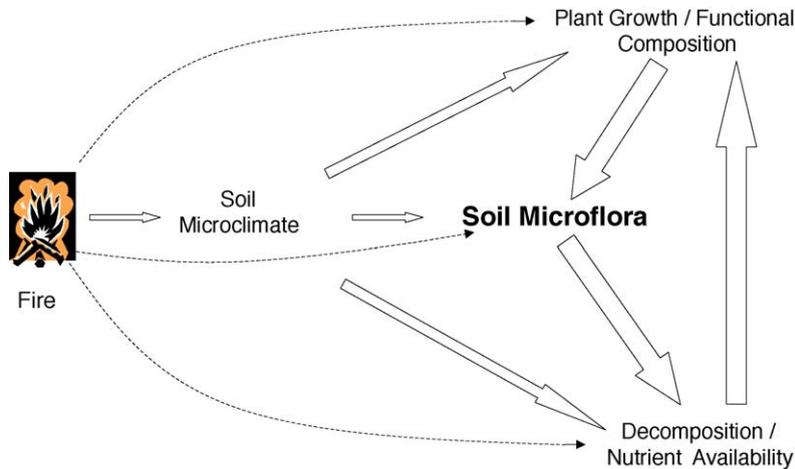


Fig. 1. Conceptual model of the effects of fire on forest ecosystems. Dotted arrows denote immediate short-term effects of fire on vegetation and soil organisms, which are transitory in nature. These include selective mortality of plants and soil microorganisms and nutrient release from combustion of organic matter. The influence of fire on soil microclimate (temperature, moisture, insolation) is the midterm mechanism driving changes in the soil microflora and vegetation (denoted by thin, block arrows), as well as changes in rates of ecosystem processes such as decomposition and nutrient mineralization (denoted by medium, block arrows). However, over time, strong feedbacks develop among the soil microflora (composition and activity), decomposition and nutrient availability, and plant growth and functional composition (grass vs. shrub, vs. tree; N fixer vs. non-N fixer). These feedbacks (denoted by thick, block arrows), caused indirectly by the fire, are primarily responsible for the long-term stability of the ecosystem. In the absence of reoccurring fire, plant succession results in changes in plant growth and functional composition, altering these feedbacks, and creating a new ecosystem state. The relative strength of the longer term interactions is noted by the thickness of the block arrows.

metal oxides, and plant litter. Therefore, fire both directly and indirectly influences the forest ecosystem (Fig. 1).

3.1. Heat transfer

The direct effects of fire on the soil microflora occur via the lysing of microbial cells and the alteration of microbial reproductive capacity from soil heating (Covington and DeBano, 1990). Biological properties of soil are more sensitive to soil heating than chemical and physical soil characteristics, with fatal temperatures for most living organisms occurring below 100 °C (DeBano et al., 1998). Fire effects on soil microorganisms are greatest in the surficial soil layers (organic horizon, if present, and upper few cm of mineral soil) where organism abundance is highest (Neary et al., 1999). Through soil heating, fire can directly alter the size, activity, and composition of the microbial biomass.

The degree and extent to which heat generated during combustion of forest fuels (organic matter) is transferred to the soil depends on a variety of factors,

including fire intensity, the rate of spread (residence time), the thickness and characteristics of the organic layer (O horizon) overlying the mineral soil, and the relative abundance of organic matter, mineral matter, water, and air within the mineral soil (DeBano et al., 1998). In general, only about 10–15% of the heat energy released during combustion of aboveground organic matter is transmitted to and absorbed by the underlying mineral soil (DeBano, 1974; Raison et al., 1986). Higher fire intensities and longer residence times result in greater heat transferred belowground. The O horizon can act as an insulating layer to the mineral soil when it itself does not combust because of the relatively low thermal diffusivity (ratio of thermal conductivity to volumetric heat capacity) of organic materials (Hillel, 1998). However, the impact of fire on the soil microflora increases dramatically if this horizon combusts and becomes a source of heat itself (DeBano et al., 1998).

Water content is a major factor affecting heat transfer in soils and the effectiveness of the heat for lysing microbial cells. As water content increases, the thermal diffusivity of the soil also increases, which

increases the depth at which fire-generated heat affects the soil (Hillel, 1998). Temperatures in moist soils do not rise above 95 °C until all the water in a given layer is driven off; hence, physicochemical properties of soils are not altered substantially until the soil becomes dry. However, moist heat (pasteurization) is more effective at killing soil microorganisms than dry heat; lethal temperatures (50–210 °C) for specific microbial groups may be reduced by as much as one-half in moist compared to dry soils (Wells et al., 1979). Consequently, for a given fire severity, moist soils will likely lead to greater mortality of the soil microflora than dry soils (Choromanska and DeLuca, 2002).

3.2. Differential responses of soil organisms to heating

Some groups of microbes are more sensitive to heating than others. Fire can result in selective mortality of different microbial groups, leading to a change in the community structure of soil organisms. Threshold temperatures for nearly 100% mortality of fungi in dry and moist soil are 80 and 60 °C, respectively (Dunn et al., 1985). Bacteria, in general, are more tolerant of heat than fungi; threshold temperatures for bacteria are 120 and 100 °C for

dry and moist soils, respectively (Dunn and DeBano, 1977).

Based on the above discussion, we might expect the relative abundance of bacteria to fungi to increase following fire. For example, using selective culturing of microbial populations, Fuller et al. (1955) found this predicted increase in bacterial to fungal ratios following both wildfire and controlled burns in ponderosa pine forests of northern Arizona, USA. However, changes in the composition of the soil microflora following fire may vary greatly depending on site factors, fire severity, and the methods used to evaluate the response of the microflora (Dunn et al., 1985). For instance, Newman et al. (in review) found that the soil metabolic quotient (the ratio of respired C to microbial C) was higher in a forest subjected to a high-severity wildfire in northern New Mexico, USA than in adjacent unburned forests; this result suggests that the ratio of fungal to bacterial biomass declined as a result of the wildfire (Blagodatskaya and Anderson, 1998). However, compared to pre-fire conditions, they found that the variation in post-fire functional diversity of soil fungi increased while that of the bacteria declined (Fig. 2).

Some specialized groups of microorganisms are particularly sensitive to heat-induced mortality caused

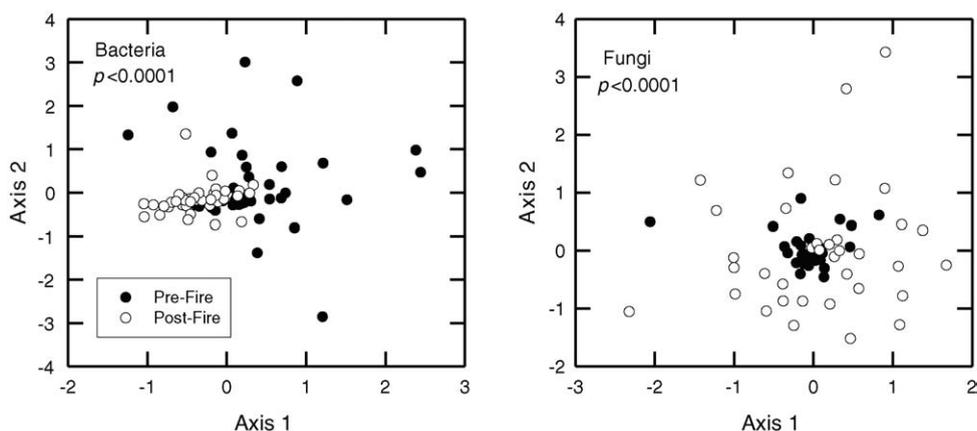


Fig. 2. Nonmetric multidimensional ordinations of bacteria and fungal community-level physiological profiles before and after a high-severity wildfire in a ponderosa pine forest near Jemez Springs, NM, USA. Each data point is a multivariate representation of the ability of the bacterial or fungal community contained in a single soil sample (0–5 cm mineral soil depth) to grow on a variety of individual carbon substrates (see Classen et al., 2003 for more details). Note that bacterial CLPPs homogenized following fire, while fungal CLPPs diversified. These results suggest that the high-severity fire increased the variation in functional diversity of the soil fungi, but reduced the variation in the functional diversity of the soil bacteria. Pre-fire samples were collected in October 2001. A wildfire burned serendipitously across the site about 11 months later, in September 2002, and post-fire samples were taken about 1 month following the fire, in October 2002. Data are from Newman et al. (in review).

by fire. For example, nitrite oxidizers (*Nitrobacter* spp.) are more heat sensitive than heterotrophic bacteria, but less than fungi; greater than 99% mortality of nitrite oxidizers occur at temperatures of 90 and 80 °C for dry and wet soils, respectively (Dunn and DeBano, 1977; Dunn et al., 1985). Despite this sensitivity, nitrate pools typically increase above pre-fire levels during the year following a fire (Covington and Sackett, 1992; Kaye and Hart, 1998a; Newman et al., in review). Increases in nitrate pools are assumed to be the result of increased activities of nitrifying organisms (i.e., nitrifiers) following fire-induced enhancement of ammonium pool sizes (White, 1991; Covington and Sackett, 1992; Klopatek and Klopatek, 1997). However, Kaye and Hart (1998a), using an ¹⁵N-based method to measure the gross rate of nitrification directly, found that greater nitrate pool sizes following a low-intensity fire occurred because of lower microbial uptake of nitrate, rather than higher rates of gross nitrification. Furthermore, Newman et al. (in review) found that the autotrophic nitrifier population size 1 month following a high-severity wildfire in northern New Mexico was over 10 times that of an adjacent unburned ponderosa pine-dominated forest. Hence, either chemoautotrophic nitrifiers are less sensitive to heat than currently believed, or the growth capacity of these organisms, when ammonium supply is high, is much greater than documented in the literature (Paul and Clark, 1996). Clearly, more research is needed that assesses both the thermal sensitivities of a wide variety of soil microorganisms under the various conditions observed in the field, as well as the growth capacities of their populations in the post-fire environment.

