Ecosystems (2005) 8: 163–181
DOI: 10.1007/s10021-004-0097-8

ECOSYSTEMS
© 2005 Springer Science+Business Media, Inc.

MINIREVIEW

Postfire Soil N Cycling in Northern Conifer Forests Affected by Severe, Stand-Replacing Wildfires

Erica A.H. Smithwick,[1]* Monica G. Turner,[1] Michelle C. Mack,[2] and F. Stuart Chapin III[3]

[1]*Department of Zoology, University of Wisconsin, Madison, Wisconsin 53706, USA;* [2]*Department of Botany, University of Florida, Gainesville, Florida 32611, USA;* [3]*Institute of Arctic Biology, University of Alaska, Fairbanks, Alaska 99775, USA*

ABSTRACT

Severe, stand-replacing fires affect large areas of northern temperate and boreal forests, potentially modifying ecosystem function for decades after their occurrence. Because these fires occur over large extents, and in areas where plant production is limited by nitrogen (N) availability, the effect of fire on N cycling may be important for long-term ecosystem productivity. In this article, we review what is known about postfire N cycling in northern temperate and boreal forests experiencing stand-replacing fires. We then build upon existing literature to identify the most important mechanisms that control postfire N availability in systems experiencing severe, stand-replacing fires compared with fires of lower severity. These mechanisms include changes in abiotic conditions caused by the opening of the canopy (for example, decreased LAI, increased solar radiation), changes in ground layer quantity and quality (for example, nutrient release, permafrost levels), and postfire plant and microbial adaptations affecting N fixation and N uptake (for example, serotiny, germination cues). Based on the available literature, these mechanisms appear to affect N inputs, internal N cycling, and N outputs in various ways, indicating that severe fire systems are variable across time and space as a result of complex interactions between postfire abiotic and biotic factors. Future experimental work should be focused on understanding these mechanisms and their variability across the landscape.

Key words: fire; nitrogen; nutrient cycling; boreal; temperate; disturbance; stand-replacing; large infrequent disturbances (LIDs).

INTRODUCTION

Severe, stand-replacing wildfires influence the structure and function of many northern temperate and boreal coniferous forests (Turner and Romme 1994; Zackrisson 1977; Kasischke and Stocks 2000). Severe fire affects ecosystem function by changing the biogeochemical cycling of critical plant nutrients, such as nitrogen (N), phosphorus, potassium, calcium, magnesium (Chorover and others 1994; Raison 1979; Boerner 1982). Changes in N cycling after severe fire are important in northern coniferous forests because plant production in these forests is generally limited by N (Vitousek and Howarth 1991; Yarie and Van Cleve in press), an element that is volatilized by fire (Raison 1979). Yet, despite the importance of both fire and N cycling in northern coniferous forests, the specific mechanisms affecting postfire N cycling after severe, stand-replacing fires, and their variation across the landscape, have not been carefully analyzed.

Received 8 July 2003; accepted 30 October 2003; published online 28 February 2005.
*Corresponding author; e-mail: easmithwick@wisc.edu

Each year extensive areas of northern temperate and boreal forests are affected by severe wildfire, despite significant regional and historical variability. Between 1980 and 1989, stand-replacing fires disturbed over 5 million ha of land annually in boreal forests, mostly in Canada and Russia (Stocks 1991). On average, wildfires affect 1.7 million ha annually in the United States, although that amount can double in severe fire years (NIFC 2003; Turner and others 2003).The mean annual area burned has increased in the northern Rockies and Canada over the past several decades (Baker 2000; Skinner and others 1999; Murphy and others 2000), while in Alaska there were no significant long-term trends in area burned between 1950 and 1999 (Kasischke and others 2002). Most (73%) of the area burned during these 40 years occurred during 10 severe fire seasons (Kasischke and others 2002).

The intensity and frequency of wildfires is expected to increase in the future as a result of predicted changes in climate (Flannigan and others 2000; Dale and others 2001; Balling and others 1992). For example, in a doubled CO_2 atmosphere, simulation results suggest lightning-caused fires will increase 30% in summer months in the northern Rockies (Baker 2000). The northern Rockies may be one of the regions in North America that is most sensitive to climate change and likely to have increases in severe or extreme fire weather (Flannigan and others 2000; Baker 2000). In Russia, the annual area burned may double or triple in a typical climate-warming scenario (Stocks and others 1998; Flannigan and Wotton 2001). Because the boreal forest is the second largest biome on Earth (Saugier and others 2001), doubling the annual area burned could have significant implications for global N and carbon (C) cycles (Flannigan and others 2000; Hobbie and others 2000).

Postfire N cycling has been studied after low-severity, managed fires (prescribed, experimental, site preparation) and in ecosystems that are either nonconiferous (grasslands, mixed hardwood forests, chaparral) or that lack stand-replacing fires (pine forests dominated by surface fires). Wan and others (2001) quantitatively summarized fire effects on N cycling in terrestrial ecosystems based on 87 studies. However, only three studies were from coniferous forests experiencing wildfire: Aleppo pine in Italy (Dumontet and others 1996), pine-wood-oak in Spain (Andreu and others 1996), and mixed spruce in Alaska (Dyrness and others 1989). Only the latter reference can be considered stand replacing.

Thus, much of what we understand about postfire N cycling is derived from low-severity fires in nonconiferous systems. From these studies, we know that fire alters N pools and fluxes via multiple mechanisms (Table 1 and Figure 1) (Ahlgren and Ahlgren 1960; Kozlowski and Ahlgren 1974; Raison 1979; Woodmansee and Wallach 1981; Boerner and others 1982; Johnson and others 1998; Wan and others 2001). First, the fire event directly changes N pools through volatilization, pyrolysis, ash deposition, translocation of N between mineral and organic soil layers, and lysis of fine root and microbial cell walls. Second, N pools and fluxes are altered by changes in rates of microbial processes after fire as a result of alteration of the soil abiotic environment (pH, temperature, moisture), changes in the quantity or quality of substrates (organic N, NH_4^+, carbon), or changes in microbial community composition and population size. Finally, N pools and fluxes are altered by the type of vegetation that persists or colonizes after fire, which affects N inputs through biological N fixation, N uptake, and the quantity of labile substrates for mineralization. The net effect of these mechanisms may affect ecosystem productivity (Wirth and others 2002; Ojima and others 1994), thus emphasizing the importance of fire to ecosystem function.

In this article, we synthesize what is known about postfire N cycling after severe, stand-replacing fires in northern temperate and boreal systems and assess the extent to which the aforementioned mechanisms are useful in understanding postfire N cycling. We place this work in context by synthesizing observations following non-stand-replacing fires and assessing spatial heterogeneity. We conclude by identifying areas of remaining uncertainty and outlining directions for future research.

Severe, Stand-Replacing Fires in Northern Conifer Forests

Stand-replacing fire regimes are common throughout the extensive boreal forests of North America, Europe, and Asia and affect a range of coniferous forest species (Turner and Romme 1994; Bourgeau-Chavez and others 2000). Fires are generally infrequent, severe, and spatially extensive. Fire return intervals range from 30 to 70 years in forests of jack pine (*Pinus banksiana*) in Canada (Rowe and others 1974), from 26 to 113 years in forests of black spruce (*Picea mariana*) in Alaska (Yarie 1981), from 100 to 300 years forests of lodgepole pine (*P. contorta*) in the northern and central Rocky Mountains (Romme 1982; Romme

Table 1. Mechanisms Affecting Postfire Internal Nitrogen Cycling in Mineral and Organic Soil

Fire event	Postfire response
(1) Volatilization	Change in mineralization rates = *f*(abiotic)
(2) Pyrolysis	(5) Temperature, Moisture
(3) Ash deposition	(6) pH
(4) Cell lysis	(7) Substrate quantity (NH_4^+)
	Change in mineralization rates = *f*(biotic)
	(8) Substrate quality
	(9) Substrate quantity (organic N)
	(10) Microbial pool size
	(11) Immobilization
	(12) Translocation
	(13) Erosion, leaching
	(14) Plant uptake
	(15) Plant community composition
	(16) Mineral soil interactions

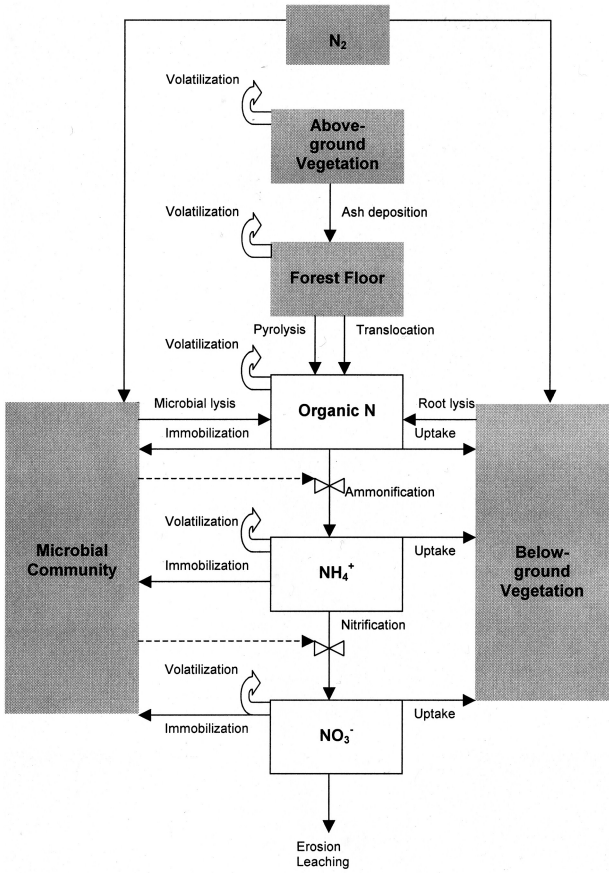

Figure 1. Flowchart showing the interactions among processes affecting postfire nitrogen cycling.

and Despain 1989), and 400 years in high-elevation forests of Douglas fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) in the Pacific Northwest, USA. The estimated fire return interval in Norway spruce (*Picea abies*), larch (*Larix* sp.), and pine (*Pinus* sp.) forests of Scandinavia and Russia extends across that entire range, from 50 to 400 years (Dahlberg 2002). Typically, very few large fires account for most of the total burned area, and these fires are driven primarily by climate, particularly prolonged regional drought (Johnson 1992; Johnson and Wowchuck 1993; Bessie and Johnson 1995; Flannigan and Wotton 2001). Under the extreme fire weather responsible for the large fires, variation in fuel structure is often of minor importance, and fires may burn through forests of all ages, structures, and compositions. Because of human influences, severe fires may be less common in regions where fuels and fires are highly managed (for example, northern Europe).

