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Forest Ecology and Management 122 (1999) 51–71

Forest Ecology and Management

Fire effects on belowground sustainability: a review and synthesis

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Abstract

The overall effects of fire on ecosystems are complex, ranging from the reduction or elimination of aboveground biomass to impacts on belowground physical, chemical and microbial mediated processes. Since a key component of overall ecosystem sustainability occurs belowground, recovery is tied to the soil's physical, chemical, and biological functions and processes. Depending on several fire severity measures, changes in belowground components can be either beneficial or deleterious to the entire ecosystem. Low-impact burning can promote a herbaceous flora, increase plant available nutrients, and thin overcrowded forests, all of which can foster healthy systems. Severe fires can often cause changes in successional rates, alter above- and belowground species composition, generate volatilization of nutrients and ash entrainment in smoke columns, produce rapid or decreased mineralization rates, alter C : N ratios, and result in subsequent nutrient losses through accelerated erosion, leaching or denitrification. In addition, changes in soil hydrologic functioning, degradation of soil physical properties, decreases in micro- and macrofauna, and alterations in microbial populations and associated processes can occur. The direct effect of fire on belowground systems is a result of the burning severity, which integrates aboveground fuel loading (live and dead), soil moisture and subsequent soil temperatures, and duration of the burn. The time for recovery of belowground systems will not only depend on the burning intensity and its effect on key ecosystem processes and components, but also on the previous land-use practices. Thus, the impacts of fire on belowground systems can be highly variable and may not be predictable. Our paper is a general review of the effects of fire on belowground systems with emphasis placed on the changes in physical, biogeochemical and biological properties of soils and the resulting consequences these changes have for ecosystem sustainability. Published by Elsevier Science B.V. All rights reserved.

Keywords: Fire; Soils; Physical properties; Microbial ecology; Nutrients; Organic matter

1. Introduction

1.1. Background

Belowground sustainability refers, in part, to meeting the vegetative demand for water and nutrients through root, biogeochemical, microbial and physical processes that regulate nutrient storage and flux and the soil's ability to hold water and nutrients. In brief, it means sustaining all the belowground processes, functions and organisms necessary to maintain aboveground ecosystem structure and function. The authors do not intend to specifically address basic concepts surrounding indicators of belowground sustainability, but rather focus on how fire affects specific

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PII: S0378-1127(99)00032-8

components of belowground systems that, in turn, may affect overall ecosystem sustainability.

Belowground systems are essential for the sustainability of all terrestrial ecosystems. This subsurface component of ecosystems harbors many of the fundamental processes and mechanisms underlying large-scale ecosystem behavior. Soils support critical processes such as hydrologic and biogeochemical cycling, and they contain a wide array of organisms ranging from bacteria, nematodes, fungi, cyanobacteria, etc., to earthworms, ants, termites, rodents, etc. They also provide a nutrient and hydrologic reservoir crucial for both below- and aboveground organism survival. Many soil processes help determine aboveground structure and function. Disruption of the belowground component may have immediate and long-lasting consequences to the whole ecosystem (Perry et al., 1989). Despite the overall importance of soils to the biosphere, limited research resources have been directed toward belowground studies that improve our understanding of the sustainability of these systems in the presence of natural or anthropogenic disturbances. One of the most common, but potentially devastating, perturbations on ecosystem dynamics is fire, both natural and anthropogenic. Our review discusses some of the major consequences of fire on belowground systems and the implications these impacts have on overall ecosystem sustainability.

Recent information indicates that the use of prescribed fire for land-management purposes and the incidence of wildfire have increased substantially in the past 15 years. Annual global biomass burning from grassland (42%), forest (18%), agricultural waste (23%), and fuelwood (17%) sources is currently estimated to consume around 8.7 billion Mg year^{-1} of fuel (Levine, 1991). The clearing and burning of partially- and fully-canopied forest and woodlands alone increased from 11.3 million ha year^{-1} in 1981 to 17.0 million ha year^{-1} in 1991 (Houghton et al., 1992). In 1991, ca. 8% of all cleared and burned forest lands in the world came from the Amazon Forest Basin of Brazil. This amount has been on a steady increase as fire is the primary site preparation tool used in these clearing activities. Although an area of 11–17 million ha represents a small percentage of the 4.1 billion ha of forest on the planet, cutting and burning presently going on in the tropical forests releases to the atmosphere twice the amount of carbon sequestered by mid- and high-latitude forests (Dixon et al., 1994). This has serious implications on sustainability.

1.2. Changes in natural weather patterns

Changes in weather patterns can often play an important role in fire frequency and intensity (see Section 1.3). For example, the prior strong El Niño period (1982–1983) produced severe droughts in Australia that resulted in extensive forest and grassland wildfires. During this same period, droughts occurred in southern and northern Africa, southern India, Indonesia, the Philippines, Mexico, Central America, and the Iberian Peninsula. This past El Niño (1997–1998) was the strongest in 150 years. Droughts and wildfires are reoccurring in the same regions that were affected in 1982–1983 (Glantz, 1996). In 1997, drought associated with the current El Niño and land clearing resulted in record levels of burning with nearly 5 million ha of forest and shrubland in Indonesia and Brazil alone (Associated Press, 1997). Recent reports from the Amazon basin indicate that fires there are occurring over a larger than normal area. Conversely, recent record rainfall totals in southwestern United States have translated into higher than normal primary productivity levels for most of the region. This has created a large fuel load, in terms of aboveground vegetation and increased surface organic matter (OM), that will no doubt result in greater fire frequency and intensity.

Other events that change weather patterns resulting in severe droughts are also common. Perhaps one of the best known examples is the Yellowstone Fire in 1988 which burned over 250 000 ha of the National Park due to prolonged drought and strong wind (Renkin and Despain, 1992). A natural fire program was established in that area in 1972 that allowed lightning-caused fires to burn themselves out without interference under prescribed conditions of weather and location. Given this policy, the resulting magnitude of that fire surprised many managers and research scientists.

1.3. Results of management practices

In some regions, vegetation and fire management has resulted in unintended consequences. Fire exclusion over the past 60 years in several areas of North American forests has resulted in large OM accumulations. As a result, when wildfires do occur, they tend to be larger and more severe. For example, the occurrence of fire in ponderosa pine (*Pinus ponderosa*) forests and pinyon–juniper woodlands in the southwestern United States decreased starting in the early 1880s. The extensive and prolonged overgrazing by sheep and cattle in this region resulted in a significant decline in the herbaceous biomass in interspace (inter-tree) areas (Kilgore, 1981). As a result, overgrazing and subsequent reduction or removal of fuel has been attributed to the decline in fire frequency and intensity. Natural, low-severity fires that occurred every 2–5 years in ponderosa pine forests (Dieterich, 1980) and every 10–30 years in pinyon–juniper (*P. edulis – Juniperus* spp.) woodlands (Wright et al., 1979) ceased primarily due to lack of adequate grass and or shrub cover. Subsequently, stand densities increased significantly.

Grazing and fire suppression in the southwestern USA decreased fire frequency (Swetnam, 1990). Between 1910 and 1990, the area (5-year smoothed average) burned annually in Arizona and New Mexico by wildfires oscillated between 2000 and 22 000 ha as woody biomass fuels increased (Fig. 1). These forest and woodland ecosystems reached a critical level in 1991. Each subsequent year, through 1996, resulted in a logarithmic increase in area burned so that the 5-year running average reached nearly 75 000 ha in 1996 with the actual 1996 wildfire-burned area exceeding 100 000 ha (personal communication, USDA Forest Service, Southwest Region, Aviation and Fire Management staff).