3.3. Mycorrhizae, roots, and fire

Arbuscular mycorrhizae (AM), generally associated with herbaceous plants in forests of the Inland West, are apparently more tolerant of heat than asymbiotic fungi. Klopatek et al. (1988) found 100% mortality of AM at temperatures of 94 °C. However, Pattinson et al. (1999) found that simulated fires in the laboratory led to almost complete loss of AM when field soils were heated above 80 °C. Some studies have also found that the effect of fire on AM in piñon–juniper woodlands can be long-lived; 10 years after burning, AM abundance was still lower than pre-burn levels (Klopatek et al., 1994).

Although most studies appear to show that fire negatively influences AM propagules (spores) and rates of AM root infection, the degree of these reductions and their persistence over time are likely a function of the fire severity (Vilarino and Arines, 1991). Fires burning through the heavy fuel loads typically found in contemporary ponderosa pine forests are likely to lead to much larger reductions in AM abundance than the lower intensity fires that were carried by the lighter fuel loads characteristic of these forests prior to Euro-American settlement. Indeed, Korb et al. (2003) found that, within 2 years following restoration treatments (thinning and burning) designed to return ponderosa pine forests to pre-Euro-American structure, the relative amount of infective propagules of AM fungi increased; this increase seemed to correspond to an enhancement in graminoid cover and herbaceous understory species richness.

The direct effect of fire on ectomycorrhizae (EM), generally associated with woody plants in forests of the Inland West, appears more variable than with AM fungi, although we were unable to find comparable lethal temperatures for this group of microorganisms in the literature. The effects of fire on EM fungi range from dramatic reductions in propagule density and diversity after an intense wildfire in a jack pine (*Pinus banksiana*) stand (Visser, 1995), to no significant changes following a stand-replacing wildfire in a Bishop pine (*Pinus muricata*) stand (Baar et al., 1999). As expected, low fire severity generally leads to little or no change in EM fungal composition, densities, or propagules (Jonsson et al., 1999; Korb et al., 2003). Jonsson et al. (1999) speculated that the effects of fire on EM would increase as the degree of consumption of the O horizon from fire increases. However, this hypothesis was based on fires in relatively mesic, boreal forests; consumption of the O horizon, per se, may not have a similar effect on EM fungi in many of the dry forests of the Inland West because tree fine roots seldom occur in this horizon (Wright, 1996).

Plant roots are generally more sensitive to heat than soil microorganisms, with lethal temperatures occurring around 50 °C (Hare, 1961). Hence, the ability of microbial symbionts with plant roots to persist following fire depends in part on their relative ability to survive in the absence of their hosts, which tends to be lower for EM than AM fungi (Amaranthus and

Perry, 1987; Allen, 1991). We hypothesize that the difference in lethal temperatures for AM and EM fungal groups will not lead to significant differences in their survival following a fire of a given severity. It is more likely that the relative abundances of these groups of organisms will be influenced indirectly by the comparative dominance of their plant hosts following fire (see below).

4. Indirect effects of fire on microbial communities: abiotic

Although the direct effects of fire on soil microbial communities are considerable, the indirect abiotic and biotic effects of fire may be the more significant drivers of change (Fig. 1). Unlike the short-term, direct heating effects of fire on microbial communities, the indirect, abiotic effects lead to long-term change in both plant and microbial communities. Indirect abiotic effects of fire include increased solar penetration and associated changes in the mineral soil microclimate, chemical alteration of the forest floor and mineral soil, formation of hydrophobic surface conditions, and the deposition of ash (mostly alkaline oxides) and charcoal.

4.1. Insolation and soil microclimate

Fire may indirectly affect the soil microbial community by altering the soil microclimate. The soil microclimate is altered following fire via the effects of fire on vegetation and O horizon densities, as well as changes in surface albedo (reflectivity). Reducing overstory and understory plant density allows for increased insolation to reach the ground surface. This, coupled with decreases in the surface albedo (blackening) following fire, leads to increased soil heating and warmer soil temperatures during the day, and more rapid heat loss and cooler soil temperatures at night. These fire-induced effects on daily soil temperature regimes also extend to seasonal changes, with more rapid warming of the soil during spring and summer months, and more rapid freezing during fall and early winter (Fisher and Binkley, 2000). Most biological reactions are exponentially related to temperature (Paul and Clark, 1996); hence, the warmer soil temperatures following fire generally

result in increased rates of microbially mediated processes, such as decomposition and nutrient release (Bissett and Parkinson, 1980; Covington and Sackett, 1984; Kaye and Hart, 1998a,b).

Changes in soil moisture following fire should also result in changes in the activities of the soil microflora (Paul and Clark, 1996). In the generally dry forest soils of the Inland West, microbial functional diversity and activity is strongly water-limited (Kaye and Hart, 1998b; Boyle, 2002; Boyle et al., in press). However, fire-mediated changes in soil moisture regimes are more difficult to predict than changes in temperature due to the number of hydrological processes affected by fire (DeBano et al., 1998). Fire-induced losses of vegetative canopies (both understory and overstory), as well as a decrease in O horizon density, result in reduced interception losses of water. Furthermore, reduction in leaf area following fire reduces evapotranspiration losses overall, even though ground surface evaporation is usually increased due to greater insolation at the soil surface. Taken together, these hydrological changes would be expected to lead to greater soil moisture following fire. However, frequently the reduction of canopy and O horizon interception and the formation of water-repellent soils (see below) result in reduced water infiltration to the soil, because of increases in water loss via overland flow. As a result of the way fire alters these competing hydrologic processes at a given site, fire has been shown to lead to higher (Klock and Hevey, 1976; Haase, 1986), lower (Campbell et al., 1977; Milne, 1979), and no change in soil moisture storage (Wells et al., 1979; Ower, 1985; Ryan and Covington, 1986) compared to pre-burn or unburned areas.

Increased input of photosynthetically active radiation at the ground surface following fire might also increase the relative abundance of phototrophic bacteria and algae, including organisms such as cyanobacteria that fix N from the atmosphere (see below). However, we know of no studies that have documented such hypothesized changes in these groups of organisms following fire in forests.

4.2. Physicochemical changes

Changes in the chemical (i.e., nutrient availability, pH) and physical (i.e., texture, structure) characteristics of the soil following fire may also indirectly alter

microbial communities and the processes they catalyze. Forest floor (O horizon) and mineral soil heating during fire result in nutrient loss by a variety of different mechanisms, including: oxidation (gasification), vaporization (volatilization), convection of ash particles, increased leaching of soluble ions, and accelerated erosion (Fisher and Binkley, 2000). However, extremely high surface temperatures must be sustained to cause a significant loss of most soil nutrients. Nitrogen, the mineral nutrient most susceptible to loss, begins to volatilize at temperatures greater than 120 °C, but total N loss rarely exceeds 50% even in the presence of sustained surface temperatures in excess of 300 °C. The combined effect of N and C loss following heating may lead to a long-term reduction in microbial activity (Choromanska and DeLuca, 2002). However, most often there is an immediate net increase in available nutrients after fire, sometimes leading to a short-term increase in microbial activity (DeLuca and Zouhar, 2000; Choromanska and DeLuca, 2001), but not always (Newman et al., in review).

The oxidation of organic matter during fire concentrates non-volatile elements in the ash layer, thereby concentrating alkaline metals, transition metals, and some oxyanions in mineral soils following fire (Neary et al., 1999; Arocena and Opio, 2003). It is unknown if increases in these compounds alter microbial communities. Organic matter oxidation also generally increases soil pH by combusting undissociated organic acids and by consuming (titrating) H⁺ from the soil (Fisher and Binkley, 2000). Increases in soil pH following fire may increase the activity of at least some soil microorganisms. For example, Montes and Christensen (1979) found that adding lime to forest soils and raising the pH by 0.5–1.7 units increased net nitrification several-fold during laboratory incubation.

During extremely high severity fires, soil physical properties such as aggregate stability or clay content may be directly altered as a result of high temperatures (Arocena and Opio, 2003). Aggregates are destroyed by the complete or partial oxidation of the organic material binding soil particles together. At exceptionally high temperatures (those found under slash piles or smoldering stumps), soil mineral particles can actually become fused, creating silt-sized particles from clays (Ulery and Graham, 1993). These changes in physical characteristics will likely lead to decreases

in soil moisture and reductions in soil aeration, with corresponding changes in soil microbial communities.