Across northern temperate and boreal ecosystems, severe, stand-replacing fires are carried by different fuels (surface vs. canopy) and are characterized by varying levels of fuel consumption. However, all severe, stand-replacing fires kill the trees and initiate secondary succession through the establishment of a new forest cohort (Johnson 1992). For example, crown fires are carried by the tree canopy, whereas severe surface fires are typically carried by ground fuels, although both may result in complete canopy mortality and substantial consumption of ground fuels. It is important to note that not all crown fires are stand-replacing in boreal coniferous systems; postfire tree mortality in Russia and Siberia ranges from 30% to 100% depending on fire intensity (Shvidenko and Nilsson 2000a). Likewise, not all severe surface fires are stand-replacing in boreal coniferous systems; postfire tree mortality ranges from 0 to 100%, and may depend on the amount of organic layer consumption, the height of tree scorching, and the tree species (Shvidenko and Nilsson 2000a). For example, mortality is higher for larch (which occupy 37% of Russian forests) than for pine after severe surface fires because of higher susceptibility to trunk scorching and superficial rooting (Shvidenko and Nilsson 2000a). In general, in Russia, Canada, and Alaska, stand-replacing fires are typically carried by ground fuels, especially litter (Shvidenko and Nilsson 2000a), whereas stand-replacing fires in northern temperate forests are typically carried by the upper canopy.

Estimates of surface and canopy consumption after severe, stand-replacing fire are variable. Crown fires consume 20%–40% of aboveground

biomass in Russia and Siberia (Shvidenko and Nilsson 2000b; Conard and others 2002; Bourgeau-Chavez and others 2000). In Alaskan black spruce forests, 20%–90% (average = 43%) of the ground layer may be consumed (Kasischke and others 1995, 2000). During the 1988 Yellowstone fires, all of the surface litter was consumed, although only 8% of the coarse woody debris (CWD) that was present on the forest floor was consumed, and an equal amount (approximately 8%) was converted to charcoal (Tinker and Knight 2000). Higher levels of CWD consumption have been observed elsewhere. After a high-intensity prescribed fire in Idaho, 30% of the CWD was consumed (Fahnestock and Agee 1983), and higher amounts may be consumed in boreal fires that are carried by surface fuels. The type of CWD remaining after severe fire will vary. Snags comprise approximately two-thirds of CWD biomass in burned stands compared with less than one-fifth of CWD in mature stands (Pedlar and others 2002; Tinker and Knight 2000). Downed CWD may increase through time as snagfall increases several decades after fire. Across northern forests, CWD consumption will be variable, depending on prefire CWD moisture content, prefire CWD biomass, spatial heterogeneity in fire intensity, and species composition.

There is still considerable uncertainty surrounding the extent of stand-replacing fires in northern temperate and boreal systems, especially in Russia. Stand-replacing crown fires may affect 0.240 million ha annually in forests and taiga of Russia (Shvidenko and Nilsson 2000a,b). In northern boreal systems, crown fires may be only 10%–20% of total area burned in normal years (Conard and others 2002) but 50%–90% in severe years (Kajii and others 2002; Conard and others 2002). In the Russian Far East, remote-sensing studies have documented that the majority of fires during the 1998 fire season were crown fires (Kasischke and Bruhwiler 2003).

Many plant species in the northern temperate and boreal coniferous forests display a range of adaptations to fire. Plants that have evolved with severe fire exhibit multiple autoecological adaptations that promote their survival or propagation (Rowe and Scotter 1973). Many of the dominant conifer species (for example, lodgepole pine, jack pine, and black spruce) are serotinous or semiserotinous, producing cones that open and release their seed when heated by fire. Postfire tree regeneration can be extremely dense in areas of high stand-level serotiny (M.G. Turner and others 1997). Many understory woody and herbaceous species can resprout following fire because belowground roots and rhizomes often survive; subsequent flowering can be followed by abundant seedling recruitment.

Lessons from Other Fire Systems

We begin by synthesizing what has been learned from studies of fire in other ecosystems. Lessons from these fire systems may guide future research on severe, stand-replacing fires in northern coniferous forests. We consider earlier reviews and published information on N inputs, internal N cycling (including nutrient pools and cycling rates), and N outputs from the system.

Fire-Nitrogen Reviews

In one of the first comprehensive reviews of fire and N cycling, Ahlgren and Ahlgren (1960) concluded there was conflicting evidence in nearly every aspect of fire ecology research, particularly N cycling, but were able to draw several general conclusions. They concluded that erosion is enhanced after severe fires because the topsoil is less capable of absorbing water, that moisture and temperature changes in the surface soil may be significant, that fire reduces soil acidity, and that burning appears to stimulate N fixation. Two decades later, Raison (1979) similarly concluded that the impact of isolated events on the nutrient cycling of entire ecosystems remained inadequately studied, concluding that fire ecological research was hampered by a lack of information from sites with a known burning history and by the necessarily complex ecological interactions affecting nutrient cycling.

Recently, Wan and colleagues (2001) used a meta-analysis method to quantitatively summarize fire research on N, reviewing literature on the effect of fire on N pools and concentrations, particularly fuel and soil N amount and concentration, and ammonium and nitrate pools. Independent variables used to compare results across numerous studies were vegetation type, fuel type, the amount (and %) of fuel consumption, the time after fire, and the soil sampling depth. They concluded that total fuel N amount was influenced by vegetation amount, fuel type, and the amount (and %) of fuel consumption. Fuel N concentration, on the other hand, was only affected by fuel type. Soil N amount was not correlated with any of the independent variables tested. Soil N concentration, ammonium, and nitrate were dependent on soil sampling depth. Ammonium and nitrate were affected by fire type and time since fire, but they differed temporally in

their response. For example, there is a pulse of ammonium that lasts up to 1 year after fire, approximately doubling prefire levels, which is followed by increases in nitrate. Wan and colleagues (2001) provided a new and more conclusive way of summarizing the effects of fire on N cycling and highlighted key areas of needed consistency among studies, such as soil sampling depth. However, in their article, they cited only three papers assessing wildfires in coniferous forests. Also, the authors did not attribute mechanisms behind the changes in ecosystem-level patterns. Finally, most of the research included in the aforementioned reviews was focused on the first 5 years after a fire event and much less is known about the effects of fires on N cycling through ecosystem succession.

In the following section, we build on these earlier reviews by focusing on important mechanisms that control N cycling (inputs, internal cycling, outputs) and which operate through initial postfire forest establishment and succession. In a subsequent section, we narrow our discussion to severe, stand-replacing fires in northern temperate and boreal systems.

Nitrogen Inputs

Determining when fire enhances N inputs is difficult because of the stochastic nature of interactions between abiotic processes that drive fire and the biological processes that control the abundance of postfire plant species, including N-fixing plants. For example, germination cues related to fire may have threshold effects that are difficult to predict. In a suite of 35 fire-following species in an Australian shrubland, 50% of the species did not germinate following fire unless soil temperatures exceeded 60°C; 100% of the species germinated when soil temperatures reached 80°C (Auld and O'Connell 1991). Germination was thus related to climate, fine fuel load, and seed bank composition (Bradstock and Auld 1995), all factors that vary independently in space and time. In another case, fire indirectly stimulated the germination of legume seeds in an African savanna by killing bruchid larvae that infested the seeds, thereby decreasing seed mortality (Sabiiti and Wein 1987). These types of fire-driven interactions between abiotic and biotic processes have the potential to generate a patchy and stochastic distribution of N inputs in space and time, and they may also operate in stand-replacing fires systems.

Whether or not fire enhances N inputs by stimulating asymbiotic fixation appears to be largely determined by the effects of fire on substrate availability. Systems in which plant community and ecosystem structure have shifted due to changes in fire regime may be particularly sensitive to these types of effects. For example, in a Hawaiian woodland invaded by fire-promoting exotic grasses, N inputs from asymbiotic fixation were reduced by more than a factor of 5 when woodlands were converted to grassland by fire (Ley and D'Antonio 1998; Mack and others 2001). This reduction was primarily due to the loss of litter inputs from the native species; fixers did not appear to use exotic grass litter as a substrate for fixation (Ley and D'Antonio 1998).

Fire may stimulate asymbiotic fixation activity by altering environmental factors that modulate rates of fixation. Because fixation activity is positively related to pH (Nohrstedt 1985; Limmer and Drake 1996) and temperature, the tendency of postfire forest floors to be more basic and warm should enhance fixation rates. Increases in soil moisture after fire, due to lower plant demand for water, should also enhance N fixation (Wei and Kimmins 1998). However, burning affected soil moisture differently among three stands in Alaska, attributed to differences in preburn drainage characteristics (O'Neill and others 2002). Thus, postfire N fixation may vary with prefire conditions that control postfire heterogeneity. The magnitude of these effects on N inputs at the ecosystem scale are likely to be substantially smaller than the effects of changes in substrate pool size (Limmer and Drake 1996; Ley and D'Antonio 1998).

Internal Nitrogen Cycling

Studies from non-stand-replacing fire systems show that soil ammonium concentrations generally increase after fire, 2–26 times above prefire levels (Table 2). The pulse of ammonium may be short-lived, often less than 2 years, as demonstrated in eucalyptus forests in Tasmania (Adams and Attiwill 1991), in white fir/giant sequoia forests in the Sierra Nevada region (Chorover and others 1994), and in Californian chaparral (Fenn and others 1993). Most studies show soil nitrate pools increase 2–5 times after fire, with one exception [44 times higher in a Mediterranean forest (Rapp 1990); Table 3]. The increase in nitrate pools often lags behind the increase in ammonium, as confirmed by Wan and others (2001). For example, nitrate levels may be comparable to prefire levels for 1 year after the fire and then increase dramatically in the following years (Covington and Sackett 1992). This temporal heterogeneity in nitrate levels may partially account for the many observations of non-significant fire effects summarized in Table 3.

Table 2. Changes in Postfire Ammonium Concentrations for Various Fire Systems

Fire type	Change	Mechanism	Location	Reference
Stand-replacing conifer forests				
Experimental	NS	14, 16	Alaska	Van Cleve and Dyrness 1983
Wildfire	200%-400%	11, 14	California	Grogan and others 2000a
Non-stand-replacing conifer forests (surface fire)				
Prescribed	300%	12	Oregon	Monleon and others 1997
Prescribed	487%-2054%	4	Arizona	Covington and Sackett 1986,1992
Prescribed	196%	5	Arizona	Kaye and Hart 1998
Prescribed	713%	—	Montana	DeLuca and Zouhar 2000
Prescribed	1026%	12, 16	Montana	Choromanska and DeLuca 2001
Prescribed	Increase	6, 8, 16	California	Chorover and others 1994
Prescribed	NS (112%)	—	Arizona	Wright and Hart 1997
Wildfire	156%-217%	4	Virginia	Groeschl and others 1993
Lab	109%-142%	5	Montana	Choromanska and DeLuca 2002
Woodland/Chaparral				
Prescribed	400%		Mediterranean	Rapp 1990
Prescribed	2648%	2, 12	Arizona	Covington and others 1991
Prescribed	382%	2, 12	Arizona	Klopatek and others 1990
Prescribed	284%	1, 2, 12	California	DeBano and others 1979
Wildfire	500%	9, 3	California	Christensen and Muller 1975
Wildfire	400%-1400%	—	California	Fenn and others 1993
Wildfire	900%	9	Israel	Kutiel and Naveh 1987
Wildfire	Increase	3, 14	South Africa	tock and Lewis 1986
Broadleaved/Mixed				
Slash	1000%	—	Australia	Adams and Attiwill 1991
Wildfire	136%	—	Australia	Weston and Attiwill 1990
Experimental	282%	3, 12, 16	Australia	Grove and others 1986
Clearing	325%	—	Costa Rica	Matson and others 1987
Prescribed	NS (56%)	8	Missouri	Vance and Henderson 1984

Values are postfire/control (%). Mechanisms attributed to the change are defined in Table 1. If authors did not clearly attribute a mechanism to their results, this is noted with a dash (—). NS = nonsignificant.