Ecosystem management and restoration ecology have resulted in a reconsideration of the role of fire in western forest, shrub, and grassland management. In contrast to the fire suppression paradigm of the past 50 years, more land managers are now reintroducing fire, as a natural process, into these ecosystems. This practice is being widely used in many areas, particularly in urban interfaces. However, some conflicts exist between fire management goals and other resource management, such as air quality. For example, in the USA, new Environmental Protection Agency standards for particulates and pollutant levels may hamper fire management efforts to reduce fuel loadings in these urban zones, as prescribed fires have been known to cause air-quality levels to be in the unhealthful range. In addition, recent congressional hearings in Washington, D.C., are investigating the usefulness of burning for forest sustainability, and the use of alternate management practices. Although this issue is under serious debate in the USA, the reintro-

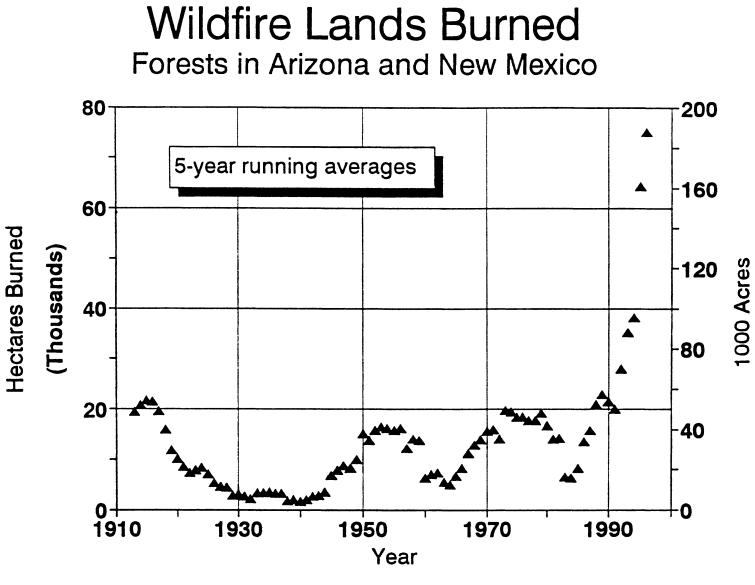

Fig. 1. Forest area burned in Arizona and New Mexico, USA, 1910–1996.

duction of fire has been approved in other countries. For example, Sweden is currently incorporating into its Code of Practices for forestry the requirement to reintroduce burning onto 5% of all forest lands annually to improve biological diversity and maintain ecosystem sustainability.

In contrast to fire suppression activities, frequent or seasonal fires, as a management tool, have been shown to have inconclusive results. Although some have suggested that repeated use of fire increases nutrient availability (Woodmansee and Wallach, 1981), others state that this practice can cause long-term cumulative negative effects on critical ecosystem processes. Frequent or regular burning can decrease surface OM and soil OM, alter C allocations in plants, reduced nitrogen (N) mineralization rates, decrease total N, change species composition of above- and belowground, and alter plant succession and evapotranspiration rates (Biederback et al., 1980; Blair, 1997; Daubenmire, 1968; Ojima et al., 1994; Towne and Owensby, 1984). Specific links between altered belowground processes following fire to aboveground processes can have positive feedbacks to the entire system. For example, decreases in plant available soil nutrient concentrations and nutrient cycling processes resulting from frequent burning can affect litter quality inputs to soil (Blair, 1997; Monleon and Cromack, 1996; Ojima et al., 1994). The widening of C : N ratios of above- and belowground inputs and subsequent increases in microbial immobilization of N can have significant long-term consequences on ecosystems.

2. Fire severity spectrum

Fire produces a spectrum of severities that depends on the interactions of burning, intensity, duration, fuel loading (i.e. live and dead materials), combustion type and degree of oxidation, vegetation type, fire climate, slope, topography, soil texture and moisture, soil OM content, time since last burned, and area burned. Severity is a qualitative measure of the effects of fire on soil and site resources that control ecosystem sustainability (Hartford and Frandsen, 1992). The impact on, and response of, forest, shrub, and grassland ecosystems can occur on a spectrum from high to low or can be seen as a chaotic matrix or patchwork, having areas of high and low impacts. Our ability to describe or predict impacts of fire on ecosystem sustainability is often confounded by inconsistent scientific data. Information is usually obtained over a limited range of fire severities and/or ecosystem types. Data of key biological, physical and chemical processes that control ecosystem sustainability may not be collected or monitored following a fire.

Fire intensity is an integral part of fire severity in that it refers to the rate at which a fire is producing thermal energy in the fuel-climate environment where it occurs (DeBano et al., 1998). It can be measured in terms of temperature, and heat release. Temperatures can range from 50° to >1500°C, and heat release can be as little as 2110 J kg^{-1} of fuel to as high as 2.1 million J kg^{-1}. Rates of spread can vary from 0.5 m $week^{-1}$ in smoldering peat fires to as much as 7 km h^{-1} in large, flaming wildfires. The intensity produced by any fire is an integration of the fuel conditions and climatic conditions that precede ignition. Fuel loading, referring to the aboveground plant biomass and the OM buildup, range from <1 Mg ha^{-1} in grasslands to >400 Mg ha^{-1} in woodland and forest stands. Size and moisture of live and dead fuel and volatile components in the fuels play a prominent role in the rate at which fires release thermal energy. Fire severity is determined by the interactions of climate conditions such as temperature, relative humidity, antecedent rainfall, and wind that affect the combustion process. Other conditions such as slope, topography, altitude, soils, and fire size may further augment the impacts of fire.

The component of fire severity that results in the greatest belowground damage to ecosystems, and hence recovery, is duration of the fire. Fast-moving fires in fine fuels, such as grass, may be intense in terms of energy release per unit area, but do not transfer the same amounts of heat to the forest floor, mineral soil or soil organisms as do slow-moving fires in moderate to heavy fuels. As discussed below, the impacts of slow-moving, low- or high-intensity fires on the belowground systems are much more severe and complex and, hence, are not as easily envisioned as they are aboveground. This makes restoration of belowground systems much more difficult.

Belowground systems are critical to the functioning of hydrological processes. On a watershed basis, possible sediment increases and water yield responses to prescribed and wildfires are often a function of fire severity and the occurrence of hydrologic events. When examining a wide range of fire severities, impacts on hydrology and sediment loss can be minimal in the absence of an immediate precipitation event. However, when a precipitation event occurs following large, moderate-to-high-severity fire, impacts can be far-reaching. For example, increased runoff, peak flows, and sediment delivery to streams can impact fish populations (Rinne, 1997). But, this concept, while workable for watershed or smaller scale soil erosion effects, does not capture other fire-induced changes in belowground systems that – when summed together – determine fire effects on ecosystem sustainability. For example, removal of partially burned OM or ash due to erosion can affect nutrient turnover and rates in soils, decomposer populations, alter stream chemistry and biological activity.

3. Soil heating

3.1. Combustion processes

Fire is the visual manifestation of the physicochemical process known as combustion. There must be a source of chemical energy (biomass fuel), thermal energy (heat from an ignition source), and oxygen (O_2) for the combustion reaction to occur. Fires typically have five phases: pre-ignition, flaming combustion, smoldering combustion, glowing combustion, and extinction (DeBano et al., 1998). Pre-ignition consists of fuel heating and thermally induced chemical decomposition of fuels. The combustion phases involve the release of solar energy stored in a chemical form in biomass fuels as heat, a variety of gases (e.g. CO_2, CO, H_2O, flammable organics, elements, etc), and particulate matter (Pyne et al., 1996). Although all three phases of combustion by-products result in impacts on belowground sustainability, the transfer of heat to the organic and mineral horizons of the soil produces the most profound impacts on the physical, chemical, and biological processes involved in sustainability.

Next to smoke, flaming combustion is the most visible aspect of fire. Although this rapid exothermic reaction can produce temperatures in the range of 300° to 1400°C, the masses of burning gases we see as flames may be highly transient in any given spot, running with the winds that feed O_2 into the fire (Pyne et al., 1996; DeBano et al., 1998). The duration of flaming combustion and transfer of heat is highly variable, and so are its effects on soils. Smoldering combustion normally follows flaming and is characterized by decreased rate of spread, temperature, and heat flux. In some fuels, such as thick litter and duff accumulations and organic soils, smoldering is the initial and dominant phase of combustion. Although smoldering temperatures of ground fires are lower than flaming combustion (300–600°C), the slow movement of this type of fire (<3 cm h^{-1}) affects a smaller area but can have more profound soil impacts. The final combustion phase of a fire is glowing combustion. It is a very slow oxidation of char residues left over from the flaming and smoldering phases. This type of combustion can persist for long periods of time in both organic and mineral soils, and still produces temperatures in the 400–760°C range.