4.3. Formation of water repellent soils

Surface soils exposed to fire may experience a short-term occurrence of increased water repellency as a result of the heating and distillation of organic materials into organic and mineral surface horizons (DeBano, 2000). Fire-induced water repellency normally exists in a shallow, discrete layer that runs parallel to the mineral soil surface. It is created at relatively low temperature (200–280 °C), short-duration heating of soils and is readily destroyed at sustained temperatures greater than 280 °C. Ideal temperatures for the formation of hydrophobic conditions are commonly found within the upper 10 cm of the mineral soil during fire (DeBano, 2000). This water repellent or hydrophobic condition has the potential to increase overland or shallow subsurface flow, resulting in decreased recharge of soil moisture and increased erosion potential (DeBano, 2000; Robichaud, 2000; Shakesby et al., 2000), and possible changes in microbial activity (Letey, 2001). Fire-induced hydrophobic conditions are not permanent, but dissipate within a year or two after fire as a result of microbial decomposition of the waxy, hydrophobic materials (Franco et al., 2000).

4.4. The charcoal effect

Charcoal is generated by the partial combustion of organic materials and is produced during most natural fire events in both forest and prairie environments. The polycyclic aromatic structure of charcoal or “black carbon” makes it chemically and biologically stable, allowing it to persist in the environment for centuries. Oxidation during charcoal formation produces carboxylic groups on the edges of the aromatic backbone, which increases the nutrient and water holding capacities of charcoal (Glaser et al., 2002).

Charcoal functions as effective sorptive surfaces for organic compounds. This functional aspect of charcoal has resulted in its use in a myriad of applications from water purification to odor reduction (Ivancev-Tumbas et al., 1998). Charcoal formed from trees burned during forest fires degrades more slowly than non-charred woody materials (Seiler and

Crutzen, 1980), and therefore tends to accumulate over time. Zackrisson et al. (1996) demonstrated that boreal forest soils lose their ability to sorb phenolic compounds approximately 100 year after charcoal deposition (Zackrisson et al., 1996).

There are only a limited number of studies addressing the chemical or biological importance of charcoal in ecosystem function. A few researchers have explored the potential role of charcoal in plant responses to fire or its absence (Keeley, 1987; Zackrisson et al., 1996; Wardle et al., 1998), and fewer yet have investigated the role of charcoal in soil processes. Glaser et al. (2002) recently reviewed the influence of charcoal on soil properties in tropical agroecosystems. These researchers suggested that charcoal has a potent effect on soil productivity by increasing water and nutrient holding capacities, but they do not address the direct or indirect influence of charcoal on microbial activity (Glaser et al., 2001, 2002). Studies of the effect of charcoal on microbial activity and community composition (Wardle et al., 1997, 1998; Pietikäinen et al., 2000) suggest that charcoal has little influence on total activity, but a significant influence on specific groups of microorganisms. For example, charcoal may play a significant role in maintaining the activity of nitrifying bacteria in late successional boreal forests (DeLuca et al., 2002). Laboratory studies have suggested that charcoal taken from western Montana forest soils effectively sorbs free phenolic compounds and enhances net nitrification (T.H. DeLuca, unpublished data), but no conclusive studies have demonstrated this relationship.

5. Indirect effects of fire on microbial communities: biotic

We hypothesize that, where frequent fire has shaped the evolutionary history of a forest, the indirect biotic effects of fire on soil microbial communities are mediated primarily by fire-induced changes in the vegetative community. The strong links between plant functional groups or species and soil microbial communities (e.g., Hobbie, 1992; Wardle, 2002) suggests that changes in vegetative community structure in the years following fire have the potential to be the more dominant driver and shaper of the soil

microflora than the direct impact of the fire disturbance itself. Other indirect biotic effects likely also occur following fire that influence soil microbial communities, such as changes in the relative abundance of microbial grazers; however, we speculate that these other biotic changes have relatively minor effects on soil microorganisms compared to vegetation-driven changes. In most cases, the biotic effects are initiated via changes in the physicochemical (abiotic) characteristics of the soil following fire (see above). However, over time, feedback loops develop between the post-fire vegetation and the soil microbial communities (Fig. 1). It is these plant–soil feedbacks that we believe are fundamental to the long-term maintenance and stability of fire-adapted forests, and not the direct nutrient mineralizing effects so often suggested (St. John and Rundel, 1976).

5.1. Post-fire vegetative dynamics as microbial drivers

As noted above, the primary mechanisms by which vegetation influences soil microbial communities are by regulating: (1) the quantity of resources added to the soil system (NPP); (2) the competition for nutrients; (3) the quality of the resources (substrate quality); and (4) by forming mutualisms with the soil microflora. All of these mechanisms are potentially influenced by the effects of fire on post-fire vegetation productivity and composition.

The fire-suppressed, contemporary forests of the Inland West likely have higher NPP than the open, park-like savanna forests that were sustained by frequent ground fires prior to Euro-American settlement (Kaye et al., *in press*; S. Hart, unpublished data). This is mainly due to the higher leaf areas that contemporary forests support. Changes in NPP resulting from the direct and indirect effects of fire on vegetation structure likely impact both the composition and biomass of the soil microflora (Wardle, 2002).

Fire-induced changes in plant communities have the potential to change the relative competitive ability between plant and microbes for limiting nutrients (Kaye and Hart, 1997; Kaye et al., *in press*), which may, in turn, modify the soil microflora as well. However, little is known about the relative importance of this plant–soil interaction as a mechanism of control on the soil microflora (Wardle, 2002).

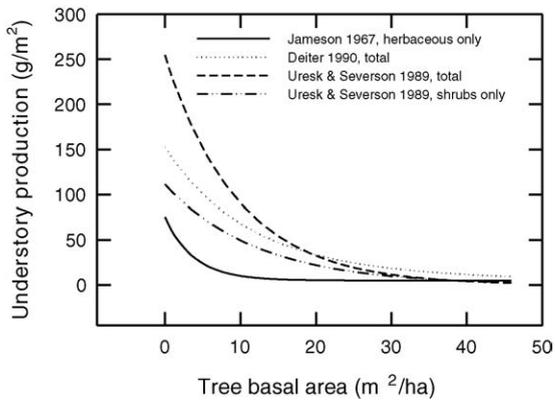


Fig. 3. Relationships between overstory stand density (basal area) and aboveground understory production in ponderosa pine-dominated ecosystems of the Inland West, USA. In all cases, understory production is strongly and negatively influenced by increasing pine density. The relationships shown for Uresk and Severson (1989) study were developed from the Black Hills, SD and included shrub and total (herbaceous plus shrubs) understory production. The relationship shown from Deiter (1991) was developed from the Kaibab Plateau, AZ and included total understory production; however, shrub production was generally a small fraction of total understory production. The relationship shown from Jameson (1967) was based on herbaceous production alone and was developed from data collected from the Wild Bill Range Study near Flagstaff, AZ.

In dry interior forests of the Inland West, the historical fire regime played a key role in maintaining stand structure, in particular the relative balance between understory vegetation (i.e., grasses, forbs, shrubs) and overstory trees (Covington et al., 1994). Due to resource competition between understory vegetation and overstory trees, understory production is tightly coupled to overstory stand density (Fig. 3); increases in the density of the tree overstory result in concomitant decreases in herbaceous or shrub production. The regulation of pine seedling recruitment by fire is the major pathway by which a balance between these two plant functional groups is maintained (Covington et al., 2001). Understory plants in these ecosystems are well adapted to grow vigorously following fire by maintaining large C reserves belowground (Ojima et al., 1994; DeBano et al., 1998).

We hypothesize that changes in the quality of organic matter inputs by the vegetation and the degree to which plant–microbial mutualisms are formed are the most important mechanisms by which post-fire

vegetation changes drive microbial community dynamics. Fire suppression activities over the past 120 years in ponderosa pine-dominated forests of the Inland West have resulted in large increases in pine and other conifer litter input, and a concurrent reduction in herbaceous litter inputs both above- and below-ground (Kaye et al., in press). The net effect of these changes in vegetation structure has been to “lignify” the ecosystem. In other words, although the total amount of organic matter input may be higher in these forests when fire is suppressed (Kaye et al., in press; S. Hart, unpublished data), a greater proportion of the input is high-lignin, low-N pine litter, as opposed to low-lignin, high-N herbaceous litter, resulting in reduced rates of N cycling (Scott and Binkley, 1997; Kaye and Hart, 1998a,b; Kaye et al., in press). These changes in litter quality have also apparently altered the mutually dependent soil microflora (see below).