Changes in soil inorganic N after fires have been attributed to a combination of direct and indirect fire effects. The volatilization of N, the pyrolysis of organic matter (Kovacic and others 1986), and the deposition of N and cations in ash (Grove and others 1986; Christensen 1973; Christensen and Muller 1975) have been well documented in surface fires. Increased inorganic N in soil after fire may be proportional to the amount of forest floor burned (Covington and Sackett 1992) and may be positively correlated with fire severity (Weston and Attiwill 1990).

There are conflicting results about whether N mineralization rates are enhanced or diminished by fire in the studies from other systems (Table 4). Elevated soil N mineralization rates have been observed in chaparral (Singh and others 1991), tropical forest (Matson and others 1987), grassland (Hobbs and Schimel 1984), mixed hardwood (Knoepp and Swank 1993), and surface-fire systems (Kaye and Hart 1998; Rapp 1990), as well as in laboratory settings (Dunn and others 1979). Decreases in soil net mineralization rates after fire have been observed in surface-fire (Monleon and others 1997), grassland (Blair 1997), and chaparral (Dumontet and others 1996) systems.

Increases in soil N mineralization rates have been attributed to a combination of factors, both abiotic [increased soil temperatures (Hobbs and Schimel 1984), increased anion exchange at depth (Matson and others 1987), higher pH (Christensen and Muller 1975)] and biotic [reduced microbial immobilization (Klopatek and others 1990)]. Nitrification may increase as a result of increased ammonium, increased soil pH, and perhaps decreased microbial immobilization of nitrate (Stock and Lewis 1986; Chorover and others 1994; Kaye and Hart 1998). Decreased soil mineralization rates have mainly been attributed to biotic factors, increased C: N (Dumontet and others 1996) and a

Table 3. Changes in Postfire Nitrate Concentrations for Various Fire Systems

Fire type	Change	Mechanism	Location	Reference
Stand-replacing conifer forests				
Experimental	NS (25%-50%)	5, 11, 13, 16	Alaska	Van Cleve and Dyrness 1983
Wildfire	Increase	7	California	Grogan and others 2000a
Non-stand-replacing conifer forests (surface fire)				
Prescribed	Increase	7, 15	Arizona	Covington and Sackett 1986
Prescribed	273%	11	Arizona	Kaye and Hart 1998
Prescribed	192%	—	Montana	DeLuca and Zouhar 2000
Prescribed	275%	7, 11	Montana	Choromanska and DeLuca 2001
Prescribed	Increase	—	California	St. John and Rundel 1976
Prescribed	Increase	6, 7, 11	California	Chorover and others 1994
Prescribed	NS	—	Arizona	Covington and Sackett 1992
Prescribed	NS	—	Montana	Newland and DeLuca 2000
Prescribed	NS	—	Oregon	Monleon and others 1997
Prescribed	NS(+ 150%)	—	Arizona	Wright and Hart 1997
Wildfire	85%–385%	4	Virginia	Groeschl and others 1993
Woodland/Chaparral				
Prescribed	550%	7	Arizona	Covington and others 1991
Prescribed	4400%	—	Mediterranean	Rapp 1990
Prescribed	NS(−28% to + 222%)		Arizona	Klopatek and others 1990
Prescribed	NS(−19% to + 244%)		California	DeBano and others 1979
Experimental	154%	3, 9, 12, 14	India	Singh and others 1991
Wildfire	500%	Not clear	Nevada	Baldwin and Morse 1994
Wildfire	500%	6, 7	California	Christensen and Muller 1975
Wildfire	200%	—	Israel	Kutiel and Naveh 1987
Wildfire	Increase	14	South Africa	Stock and Lewis 1986
Wildfire	NS (increase)	—	California	Fenn and others 1993
Broadleaved/Mixed				
Prescribed	NS	—	South Carolina	Binkley and others 1992
Slash	250%	—	Costa Rica	Matson and others 1987
Prescribed	NS	—	Missouri	Vance and Henderson 1984
Slash	NS	1	Costa Rica	Ewel and others 1981
Wildfire	NS	—	Australia	Weston and Attiwill 1990

Values are postfire/control (%). Mechanisms attributed to the change are defined in Table 1. If authors did not clearly attribute a mechanism to their results, this is noted with a dash (—). NS = nonsignificant.

decrease in litter quantity and quality (Monleon and others 1997).

Studies from non-stand-replacing fire systems report variable responses of total soil N to fire, from 65% to 310% of prefire levels (Table 5), largely depending on the balance between N inputs to the soil from ash and canopy litter versus combustion and leaching losses.

Changes in inorganic N availability may be due to changes in microbial activity or populations. Studies from non-stand-replacing fire systems report that microbial immobilization decreases (Klopatek and others 1990) or increases (Adams and Attiwill 1991). Decreased immobilization has been attributed to a loss of C inputs following fire (Klopatek and others 1990). Increased immobilization has been attributed to enhanced microbial activity (Ojima and others 1994), increases in available organic C concentrations, and/or increases in phosphorus supply (Adams and Attiwill 1991). If microbial immobilization is enhanced by fire, it may restrict off-site N losses (Adams and Attiwill 1991).

There are conflicting reports on the effect of fire on microbial biomass shortly after fire. Decreases in microbial biomass have been observed in the tropics (Matson and others 1987) and in pine forests dominated by surface fires (Dumontet and others 1996; Prieto-Fernandez and others 1998). Increases in microbial biomass have been documented after fire in Californian chaparral (Christensen and Muller 1975) and immediately after a

Table 4. Changes in Postfire Mineralization Rates for Various Fire Systems

System	Change	Mechanism	Location	Reference
Net Mineralization				
Stand-replacing conifer forests				
Wildfire	NS	5, 10	Quebec	Simard and others 2001
Non-stand-replacing conifer forests (surface fire)				
Prescribed	200%–300%	7	Arizona	Kaye and Hart 1998
Prescribed	1278%	—	Mediterranean	Rapp 1990
Prescribed	134%	—	North Carolina	Schoch and Binkley 1986
Prescribed	53%–524% (PMN)	9, 12, 14	Montana	DeLuca and Zouhar 2000
Prescribed	370% (PMN)	8	Montana	Choromanska and DeLuca 2001
Prescribed	Decrease	8, 9	Oregon	Monleon and others 1997
Prescribed	79%(PMN)	1, 9	Montana	Newland and DeLuca 2000
Prescribed	73% (AMN)	8, 10	Arizona	Wright and Hart 1997
Woodland/Chaparral				
Experimental	120%	9, 15	India	Singh and others 1991
Wildfire	Decrease	8	Italy	Dumontet and others 1996
Broadleaved/Mixed				
Slash	50%	16	Costa Rica	Matson et al 1987
Slash	252% (PMN)	5, 14	Australia	Adams and Attiwill 1991
Slash	158%	5, 14	Australia	Adams and Attiwill 1991
Wildfire	22%	11	Australia	Weston and Attiwill 1990
Grassland				
Experimental	32%	—	Kansas	Blair 1997
Experimental	27%, 134%	8, 11	Kansas	Ojima and others 1994
Experimental	15%	5, 8, 9	Kansas	CL Turner and others 1997
Prescribed	200%–400%	5, 8	Colorado	Hobbs and Schimel 1984
Nitrification				
Stand-replacing conifer forests				
Wildfire	NS	6, 7	Quebec	Simard and others 2001
Non-stand-replacing conifer forests (surface fire)				
Prescribed	Increase	6, 7, 11	California	Chorover and others 1994
Prescribed	300%–500%	11	Arizona	Kaye and Hart 1998
Prescribed	−367%	11	North Carolina	Schoch and Binkley 1986
Prescribed	NS	—	Oregon	Monleon and others 1997
Prescribed	2% (NS)	11	South Carolina	Bell and Binkley 1989
Woodland/Chaparral				
Experimental	125%	—	India	Singh and others 1991
Grassland				
Experimental	22%	—	Kansas	CL Turner and others 1997
Ammonification				
Non-stand-replacing (surface fire)				
Prescribed	78%	9	North Carolina	Schoch and Binkley 1986
Prescribed	46% (NS)	11	South Carolina	Bell and Binkley 1989

Values are postfire/control (%). Mechanisms attributed to the change are defined in Table 1. If authors did not clearly attribute a mechanism to their results, this is noted with a dash (—). Values are net rates, unless otherwise noted. PMN = potentially mineralizable N; AMN = aerobically mineralization N. NS = nonsignificant.

Table 5. Changes in Postfire Total Soil Nitrogen for Various Systems

System	Change	Mechanism	Location	Reference
Stand-replacing conifer forests				
Prescribed	NS	—	Canada	Beaton 1959
Experimental	Increase	4, 12, 15	Canada	Lynham and others 1998
Experimental	50% (FF)	4, 12, 15	Canada	Lynham and others 1998
Wildfire	67%	1	Washington	Grier 1975
Wildfire	3% (FF)	1	Washington	Grier 1975
Wildfire	99%–117%	1	Alaska	Dryness and others 1989
Wildfire	36%–98% (FF)	1	Alaska	Dryness and others 1989
Wildfire	50%–115% (FF)	1	Quebec	Simard and others 2001
Wildfire	Decrease (FF)	1	Oregon	Little and Ohmann 1988
Slash	Decrease (FF)	1	British Columbia	Feller 1988
Slash	NS (106%) (FF)	11, 14	British Columbia	Feller and Kimmins 1984
Slash	76%–106% (FF)	—	British Columbia	Bellilas and Feller 1998
Non-stand-replacing conifer forests (surface fire)				
Prescribed	Decrease	2, 4, 5	California	St. John and Rundel 1976
Prescribed	275%	—	Montana	Choromanska and DeLuca 2001
Prescribed	120%	8, 12	Montana	DeLuca and Zouhar 2000
Prescribed	108%–152%	—	California	Chorover and others 1994
Prescribed	116%	—	Arizona	Kaye and Hart 1998
Prescribed	Decrease	—	Southwest U.S	Johnson and others 1997
Prescribed	94%	1	Arizona	Wright and Hart 1997
Prescribed	82%	4	South Carolina	Bell and Binkley 1989
Prescribed	NS	—	South Carolina	Binkley and others 1992
Prescribed	104% (FF)	—	North Carolina	Schoch and Binkley 1986
Wildfire	65%	1, 4	Virginia	Groeschl and others 1993
Woodland/Chaparral				
Prescribed	152%	—	Arizona	Covington and others 1991
Prescribed	88%	—	California	DeBano and Conrad 1978
Experimental	118%	—	India	Singh and others 1991
Wildfire	128%	9	South Africa	Stock and Lewis 1986
Wildfire	75%	1	Israel	Kutiel and Naveh 1987
Wildfire	Variable	—	California	Christensen and Muller 1975
Broadleaved/Mixed				
Wildfire	237%	3	Spain	Andreu and others 1996
Wildfire	310%	4	Australia	Weston and Attiwill 1990
Clearing	85%	15	Amazon	Uhl and Jordan 1984
Grassland				
Experimental	83%	—	Kansas	Ojima and others 1994

Values are postfire/control (%). Values represent mineral soil nitrogen unless otherwise noted. FF = forest floor-nitrogen. Mechanisms attributed to the change are defined in Table 1. If authors did not clearly attribute a mechanism to their results, this is noted with a dash (—). NS = nonsignificant.

prescribed fire in mixed ponderosa pine/Douglas-fir forests of northwest Montana (DeLuca and Zouhar 2000). However, in a chronosequence of sites with increasing time since fire, Fenn and others (1993) observed no differences in microbial biomass patterns beneath chamise/*Ceanothus* vegetation in California.