3.2. Heat-transfer processes

Heat is transferred from burning fuels to the organic and mineral layers of soils by the processes of radiation, convection, conduction, mass transport, and vaporization/condensation (Chandler et al., 1983). Radiation is the transfer of heat via electromagnetic wave motion. It is the major mechanism for heat transfer at the initiation of vegetation fires and in calm air. Radiation and convection are responsible for most heat transfer from light fuels (e.g. grass, foliage, branches) and to the soil. Convection is the process of heat transfer from one location to another by the mixing of air masses. It is the cause of aggressive and explosive fire behavior. Heat transfer by conduction occurs from physical contact between a heat source and fuel or mineral body. It is the major heat-transfer mechanism in heavy fuels like duff, organic soils, and slash piles. Mass transport occurs when firebrands or other burning fuels are spotted ahead of a fire by convective air columns or rolled down steep slopes by gravity. This heat-transfer process affects fire spread and does not play much of a role in soil heating. Vaporization and condensation play an important role in rapid heat movement into soils. These processes involve phase changes of water and organic compounds distilled by the combustion process. Liquid water requires 560 $\mathrm{cal}^{-1}\ \mathrm{g}^{-1}{}^{\circ}\mathrm{C}^{-1}$ to raise its temperature to the vaporization point. Water moves much faster through soil pores as a vapor, and releases the same amount of heat when condensation occurs, thereby raising soil temperature.

Heat transfer from vegetation or OM combustion is a function of a complex number of variables. These include fuel characteristics (e.g. loading, size, arrangement, moisture content, etc.), weather conditions (e.g. temperature, wind, humidity, etc.), and fire behavior (e.g. rate of spread, flame length, intensity, duration, etc.). In general, surface organic layers and dry soil conditions retard soil heating, whereas bare mineral-soil surfaces, which are somewhat wet, can be heat rapidly. It is difficult to characterize heat transfer within individual fires and between different fires because of the enormous variability of combustion and soil conditions. Mathematical models have been developed to begin to address this problem (Aston and Gill, 1976).

3.3. Temperatures

Soil temperatures reflect both, the diurnal and seasonal variations of the climates in which they form. Soil organisms and their ecological processes, in turn, reflect the thermal and hydrological regimes of the soils they inhabit. The largest and significant effect of fires in forest, shrub, and grass ecosystems is the transfer of heat from burning biomass to the soil system (DeBano et al., 1998). The quantity and duration of this heat transfer determines the severity of impact to the physical soil system, its chemical constituents, and biological components.

During forests fires, maximum ground temperatures are typically in the range of 200° to 300°C (Fig. 2; Rundel, 1983). In heavy fuels like slash, where loadings can reach >400 Mg ha^{-1}, soil surface maximum temperatures are usually around 500–700°C, but instantaneous temperatures in excess of 1500°C can occur (Dunn and DeBano, 1977). Fire-prone shrubland vegetation types commonly burn at lower temperatures, but have a wider range (Woodmansee and Wallach, 1981; Rundel, 1983; DeBano et al., 1998). On the other end of the fuel spectrum, fires in grasslands with fuel loadings of <1 Mg ha^{-1} usually have ground-level temperatures of <225°C although higher instantaneous temperatures have been measured (Raison, 1979).

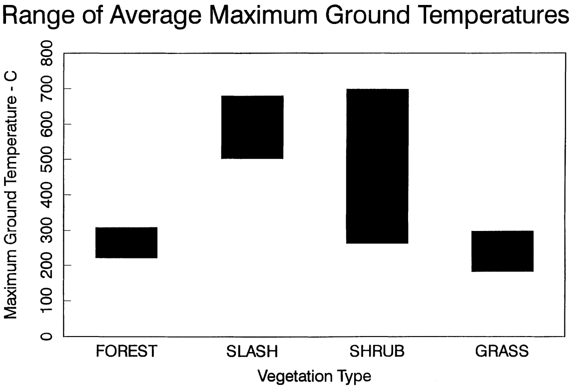

Fig. 2. Maximum ground temperatures during fires in forest, shrubland, and grassland ecosystems (Adapted from Rundel, 1983).

Biological disruptions begin in the 40–70°C range with protein degradation and plant tissue death (Table 1). At soil temperatures of 48–54°C, roots can desiccate or are killed, and seed mortality occurs in the 70–90°C range. Depending on the microbe, mortality generally occurs between temperatures in the 50–121°C range with fungi usually less resistant to thermal effects than bacteria. Burning under wet and dry conditions can have varying effects on soil microflora. For example, Klopatek et al. (1990) showed that 90 days following a burn, soil microbial biomass was lower when burned under wet than under dry conditions. This trend was also seen for VAM populations (Klopatek, 1987). In contrast, nitrifier populations in the same experiment were more affected by burning

Table 1
Threshold temperatures for biological disruptions in soils (adapted from DeBano et al., 1998)

Biological component threshold	Temperature (°C)	Reference
Plant roots	48	Hare, 1961
Small mammals	49	Lyon et al., 1978
Protein coagulation	60	Precht et al., 1973
Fungi – wet soil	60	Dunn et al., 1985
Seeds – wet soil	70	Martin et al., 1975
Fungi – dry soil	80	Dunn et al., 1985
Nitrosomonas spp. – wet soil	80	Dunn and DeBano, 1977
Nitrosomonas spp. – dry soil	90	Dunn and DeBano, 1977
Seeds – dry soil	90	Martin et al., 1975
VA mycorrhizae	94	Klopatek et al., 1988

under dry than under wet conditions (Klopatek et al., 1990).

Physico-chemical disruptions occur at much higher temperatures than biological ones. Organic matter distillation normally starts in the 200–315°C range. However, substantial OM matter loss can occur at lower temperatures (DeBano et al., 1998). Litter scorch and distillation of volatile organic compounds occurs at temperatures up to 180–200°C. Nutrient volatilization (particularly N) begins when temperatures climb to 200–400°C. In the 180–300°C range, destructive distillation and combustion of about 85% of the litter layer occurs. At temperatures >300°C, the entire surface organic horizon of the soil is usually consumed. Nearly all OM is consumed in regions of the soil heated to 450°C.

Temperature profiles in the organic horizons and the mineral soil depend on the intensity of the fire, fuel loads, duration of the burning, and antecedent soil moisture (Hartford and Frandsen, 1992; Hungerford et al., 1995). With low-severity soil heating, mineral soil temperatures typically do not exceed 100°C at the surface and 50°C at 5 cm depth (Agee, 1973). Hot fires in thick organic horizons (litter and duff), such as those currently found in some ponderosa pine stands in the southwestern USA, can raise soil surface temperatures to 275°C (Sackett and Haase, 1992). However, where severe soil heating occurs (e.g. underneath slash accumulations, slow-moving fires, etc), temperatures can be nearly 700°C at the soil surface, yet can reach temperatures >250°C at a depth of 10 cm, and exceed 100°C as far as 22 cm belowground surface. The result is mortality to soil organisms, plant roots, alteration of physical properties, changes in nutrient cycling patterns and nutrient volatilization (Fig. 3; Roberts, 1965). Soil temperatures can remain elevated from a few minutes to an hour in cool prescribed fires to over five days during severe fires. If the entire organic horizon is consumed, surface mineral soil temperature can remain elevated above normal levels for months or years due to direct solar radiation heating on exposed soil.

Differences in microclimates between newly burned and unburned canopy-covered areas can be substantial (Pickett and White, 1985; Woodmansee and Wallach, 1981). Christensen and Muller (1975) showed that surface soil temperatures in newly burned areas exceeded 70°C. This heating is a result of:

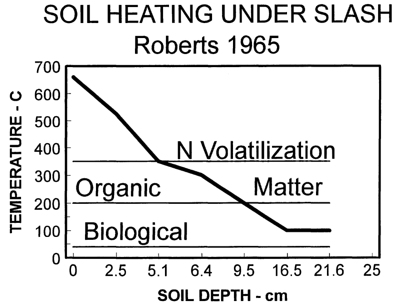

Fig. 3. Soil heating under slash piles (Adapted from Roberts, 1965).