This mechanism of change can be illustrated from a forest restoration experiment conducted at the Gus Pearson Natural Area (GPNA), near Flagstaff, AZ (Covington et al., 1997). In 1993, a study was initiated to determine if restoring forest structure to pre-Euro-American patterns and reintroducing the natural fire regime would reestablish ecosystem function. The restoration treatment included whole-tree harvesting of the majority of ponderosa pine trees established post-settlement (ca. 1876), followed by forest floor manipulation and a prescribed burn. Forest floor manipulation prior to the prescribed burn included raking aside the Oi layer and removing the Oa and Oe layers from the site. The Oi layer (2–4 years of litterfall) was then returned to the soil surface, along with ~670 kg/ha of native grasses and forbs mowed from nearby Hart Prairie. These forest floor manipulations were intended to emulate the fuel load of forests prior to fire exclusion; they were based on previous local experience suggesting that old growth tree mortality is high when prescribed burns are not preceded by the reduction of forest floor fuels that accumulated over 120 years of fire suppression (Covington et al., 1997).

Within only 1–2 years following restoration treatments, aboveground inputs of herbaceous litter increased and pine litter decreased in the restored plots relative to the controls (Table 2). These changes, coupled with the higher N and lower lignin

Table 2

Mean annual amount and chemical quality of aboveground litter inputs in control and restored (thinned and burned) plots one to two years after treatment at the Gus Pearson Research Area^a

Chemical constituent	Control			Restored		
	Herb	Tree	Total	Herb	Tree	Total
C (g/m ²)	2.4	128.4	130.8	12.6	95.7	108.3
N (g/m ²)	0.07	1.18	1.25	0.36	0.86	1.22
C:N (kg/kg)	34	109	105	35	112	89
Lignin ^b (%)	9.0	28.5	28.1	9.0	28.5	26.2

^a Data from Kaye et al. (in press).

^b Lignin values assumed to be 5.2% for herbaceous understory litter (Hannemann, 1991) and 28.5% for ponderosa pine tree litter (Hart et al., 1992).

concentrations of herbaceous litter relative to pine litter, led to a decrease in the C:N ratio and a reduction in the lignin concentration of the total aboveground litterfall. Ongoing studies at GPNA suggest that these differences in the quality of litter inputs have been widening between these two treatments over time (W.

Covington, P. Fulé, S. Hart, M. Moore, Northern Arizona University, unpublished data).

Preliminary data from the restoration experiment at GPNA are consistent with the hypothesis that fire-driven changes in vegetation modify soil microbial communities. Table 3 summarizes various microclimatic and biological characteristics of soils under contrasting canopy types at GPNA. Canopy patches dominated by relict grass openings had higher growing season soil temperatures and water contents than soils under pine canopies. These changes are likely responsible, at least in part, for the observed higher rates of soil processes mediated by soil microorganisms, and may directly induce changes in the composition of the microflora (Kaye and Hart, 1998a,b; Boyle, 2002; Wardle, 2002; Boyle et al., in press).

Although the microbial biomass was similar among these contrasting canopy types, the mean growing season activities of a suite of eight different soil enzymes involved in microbially mediated decom-

Table 3

Comparison of microclimatic and biological characteristics of soils under contrasting canopy types at the Gus Pearson Natural Area^a

Soil characteristic	Canopy type		
	Presettlement	Postsettlement	Grass
Median growing season soil temperature ^b (°C)	16.0 a	15.5 a	17.0 b
Mean growing season soil water content ^b (m ³ /m ³)	0.194 a	0.193 a	0.199 b
Soil respiration ^c (g C m ⁻² y ⁻¹)	511 a	476 a	636 b
Net N mineralization ^d (g N m ⁻² y ⁻¹)	2.2 a,b	1.5 a	2.7 b
Net nitrification ^d (g N m ⁻² y ⁻¹)	1.2 a	1.3 a	2.3 b
Nitrifier biomass/activity ^e (mg N m ⁻² d ⁻¹)	58 a	91 b	97 b
Mean growing season enzyme activity index ^f (μg product kg ⁻¹ h ⁻¹)	157 a	255 b	263 b
Mean growing season microbial N ^g (g/m ²)	5.65 a	4.37 a	5.15 a

^a These canopy types were nested within control and ecological restoration treatments that included thinning and prescribed fire. However, in all cases, no significant treatment by canopy-type interaction occurred (see Kaye and Hart, 1998a,b; Boyle et al., in press). Values followed by different letters within a row are significantly different ($P < 0.10$).

^b Mean daily soil temperature (7.5 cm mineral soil depth) and soil volumetric water content (0–15 cm mineral soil depth) were measured between 4 June and 30 September 2001.

^c Soil respiration rates were measured during 1995; rates measured during 1996, 2001, and 2002 showed very similar patterns among canopy types (Kaye and Hart, 1998b; S. Hart unpublished data).

^d Net N mineralization and nitrification rates were measured between May 1995 and 1996 (O horizon + 0–15 cm mineral soil depth; Kaye and Hart, 1998a).

^e Nitrification potential (0–15 cm mineral soil depth) determined using the method of Belser and Mays on soil sampled in August 1995. This method is essentially an enzyme assay that measures the activity of ammonia monooxygenase, which covaries well with chemoautotrophic nitrifier population size (Hart et al., 1994).

^f The mean enzyme activity of eight different soil enzymes involved in organic matter decomposition and nitrogen, phosphorus, and sulfur mineralization averaged over two sampling periods: when soils were dry early in the growing season, and when soils were moist late in the growing season. Calculated from values given in Boyle et al. (in press).

^g Determined using the chloroform-fumigation extraction method and assuming a k_{en} of 0.2, averaged over two sampling periods: when soils were dry early in the growing season and when soils were moist late in the growing season. Calculated from values given in Boyle et al. (in press).

position and N, phosphorus (P), and sulfur (S) release were over 60% higher under grass than under presettlement pine canopies. The biomass of autotrophic nitrifying organisms responsible for nitrification was also over 60% higher in grass patches than under presettlement pines, and the in situ rate of net nitrification was over 90% higher. Although in situ rates of net N mineralization were similar between these two canopy types, soil respiration rates (a measure of the biological activity belowground) was higher from soils beneath grass than presettlement vegetation. For all of these measurements, there was no significant treatment (control, thinning only, thinning and prescribed burning) by canopy-type interaction, suggesting that these differences among canopy types were not directly altered by thinning or prescribed fire. Rather, these data suggest that microclimatic and biological characteristics of soils beneath the various canopy types are intrinsic differences of the vegetation patch; restoration treatments (thinning and prescribed fire) alter these characteristics at the stand-level by converting postsettlement tree patches to grass patches (Kaye and Hart, 1998a,b; Boyle, 2002; Boyle et al., in press).

In contrast to successional patterns of ponderosa pine ecosystems of the Southwestern USA, ponderosa pine–Douglas-fir ecosystems of the wetter Inland Northwest are shaped from longer fire-return intervals and a longer successional pathway. To date, the succession pattern of understory vegetation in these northwestern ecosystems has been poorly described. Recent evidence (MacKenzie et al., 2004) suggests that, although there is little change in total graminoid cover with time since last fire, woody shrub cover increases significantly with time (Fig. 4). This shift to a woody shrub-dominated understory along with an increase in forest basal area may reduce nutrient availability with succession. This hypothesis is supported by the corresponding increase in total phenols in the forest floor with the increase in woody shrubs, and the decline in net nitrification (as estimated by sorption of nitrate to anion exchange resins) with increasing total phenols in the mineral soil (Fig. 5).

In these northwestern forests, fire results in the retreat of the shrub community and a renewed dominance by graminoids and herbaceous species. The increased presence of graminoids and herbaceous species are more likely to provide the soil with greater

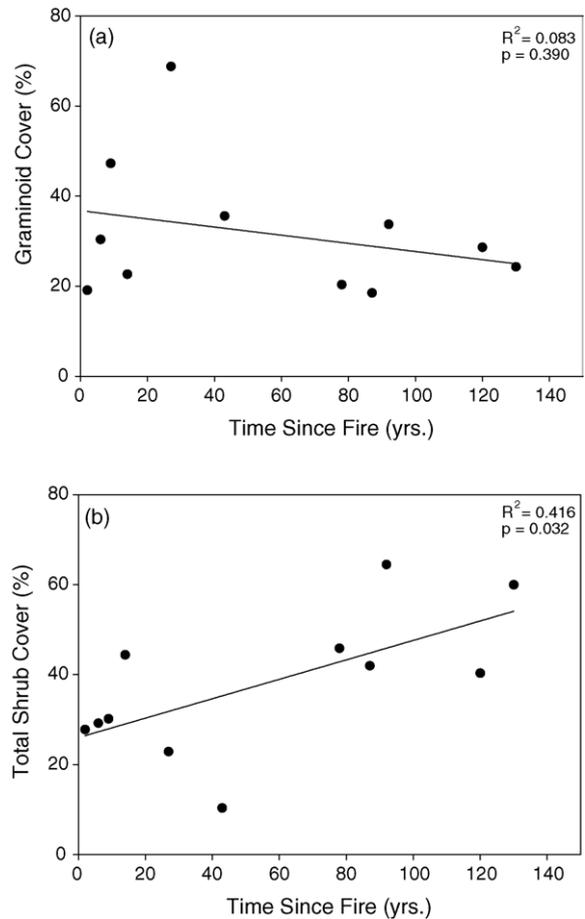


Fig. 4. Successional recovery of understory plants from Inland Northwest ponderosa pine forests with increasing time since fire. The percent cover of graminoids (a) shows no significant trend, while the percent cover of total shrubs (b) increases significantly with time since fire. Results were normalized to the amount of bare ground per site to account for moisture differences; bare ground did not change significantly with time since fire (MacKenzie et al., 2004).