Microbial populations are affected by temperature and moisture changes caused by burning. Ground surface temperatures during fire are typically 100°C–200°C but may approach 1500°C in intense fires (Neary and others 1999). Microbial populations, especially fungi, are negatively affected when temperatures are greater than 50°C (Neary and others 1999). The transfer of this heat to lower soil depths determines the extent to which microbial populations are affected. Postfire microbial mortality may be greater in moist soils compared with drier soils (Klopatek and others 1990; Choromanska and DeLuca 2002), potentially

because moister soils may result in higher temperatures at depth due to higher thermal conductivity up to 90°C (Campbell and others 1994). However, in an open system at higher soil temperatures, latent heat transport does not influence thermal conductivity (Campbell and others 1994). The concomitant effects of higher soil temperatures and changes to soil moisture are not well studied. Postfire microbial mortality may be less in drier soils if microbial populations are adapted to stressful environments (Choromanska and DeLuca 2002). Site fire history may be important in affecting microbial community responses (Choromanksa and DeLuca 2002). Finally, the postfire microbial community may be determined both by survival of the extant community as well as by reinvading communities from neighboring sites not affected by fire (Dunn and others1979).

Nitrogen Outputs

Several factors influence plant uptake after fire. As described above, N availability usually increases following fire (see also Wan and others 2001). However, root biomass declines following fire due to both death of fire-sensitive species and to reallocation to aboveground tissues of species that resprout following fire, as occurs following clipping or aboveground herbivory. The overall effect is a radical decline in root biomass and therefore in N uptake by vegetation (Chapin and Van Cleve 1981). The rate at which uptake recovers following fire depends on the proportion of surviving vegetation and on the rate of establishment and growth of colonizing species. Early successional postfire species are typically shrubs, grasses, and herbs with high relative growth rates and high capacity for N uptake per gram root (Chapin 1980). Some of these species, such as fireweed (*Epilobium angustifolium*), are typically associated with soils of high nitrate availability and have particularly high tissue N concentrations. Seven of 15 species sampled before and after fire in eight separate studies showed a significant increase in leaf N after fire, and no species showed a significant decrease in leaf N; the median change after fire was a 29% increase in leaf N (Chapin and Van Cleve 1981). Given that root biomass declines after fire, this increase in leaf N concentration probably reflects both increased N availability and perhaps increased N uptake capacity per gram of root, a physiological change that typically accompanies a change to conditions that are more favorable for growth and leads to an increase in plant demand for N (Chapin 1980). Changes in species composition can also influence plant N uptake. Most early successional postfire species grow rapidly, have a high capacity for N uptake, and produce litter that decomposes and mineralizes N readily (Chapin and others 2002).

After slash fires and natural wildfires, there is generally a decline in total ecosystem N. The magnitude of this N loss correlates with the degree to which humic layers are consumed (Table 5; Little and Ohmann 1988; Feller 1988; Bellilas and Feller 1998; Simard and others 2001; Grier 1975). Except following the most severe fires (Stark 1977), there are surprisingly few reports of increased N losses to streams (McColl and Grigal 1977), suggesting that most of the N loss associated with fire is directly to the atmosphere during combustion, although deep-soil retention or postfire denitrification in wet sites such as riparian zones could also account for some of the N loss associated with fire (Grier 1975).

N Cycling After Severe, Stand-Replacing Fires

There are several important characteristics of severe, stand-replacing fire systems that may affect postfire N cycling differently compared with fires of lower severity. First, the opening of the canopy after a severe fire may modify the temperature and moisture conditions at the soil surface by increasing solar radiation and reducing plant water uptake, potentially altering N mineralization rates. Second, where prefire organic layers are important, a thinner or charred organic layer is likely to have reduced capacity to store moisture and insulate the underlying soil (Viro 1974; Rowe and Scotter 1973; Van Cleve and others 1983), potentially modifying soil N mineralization rates. Thermal decomposition of organic matter by fire (pyrolysis) causes a release of available N from organic layers that may be translocated to mineral soil (Rowe and Scotter 1973). Third, many plants have adapted to severe, stand-replacing fires by acquiring traits that confer their successful establishment postfire. The resulting postfire plant abundance and composition affects N availability by modifying ecosystem N inputs, mineralization rates, and plant N uptake. For example, after severe fire in areas of high prefire serotiny, high tree density affects litter lignin content, potentially constraining mineralization rates. Below, we synthesize what is known about postfire N cycling after severe, stand-replacing fires in northern temperate and boreal systems.

In general, fires alter N cycling over the long term (several centuries) by influencing successional trajectories and altering landscape-level

age-class structures (Harden and others 2003; O'Neill and others 2003 ; Wirth and others 2002). In particular, the influence of severe fires may be significant if they initiate heterogeneous patterns of postfire succession over broad areas (Turner and others 2003) that set the template of successional dynamics, and thus N cycling, for centuries. However, these long-term changes are not within the scope of this review. Rather, we focus on ecosystem effects on N cycling after severe fire through initial postfire stand development (less than 100 years), focusing on N inputs, internal cycling, and outputs.

Nitrogen Inputs

Severe fires affect ecosystem N inputs by increasing the abundance of N-fixing plants. In addition, severe fires may affect N inputs by altering the composition and activity of asymbiotic fixers and affecting canopy interception of precipitation. Alteration of the abundance of N-fixing plants has the largest effect on inputs because this group has the potential to attain the highest rates of fixation. For example, *Ceanothus* spp. fix between 20 and 100 kg N ha^{-1} y^{-1} in the understory of early to midsuccessional ponderosa pine stands in the intermontane west (Busse 2000). This amount is over an order of magnitude greater than estimated annual inputs from asymbiotic fixation (Cleveland and others 1999) or atmospheric deposition in the western United States (Binkley and others 2000) (although N fixation may account for a small proportion of inputs in systems that receive high levels of atmospheric N deposition from industrial and agricultural sources). Although we found few studies that compared these fluxes before and after fire, we identify several reasons why N inputs may respond differently to stand-replacing fires than to fires of lower severity.

First, severe fires alter the abundance of N-fixing plants by drastically decreasing canopy LAI. Simulation models suggest that the high C cost of N fixation decreases the ability of these species to compete effectively for light with nonfixing species (Vitousek and Field 1999), and they predict that abundance of fixers should decline as the canopy closes following severe disturbance (Rastetter and others 2001). These modeling results are supported by observations that N-fixing plants are largely absent from late successional stages of boreal and temperate forests (Schlesinger 1991; Cleveland et al 1999; Crews 1999), although they may persist later in succession in drier systems (Zavitovski and Newton 1967; Vogel and Gower 1998) or in canopy gaps (Wurtz 1995), where competition for light is likely to be low.

A second unique effect of stand-replacing fires is their potential effect on soil seed banks. Many of the common N-fixing species that sprout following fire create seed banks that may endure for several fire cycles (Fenner 1985), allowing persistence through the late successional stages when the canopy is closed. For example, Zavitkovski and Newton (1967) estimated that germinable seeds of *Ceanothus velutinus* had persisted for hundreds of years in the seed bank of a conifer forest in central Oregon despite limited abundance in mature stands. High soil temperatures associated with severe fires may be necessary to break innate dormancy and stimulate germination of some N-fixing species such as *Lupinus arcticus* and *Astragalus umbellatus*, leguminous forbs common in postfire boreal forest stands.

For smaller inputs of N associated with lichens, asymbiotic fixers, and atmospheric deposition, severe fires may variably increase and decrease rates of inputs by altering C substrates for asymbiotic fixers and environmental conditions. There are several possible mechanisms through which severe fires are likely to have unique effects on asymbiotic fixation. First, the death of canopy trees results in large inputs of woody debris and root litter, which may have a positive effect on N inputs in systems where these substrates are important for asymbiotic fixation. In a ponderosa pine stand killed by wildfire in interior British Columbia, for example, decomposer bacteria colonizing decaying roots contributed the most to asymbiotic N fixation on an annual basis (Wei and Kimmins 1998). Second, severe fires may disrupt the physical habitat preferred by asymbiotic N fixers. Feathermoss species on the forest floor of mature boreal conifer stands support epiphytic *Nostoc* spp. that may fix up to 1.5 kg N ha^{-1} y^{-1} and may represent the primary source of biological N fixation in the late succession ecosystem (DeLuca and others 2002). Mosses that have been shown to be associated with N fixation are killed by severe fire and the moss litter layer is consumed. These do not reestablish until the canopy closes again (Van Cleve and others 1983). Similarly, lichens may contribute substantial amounts of N in the canopy of old growth conifer stands in the Pacific Northwest; these epiphytes do not regenerate immediately following fire (Denison and others 1977). Overall, whether asymbiotic N inputs are likely to increase or decrease following severe fires is unclear. Finally, stand replacing fires have the potential to decrease in canopy interception of atmospheric N deposition due to the positive

relationship between LAI and interception in conifer canopies (Chapin and others 2002), but the magnitude of this mechanism is generally poorly understood. Although asymbiotic fixation and deposition fluxes of N are generally low both before and after fire, these mechanisms may be particularly important for between-fire N accumulation in ecosystems where N-fixing plants are rare or absent.

Internal Nitrogen Cycling

In addition to changes in N inputs, severe, stand-replacing fires will also affect internal N cycling because of substantial changes in biotic and abiotic conditions. Internal N cycling in boreal forests after severe fire will be largely affected by postfire changes to the organic layer. Thick organic layers insulate underlying mineral soil from heating and limit downward conduction of heat due to high porosity and high moisture content. Stand-replacing fires result in several changes to the radiative balance at the ground surface: (a) tree canopies are killed, increasing solar insolation; (b) organic layer thickness is reduced, causing decreased insulation, and; (c) the ground surface is charred, decreasing albedo. If the area is underlain by permafrost, this change in radiative forcing causes the permafrost layer to thaw, resulting in increased soil temperatures and biological activity (Bourgeau-Chavez and others 2000; Richter and others 2000). Soil temperature at 20-cm depth may increase fourfold during the 3 years after fire (O'Neill and others 2003), although effects may last for decades (Richter and others 2000). Changes in soil temperature are a function of the temperature gradient at the surface, changes in thermal diffusivity of the organic layer, and the amount of organic matter remaining. In addition to changes in soil temperature, changes in soil moisture and nutrients may also be significant. Changes in soil moisture are a function of soil type, fire severity, and the degree to which permafrost is altered (O'Neill and others 2003; Bourgeau-Chavez and others 2000). Rapid increases in understory vegetation and mosses within a decade after fire may ameliorate immediate abiotic changes.