1. removal of overstory, allowing direct insolation to the soil surface; and
2. blackening of soil surfaces due to incomplete combustion of organic material, producing additional heat absorption.

These surface temperature increases have implications on seedling establishment, nutrient cycling, water relations and microbial community structure.

4. Belowground ecosystem structure, functions, and processes

The cumulative impacts of fires on belowground sustainability arise from changes in above- and belowground structure, functions and processes. For example, changes or removal of aboveground structure can directly affect belowground systems by:

1. altering nutrient inputs that in turn, affect soil and litter macro- and microflora and fauna;
2. increasing surface soil temperatures as a result of increased solar heating; and
3. changing evapotranspiration rates due to losses in vegetation that in turn, alter soil moisture availability, etc.

Thus, there are a multitude of interactions between above- and belowground systems following fire. In this section, we choose only a subset of key belowground components, which have direct linkages to the aboveground, that may be altered as a result of fire. These components are divided under physical, chemical, and biological properties and processes.

Cumulative negative impacts that occur belowground as a result of fire manifest themselves in changes or breakdown in soil structure, reduced moisture retention and capacity, development of water repellency, changes in nutrient cycling rates and fluxes, atmospheric losses of elements, off-site erosional losses, loss of forest floor, reduction or loss of soil OM, alterations or loss of microbial species and population dynamics, reduction or loss of invertebrates, and partial elimination (through decomposition) of plant roots. Although the most serious and widespread impacts on belowground sustainability occur with stand-replacing wildfires, prescribed fires started for planting site preparation, site conversion, and fuel reduction purposes can produce localized problems.

4.1. Soil physical characteristics

The physical nature and processes of soils have direct effects on productivity and the sustainability of any ecosystem (Pickett and White, 1985; Childs et al., 1989). Properties such as structure, porosity, infiltration, thermal regime, and water storage are key factors in sustainability, and can be profoundly affected by disturbances such as fire (Powers et al., 1990).

In most soils, primary soil particles (e.g. sand, silt, clay) are aggregated together into structural units under the influence of OM and clay minerals. Some soils remain structureless as loose accumulations of sand grains or massive deposits of clay minerals. Organic matter is more crucial to the formation of structure in the surface A horizon. Clay minerals and soil solution cation contents have the dominant role in structure development in the deeper horizons. Structure is an important determinant of proper hydrologic functioning in soils. Well-structured soils provide the macropore spaces needed for water movement and storage and root growth (Neary et al., 1990; Paul and Clark, 1989). Water that infiltrates the soil is not only available for plants, but for microbial and micro- and macrofauna use, sustains the baseflow of streams, and generally does not produce erosion of the soil surface.

Soil structure can be affected by fire through alteration of clay minerals and OM combustion. Clay minerals are usually not altered to any great extent during a fire because of their low content in surface soil horizons, and the high temperatures needed to produce a loss of OH groups (>460°C; Giovannini et al., 1988) or irreversible changes in water of hydration (>980°C; DeBano et al., 1977). The abundant OM that contributes to surface soil structure and porosity is profoundly affected by fires (see Section 3.3). Soil-structure degradation can persist from a year to decades, depending on the severity of the fire and post-fire ecosystem conditions. Cold and arid climates have the most problems with persistent soil structure deterioration following fire (DeBano et al., 1998). When soil structure degrades, the macropores (>0.6 mm diameter) responsible for water infiltration become limiting, and surface runoff increases.

When fire consumes vegetation and underlying litter layers that mitigate the impact of rainfall on the soil, bare soil surfaces can seal off under the impact of raindrops, resulting in much higher rates of surface runoff. The net effect is a reduction in soil-moisture contents, erosion of nutrient-rich ash and A horizon sediments, and ultimately watershed drying. Apart from the physical removal of nutrients in runoff (discussed in a following section), the drying of soils diminishes the ability of recovering and recolonizing of microbes that are involved in biogeochemical cycling. Desiccation of soil can also create a negative feedback on nutrient cycling by inhibiting recolonization of plants that stabilize soils, resulting in increased surface erosion of nutrient-rich sediments.

Another physical response to fire in soils that is linked to the processes discussed above is water repellency (DeBano, 1981). This condition can be found in the presence of high-intensity fires and certain litter types. Water repellency develops as a discreet layer of soil parallel to the surface where hydrophobic organic compounds coat soil aggregates or minerals. It is formed when soil temperatures rise above 176°C and destroyed at temperatures >288°C (DeBano, 1981; DeBano et al., 1976). When soils are in this condition, water is prevented from wetting aggregates and infiltration declines greatly. In flat terrain, water repellency just contributes to soil desiccation, but in steep terrains it can significantly accelerate erosion. It produces both, long-term (mass wasting, soil erosion, site degradation, etc.) and short-term effects (increased runoff, ash and soil transport, etc.) that affect nutrient cycling processes. On a large-area basis, nutrients lost in mass wasting and surface erosion due to water repellency may only be 10% of the total plant-litter-soil losses (DeBano and Conrad, 1978). However, areas stripped of their upper soil layers become depauperized of available nutrients and result in severe sites for re-establishing a plant community. Hence, soil properties such as infiltration rate, porosity, conductivity, and storage capacity that lead to good hydrologic functioning can be adversely affected by fire. Deterioration of hydrologic functioning can quickly lead to decreases in ecosystem sustainability.

4.2. Impacts on organic matter and nutrients

The organic horizon is a critical component of ecosystem sustainability in that it provides a protective soil cover that mitigates erosion, aids in regulating soil temperature, provides habitat and substrates for soil biota and can be the major source of readily mineralizable nutrients. Many arid and semiarid systems have most of their organic inputs from belowground sources. The organic horizon contains newly fallen and partially decomposed plant, animal and microbial residues which is made up of readily decomposable materials such as cellulose, slow to decompose material (e.g. holo-celluloses) and recalcitrant humic materials (e.g. lignins) (McColl and Gressel, 1995). Organic matter input from above- and belowground can significantly affect the nutrient pools and storage in soils, and is the major factor controlling total cation exchange capacity (organic and clay mineral).

Tiedemann (1987) contrasted aboveground and belowground biomass, litter, and N on a shrub-grass-forb to sagebrush-grass to pinyon–juniper ecotone in the semi-arid intermountain region of western USA. Across this gradient, the amount of litter increased from 3.0 to 100.0 Mg ha^{-1}, and the percent of ecosystem N tied up in litter increased from <0.1% to 12.4% (Table 2). Conant et al. (1998) showed that C pools and storage significantly increased across a gradient from Great Basin shrub lands, through pinyon–juniper up to ponderosa pine in northern Arizona. But, they also found that aboveground litter inputs in the pinyon–juniper system were 33% greater than ponderosa pine and 95% greater than in the shrubland community. In a companion study, Murphy et al. (1998) showed that the amount of N tied-up in litter did not increase proportionally up the gradient, with juniper (*Juniperus monosperma*) having the greatest N concentrations, followed by ponderosa pine, snakeweed (*Gutierrezia sarothrae*), pinyon pine and blue grama grass (*Bouteloua gracilis*).