daily and annual inputs of labile N and C than are the perennial woody shrubs. Thus, N turnover rates may be increased in spite of a reduction in mineralizable N and total N following fire (e.g., Monleon et al., 1997; Kaye and Hart, 1998a,b; DeLuca and Zouhar, 2000). It is clear that the quality of substrate (e.g., low lignin to N ratios) that is delivered to the soil by the existing plant community can directly influence N turnover rates (e.g., Scott and Binkley, 1997). Increases in polyphenol-rich litter may also directly or indirectly influence nutrient turnover and microbial activity

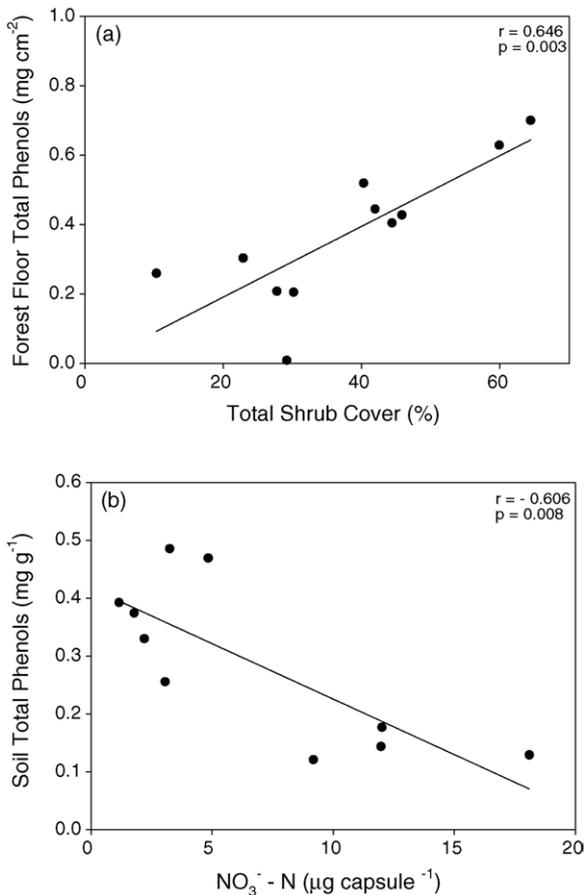


Fig. 5. The relationship between secondary metabolites, ground cover, and net nitrification. Uncorrected Pearson correlations showed that total shrub cover (a) was positively related to forest floor total phenols (mg cm^{-2}), and that resin accumulated nitrate ($\mu\text{g capsule}^{-1}$) from the mineral soil (b) was negatively related to mineral soil total phenols (mg g^{-1}) (MacKenzie et al., 2004).

(Hättenschwiler and Vitousek, 2000; Schweitzer et al., 2004).

Rates of biological N fixation may increase after burning in response to changes in resource availability (e.g., C, light, P) following fire (Wells et al., 1979). Although several researchers have speculated that asymbiotic N fixation (free-living and associative) increases after fire (Woodmansee and Wallach, 1981; Boerner, 1982; Christensen, 1987), available evidence does not support this hypothesis (Fisher and Binkley, 2000). However, the relative abundance of symbiotic N-fixing plants frequently increases following fire, and this keystone mutualism may dramatically alter

both the rates of N cycling and the soil microbial community. The rate of N fixation in temperate forest ecosystems is predominantly the result of symbiotic N fixation and has been estimated to average about $0.7 \text{ g N m}^{-2} \text{ y}^{-1}$ (Cleveland et al., 1999); increases in symbiotic N-fixing vegetation density following fire events generally results in N-fixation rates much higher than this average. For instance, in semi-arid forests in the eastern Sierra Nevada mountains of California, dense stands of the N-fixing shrub snowbush (*Ceanothus velutinus*) have been reported following fire. Symbiotic N fixation by this species over a 16-year period can return more N to the soil than was lost during the fire (Johnson and Curtis, 1998). Post-fire stands of red alder (*Alnus rubra*) in the Pacific Northwest have been reported to fix between 5 and $20 \text{ g N m}^{-2} \text{ y}^{-1}$ (Binkley, 1981).

Exclusion of fire from Inland Northwest, second-growth ponderosa pine forests may reduce the abundance of N-fixing lupine (*Lupinus* spp.) that would normally colonize these sites following fire (Newland and DeLuca, 2000). In ponderosa pine forests of the Southwest, increased abundance and production of the N-fixing plants lupine (Casey, 2004) and fendler ceanothus (*Ceanothus fenderi*; Huffman, 2003) occur following fire. In one of the only studies to evaluate biological N-fixation rates in southwestern ponderosa pine forests, Story (1974) estimated that as much as $2 \text{ g N m}^{-2} \text{ y}^{-1}$ might be fixed in very dense stands of lupine or ceanothus, but more typical values are less than $0.08 \text{ g N m}^{-2} \text{ y}^{-1}$. Nevertheless, increases in biological N fixation following fire are likely important for replacing any ecosystem N lost directly from combustion during burning. We speculate that N loss following burning with the low fuel loads historically found in these forests prior to Euro-American settlement would be similar in magnitude (Covington et al., 1997) to these more typical rates of N fixation.

Biological N fixation is known to increase rates of soil N cycling primarily through increased input of high quality litter to the soil (Hart et al., 1997). For reasons noted above, we expect that an increase in the relative abundance of N-fixing plants following fire would not only alter the abundances of the N-fixing symbionts, but also would alter the relative composition and activities of other soil microorganisms (Wardle, 2002).

The indirect impact of fire on post-fire vegetation composition undoubtedly affects other microbial

mutualisms, such as mycorrhizae, that are plant-host dependent. We expect that these effects are greater for EM than AM associations because of the greater host specificity of EM fungi (Perry, 1994).

5.2. Fire as a nutrient mineralizer versus vegetation maintainer

Ever since the classic study by St. John and Rundel (1976), most fire researchers have stressed the importance of fire as a nutrient mineralizer in fire-evolved forest ecosystems with historically frequent fire regimes. Several studies have noted large increases in inorganic N and other mineral nutrients following prescribed fire in semi-arid forests of the Inland West (St. John and Rundel, 1976; Stark, 1977; Covington and Sackett, 1986, 1992; Ryan and Covington, 1986; Choromanska and DeLuca, 2001). For example, Ryan and Covington (1986) found an increase of up to 7 g N m^{-2} in the upper 15 cm of mineral soil during the summer following a fall prescribed burn.

However, two lines of evidence suggest that N availability in forests with a naturally frequent fire regime is regulated primarily by the effect of fire on the balance between understory and overstory vegetation, rather than due to fire as an N-mineralizing agent. Firstly, the dramatic increases in available N typically observed following fire are short-lived relative to the length of the fire-free return interval in these forests; most significant increases in inorganic

N following fire last only a few growing seasons or less following burning (St. John and Rundel, 1976; Covington and Sackett, 1992; Monleon et al., 1997; Fisher and Binkley, 2000). Secondly, all of these documented increases in available N following prescribed fire have been conducted in forests that have had unnaturally high fuel buildups due to long-term, fire suppression activities. Hence, the observed large increases in available N following fire are, in part, an artifact of the extremely high fuel loads prior to burning. For instance, Wright and Hart (1997) found that, after 20 years of reinstating the historical 2-year burning frequency to a ponderosa pine forest near Flagstaff, AZ, no significant increase in available N occurred over the entire 2-year burn cycle.

The relative importance to ecosystem function of fire as a maintainer of vegetation structure versus as a nutrient mineralizer is illustrated in Table 4. This table compares the plant demand for N (plant uptake) to the net release of N from ponderosa pine litter decomposition, N release directly by fire, and net N mineralization from soil organic matter (both in the forest floor and mineral soil) in the restoration treatments described previously at GPNA. The complete restoration treatment included the return of the forest structure to pre-Euro-American condition by thinning postsettlement trees, and the forest floor fuels had been manipulated to emulate a forest that had a frequent fire regime before prescribed burning was implemented (Covington et al., 1997). The partial restoration treatment included a similar thinning

Table 4
Comparison of N supplies and plant demand ($\text{g m}^{-2} \text{ y}^{-1}$) in restored and unrestored ponderosa pine ecosystems

Treatment	Net release from decomposition ^a	Net release from fire ^b	Net mineralization from forest floor ^c	Net mineralization from mineral soil ^c	Plant uptake ^d
Control	-0.05	-	0.19	0.75	3.17
Partial restoration (thinning only)	-0.05	-	0.63	2.31	3.09
Complete restoration (thinning and burning)	-0.11	0.83	0.22	1.75	2.94

^a Calculated from litterbag decomposition and litterfall data collected over a 40.5-month period. Only pine needle litter was considered in this calculation. Negative values denote net accumulation.