There are surprisingly few studies that have examined change in soil ammonium or nitrate pools and concentrations after severe, stand-replacing fires (Tables 2 and 3). In a California bishop pine forest, Grogan and colleagues (2000a) observed 2–4 times higher ammonium and nitrate concentrations after fire. N availability has been shown to increase 2–12 times after fire in Alaska (Heilmann 1966; Van Cleve and Dyrness 1985). No changes in nitrate concentration were observed in a Douglas-fir/larch forest (Stark 1977). Van Cleve and Dyrness (1983) observed no significant changes in pools of ammonium and nitrate after experimental fires in Alaska. Similarly, N mineralization rate measured 2, 14, and 21 years after fire was unaffected by wildfire in black spruce forests in Quebec (Simard and others 2001). We are aware of no published studies in severe, stand-replacing systems that quantify significant changes in mineralization rates immediately after fire (Table 4). However, increases in decomposition after severe fire that are a result of altered soil temperature and moisture conditions have been observed (Stark 1977; Van Cleve and Dyrness 1985; O'Neill and others 2003). Decomposition rates may increase 50%–100% when soil temperatures increase 5°C–10°C (Richter and others 2000). Modeling results have shown that 20% of the ground layer in boreal forests may be lost via decomposition 25 years after fire because of increased soil temperatures (Kasischke and others 1995). Increased decomposition may result in releases of C that are the same order of magnitude as combustion (O'Neill and others 2003), although the effects on N cycling are not clear. The effect of severe, stand-replacing fires on total soil or forest floor N is variable (Table 5). Ash deposition to the ground surface may be a source of mineral and organic N (Christensen 1973), but losses of N due to volatilization, ash convection, and leaching may be greater (Boerner 1982; DeBano and Conrad 1978). Postfire total soil N was two-thirds of prefire values in Washington, USA (Grier 1975). Studies in Alaska and Canada have shown either large reductions (Simard and others 2001) or nonsignificant/ variable effects of severe fire on total soil N (Dyrness and others 1989; Beaton 1959; Van Cleve and Dyrness 1985).

There are several reasons to expect greater changes in N mineralization after severe, stand-replacing fires compared with non-stand replacing fires. First, there may be a pulse of organic N as roots turnover after the death of the canopy and understory. Also, severe fires may release N that was previously held in inaccessible forms. In addition, stand-replacing fires in boreal systems may moderate thermal conditions for several years by modifying the properties of the permafrost layer after fire. The combination of increased organic N substrates and enhanced abiotic conditions may stimulate mineralization rates after severe fire.

Despite the radical change in physical environment and soil organic content that accompanies stand-replacing fire, the magnitude of changes in N

availability is similar to that in non-stand-replacing systems. There are, however, many fewer studies in severe, stand-replacing systems, limiting our confidence in this generalization. There are several reasons why N availability may not be enhanced dramatically after severe fires. First, the death of the canopy and understory reduces microbial carbon substrates for mineralization. Also, fires tend to consume the relatively young portions of litter and organic mat substrates, leaving older, more decomposed and recalcitrant layers behind, potentially constraining mineralization rates. Second, losses of total N from the soil may be large due to the high temperature of the fires, because N volatilizes at relatively low temperatures (greater than 200°C) (Knight 1966; Boerner 1982). Finally, levels of mineralization are generally low in late-successional conifer forests [1.5–10.2 kg N ha^{-1} y^{-1}) in mature lodgepole pine forests in Yellowstone (Romme and Turner in press)], so fire-induced changes in net N mineralization may be difficult to detect.

Inorganic N concentration, mineralization rates, and total soil N amount are affected by changes in the microbial community. Bissett and Parkinson (1980) observed increases in microbial populations after stand-replacing fires in British Columbia, Canada, attributed to warmer soil temperatures over the growing season and an earlier spring thaw. Recovery of microbial populations is also dependent on adequate soil moisture throughout the growing season following fire (Grogan and others 2000b), which is partially dependent on the depth and quality of organic material that survives the fire. Microbial populations may decrease in size following severe, stand-replacing fires, potentially as a result of intense soil heating (Grogan and others 2000b). Decreases are most dramatic within a year of the fire event but are still evident over a decade later (Dumontet and others 1996). Six years after the fire, the ratio of fungal to bacterial biomass was lower in burned soils despite similar microbial biomass. Changes in fungal-to-bacterial ratios has been attributed to the decreased acidity of burned sites (Bissett and Parkinson 1980), although Grogan and others (2000b) showed that ash deposition did not appear to directly influence microbial populations. Higher charcoal amounts after severe fires may change community composition of understory vegetation and associated fungi (Wardle and others 1997; Pietikäinen and others 2000).

The abundance of mycorrhizal fungi after severe fire may be dependent on the survival of the host tree and the ability of postfire mycorrhizae to colonize new tree seedlings. Thus, following canopy death resulting from severe fire, mycorrhizal communities may be negatively affected (Dahlberg 2002; Visser 1995), although some of the mycorrhizal community may survive because severe heat may extend only to the top few centimeters. It is reasonable to assume that because mycorrhizae have evolved with their hosts, higher plants adapted to severe fires, they would also exhibit adaptations to fire such as dormant spores and/or resistant propagules (Baar and others 1999; Visser 1995). Evidence of the resiliency of mycorrhizae was exhibited by widespread mycorrhizal colonization of lodgepole pine seedlings 1 or 2 years after severe fire near Grand Teton National Park, Wyoming (Miller and others 1998). The species composition of postfire fungal communities may be a function of the surviving mycelial network among trees (even if those trees are killed) and of successional trajectories initiated by fire (Jonsson and others 1999; Visser 1995; Grogan and others 2000b). In Fenno-Scandinavia, only two ectomycorrhizal fungal taxa exclusively fruit after severe fires (Dahlberg 2002), although three morphologically distinct types of mycorrhizae were found after severe fire in Grand Teton National Park (Miller and others 1998).

The primary factors controling microbial community survival immediately after fire are fire severity (which affects survival of the host tree, combustion of the organic layer, and postfire abiotic conditions) and the prefire fungal or bacterial community composition (including characteristics that convey survival or propagation). The survival of the microbial bacterial and fungal communities determines the rates of mineralization and the ability of plants to acquire N from the soil. Subsequent changes in the microbial community biomass and composition will increasingly reflect changes in quantity/quality of soil organic matter and vegetation recovery (species and biomass) rather than direct fire effects on the microbial community. Perhaps because of a combination of these direct and indirect factors, several authors have shown that changes in microbial communities extend at least a decade following a severe fire event.

Nitrogen Outputs

The death of most trees following stand-replacing fires results in the death of tree roots, loss of mycorrhizal associations (Grogan and others 2000b), and, therefore, a loss of nutrient uptake by trees. However, nutrient uptake from resprouting understory vegetation can be large enough to prevent

most N loss to streams and lakes (McColl and Grigal 1977). If fires are sufficiently severe to eliminate resprouting vegetation, this also eliminates most plant uptake, causing N losses to groundwater (Stark 1977). The extent to which this N retention results from plant uptake, microbial uptake, or residual exchange capacity of organic matter has not been evaluated. Nutrient uptake gradually increases after fire as root biomass recovers. In Alaska, postfire aspen has a three-fold higher capacity to absorb phosphate per gram of root than in late successional stands; in black spruce, uptake capacity per gram root remains high for about 60 years after fire before declining (Chapin and Van Cleve 1981). These successional changes in uptake capacity and in nutrient availability are much smaller than the changes in root biomass that occur through postfire succession, suggesting that root biomass is the primary determinant of successional changes in nutrient uptake by vegetation after fire. In a *Pinus banksiana* forest, it takes approximately 20 years (one-third of the typical fire return interval) before plant N stock returns to 50% of the prefire quantity present before the fire (MacLean and Wein 1977; Chapin and Van Cleve 1981).

There is a positive correlation between fire return time and the time required for biomass and nutrient stocks to return to prefire levels (Chapin and Van Cleve 1981). Ecosystems characterized by stand-replacing fires are therefore at one extreme of fire-prone ecosystems in the time required for recovery of stand-level nutrient uptake and accumulation. The 20-year period required for *Pinus banksiana* stands to accumulate 50% of the original N stock following a stand-replacing fire (33% of the average fire interval; MacLean and Wein 1977) contrasts with 8 years for resprouting heath (75% of the average fire interval; Chapman 1967) and 9 months for a resprouting subtropical marsh (25% of the average fire interval; Steward and Ornes 1975).

Spatial Heterogeneity in Postfire N Cycling

Understanding postfire N cycling in any system is complicated by spatial variation in ecosystem responses. Stand-replacing fires do not homogenize the landscape; rather, they produce a spatially complex mosaic of burned patches encompassing a wide range of burn severities (Christensen and others 1989; Turner and others 1994; Foster and others 1998). Variation in patch size and burn severity in turn influence postfire plant communities (M.G. Turner and others 1997, 1999), and N cycling following stand-replacing fire is also likely to exhibit significant spatial variation. However, postfire spatial variation in N cycling is not well documented.

Soon after fire, the redistribution of ash by wind and water can produce substantial spatial heterogeneity in soil N availability, as observed in a *Pinus muricata* stand in California (Grogan and others 2000a). Ash stimulated postfire primary production and ecosystem N retention through direct inputs from ash to soils, accounting for one-third of the increases in total N, and indirect effects on soil N availability to plants (Grogan and others 2000a). Species that resprout following fire were stimulated in the presence of ash (Grogan and others 2000a). Because surface ash is rapidly displaced following fire, accumulating in local depressions or the leeward side of stumps and fallen trees (Wright 1976), this redistribution is likely to create heterogeneity in postfire N availability.

The spatial heterogeneity of fire influences the composition and abundance of herbaceous vegetation for several years following fire. Between vegetated and open areas, differences in soil moisture may lead to significant variability in rates of N cycling (Klopatek and others 1990; Binkley and others 1992). In addition, differences in N utilization, leaching, or soil microclimates among different plant species also may produce spatial variation in concentrations of ammonium or nitrate (Stock and Lewis 1986) or N cycling rates (Christensen and Muller 1975). Over longer periods of time, feedback between the postfire plant community and the soil (for example, Hobbie 1992) should lead to patterns of variability associated with heterogeneity in postfire vegetation.