These differences in the above-mentioned examples emphasize the need to examine not only total organic C pools, but amount and source of organic inputs to systems, litter quality (in terms of C quality and N concentrations), decomposition rates and various climate forcing factors when assessing C dynamics (Klopatek et al., 1995; Waring and Schlesinger, 1985). Since temperature and moisture regulate many ecosystem functions, such as microbial activity and nutrient storage, they are the most critical driving forces in ecosystems (Swift et al., 1979). Klopatek et al. (1995) and later Murphy et al. (1998) showed that, for three semi-arid ecosystem types, N is not a driving factor for decomposition, unlike more mesic systems (Meentemeyer, 1978; Aber and Melillo, 1982). Rather, moisture availability and C quality of the litter play a much greater role in controlling decomposition. Thus, most semi-arid ecosystems are complex not only due to their overall decomposition processes and drivers, but their unique spatial patterning (Klopatek et al., 1998), low water availability, and

Table 2
Distribution of biomass and percentage of N capital contained in biomass, litter, and soil components of three semi-arid ecosystems in the Intermountain USA (Adapted from Tiedemann, 1987)

Ecosystem	Biomass (Mg ha^{-1})		Nitrogen capital (N%)		
			Aboveground		Belowground
	Plants	Litter	Plants	Litter	Soil
Shrub-grass–forb	0.6	3.0	0.1	<0.1	99.8
Sagebrush–grass	12.0	5.4	2.6	0.2	97.2
Pinyon pine–juniper	97.4	100.0	5.3	12.4	82.3

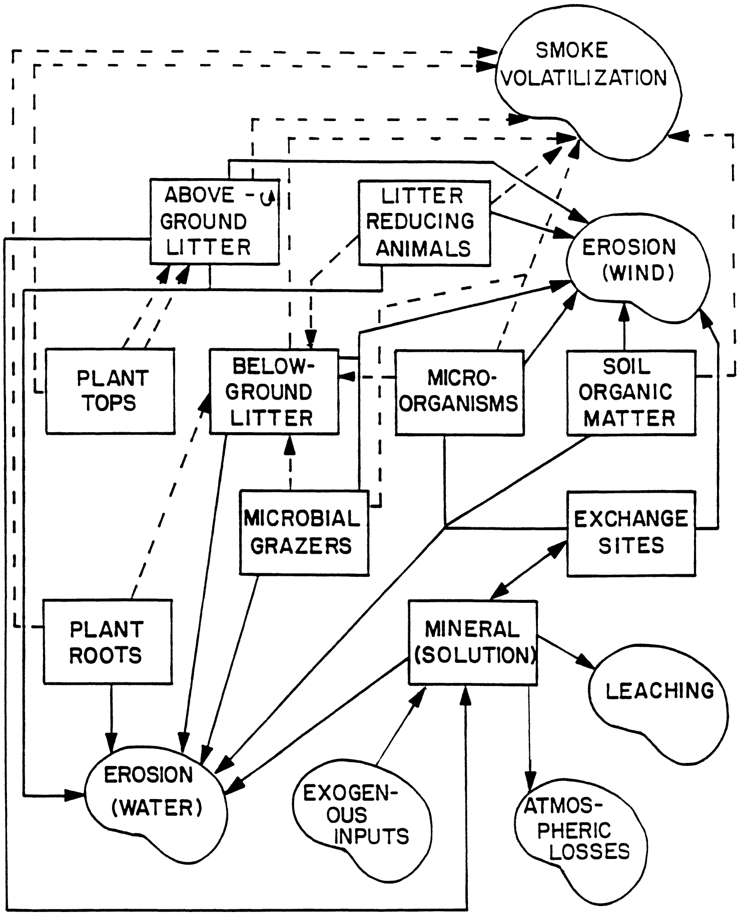

Fig. 4. Nitrogen flux pathways in an ecosystem affected by fire (Adapted from Woodmansee and Wallach, 1981)

past land-use and management practices and intensities.

One of the best studied and understood nutrient cycling pathways is N since it is a critical component to all living organisms. This cycle is unique in that it is predominantly controlled by microorganisms. Fig. 4 is a generalized diagram showing the major N fluxes and storage in an undisturbed forest ecosystem. In semi-arid ecosystems, the proportion of the ecosystem N pool reported in litter ranges from <0.1% sagebrush (*Artemisia rigida – Stipa occidentalis*) to 1.24% in pinyon–juniper communities (DeBano and Conrad, 1978; Klopatek et al., 1995; Tiedemann, 1987). In boreal forest ecosystems, the percentage of ecosystem N contained in the forest floor is in the range of 7.8% jack pine (*P. banksiana*) to 72.4% black spruce (*Picea mariana*) (Morris and Miller, 1994). Temperate forest ecosystems have variable proportions of ecosystem N in their litter (*Quercus* spp. – 0.7%, *Tsuga* spp./*Picea* spp. – 0.7%, *Fagus* spp. – 2.5%, *Pseudotsuga menziesii* – 5.2–18.5%, *P. taeda* – 6.3%, and *P. elliottii* – 8.1%) (Van Lear et al., 1990; Morris and Miller, 1994). Tropical forest ecosystems tend to have higher proportions of their N pools in litter (*Celtis* spp. – 7.7%, and *Cordia – Mimosa* spp. 13.3% (Kaufmann et al., 1993; Morris and Miller, 1994) and aboveground biomass.

As mentioned earlier, fire can alter soil physical properties (e.g. clay minerals), but one of the most important impacts on belowground systems is on combustion of OM. Analysis of aboveground/belowground allocation of organic C pools provides a means

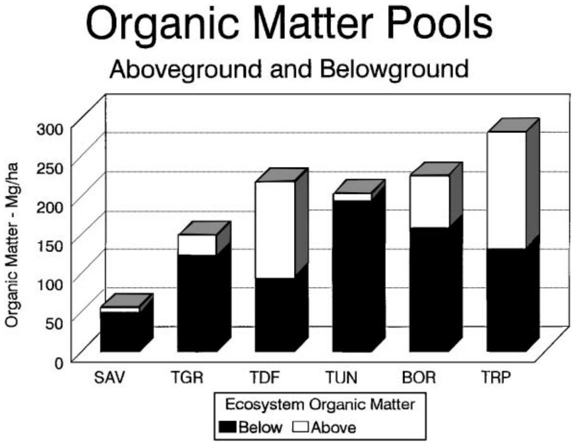

Fig. 5. Aboveground and belowground organic matter pools in savanna (SAV), temperate grassland (TGR), temperate deciduous forest (TDF), tundra (TUN), boreal forest (BOR), and tropical forest (TRP) ecosystems (Adapted from Anderson, 1991).

of assessing ecosystem risks for fire disruption. Ecosystems with greater proportions of OM reserves belowground may be less susceptible to fire-related nutrient losses and sustainability declines (Fig. 5; Anderson, 1991). Humid tropical forest are the most sensitive to fire-related nutrient losses, since only 45% of their C pool is belowground. Grasslands and savanna are the most fire-adapted ecosystems, with 83–85% of their C belowground. This rationale, of course, is subject to the fire severity and intensity.

Depending on the fire intensity, the dryness of the surface OM and underlying soil, thickness of the organic layer itself, consumption of organics can range from scorching (producing black ash) to complete ashing (producing white ash) (Table 3). Nutrients that reside in the remaining organic material can be further lost through biological and nonbiological processes (see below). Campbell et al. (1977) described the effects of moderate and severe fire severities within a ponderosa pine wildfire on the Mogollon Rim of Arizona. They found that the moderately burned areas maintained 38% of the vegetative and litter cover while the severely burned areas had 0–23% vegetation and litter, respectively. Although generally not severe, prescribed fires can also significantly decrease surface organic material from 21% to 80% (Pase and Lindenmuth, 1971; Covington and Sackett, 1992). Personal observations by the authors (Klopatek, C.C. and D.G. Neary, personal communication) found that litter losses in pinyon–juniper woodlands and ponderosa pine forests of Arizona following catastrophic stand replacing fires ranged from 75% to complete loss of organic material.

Table 3
Comparison of fire severity classes for temperature, organic matter (OM), microorganisms, and roots in soils under chaparral (adapted from DeBano et al., 1977)

Parameter	Light	Fire severity Moderate	High
Surface temperature	250°C	400°C	675°C
Temperature – 25 mm	100°C	175°C	190°C
Temperature – 50 mm	<50°C	50°C	75°C
Surface litter, OM [a]	partially scorched	mostly consumed	totally consumed
Soil OM – 25 mm	OM distillation start	partially scorched	consumed/scorched
Soil OM – 50 mm	not affected	OM distillation start	OM distillation start
Surface roots	dead	dead	dead
Roots – 25 mm	dead	dead	dead
Roots – 50 mm	live	live	dead
Surface microbes	dead	dead	dead
Microbes – 25 mm	live	selective die-off	dead
Microbes – 50 mm	live	selective die-off	selective die-off
Surface nutrient Vol [b]	N	N, organic P	N, K, P, S
Nutrient Vol [b] – 25 mm	none	none	none
Nutrient Vol [b] – 50 mm	none	none	none

[a] Organic matter.
[b] Volatilization.