^b Calculated by subtracting the nutrient content of the forest floor 12 months following the burn (not including newly fallen needles) from pre-burn values, and then dividing this value by a putative 3-year, fire-free period. Covington and Sackett (1984) have shown previously in a nearby ponderosa pine stand that fire-stimulated changes in forest floor nutrient content over a year following a fire can be significant relative to those resulting immediately following the fire. Thus, the values given here are likely overestimates of the actual amount of nutrients released immediately following the fire. No fire occurred in the control and partial restoration treatments. See Covington et al. (1997) for more information on treatments.

^c Data from Kaye and Hart (1998a).

^d Data from Kaye et al. (in press). Values include above- and below-ground N uptake of all forest vegetation.

treatment to restore structure only. In both of these restoration treatments, understory productivity was greatly increased (Kaye et al., in press). The prescribed fire with more natural fuel loads released only a very small amount of N relative to annual demand by the vegetation. In contrast, net N mineralization from soil organic matter in both restoration treatments, where the herbaceous productivity in the understory had increased dramatically, was much higher than in the control treatment, and appeared to account for most of the annual plant uptake of N. These results, along with the higher rates of net N mineralization found under grass openings compared to under presettlement pines (Table 3), suggest that N availability in presettlement forests was driven by the open canopy structure and abundant understory vegetation rather than the direct mineralization of N from the frequent fires themselves; frequent fire maintained this vegetation structure by preventing pine seedling establishment in grass openings (Kaye and Hart, 1998a; Covington et al., 2001). We believe that this paradigm of the role of fire in these forests is generalizable to semi-arid forests throughout the Inland West, where a frequent fire regime historically occurred.

6. Future research needs

We hope that that this paper has achieved our overarching objective of creating interest in the reader to develop and test hypotheses related to the importance of plant–soil interactions in fire-dependent forest ecosystems. Here, we highlight three important areas of research needed to elucidate the feedbacks among fire, plants, and microorganisms in forests.

6.1. The role of fire severity

We have purposefully avoided a discussion throughout this paper of the importance of fire severity as a moderator of the response of the plant and soil microbial communities to burning. We took this approach because little is known about these relationships other than more intense burns will likely lead to greater effects on the biota. How are the responses of the soil and plant biota different following a controlled burn versus a wildfire? To

answer this question, we need to understand the qualitative and quantitative relationships between fire severity and specific changes in ecosystem structure and function. In particular, we need to know the nature of the responses: are there thresholds in fire severity where the ecological response changes dramatically with a small change in fire severity, or is there more of a continuous, linear response to changes in fire severity?

6.2. Fire: the ultimate vegetation manager?

We hypothesize that the relative importance of fire as a vegetation manager compared to a nutrient mineralizer increases as the mean fire-return interval increases. This is because as the fire frequency lengthens, the pulse of nutrients released from the fire, although greater in magnitude, has a lower potential to affect plant growth over the entire fire-free period. Furthermore, in forests with a low fire frequency and hence stand-replacing behavior, the impact of fire on vegetation structure is long-lasting (DeBano et al., 1998). If this hypothesis is correct, then the ponderosa pine examples we have provided in this paper, with some of the highest fire frequencies of any forest type (Table 1), should be robust; they clearly demonstrate the principal importance of fire as a shaper of vegetation structure and, in turn, of microbial communities. To fully evaluate this hypothesis, more research is needed to clarify these roles in a variety of contrasting forest types with varying fire regimes.

6.3. The importance of long-term studies

At this point in time, we have only a limited appreciation for the interrelationships among plant and microbial communities and ecosystem processes as they change in the months, as well as years, following fire. It is apparent that fire serves as an immediate and significant disturbance to the soil ecosystem, and has a dramatic, typically short-term change in the understory plant community. However, it is unclear whether fire has a considerable influence on long-term changes in understory species composition, and how such changes in plant dynamics might influence microbial communities and the processes they mediate. We call for long-term, interdisciplinary studies to be developed, in a range of forests with

varying fire regimes, to evaluate the interrelationships among reoccurring fire, vegetation structure, microbial communities, and ecosystem function. Through such long-term, integrative studies, we will be able to unequivocally link plant community responses to fire with those of the mutually dependent soil microflora, and ultimately improve our understanding of the ecological role of fire in forest ecosystems.

Acknowledgements

This research was supported by National Science Foundation grant DEB-9322706, McIntire-Stennis appropriations to NAU's School of Forestry with matching funds from the State of Arizona, Joint Venture Agreements RMRS-99161-RJVA and RMRS-00-JV-11221615-233 with the US Forest Service Rocky Mountain Research Station, the Southwest Fire Initiative, and NAU's Ecological Restoration Institute. This is Contribution No. 54 of the National Fire and Fire Surrogate Project, funded by the US Joint Fire Sciences Program. We thank W.W. Covington, P. Fulé, M. Moore, and the US Forest Service for maintaining the field site at the GPNA, M. Moore for helpful discussions regarding overstory–understory relationships, and R.F. Powers and two anonymous reviewers for their constructive comments on an earlier version of this manuscript.

References

- Agrios, G.N., 1997. Plant Pathology. Academic Press, San Diego, CA, USA.
- Allen, M.F., 1991. The Ecology of Mycorrhizae. Cambridge University Press, Cambridge.
- Amaranthus, M.P., Perry, D.A., 1987. Effect of soil transfer on ectomycorrhiza formation and the survival and growth of conifer seedlings on old, nonreforested clear-cuts. *Can. J. For. Res.* 17, 944–950.
- Arno, S.F., Harrington, M.G., Fiedler, C.E., Carlson, C.E., 1995. Restoring fire-dependent ponderosa pine forests in western Montana. *Restor. Manage. Notes* 13, 32–36.
- Arocena, J.M., Opio, C., 2003. Prescribed fire-induced changes in properties of sub-boreal forest soils. *Geoderma* 113, 1–16.
- Baar, J., Horton, T.R., Kretzer, A., Bruns, T.D., 1999. Mycorrhizal recolonization of *Pinus muricata* from resistant propagules after a stand-replacing wildfire. *N. Phytol.* 143, 409–418.
- Bear, M.H., Neely, C.L., Coleman, D.C., Hargrove, W.L., 1991. Characterization of a substrate-induced respiration method for measuring fungal, bacterial and total microbial biomass on plant residues. *Agric. Ecosyst. Environ.* 34, 65–73.
- Bever, J.D., 2003. Soil community feedback and the coexistence of competitors: conceptual frameworks and empirical tests. *N. Phytol.* 157, 465–486.
- Binkley, D., 1981. Nodule biomass and acetylene reduction rates of red alder and Sitka alder on Vancouver Island, BC. *Can. J. For. Res.* 11, 281–286.
- Bissett, J., Parkinson, D., 1980. Long-term effects of fire on the composition and activity of the soil microflora of a subalpine, coniferous forest. *Can. J. Bot.* 58, 1704–1721.
- Blagodatskaya, E.V., Anderson, T.H., 1998. Interactive effects of pH and substrate quality on the fungal-to-bacterial ratio and qCO₂ of microbial communities in forest soils. *Soil Biol. Biochem.* 30, 1269–1274.
- Boerner, R., 1982. Fire and nutrient cycling in temperate ecosystems. *BioScience* 32, 187–192.
- Boyle, S.I., 2002. Impact of ecological restoration on soil microbial communities in *Pinus ponderosa* ecosystems of northern Arizona. M.S. Thesis. Northern Arizona University, Flagstaff, AZ, USA.
- Boyle, S.I., Hart, S.C., Kaye, J.P., Waldrop, M.P., in press. Restoration and canopy type influence soil microflora in a ponderosa pine forest. *Soil Sci. Soc. Am. J.*
- Campbell, R.E., Baker Jr., M.B., Ffolliott, P.F., Larson, F.R., Avery, C.C., 1977. Wildfire effects on a ponderosa pine ecosystem: an Arizona case study. USDA For. Serv. Res. Pap. RM-191.
- Casey, C.A., 2004. Herbaceous biomass and species composition responses to ponderosa pine restoration treatments. M.S. Thesis. Northern Arizona University, Flagstaff, AZ, USA.
- Choromanska, U., DeLuca, T.H., 2001. Prescribed fire alters the effect of wildfire on soil biochemical properties in a ponderosa pine forest. *Soil Sci. Soc. Am. J.* 65, 232–238.
- Choromanska, U., DeLuca, T.H., 2002. Microbial activity and nitrogen mineralization in forest mineral soils following heating: evaluation of post-fire effects. *Soil Biol. Biochem.* 34, 263–271.
- Christensen, N.L., 1987. The biogeochemical consequences of fire and their effects on the vegetation of the coastal plain of the Southeastern United States. In: Trabaud, L. (Ed.), *The Role of Fire in Ecological Systems*. SPB Academic Publishing, The Hague, The Netherlands, pp. 1–21.
- Classen, A.T., Boyle, S.I., Haskins, K.E., Overby, S.T., Hart, S.C., 2003. Community-level physiological profiles of bacteria and fungi: plate type and incubation temperature influences on contrasting soils. *FEMS Microbiol. Ecol.* 44, 319–328.
- Cleveland, C.C., Townsend, A.R., Schimel, D.S., Fisher, H., Howarth, R.W., Hedin, L.O., Perakis, S.S., Latty, E.F., Von Fischer, J.C., Elseroad, A., Wasson, M.F., 1999. Global patterns of terrestrial biological nitrogen (N₂) fixation. *Global Biogeochem. Cycles* 13, 623–645.
- Covington, W.W., Sackett, S.S., 1984. The effect of a prescribed burn in southwestern ponderosa pine on organic matter and nutrients in woody debris and forest floor. *For. Sci.* 30, 183–192.