After stand-replacing fires, we expect to see significant spatial variation in N cycling at different spatial scales. At broad scales, N cycling may vary with postfire tree density throughout the burned forest. Controls on serotiny, which control postfire density in several conifer species, are not well understood but are likely a response to repeated, severe fires (Turner and others 2003; Schoennagel and others in press). At fine scales, N cycling should vary with local species composition, as well as CWD and organic matter consumption. Severe, stand-replacing fires may differentially affect these postfire characteristics compared with fires of lower severity.

Future Directions

To further understanding of postfire N cycling after severe, stand-replacing fires in northern coniferous systems, we recommend three broad categories of

research and suggest several questions to stimulate research in these areas.

(1) The Role of the Organic Layer in Postfire N Availability

As an important characteristic of northern coniferous forests, understanding how the organic layer is altered by severe, stand-replacing fire is critical for understanding effects on N cycling. Based on the published literature, the thermal properties of the organic layer are substantially altered by severe fire, which may affect microbial activity and mineralization rates. Changes to organic layers may also affect residual exchange capacity controling N outputs and germination of soil seed banks controling N inputs. However, several questions remain. How does severe, stand-replacing fire affect postfire N and C availability from the organic and the mineral soil layers? Are changes in abiotic properties of the organic layer more or less important than changes in substrate availability in affecting microbial activity and N cycling?

(2) Plant and Microbial Adaptation to Severe, Stand-Replacing Fire

The composition and abundance of plant and microbial communites after severe, stand-replacing fires control N inputs by influencing N fixation, control internal N cycling by affecting mineralization and immobilization rates, and control N outputs by affecting root biomass and N uptake patterns through time. Severe fires may particularly control biotic adaptation to fire. However, there are few studies relating specific plant adaptations to severe fire and N cycling, and even fewer studies on how microbial communities may be (or not be) adapted to severe fire or how these adaptations may affect N cycling. Several interesting research questions remain. Is there a predictable successional trajectory of microbial communities after severe, stand-replacing fire? How has the microbial community adapted to severe fires (resistant spores, seed banks in the soil)? What is the relative importance of changes in abiotic conditions, substrate, and plant composition on postfire microbial populations and N uptake?

(3) Fine- and Broad-Scale Postfire Spatial Heterogeneity

Severe, stand-replacing fires do not homogenize the landscape. Rather, they create spatial patterns (for example, in postfire tree density, CWD biomass, ash deposition) that are likely to influence N cycling for decades. However, several questions remain. What are the dominant mechanisms creating spatial variability in postfire mineral soil N availability? To what extent are these mechanisms a result of prefire conditions (variation in drainage patterns), the fire event itself (variation in fire behavior), or postfire circumstances (tree density, location of N fixers)? Under what circumstances does fine-scale variability in drainage patterns, ash deposition, or positioning of CWD impede the ability to make broad-scale conclusions? At broad scales, are off-site emission losses from severe fires transferred to the stratosphere and deposited at other locations?

Conclusion

Large, infrequent disturbances (LIDs) are known to affect ecosystem processes for decades after the disturbance event. Their lasting impact is manifested in heterogeneity in the spatial distribution of disturbance severities, as well as biotic and abiotic legacies (Turner and others 1998; Foster and others 1998). As one type of LID, severe, stand-replacing fires may have an immediate and lasting effect on N availability in northern coniferous systems. The articles described herein clearly demonstrate that ecologists have observed differing patterns of postfire N availability. However, predicting postfire N availability among systems is hampered by a lack of understanding of the mechanisms controling these patterns. Changes in abiotic conditions caused by the opening of the canopy, changes in ground layer depth and characteristics, and postfire plant adaptations affecting N fixation and uptake are mechanisms that may strongly affect N cycling after stand-replacing fires compared with fires of lower severity. More experimental work, in conjunction with synthetic efforts, is necessary to inform managers and policymakers of the effects of natural wildfires on long-term ecosystem function.

ACKNOWLEDGEMENTS

This article was greatly improved by comments from two anonymous reviewers.

REFERENCES

Adams MA, Attiwill PM. 1991. Nutrient balance in forests of northern Tasmania. 2. Alternation of nutrient availability and soil-water chemistry as a result of logging, slash-burning and fertilizer application. For Ecol Manage 44:115–131.

Ahlgren IF, Ahlgren CE. 1960. Ecological effects of forest fires. Bot Rev 26:483–533.

Andreu V, Rubio JL, Forteza J, Cerni R. 1996. Postfire effects on soil properties and nutrient losses. Int J Wildl Fire 6:53–58.

Auld TD, O'Connell MA. 1991. Predicting patterns of postfire germination in 35 eastern Australian Fabaceae. Austral J Ecol 16:53–70.

Baar J, Horton TR, Kretzer AM, Bruns TD. 1999. Mycorrhizal colonization of Pinus muricata from resistant propagules after a stand-replacing wildfire. New Phytol 143:409–18.

Baker W. 2000. Fires and climate in forested landscapes of the U.S. Rocky Mountains. In: Kasischke ES, Stocks BJ, editors. Fire, Climate Change, and Carbon Cycling in the Boreal Forest. New York: Springer-Verlag. p 120–57.

Baldwin IT, Morse L. 1994. Up in smoke II. Germination of *Nicotiana attenuatua* in response to smoke-derived cues and nutrients in burned and unburned soils. J Chem Ecol 20:2373–91.

Balling RC Jr, Meyer GA, Wells SG. 1992. Relation of surface climate and burned area in Yellowstone National Park. Agric For Meteorol 60:285–93.

Beaton JD. 1959. The influence of burning on the soil in the timber range area of Lac le Jeune, British Columbia. Can JSoil Sci 39:6–11.

Belillas CM, Feller MC. 1998. Relationships between fire severity and atmospheric and leaching nutrient losses in British Columbia's coastal western hemlock zone forests. Int J Wildl Fire 8:87–101.

Bell RL, Binkley D. 1989. Soil nitrogen mineralization and immobilization in response to periodic prescribed fire in a loblolly pine plantation. Can J For Res 19:816–20.

Bessie WC, Johnson EA. 1995. The relative importance of fuels and weather on fire behavior in subalpine forests. Ecology 76:747–62.

Binkley D, Richter D, David MB, Caldwell BA. 1992. Soil chemistry in a loblolly/longleaf pine forest with interval burning. Ecol Applications 2:157–164.

Binkley D, Son Y, Valentine DW. 2000. Do forests receive occult inputs of nitrogen?. Ecosystems 3:321–31.

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 58:1704–21.

Blair JM. 1997. Fire, N availability, and plant response in grasslands: a test of the transient maxima hypothesis. Ecology 78:2359–68.

Boerner REJ. 1982. Fire and nutrient cycling in temperate ecosystems. Bioscience 32:187–92.

Bourgeau-Chavez LL, Alexander ME, Stocks BJ, Kasischke ES. 2000. Distribution of forest ecozones and carbon in the North American boreal zone. In: Kasischke ES, Stocks BJ, editors. Fire, Climate Change, and Carbon Cycling in the North American Boreal Forest. New York: Springer-Verlag. p 111–31.

Bradstock RA, Auld TD. 1995. Soil temperatures during experimental bushfires in relation to fire intensity: consequences for legume germination and fire management in south-eastern Australia. J Appl Ecol 32:76–84.

Busse MD. 2000. Suitability and use of the 15N-isotope dilution method to estimate nitrogen fixation by actinorhizal shrubs. For Ecol Manage 136:85–95.

Campbell GS, Jungbauer JD, Bidlake WR, Hungerford RD. 1994. Predicting the effect of temperature on soil thermal conductivity. Soil Sci 158:(5)307–13.

Chapin FS III. 1980. The mineral nutrition of wild plants. Annu Rev Ecol Syst 11:233–60.

Chapin FS III, Van Cleve K. 1981. Plant nutrient absorption and retention under differing fire regimes. In: Mooney HA, Bonnickson TM, Christensen NL, Lotan JE, Reiners WA, editors. Fire Regimes and Ecosystem Processes. USDA Forest Service General Technical Report WO-26. Washington, DC: p 301–321.

Chapin FS III, Matson PA, Mooney HA. 2002. Principles of Terrestrial Ecosystem Ecology New York: Springer-Verlag.

Chapman SB. 1967. Nutrient budgets for a dry heath ecosystem in the south of England. J Ecol 55:677–89.

Choromanska U, DeLuca TH. 2001. Prescribed fire alters the impact of wildfire on soil biochemical properties in a ponderosa pine forest. Soil Sci Soc Am J 65:232–8.

Choromanska U, DeLuca TH. 2002. Microbial activity and nitrogen mineralization in forest mineral soils following heating: evaluation of postfire effects. Soil Biol Biochem 34:263–71.

Chorover J, Vitousek PM, Everson DA, Esperanza AM, Turner D. 1994. Solution chemistry profiles of mixed-conifer forests before and after fire. Biogeochemistry 26:115–44.

Christensen NL. 1973. Fire and the nitrogen cycle in California chaparral. Science 181:66–8.

Christensen NL, Muller C. 1975. Effects of fire on factors controlling plant growth in Adenostoma chaparral. Ecol Monogr 45:29–55.

Christensen NL, Agee JK, Brussard PF, Hughes J, Knight DH, Minshall GW, Peek JM, Pyne SJ, Swanson FJ, Thomas JW, Wells S, Williams SE, Wright HA. 1989. Interpreting the Yellowstone fires of 1988. BioScience 39:678–85.

Cleveland CC, Townsend AR, Schimel DS, Fisher H, Howarth RW, Hedin LO, Perakis SS, Latty EF, Von Fischer JC, Elseroad A, Wasson MF. 1999. Global patterns of terrestrial biological nitrogen (N2) fixation in natural ecosystems. Global Biogeochem Cycles 13:623–45.

Conard SG, Sukhinin AL, Stocks BJ, Cahoon DR, Davidenko DP, Ivanova GA. 2002. Determining effects of area burned and fire severity on carbon cycling and emissions in Siberia. Climatic Change 55:(1-2)197–211.

Covington WW, Sacket SS. 1986. Effect of periodic burning on soil nitrogen concentrations in Ponderosa Pine. Soil Sci Soc Am J 50:452–7.

Covington WW, Sacket SS. 1992. Soil mineral nitrogen changes following prescribed burning in ponderosa pine. For Ecol Managet 54:175–91.

Covington WW, DeBano LF, Huntsberger TG. 1991. Soil nitrogen changes associated with slash pile burning in pinyon-juniper woodlands. For Sci 37:347–55.

Crews TE. 1999. The presence of nitrogen fixing legumes in terrestrial communities: evolutionary vs. ecological considerations. Biogeochemistry 46:233–46.

Dahlberg A. 2002. Effects of fire on ectomycorrhizal fungi in Fennoscandian Boreal forests. Silva Fennica 36:69–80.

Dale VH, Joyce LA, McNulty S, Neilson RP, Ayres MP, Flannigan MD, Hanson PJ, Irland LC, Lugo AE, Peterson CJ, Simberloff D, Swanson FJ, Stocks BJ, Wotton BM. 2001. Climate change and forest disturbances. Bioscience 51:723–34.

DeBano LF, Conrad CE. 1978. The effects of fire on nutrients in a chaparral ecosystem. Ecology 59:489–97.