Nutrient losses from the litter layer and surface soil during fires is a function of fire severity. The key pathways during, and immediately following, fires are ash convection, volatilization, mineralization, erosion, runoff and leaching. Nutrient-rich ash materials remaining after a fire can be removed off-site or redistributed within a burned area by convection in a smoke column or surface wind transport. These processes account for a small portion of atmosphere-related nutrient losses during, and immediately after, small, low-intensity fires, but are a more important consideration after large wildfires and in windy regions. For low-intensity eucalyptus (*Eucalyptus* spp.) fires, ash lost in convective smoke plumes can amount to 1–4% of the mass of the burned fuel (Raison et al., 1985a). With higher intensity fires, they found ash losses in convective columns can exceed 11%. Data on nutrient losses in wind-borne ash after fires are very scarce, but losses are estimated to be low because of the relatively low mass transport of soil and ash in wind from most burned areas.

Direct loss of nutrients to the atmosphere is temperature dependent. Nitrogen is the element most prone to this type of loss as it starts to volatilize at 200°C. At temperatures >500°C, over half the N in OM can be volatilized. Higher temperatures are needed to vaporize potassium (K – >760°C), phosphorus (P – >774°C), sulfur (S – >800°C), sodium (Na – >880°C), magnesium (Mg – >1107°C) and calcium (Ca – >1240°C) (Weast, 1988).

Combustion of large woody debris and other surface organic materials produces the most significant volatilization losses of nutrients and has significant effects on biogeochemical cycles. Harwood and Jackson (1975) reported nutrient losses to the atmosphere from low-intensity slash burning of 10–17% of total nutrients (P, K, Ca, and Mg) in eucalyptus fuels. Raison et al. (1985b) measured higher, non-particulate elemental transfers to the atmosphere from low-intensity eucalyptus slash burning of 54–75% (N), 37–50% (P), 43–66% (K), 31–34% (Ca), 25–49% (Mg), 25–43% (manganese – Mn), and 35–54% (boron – B). Grier (1975) documented nutrient losses to the atmosphere through volatilization and ash convection from the Entiat wildfire in Washington State, USA (mixed conifer forest). Although most of the N loss (39%) was through volatilization, much of the monovalent cation losses (35% for K and 83% for Na) could have also been through volatilization due to the high fire intensity. DeBano and Conrad (1978) measured N and P changes in the litter layer after a prescribed fire in California chaparral. While the N loss from litter totaled 5% of the pre-burn litter N, the P pool in litter increased 43% due to the accretion of ash from the burned vegetation. For the system as a whole, the N loss was 10% (half coming from the litter), and the P loss was 2% (mainly from reductions in soil P in the top 2 cm) (DeBano et al., 1979).

Biogeochemical processes in the mineral soil may also change as a result of burning and are the most pronounced when burning is of high intensity. Carbon (as stated above) and N, are perhaps the key nutrients affected by burning. The significance of these changes is directly tied to the net primary productivity (NPP) of a given ecosystem. For example, in a low-to-moderate intensity fire, a given change in N capital of a highly productive system (Ah to Bh in Fig. 6) does not significantly affect productivity (Dh) following burning. This assumes that the available N does not become immobilized or mineralized above or below the normal rate. Nevertheless, similar change in N capital (Al to Bl) in a nutrient stressed system will result in a much greater change in productivity (Dl in Fig. 6). This assumes that fire may result in further alterations of C and N cycling in systems that are already stressed. Thus, N capital and productivity of systems may be used as predictive measures of potential post-fire ecosystem recovery.

The effect of burning on soil N presents an interesting paradox that has been vigorously debated for

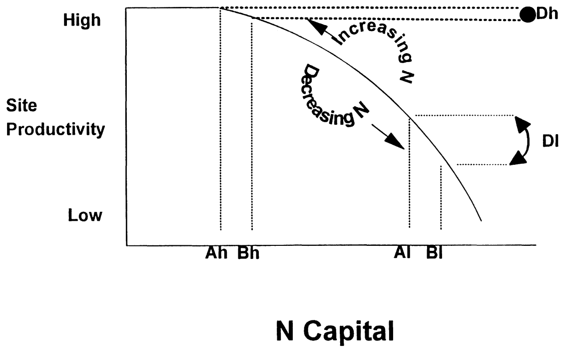

Fig. 6. Changes in site productivity in high-nitrogen and low-nitrogen ecosystems with equal reductions in nitrogen capital (Adapted from DeBano et al., 1998).

years (Knight, 1966; McKee, 1982). As opposed to N losses to the atmosphere, soil N can be made more available following low-intensity burning by non-biological and biological means, converting organic forms to inorganic ammonium nitrogen (NH_4–N) and nitrate nitrogen (NO_3–N) (Hungerford et al., 1995; Pickett and White, 1985) (Fig. 4). On the other hand, Klopatek et al. (1990) found that burning in a microcosm experiment caused significant losses in N in pinyon and juniper litter and soil compared to interspaces which contained very little litter and no duff. This was later verified with an in situ, stand replacing fire that occurred in the same area in which the soils from the 1990 study were collected (Klopatek et al., 1994). High-intensity fires can cause large losses of N directly through consumption or NH_4 volatilization (see Section 4.3 for further details on N cycling and losses through biologic processes). Furthermore, NO_3, that was converted following fire can be lost through denitrification, leaching or overland flow.

The main pool for P, a critical plant nutrient, is in the soil (94–98%) and not in the litter. Severe burning of vegetation and litter does not necessarily have the same potential impact on P pools as on N. However, organic forms of P in the litter are more readily available to plants. Thus, the impact of complete litter combustion on P cycling can be more severe than that indicated by the size of the individual nutrient pools. Also, P in soils with high Ca levels can be complexed into non-available forms which have detrimental consequences for ecosystem productivity. Since the cycling of P is primarily through the organic-P pools, removal of vegetation, all at the same time, by burning results in depletion of the aboveground P pool at a rate greater than mineral weathering can replace P (DeBano and Klopatek, 1987).

Recovery of soil-nutrient levels can be fairly slow in some ecosystems, particularly those with limited N and in semi-arid regions like the southwestern USA and northern Mexico, where decomposition rates are slow. Klopatek (1987) determined that N and P concentrations beneath pinyon–juniper canopies, 35 years after a wildfire, had not recovered to levels found in stands that had not burned in 300 years. In addition, when contrasting soils beneath burned and unburned stands, two-fold differences were noted in the percent of total N that was mineralized. This difference indicates that mineralization and nitrification may be enhanced by fire disturbance.

4.3. Microbes

Regulation of nutrient availability to vegetation is a property resulting from actions of soil biota on substrate quality and quantity. Sustainability, in the general sense, depends upon synchrony between vegetation demand and the microbial processes regulating the storage and flux of nutrients. Nutrient storage depends not only on immediate actions of biota, but upon their past activities. One sees interesting plant–mycorrhizae–nutrient interactions, with linkages being made across genera and families of plants by mycorrhizal hyphal bridges (Read et al., 1985). Soil detrital food web studies are new to science, but some initial progress has been made with these taxonomically complex interactions (Moore and de Ruiter, 1991). The structure of the soil, its capacity to hold water and nutrients, and indeed to sustain life, is the result of long years of activity by soil biota.

Although the importance of microbes in fundamental ecosystem processes is well known, the role belowground diversity plays in maintaining ecosystem sustainability is not so well understood. Belowground biologic diversity may be described as an integration of physical and biological variables across all scales – from genetic, species, ecosystem and landscapes (Solbrig, 1991). At present, it is difficult to assess the biological diversity of soil organisms. Traditional soil biological diversity surveys that estimated biomass or population size tended to assign soil organisms to general categories such as ‘bacteria’, ‘fungi’, ‘microarthropods’, ‘macroarthropods’, etc. There is a lack of information on the numbers and subsequent identification of soil organisms. For example, it has been estimated that fewer than 1% of all bacteria living in soil or water have been identified, compared to 3% of nematodes and 13% of insects (Edwards and Walton, 1992). Furthermore, populations of soil organisms are dynamic; numbers as well as species composition often change on several scales, both in time and space–just within one ecosystem (Moore and de Ruiter, 1991).