- Covington, W.W., Sackett, S.S., 1986. Effect of periodic burning on soil nitrogen concentrations in ponderosa pine. *Soil Sci. Soc. Am. J.* 50, 452–457.
- Covington, W.W., DeBano, L.F., 1990. Effects of fire on pinyon-juniper soils. In: Krammes, J.S. (Technical Coordinator), *Effects of Fire Management of Southwestern Natural Resources*. USDA For. Serv. Gen. Tech. Re RM-191, pp. 78–86.
- Covington, W.W., Sackett, S.S., 1992. Soil mineral nitrogen changes following prescribed burning in ponderosa pine. *For. Ecol. Manage.* 54, 175–191.
- Covington, W.W., Moore, M.M., 1994. Southwestern ponderosa pine forest structure: changes since Euro-American settlement. *J. For.* 92, 39–47.
- Covington, W.W., Fulé, P.Z., Hart, S.C., Weaver, R.P., 2001. Modeling ecological restoration effects on ponderosa pine forest structure. *Restor. Ecol.* 9, 421–431.
- Covington, W.W., Everett, R.L., Steele, R., Irwin, L.L., Daer, T.A., Auclair, A.N.D., 1994. Historical and anticipated changes in forest ecosystems of the Inland West of the United States. *J. Sustain. For.* 2, 13–63.
- Covington, W.W., Fulé, P.Z., Moore, M.M., Hart, S.C., Kolb, T.E., Mast, J.N., Sackett, S.S., Wagner, M.R., 1997. Restoration of ecosystem health in southwestern ponderosa pine forests. *J. For.* 95, 23–29.
- DeBano, L.F., 1974. Chaparral soils. In: Rosenthal, C. (Conference Chairman), *Proceedings of a Symposium on Living with the, Chaparral*, Sierra Club, San Francisco, CA, USA, pp. 19–26.
- DeBano, L.F., 2000. The role of fire and soil heating on water repellency in wildland environments: a review. *J. Hydrol.* 231–232, 195–206.
- DeBano, L.F., Neary, D.G., Ffolliott, P.F., 1998. *Fire's Effects on Ecosystems*. John Wiley and Sons Inc., New York, USA.
- Deiter, D.A., 1991. A comparison of ponderosa pine stand density measures for predicting understory production in the Kaibab Plateau, northern Arizona. M.S. Thesis. Northern Arizona University, Flagstaff, AZ, USA.
- DeLuca, T.H., Zouhar, K.L., 2000. Effect of selection cutting and prescribed fire on N dynamics in ponderosa pine forests. *For. Ecol. Manage.* 138, 263–271.
- DeLuca, T.H., Nilsson, M.-C., Zackrisson, O., 2002. Nitrogen mineralization and phenol accumulation along a fire chronosequence in northern Sweden. *Oecologia* 133, 206–214.
- Dunn, P.H., DeBano, L.F., 1977. Fire's effects on biological and chemical properties of chaparral soils. In: Mooney, H.A., Conrad, C.E. (Technical Coordinators), *Proceedings of a Symposium on Environmental Conservation: Fire and Fuel Management in Mediterranean Ecosystems*, Palo Alto, CA, August 4–5, 1988. USDA For. Serv. WO-3, Washington, DC, pp. 75–84.
- Dunn, P.H., Barro, S.C., Poth, M., 1985. Soil moisture affects survival of micro-organisms in heated chaparral fire. *Soil Biol. Biochem.* 17, 143–148.
- Fisher, R.F., Binkley, D., 2000. *Ecology and Management of Forest Soils*, 3rd ed. John Wiley and Sons Inc., New York, USA.
- Franco, C.M.M., Clarke, P.J., Tate, M.E., Oades, J.M., 2000. Hydrophobic properties and chemical characterisation of natural water repellent materials in Australian sands. *J. Hydrol.* 231–232, 47–58.
- Fuller, W.H., Shannon, S., Burgess, P.S., 1955. Effect of burning on certain forest soils of northern Arizona. *For. Sci.* 1, 44–50.
- Glaser, B., Haumaier, L., Guggenberger, G., Zech, W., 2001. The 'Terra Preta' phenomenon: a model for sustainable agriculture in the humid tropics. *Naturwissenschaften* 88, 37–41.
- Glaser, B., Lehmann, J., Zech, W., 2002. Ameliorating physical and chemical properties of highly weathered soils in the tropics with charcoal—a review. *Biol. Fertil. Soils* 35, 219–230.
- Haase, S.M., 1986. Effect of prescribed burning on soil moisture and germination of southwestern ponderosa pine seed on basaltic soils. USDA For. Serv., Rocky Mt. For. Range Exp. Stn. Res. Note RM-462.
- Hannemann, M.D., 1991. Effects of cattle, elk and mule deer on a narrowleaf cottonwood riparian community under a short rotation grazing system in northern Arizona. M.S. Thesis. Northern Arizona University, Flagstaff, AZ, USA.
- Hare, R.C., 1961. Heat effects on living plants. USDA For. Serv. Occ. Pap. 183. USDA For. Serv. South. Exp. Stn., New Orleans, LA.
- Hart, S.C., Firestone, M.K., Paul, E.A., 1992. Decomposition and nutrient dynamics of ponderosa pine needle litter in a Mediterranean-type climate. *Can. J. For. Res.* 22, 306–314.
- Hart, S.C., Stark, J.M., Davidson, E.A., Firestone, M.K., 1994. Nitrogen mineralization, immobilization, and nitrification. In: Weaver, R.W., et al. (Eds.), *Methods of Soil Analysis, Part 2: Microbiological and Biochemical Properties*, SSSA Book Series No. 5, Madison, WI, USA, pp. 985–1018.
- Hart, S.C., Binkley, D., Perry, D.A., 1997. Influence of red alder on soil nitrogen transformations in two conifer forests of contrasting productivity. *Soil Biol. Biochem.* 29, 1111–1123.
- Hättenschwiler, S., Vitousek, P.M., 2000. The role of polyphenols in terrestrial ecosystem nutrient cycling. *Trends Ecol. Evol.* 15, 238–243.
- Hillel, D., 1998. *Environmental Soil Physics*. Academic Press Inc., San Diego, CA, USA.
- Hobbie, S.E., 1992. Effects of plant species on nutrient cycling. *Trends Ecol. Evol.* 7, 336–339.
- Huffman, D.W., 2003. Population ecology of fender ceanothus: responses to herbivory and forest restoration experiments. Ph.D. Dissertation. Northern Arizona University, Flagstaff, AZ, USA.
- Ivancev-Tumbas, I., Dalmacija, B., Tamas, Z., Karlovic, E., 1998. Reuse of biologically regenerated activated carbon for phenol removal. *Water Res.* 32, 1085–1094.
- Jameson, D.A., 1967. The relationship of tree overstory and herbaceous understory vegetation. *J. Range Manage.* 20, 247–249.
- Johnson, D.W., Curtis, P.S., 1998. Effects of forest management on forest soil C and N storage: a meta analysis. *For. Ecol. Manage.* 140, 227–248.
- Jonsson, L., Dalhberg, A., Nilsson, M.-C., Zackrisson, O., Kårén, O., 1999. Ectomycorrhizal fungal communities in late-successional boreal forests, and their composition following wildfire. *Mol. Ecol.* 8, 205–215.
- Kaye, J.P., Hart, S.C., 1997. Competition for nitrogen between plants and soil microorganisms. *Trends Ecol. Evol.* 12, 139–143.