DeBano LF, Eberlein GE, Dunn PH. 1979. Effects of burning on chaparral soils: I. Soil Nitrogen. Soil Sci Soc Am J 43:503–9.

DeLuca TH, Zouhar KL. 2000. Effects of selection harvest and prescribed fire on the soil nitrogen status of ponderosa pine forests. For Ecol Manage 138:263–71.

DeLuca TH, Zackrisson O, Nilsson M-C, Sellstedt A. 2002. Quantifying nitrogen-fixation in feather moss carpets of boreal forests. Nature 419:917–20.

Denison R, Caldwell B, Bormann B, Eldred L, Swanberg C, Anderson S. 1977. The effects of acid rain on nitrogen fixation in Western Washington USA coniferous forests. Water Air Soil Pollut 8:21–34.

Dumontet S, Dinel H, Scopa A, Mazzatura A, Saracino A. 1996. Postfire soil microbial biomass and nutrient content of a pine forest soil from a dunal Mediterranean environment. Soil Biol Biochem 28:1467–75.

Dunn PH, DeBano LF, Eberlein GE. 1979. Effects of burning on chaparral soils: II. Soil microbes and nitrogen mineralization. Soil Sci Soc Am J 43:509–14.

Dyrness CT, Van Cleve K, Levison JD. 1989. The effect of wildfire on soil chemistry in four forest types in interior Alaska. Can J For Res 19:1389–96.

Ewel JJ, Berish C, Brown B, Price N, Raich J. 1981. Slash and burn impacts on a Costa Rican wet forest site. Ecology 62:816–29.

Fahnestock GR, Agee JK. 1983. Biomass consumption and smoke production by prehistoric and modern forest fires in western Washington. J Forestry 81:653–7.

Feller MC. 1988. Relationships between fuel properties and slashburning-induced nutrient losses. For Sci 34:998–1015.

Feller MC, Kimmins JP. 1984. Effects of clearcutting and slash burning on streamwater chemistry and watershed nutrient budgets in Southwestern British Columbia. Water Resour Res 20:29–40.

Fenn ME, Poth MA, Dunn PH, Barro SC. 1993. Microbial N and biomass, respiration and N mineralization in soils beneath two chaparral species along a fire-induced age gradient. Soil Biol Biochem 25:457–66.

Fenner M. 1985. Seed Ecology London: Chapman and Hall, 151 p.

Flannigan MD, Wotton BM. 2001. Climate, weather and area burned. In: EA Johnson, Miyanishi K, editors, Forest fires. New York: Academic Press. p 351–73.

Flannigan MD, Stocks BJ, Wotton BM. 2000. Climate change and forest fires. Sci Total Environ 262:221–9.

Foster DR, Knight DH, Franklin JF. 1998. Landscape patterns and legacies resulting from large, infrequent forest disturbances. Ecosystems 1:497–510.

Grier CC. 1975. Wildfire effects on nutrient distribution and leaching in a coniferous ecosystem. Can J For Res 5:599–607.

Groeschl DA, Johnson JE, Smith DW. 1993. Wildfire effects on forest floor and surface soil in a table mountain pine-pitch pine forest. Int J Wildl Fire 3:149–54.

Grogan P, Bruns TD, Chapin FS III. 2000a. Fire effects on ecosystem nitrogen cycling in a Californian bishop pine forest. Oecologia 122:537–44.

Grogan P, Baar J, Bruns TD. 2000b. Below-ground ectomycorrhizal community structure in a recently burned bishop pine forest. J Ecol 88:1051–62.

Grove TS, O'Connell AM, Dimmock GM. 1986. Nutrient changes in surface soils after an intense fire in jarrah (*Eucalyptus marginata* Donn ex Sm.) forest. Austral J Ecol 11:303–17.

Harden JW, Mack M, Veldhuis H, Gower ST. 2003. Fire dynamics and the implications for nitrogen cycling in boreal forests. J Geophys Res 108(D3):WFX 4-1-4–8.

Heilman PE. 1966. Change in distribution and availability of nitrogen within forest succession on north slopes in interior Alaska. Ecology 47:825–31.

Hobbie SE. 1992. Effects of plant species on nutrient cycling. Trends Ecol Evol 7:336–9.

Hobbie SE, Schimel JP, Trumbore SE, Randerson JR. 2000. Controls over carbon storage and turnover in high-latitude soils. Global Change Biol 6:196–210.

Hobbs NT, Schimel DS. 1984. Fire effects on nitrogen mineralization and fixation in mountain shrub grassland communities. J Range Manage 37:402–5.

Johnson EA. 1992. Fire and vegetation dynamics New York: Cambridge University Press.

Johnson EA, Wowchuck DR. 1993. Wildfires in the southern Canadian Rocky Mountains and their relationship to mid-tropospheric anomalies. Can J For Res 23:1213–22.

Johnson DW, Susfalk RB, Dahlgren RA. 1997. Nutrient fluxes in forests of the eastern Sierra Nevada mountains, United States of America. Global Biogeochem Cycles 11:673–81.

Johnson DW, Susfalk RB, Dahlgren RA, Klopatek JM. 1998. Fire is more important than water for nitrogen fluxes in semi-arid forests. Environ Sci Policy 1:79–86.

Jonsson L, Dahlberg A, Nilsson M-C, Karen O, Zackrisson O. 1999. Continuity of ectomycorrhizal fungi in self-regenerating boreal *Pinus sylvestris* forests studied by comparing mycobiont diversity on seedlings and mature trees. New Phytol 142:151–62.

Kajii Y, Kato S, Streets DG, Tsai NY, Shvidenko A, Nilsson S, McCallum I, Minko NP, Abushenko N, Altyntsev D, Khodzer TV. 2002. Boreal forest fires in Siberia in 1998:estimation of area burned and emissions of pollutants by advanced very high resolution radiometer data. J Geophys Res 107:(D24)4-1-4–8.

Kasischke ES, Bruhwiler LM. 2003. Emissions of carbon dioxide, carbon monoxide and methane from boreal forest fires in 1998. J Geophys Res 108:(DA)FF 2-1-2–14.

Kasischke ES, Stocks BJ, editors. 2000. Fire, Climate Change, and Carbon Cycling in the Boreal Forest New York: Springer-Verlag.

Kasischke ES, Christensen NL Jr, Stocks BJ. 1995. Fire, global warming, and the carbon balance of boreal forests. Ecol Appl 5:437–51.

Kasischke ES, O'Neill KP, French NHF, Bourgeau-Chavez LL. 2000. Controls on patterns of biomass burning in Alaskan boreal forests. In: Kasischke ES, Stocks BJ, editors. Fire, Climate Change, and Carbon Cycling in the North American Boreal Forest. New York: Springer-Verlag. p 173–96.

Kasischke ES, Williams D, Barry D. 2002. Analysis of the patterns of large fires in the boreal forest region of Alaska. Int J Wildl Fire 11:131–44.

Kaye J, Hart SC. 1998. Ecological restoration alters nitrogen transformations in a ponderosa pine-bunchgrass ecosystem. Ecol Appl 8:1052–60.

Klopatek J, Klopatek CC, DeBano LF. 1990. Potential variation of nitrogen transformations in pinyon-juniper ecosystems resulting from burning. Biol Fertil Soils 10:35–44.

Knight DH. 1966. Loss of nitrogen from the forest floor by burning. Forestry Chronicle 42:149–52.

Knoepp JD, Swank WT. 1993. Site preparation burning to improve southern Appalachian pine-hardwood stands: nitrogen responses in soil, soil water, and streams. Can J For Res 23:2263–70.

Kovacic DA, Swift DM, Ellis JE, Hakonson TE. 1986. Immediate effects of prescribed burning on mineral soil nitrogen in ponderosa pine of New Mexico. Soil Sci 141:(1)71–6.

Kozlowski TT, Ahlgren CE. 1974. Fire and Ecosystems New York: Academic Press.

Kutiel P, Naveh Z. 1987. The effect of fire on nutrients in a pine forest soil. Plant Soil 104:269–74.

Ley RE, D'Antonio CM. 1998. Exotic grass invasion alters potential rates of N fixation in Hawaiian woodlands. Oecologia 113:179–87.

Limmer C, Drake HL. 1996. Non-symbiotic N_2-fixation in acidic and pH-neutral forest soils: aerobic and anaerobic differentials. Soil Biol Biochem 28:177–83.

Little SN, Ohmann JL. 1988. Estimating nitrogen lost from forest floor during prescribed fires in douglas-fir/western hemlock clearcuts. For Sci 34:152–64.

Lynham TJ, Wickware GM, Mason JA. 1998. Soil chemical changes and plant succession following experimental burning in immature jack pine. Can J Soil Sci 78:93–104.

MacLean DA, Wein RW. 1977. Nutrient accumulation for postfire jack pine and hardwood succession patterns in New Brunswick. Can J For Res 7:562–78.

Mack MC, D'Antonio CM, Ley RE. 2001. Alteration of ecosystem nitrogen dynamics by exotic plants: A case study of C4 grasses in Hawaii. Ecol Appl 11:1323–35.

Matson PA, Vitousek PM, Ewel JJ, Robertson FP. 1987. Nitrogen transformations following tropical forest felling and burning on a volcanic soil. Ecology 68:491–502.

McColl JG, Grigal DF. 1977. Nutrient changes following a forest wildfire in Minnesota: Effects in watersheds with differing soils. Oikos 28:105–12.

Miller SL, McClean TM, Stanton NL, Williams SE. 1998. Mycorrhization, physiognomy, and first-year survivability of conifer seedlins following natural fire in Grand Teton Naitonal Park. Can J For Res 28:115–22.

Monleon VJ, Cromack K Jr, Landsberg JD. 1997. Short- and long-term effects of prescribed underburning on nitrogen availability in ponderosa pine stands in central Oregon. Can J For Res 27:369–78.

Murphy PJ, Mudd JP, Stocks BJ, Kasischke ES, Barry D, Alexander ME, French NHF. 2000. Historical fire records in the North American boreal forest. In: Kasischke ES, Stocks BJ, editors. Fire, Climate Change and Carbon Cycling in the North American Boreal Forests. New York: Springer-Verlag. p 275–88.

Neary DG, Klopatek CC, DeBano LF, Folliott PF. 1999. Fire effects on belowground sustainability: a review and synthesis. For Ecol Manage 122:51–71.

Newland JA, DeLuca TH. 2000. Influence of fire on native nitrogen-fixing plants and soil nitrogen status in ponderosa pine—Douglas-fir forests in western Montana. Can J For Res 30:274–82.

NIFC (National Interagency Fire Center). Fire statistics. www.nifc.gov/stats/index.html. Viewed 9/18/2003.

Nohrstedt HO. 1985. Nonsymbiotic nitrogen fixation in the topsoil of some forest stands in central Sweden. Can J For Res 15:715–22.

Ojima D, Schimel DS, Parton WJ, Owensby CE. 1994. Long- and short-term effects of fire on nitrogen cycling in tallgrass prairie. Biogeochemistry 24:67–84.