In view of the aforementioned uncertainties, the short- and long-term effect of fire on belowground microorganisms, and the resulting effect on ecosystem sustainability, is uncertain and often debatable. There are studies that demonstrate that fire can affect soil microorganism populations and species composition depending on the intensity of the fire, maximum temperatures, soil-water content, duration of heating, and depth of heating (e.g. Hungerford et al., 1995). Site conditions (fuel loadings, aspect, elevation, etc.) and pre- and post-fire weather conditions are important since they can influence the nature of the fire and site recovery. Klopatek et al. (1990) found that after 90 days following burning, microbial N biomass was greater in burned rather than in pre-burn pinyon–juniper woodland soils. They found that as time elapsed, microbial N biomass decreased significantly below pre-burning conditions. Microorganism responses within, and between, fires on any given site, and between sites, will fall along a continuum determined by the factors mentioned here (DeBano et al., 1995). Low-intensity, rapidly-moving fires, such as in low fuel load grass understories or grasslands, do not have a major effect on microbial populations. High-intensity fires of long durations, such as in mixed conifers with high fuel loads, cause the greatest impact on soil microbes.

Fire effects on microorganisms are greatest in organic horizons (if present) and top 1–2 cm of soil where microorganism populations are most abundant. This is where heating effects are the greatest, or where fires reach moderate to high severity (Table 3). Depending on the microbe, soil heating can be lethal (50–210°C) or can alter their reproductive capabilities (Covington and DeBano, 1990; Klopatek et al., 1988). Whereas temperatures as high as 210°C may be needed to kill specific groups of bacteria in dry soils, soil moisture can reduce lethal levels to around 110°C (Wells et al., 1979).

Fire can significantly alter microbes that affect large-scale processes such as nutrient cycling. For example, following a moderate-or greater intensity fire, the general trend is for heterotrophic microbes to decline significantly. These microbes can be killed directly through consumption. Indirectly, heterotrophic microbes can be affected by totally or partially oxidizing organic C in and above the soil surface or remove the vegetation completely, thus, reducing the potential OM inputs to soil. Conversely, remaining roots at lower depths of fire-killed vegetation can be the primary C source for heterotrophic microbes, often resulting in a large efflux in CO_2 and, hence, a C loss in the system (Klopatek and Klopatek, 1987). These processes can then alter C : N ratios, mineralization rates, etc.

In contrast to the various heterotrophic responses, certain autotrophic microbes may increase dramatically above pre-fire levels. Particularly affected are organisms involved in N cycling (Fig. 4). Vitousek and Matson (1985) stated that microbial immobilization is the most important process preventing N losses in harvested loblolly pine sites. Fire can release or increase soil inorganic N concentrations through abiotic and biotic means that can result in net N losses (see Section 4.2 above). In most environments, *Nitrosomonas* spp. and *Nitrobacter* spp., which are involved with nitrification, are normally in low densities when systems are in the 'steady state'. This is believed to be a result of strong competition for NH_4^+ by vegetation as well as growth inhibition due to the presence of allelopathic compounds, such as terpenes and phenolics in the litter (Klopatek and Klopatek, 1997; Rice, 1982; White, 1991). Through consumption of the organic layer, these compounds volatilize even in the soil. By removing the N sink (e.g. vegetation) and removal of allelopathic compounds, any available NH_4^+ can then be oxidized by nitrifiers (Klopatek et al., 1990a, b). Without any potential plant uptake, resulting NO_3^- can either be denitrified or leached. This loss of N can have subsequent impacts on plant succession and C cycling, hence, ecosystem restoration.

The importance of mycorrhizae in ecosystem function is well documented (Allen, 1991; Safir, 1987). Studies have shown that this symbiosis is fragile, and that mycorrhizal activity decreases with increasing levels of anthropogenic disturbance (Allen, 1988; Janos, 1980; Klopatek et al., 1991, 1994). For example, the abundance and frequency of vesicular–arbuscular mycorrhizae (VAM) propagules decreases precipitously from a moderate disturbance, such as livestock grazing (Bethlenfalvay and Dakessian, 1984; Reece and Bonham, 1978), to a severe disturbance, such as surface mining (Gould and Liberta, 1981; Zac and Parkinson, 1982). However, the effects of natural disturbances, such as fire, have shown contrasting results.

Until recently, little was known about the response of VAM symbionts to fire. Klopatek et al. (1988) found that colonization of VAM on host plants were moderately affected at soil temperatures <50°C, significantly reduced between 50–60°C, and severely reduced when burning temperatures reached 80–90°C. At 94°C, there was a total loss of VAM. Soil-water availability at the time of burning played an important role in VAM survival, with dry soils being more of a detriment than wet soils because of higher resultant temperatures. Gibson and Hetrick (1988) found significant reductions of three VAM species following a fire in the tall grass prairie of Kansas. In a similar experiment, Bentivenga and Hetrick (1991) found that burning temporarily increased mycorrhizal activity in a tall grass prairie ecosystem. Dhillion et al. (1988) found that colonization levels of VAM fungi in little bluestem roots were significantly reduced on burned sites when compared to unburned sites, but increased significantly after one growing season. Their results suggest that the response of VAM fungi to fire may be attributed to changes in the host plant rather than the direct effect of fire. Fire temperatures usually do not reach a level high enough to kill all the plants, thereby leaving a large residual VAM pool in the soil and in plant roots. In fact, some research has shown that fire actually stimulated plant growth. In contrast, Vilarino and Arines (1991) examined a forested ecosystem in Spain a year following a wildfire and found lower soil propagule densities and lower VAM colonization in post-fire herbaceous vegetation than in neighboring unburned areas. Although they had no information on the VAM distribution or activity prior to the fires, Vilarino and Arines (1991) suggest that VAM are negatively affected by fire and that mycorrhizal recovery in forested ecosystems is a slow process. In addition, they theorized that topographical and pedological properties may have played an important role in the losses and re-establishment of mycorrhizae on their study areas.

Natural and prescribed fires may impact the spatial mosaic of both, VAM (Klopatek et al., 1988; Vilarino and Arines, 1991) and ectomycorrhizae in forest ecosystems (Mikola et al., 1964; Schoenberger and Perry, 1982). Klopatek et al., 1988, 1990, 1994 examined the effects of fire in pinyon–juniper ecosystems in both laboratory and field studies. They specifically examined N and C dynamics, nitrifing bacteria and mycorrhizae. In both studies, a bioassays was performed to determine propagule densities. Results showed that bioassay performed on field burned soils were remarkably similar to those that were burned under laboratory conditions. All post-burn bioassays were significantly reduced and overall propagule losses under canopies were greater (up to 81%) than interspaces (34%). Although moisture generally aggravates heat damage in soils during fires, they found that damage was greater when the soils were dry than when they were wet. In both, field and laboratory studies, the reduction of mycorrhizal propagules was correlated with soil temperature and heating duration. Spore numbers found in the field study revealed that interspaces between pinyon and juniper trees had significantly lower spore numbers than under tree canopies prior to burning. But, post-burn spore numbers were significantly reduced in canopy areas (up to 88% loss) as compared with the interspaces (47% loss). In addition to the biological parameters, N and C losses were significantly greater under canopies than interspaces, again as a result of the fuel loading. The field study results showed that ten years after burning mycorrhizae numbers, soil nutrients, and vegetation under severely burned canopies had not recovered to pre-burn levels. However, successional processes in interspaces have occurred and the soils are nearly fully recovered.