- Kaye, J.P., Hart, S.C., 1998a. Ecological restoration alters nitrogen transformations in a ponderosa pine–bunchgrass ecosystem. *Ecol. Appl.* 8, 1052–1060.
- Kaye, J.P., Hart, S.C., 1998b. Restoration and canopy type effects on soil respiration in a ponderosa pine–bunchgrass ecosystem. *Soil Sci. Soc. Am. J.* 62, 1062–1072.
- Kaye, J.P., Hart, S.C., Fulé, P.Z., Covington, W.W., Moore, M.M., Kaye, M.W., in press. Initial carbon, nitrogen, and phosphorus fluxes following ponderosa pine restoration treatments. *Ecol. Appl.*
- Keeley, J.E., 1987. Role of fire in seed germination of woody taxa in California chaparral. *Ecology* 68, 434–443.
- Klock, G.O., Hevey, J.D., 1976. Soil-water trends following wildfire on the Entiat Experimental Forest. *Ann. Proc. Tall Timber Fire Ecol. Conf.* 15, 193–200.
- Klopatek, C.C., DeBano, L.F., Klopatek, J.M., 1988. Effects of simulated fire on vesicular-arbuscular mycorrhizae in pinyon–juniper woodland soil. *Plant Soil* 109, 245–249.
- Klopatek, C.C., Freise, C.F., Allen, M.F., Klopatek, J.M., 1994. Comparisons of laboratory and field burning experiments on mycorrhizae distribution, density and diversity. *J. Soc. Am. For.* 94, 762–776 (12th Conference on Fire and Forest Mineralogy, Special Issue).
- Klopatek, C.C., Klopatek, J.M., 1997. Nitrifiers, mineralization and microbes in pristine and disturbed pinyon–juniper ecosystems. *J. Arid Soil Res. Rehab.* 11, 331–342.
- Korb, J.E., Johnson, N.C., Covington, W.W., 2003. Arbuscular mycorrhizal propagule densities respond rapidly to ponderosa pine restoration treatments. *J. Appl. Ecol.* 40, 101–110.
- Letej, J., 2001. Causes and consequences of fire-induced soil water repellency. *Hydrol. Process.* 15, 2867–2875.
- Lynch, J.M., Whipps, J.M., 1991. Substrate flow in the rhizosphere. In: Keister, D.L., Cregan, P.B. (Eds.), *The Rhizosphere and Plant Growth*. Kluwer Publication, The Netherlands, pp. 15–24.
- MacKenzie, D.M., DeLuca, T.H., Sala, A., 2004. Forest structure and organic horizon analysis along a fire chronosequence in low elevation forests of western Montana. *For. Ecol. Manage.* 203, 331–343.
- Milne, M.M., 1979. The effects of burning root trenching, and shading on mineral soil nutrients in southwestern ponderosa pine. M.S. Thesis. Northern Arizona University, Flagstaff, AZ, USA.
- Monleon, V.J., Cromack Jr., K., Landsberg, J.D., 1997. Short- and long-term effects of prescribed underburning on nitrogen availability in ponderosa pine stands in central Oregon. *Can. J. For. Res.* 27, 369–378.
- Montes, R.A., Christensen, N.R., 1979. Nitrification and succession in the Piedmont of North Carolina. *For. Sci.* 25, 287–297.
- Nearly, D.G., Klopatek, C.C., DeBano, L.F., Ffolliott, P.F., 1999. Fire effects on belowground sustainability: a review and synthesis. *For. Ecol. Manage.* 122, 51–71.
- Newland, J., DeLuca, T.H., 2000. Influence of fire on native nitrogen fixing plants and the soil N status of ponderosa pine forests in western Montana. *Can. J. For. Res.* 30, 274–282.
- Newman, G.S., Hart, S.C., Guido, D.R., Overby, S.T., in review. Wildfire effects on soil microbial function *Oecologia*.
- Ojima, D.S., Schimel, D.S., Parton, W.J., Owensby, C.E., 1994. Long- and short-term effects of fire on nitrogen cycling in tallgrass prairie. *Biogeochemistry* 24, 67–84.
- Ower, C.L., 1985. Changes in ponderosa pine seedling growth and soil nitrogen following prescribed burning and manual removal of the forest floor. M.S. Thesis. Northern Arizona University, Flagstaff, AZ, USA.
- Packer, A., Clay, K., 2000. Soil pathogens and spatial patterns of seedling mortality in a temperate tree. *Nature* 404, 278–281.
- Pattinson, G.S., Hammill, K.A., Sutton, B.G., McGee, P.A., 1999. Simulated fire reduces the density of arbuscular mycorrhizal fungi at the soil surface. *Mycol. Res.* 103, 491–496.
- Paul, E.A., Clark, F.E., 1996. *Soil Microbiology and Biochemistry*, 2nd ed. Academic Press Inc., San Diego, CA, USA.
- Perry, D.A., 1994. *Forest Ecosystems*. The John Hopkins University Press, Baltimore, MD, USA.
- Pietikäinen, J., Fritze, H., 1995. Clear-cutting and prescribed burning in coniferous forest: comparison of effects on soil fungal and total microbial biomass, respiration activity and nitrification. *Soil Biol. Biochem.* 27, 101–109.
- Pietikäinen, J., Kiikkilä, O., Fritze, H., 2000. Charcoal as a habitat for microbes and its effect on the microbial community of the underlying humus. *Oikos* 89, 231–242.
- Raison, R.J., Woods, P.V., Jakobsen, B.F., Bary, G.A.V., 1986. Soil temperatures during and following low intensity prescribed burning in a *Eucalyptus pauciflora* forest. *Aust. J. Soil Res.* 24, 33–47.
- Robichaud, P.R., 2000. Fire effects on infiltration rates after prescribed fire in Northern Rocky Mountain forests, USA. *J. Hydrol.* 231–232, 220–229.
- Ryan, M.G., Covington, W.W., 1986. Effect of a prescribed burn in ponderosa pine on inorganic nitrogen concentrations of mineral soil. USDA For. Serv., Rocky Mt. For. Range Exp. Stn. Res. Note RM-464.
- Schweitzer, J.A., Bailey, J.K., Rehill, B.J., Martinsen, G.D., Hart, S.C., Lindroth, R.L., Keim, P., Whitham, T.G., 2004. Genetically based trait in a dominant tree affects ecosystem processes. *Ecol. Lett.* 7, 127–134.
- Scott, N.A., Binkley, D., 1997. Foliage litter quality and annual net N mineralization: comparison across North American forest sites. *Oecologia* 111, 151–159.
- Seiler, W., Crutzen, P.J., 1980. Estimates of gross and net fluxes of carbon between the biosphere and the atmosphere from biomass burning. *Clim. Change* 2, 207–247.
- Shakesby, R.A., Doerr, S.H., Walsh, R.P.D., 2000. The erosional impact of soil hydrophobicity: current problems, and future research directions. *J. Hydrol.* 231–232, 178–191.
- Staddon, P.L., Ramsey, C.B., Ostle, N., Ineson, P., Fitter, A.H., 2003. Rapid turnover of hyphae of mycorrhizal fungi determined by AMS microanalysis of ¹⁴C. *Science* 300, 1138–1140.
- Stark, N.M., 1977. Fire and nutrient cycling in a Douglas-fir/larch forest. *Ecology* 58, 16–30.
- St. John, T.V., Rundel, P.W., 1976. The role of fire as a mineralizing agent in a Sierran coniferous forest. *Oecologia* 25, 35–45.
- Story, M.T., 1974. Nitrogen fixation by *Ceanothus fendleri* and *Lupinus argenteus* as a function of parent material and vegetal cover. M.S. Thesis. University of Arizona, Tucson, AZ, USA.

- Ulery, A.L., Graham, R.C., 1993. Forest fire effects on soils color and texture. *Soil. Sci. Soc. Am. J.* 57, 135–140.
- Uresk, D.W., Severson, K.E., 1989. Understory–overstory relationships in ponderosa pine forests, Black Hills, South Dakota. *J. Range Manage.* 42, 203–208.
- Vilarino, A., Arines, J., 1991. Numbers and viability of vesicular–arbuscular fungal propagules in field soil samples after wildfire. *Soil Biol. Biochem.* 23, 1083–1087.
- Visser, S., 1995. Ectomycorrhizal fungal succession in jack pine stands following wildfire. *N. Phytol.* 129, 389–401.
- Wardle, D.A., Zackrisson, O., Hörnberg, G., Gallet, C., 1997. The influence of island area on ecosystem properties. *Science* 277, 1296–1299.
- Wardle, D.A., Zackrisson, O., Nilsson, M.-C., 1998. The charcoal effect in Boreal forests: mechanisms and ecological consequences. *Oecologia* 115, 419–426.
- Wardle, D.A., 2002. *Communities and Ecosystems: Linking the Aboveground and Belowground Components*. Princeton University Press, Princeton, NJ, USA.
- Wells, C.G., Campbell, R.E., DeBano, L.F., Lewis, C.E., Fredrickson, R.L., Franklin, E.C., Froelich, R.C., Dunn, P.H., 1979. Effects of fire on soil: a state-of-the knowledge review. USDA For. Serv. Gen. Tech. Re WO-7, Washington, DC, USA.
- White, C.S., 1991. The role of monoterpenes in soil nitrogen cycling processes in ponderosa pine. *Biogeochemistry* 12, 43–68.
- Woodmansee, R.G., Wallach, L.S., 1981. Effects of fire regimes on biogeochemical cycles. In: Mooney, H.A., et al. (Eds.), *Fire regimes and Ecosystem Properties*, USDA For. Serv. Gen. Tech. Rep. WO-26, Washington, DC, USA.
- Wright, R.J., 1996. Fire effects on fine roots, mycorrhizae, and nutrient dynamics in a southwestern ponderosa pine forest. M.S. Thesis. Northern Arizona University, Flagstaff, AZ, USA.
- Wright, R.J., Hart, S.C., 1997. Nitrogen and phosphorus status in a ponderosa pine forest after 20 years of interval burning. *Ecoscience* 4, 526–533.
- Zackrisson, O., Nilsson, M.-C., Wardle, D.A., 1996. Key ecological function of charcoal from wildfire in the Boreal forest. *Oikos* 77, 10–19.