O'Neill K, Kasischke ES, Richter DD. 2002. Environmental controls on soil CO_2 flux following fire in black spruce, white spruce, and aspen stands of interior Alaska. Can J For Res 32:(9)1525–41.

O'Neill KP, Kasischke ES, Richter DD. 2003. Seasonal and decadal patterns of soil carbon uptake and emission along an age-sequence of burned black spruce stands in interior Alaska. J Geophys Res 108:(D1)FFR 11-1-11–15.

Pedlar JH, Pearce JL, Venier LA, McKenney DW. 2002. Coarse woody debris in relation to disturbance and forest type in boreal Canada. For Ecol Manage 158:189–94.

Pietikäinen J, Kiikkila O, Fritze H. 2000. Charcoal as a habitat for microbes and its effect on the microbial community of the underlying humus. Oikos 89:231–42.

Prieto-Fernandez A, Acea MJ, Carballas T. 1998. Soil microbial and extractable C and N after wildfire. Biol Fertil Soils 27:132–42.

Raison RJ. 1979. Modification of the soil environment by vegetation fires, with particular reference to nitrogen transformations: a review. Plant Soil 51:73–108.

Rapp M. 1990. Nitrogen status and mineralization in natural and disturbed mediterranean forests and coppices. Plant Soil 128:21–30.

Rastetter EB, Vitousek PM, Field C, Shaver GR, Herbert D, Agren GI. 2001. Resource optimization and symbiotic nitrogen fixation. Ecosystems 4:369–88.

Richter DD, O'Neill KP, Kasischke ES. 2000. Postfire stimulation of microbial decomposition in black spruce (*Picea mariana* L.) forest soils: a hypothesis. In: Kasischke ES, Stocks BJ, editors. Fire, Climate Change, and Carbon Cycling in the Boreal Forest. New York: Springer-Verlag. p 197–213.

Romme WH. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. Ecol Monogr 52:199–221.

Romme WH, Despain DG. 1989. Historical perspective on the Yellowstone fires of 1988. BioScience 39:695–9.

Romme WH, Turner MG. 2004. Ten years after the 1988 Yellowstone fires: is restoration needed? In: Wallace LL, editor. After the Fires: The Ecology of Change in Yellowstone National Park. New Haven (CT): Yale University Press.

Rowe JS, Scotter GW. 1973. Fire in the boreal forest. Quat Res 3:444–64.

Rowe JS, Bergsteinsson JL, Padbury GA, Hermesh R. 1974. Fire studies in the Mackenzie Valley. Canadian Department of Indian and Northern Affairs, Arctic Land Use Research Program. Publication No. Q5-1567-000-EE-A1. Ottawa, 123 pp.

Sabiiti EN, Wein RW. 1987. Fire and *Acacia* seeds: a hypothesis of colonization success. J Ecol 74:937–46.

Saugier, Roy J, Mooney HA. 2001. Estimations of global terrestrial productivity: Converging toward a single number? In: Roy J, Saugier B, Mooney HA, editors. Terrestrial Global Productivity. San Diego: Academic Press. p 543–57.

Schlesinger WH. 1991. Biogeochemistry: an Analysis of Global Change. San Diego: Academic Press, 443 p.

Schoch P, Binkley D. 1986. Prescribed burning increased nitrogen availability in a mature loblolly pine stand. For Ecol Manage 14:13–22.

Schoennagel T, Turner MG, Romme WH. 2003. The influence of fire interval and serotiny on postfire lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) density in Yellowstone National Park (USA). Ecology 84:2967–2978.

Shvidenko AZ, Nilsson S. 2000a. Extent, distribution and ecological role of fire in Russian forests. In: Kasischke ES, Stocks BJ, editors. Fire, Climate Change, and Carbon Cycling in the Boreal Forest. New York: Springer-Verlag. p 132–50.

Shvidenko AZ, Nilsson S. 2000b. Fire and the carbon budget of Russian forests. In: Kassischke ES, Stock BJ, editors, Fire, Climate change and Carbon cycling in the Boreal Forest. 289–311.

Simard DG, Fyles JW, Paré D, Nguyen T. 2001. Impacts of clearcut harvesting and wildfire on soil nutrient status in the Quebec boreal forest. Can J Soil Sci 81:229–37.

Singh RS, Raghubanshi AS, Singh JS. 1991. Nitrogen-mineralization in dry tropical savanna: effects of burning and grazing. Soil Biol Biochem 23:269–73.

Skinner WR, Stocks BJ, Martell DL, Bonsal B, Shabbar A. 1999. The association between circulation anomalies in the Mid-Troposphere and area burned by wildland fire in Canada. Theor Appl Climatol 63:89–105.

St. John TV, Rundel PW. 1976. The role of fire as a mineralizing agent in a Sierran coniferous forest. Oecologia 25:35–45.

Stark NM. 1977. Fire and nutrient cycling in a Douglas-fir/larch forest. Ecology 58:16–30.

Steward KK, Ornes WH. 1975. The autecology of sawgrass in the Florida Everglades. Ecology 56:162–71.

Stock WD, Lewis OAM. 1986. Soil nitrogen and the role of fire as a mineralizing agent in a South African coastal fynbos ecosystem. J Ecol 74:317–28.

Stocks BJ. 1991. The extent and impact of forest fires in northern circumpolar countries. In: Levine JS, editor. Global Biomass Burning: Atmospheric, Climatic, and Biospheric Implications. Cambridge: The MIT Press. p 197–202.

Stocks BJ, Fosberg MA, Lynham TJ, Mearns L, Wotton BM, Yang Q, Jin J-Z, Lawrence K, Hartley GR, Mason JA, McKenney DW. 1998. Climate change and forest fire potential in Russian and Canadian boreal forests. Climatic Change 38:1–13.

Tinker DB, Knight DH. 2000. woody debris following fire and logging in Wyoming lodgepole pine forests. Ecosystems 3:472–83.

Turner CL, Blair JM, Schartz RJ, Neel JC. 1997. Soil N and plant responses to fire, topography, and supplemental N in tallgrass prairie. Ecology 76:1832–43.

Turner MG, Romme WH. 1994. Landscape dynamics in crown fire ecosystems. Landscape Ecol 9:59–77.

Turner MG, Hargrove WH, Gardner RH, Romme WH. 1994. Effects of fire on landscape heterogeneity in Yellowstone National Park, Wyoming. J Veget Sci 5:731–42.

Turner MG, Romme WH, Gardner RH, Hargrove WW. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. Ecol Monogr 67:411–33.

Turner MG, Baker WL, Peterson C, Peet RK. 1998. Factors influencing succession: lessons from large, infrequent natural disturbances. Ecosystems 1:511–23.

Turner MG, Romme WH, Gardner RH. 1999. Prefire heterogeneity, fire severity and plant reestablishment in subalpine forests of Yellowstone National Park, Wyoming. Int J Wildl Fire 9:21–36.

Turner MG, Romme WH, Tinker DB. 2003. Surprises and lessons from the 1988 Yellowstone fires. Front Ecol Environ 1:(7)351–8.

Uhl C, Jordan CF. 1984. Succession and nutrient dynamics following forest cutting and burning in Amazonia. Ecology 65:1476–90.

Van Cleve K, Dyrness CT. 1983. Effects of forest-floor disturbance on soil-solution nutrient composition in a black spruce ecosystem. Can J For Res 13:894–902.

Van Cleve K, Dyrness CT. 1985. The effect of the Rosie Creek fire on soil fertility. Miscellaneous Publication 85-2, Agricultural and Forestry Experiment Station, University of Alaska-Fairbanks, Fairbanks, AL.

Van Cleve K, Dyrness CT, Viereck LA, Fox J, Chapin FS III, Oechel WC. 1983. Taiga ecosystems in interior Alaska. BioScience 33:39–44.

Vance ED, Henderson GS. 1984. Soil nitrogen availability following long-term burning in an oak-hickory forest. Soil Sci Soc Am J 48:184–90.

Viro PJ. 1974. Effects of forest fire on soil. In: Kozlowski TT, Ahlgren CE, editors. Fire and Ecosystems. New York: Academic Press. p 7–45.

Visser S. 1995. Ectomycorrhizal fungal succession in jack pine stands following wildfire. New Phytol 129:389–401.

Vitousek P, Howarth RW. 1991. Nitrogen limitation on land and in the sea: How can it occur? Biogeochemistry 13:87–115.

Vitousek PM, Field CB. 1999. Ecosystem constraints to symbiotic nitrogen fixers: a simple model and its implications. Biogeochemistry 46:179–202.

Vogel JG, Gower ST. 1998. Carbon and nitrogen dynamics of boreal jack pine stands with and without a green alder understory. Ecosystems 1:386–400.

Wan S, Hui D, Luo Y. 2001. Fire effects on nitrogen pools and dynamics in terrestrial ecosystems: a meta-analysis. Ecol Appl 11:1349–65.

Wardle DA, Zackrisson O, Hornberg G, Gallet C. 1997. The influence of island area on ecosystem properties. Science 277:1296–9.

Wei X, Kimmins JP. 1998. Asymbiotic nitrogen fixation in harvested and wildfire-killed lodgepole pine forests in the central interior of British Columbia. For Ecol Manage 109:343–53.

Weston CJ, Attiwill PM. 1990. Effects of fire and harvesting on nitrogen transformations and ionic mobility in soils of *Eucalyptus regnans* forest of south-eastern Australia. Oecologia 83:20–6.

Wirth C, Schulze E-D, Luhker B, Grigoriev S, Siry M, Hardes G, Ziegler W, Backor M, Bauer G, Vygodskaya N.N. 2002. Fire and site type effects on the long-term carbon and nitrogen balance in pristine Siberian Scots pine forests. Plant Soil 242:41–63.

Woodmansee RG, Wallach LS. 1981. Effects of fire regimes on biogeochemical cycles. In: Clark EE, Rosswall T, editors. Terrestrial Nitrogen Cycles. Ecol Bull 33: Stockholm Swedish Lond Use Research Council . p 649–69.

Wright RF. 1976. The impact of forest fire on the nutrient influxes to small lakes in northeastern Minnesota. Ecology 57:649–63.

Wright RJ, Hart SC. 1997. Nitrogen and phosphorus status in a ponderosa pine forest after 20 years of interval burning. Ecoscience 4:526–33.

Wurtz TL. 1995. Understory alder in three boreal forests of Alaska: local distribution and effects on soil fertility. Can J For Res 25:987–96.

Yarie J. 1981. Forest fire cycles and life tables: a case study from interior Alaska. Can J For Res 11:554–62.

Yarie J, Van Cleve K. 2004. Controls on taiga forest production in interior Alaska. In: Chapin FS III, Oswood M, Van Cleve K, Viereck L, Verbyla D, eds. Alaska's Changing Boreal Forest. Oxford: Oxford University Press. p XXX–XXX.

Zackrisson O. 1977. Influence of forest fires on the North Swedish boreal forest. Oikos 29:22–32.

Zavitkovski J, Newton M. 1967. Ecological importance of snowbrush *Ceanothus velutinus* in the Oregon Cascades. Ecology 39:1134–45.