Studies in progress in central New Mexico, in cooperation with the Sevelleta Long Term Ecological Reserve, are showing that burning of arid grasslands results in initial decreases in VAM and soil nutrients only under shrub canopies (Klopatek, C.C., personal communication). This trend was evident for at least one year following burning. Fire in these grassland systems does not cause as great a reduction in mycorrhizae and nutrient pools compared to other southwestern USA systems, such as pinyon–juniper ecosystems.

The studies by Klopatek et al., 1988, 1990, 1994 concur with Vilarino and Arines (1991), who suggested that high fuel loads in forested ecosystems generate more intense and prolonged burning and incur heavier losses of VAM fungi compared to areas like grasslands with lower fuel loads and less-intense burning conditions. Janos (1980), MacMahon (1987), and Allen and Allen (1988) suggest that mycorrhizal fungi are essential in ecosystem recovery, facilitating plant establishment by regulating nutrient flow from the soil to the plant. Thus, given the importance of mycorrhizae, it is necessary to understand not only mycorrhizal response to fire, but how fire affects the patch dynamics of this ecosystem and how this affects the mosaic landscape pattern.

4.4. Soil-dwelling invertebrates and vertebrates

Invertebrates play an important role in litter decomposition, C and nutrient mineralization, soil turnover, and soil structure formation. For example, termites and beetles can be particularly critical in arid and semi-arid systems as they are the initial decomposer-colonizers of surface litter followed by microbes (Whitford, 1987). Ants have been shown in a variety of ecosystems to increase OM, N, and P concentrations, as well as to increase densities of mycorrhizal spores (Friese and Allen, 1993; Gentry and Stiritz, 1972; Wagner, 1997). Many of the macropores that govern rapid movement of water into, and through, soils are created by invertebrate activity.

The effects of fire on invertebrates and subsequent effects on belowground sustainability are difficult to assess and generalize because of fire severity variability, high pre-fire invertebrate species variability, selective modification of the balance of species by fires, and post-fire invertebrate community response to changes in litter and OM changes (Campbell and Tanton, 1981). Indirect effects of fire, such as litter mass reduction, can decrease both, the number of species and density of soil and litter invertebrates (Springett, 1976). Particularly susceptible are those belowground dwelling invertebrates which are not highly mobile and primarily reside in litter or the surface soil horizons as they are most vulnerable to the direct effects of intense surface fires or ground fires (DeBano et al., 1998).

Fire adaptations (high mobility, water conservation, and heat resistance) exhibited by invertebrates in fire-affected ecosystems appear to be more species-specific characteristics rather than fire-specific. In fire-adapted ecosystems, such as tallgrass prairies, increased plant productivity seems to be intricately linked with greater earthworm activity as well as nutrient mobilization (James, 1982). In grassland ecosystems, fires rarely reach the severity needed to adversely affect invertebrate populations. In forest ecosystems, both adverse (Sgardelis et al., 1995) and neutral (Coults, 1945) effects of fires on predominantly litter-dwelling macroinvertebrates have been documented. However, as Campbell and Tanton (1981) stated, cause and effect of fire on invertebrates relative to belowground sustainability are difficult to predict.

Vertebrates such as amphibians, reptiles, and rodents, also participate in the formation or alteration of belowground ecosystems and their physical properties. For example, in arid and semi-arid systems, the activity of burrowing mammals creates patches in which plant diversity increases (Thorsten et al., 1997). Accumulation of nutrients, water and seeds trapped in these depressions can be partially attributed to this phenomenon.

The direct effects of fire on most soil vertebrates are minimal as they are mobile enough to escape fires by burrowing deep enough into the soil to escape lethal temperatures or by fleeing on the surface. Indirect effects, such as loss of habitat, exposure of soil burrow openings, and increased predation, are more effective in reducing vertebrate diversity and abundance for several years following fires (Ream, 1981).

In conclusion, for various reasons listed above, fire can be more detrimental to invertebrate than vertebrate populations. However, catastrophic stand-replacing fires can result in significant soil invertebrate and vertebrate mortality. The overall effects of these losses on belowground sustainability may be insignificant compared to other belowground components and processes that are lost or significantly altered. Perhaps what is more important following a catastrophic fire is the rate of recruitment of micro- and macro-soil fauna from landscape boundaries (see, e.g. Bell et al., 1997) once other successional processes are underway.

5. Summary and conclusions

We have found that extensive, long-term, and or conclusive studies documenting fire's effect on belowground processes that result in sustainability declines (or increases) are scarce. This situation is of great concern to ecologists, land managers and, more recently, many state and federal agencies. We conclude that the overall effects of fire on belowground systems and the resulting processes that feedback to aboveground systems are complex and highly variable. Depending on fire severity, changes in belowground processes can be either beneficial or deleterious to the entire ecosystem and the resulting impacts can vary from short- to long-term effects. Low-impact burning can cause short-term increases in the availability of plant nutrients, reduction in disease or pathogens, and thinning of over-crowded forests, all of which can promote heathy systems. Frequent or seasonal fires, as a management tool, have been shown to have inconclusive results. In some cases, this practice can have long-term negative effects on belowground systems. Decreases in plant available soil-nutrient concentrations and nutrient cycling processes can affect litter quality inputs and, hence, have a long-term effect on overall ecosystem sustainability (Blair, 1997; Monleon and Cromack, 1996; Ojima et al., 1994). Moderate-to-severe fires can result in a large flux of nutrients leaving the ecosystem through volatilization and rapid mineralization of nutrients and increased microbiological processes (e.g. increased decomposition, nitrification and denitrification rates). Subsequent losses of nutrients through accelerated erosion and leaching are also common. Adverse changes in soil hydrologic functioning, degradation of soil physical properties, and losses or decreases in microbial populations and associated processes can occur following moderate-to-severe fires.

The time for recovery of belowground systems will not only depend on burning intensity, but also on previous disturbances and recruitment of organisms. Land-use practices, such as long-term grazing, may further intensify fire effects on belowground systems (e.g. Bock and Bock, 1997). Recruitment of soil flora and fauna from landscape boundaries (see, e.g. Bell et al., 1997) is also critical following disturbance, particularly if the disturbance is severe. The rate of vegetative succession, i.e. the primary C source to the belowground, is also a key to recovery and sustainability of these systems.

Predicting future scenarios of fire frequency and intensity as well as rates of recovery of belowground systems is further complicated by the potential of global change. Increases in greenhouse gases released by biomass burning may lead to a potential positive feedback loop, resulting in greater fire frequency. Evidence suggests that climatic changes induced by increases in greenhouse gases may be raising the frequency of drought and vegetation fires in some regions of the world (Subcommittee On Global Change Research, 1996). Current projections suggest a global warming between 1.5° and 4.5°C in the coming century (Intergovernmental Panel on Climate Change estimates: Schneider, 1989, Mitchell et al., 1990). A potential climate warming may seriously affect the arid and semi-arid regions, such as the southwestern United States, where researchers forecast a 17% increase in the desert land area. Schneider (1989) and Neilson et al. (1989) and others have shown, using general circulation models (GCMs), that the southwestern United States will not only experience a rise in temperature but a change in precipitation as well. In spite of high variability in predicted rainfall, soil moisture is anticipated to decrease in most of the region (Manabe and Weatherford, 1987; Washington and Meehl, 1989). The effects of a temperature increase and soil-moisture depletion could further compound fire dynamics in this region. As a result of the change in climate, the GCMs forecast regional spatial shifts in vegetation (Solomon and Shugart, 1993) that will have an effect on C dynamics across the landscape (Anderson, 1991; Klopatek et al., 1992). The alteration of the landscape fuel loadings caused by global change as well as the potential for drought will undoubtedly cause an increase in the overall fire frequency of this region. Other semi-arid and temperate ecosystems elsewhere in the world may experience similar scenarios.

In order to understand the impact of these global changes, increased research must be focused on belowground sustainability, particularly primary productivity and the impacts of land management practices, such as fire on this parameter of ecosystem function (Schoen, 1997). Research results are insufficient, lacking, or contradictory in regard to the effects of fire on belowground primary productivity, microbial processes, organic matter quality, nutrient depletion, and soil physical processes. This is especially true in the fragile ecosystems of semi-arid climates where small changes may have long-lasting consequences.

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