

**FIRE EFFECTS ON SOIL NITROGEN DYNAMICS IN CONIFEROUS FORESTS OF CENTRAL**

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## ABSTRACT

Forest fires are one of the most important natural disturbances in the inland Northwest, USA. Forest fires influence biogeochemical cycles of nitrogen (N) in forest ecosystems. It is critical to understand how forest fires alter N dynamics in soils because N is often a limiting nutrient in coniferous forests of the inland Northwest.

Effects of wildfires on gross fluxes of inorganic N (i.e.  $\text{NH}_4^+$  and  $\text{NO}_3^-$ ) in mineral soils were investigated using  $^{15}\text{N}$  isotope pool dilution in intact cores two years after three wildfires that occurred in summer 2003. Gross nitrification rates were not altered by the wildfires. However, microbial uptake rates of  $\text{NO}_3^-$  and  $\text{NH}_4^+$ , and ammonification rates were significantly reduced in burned soils relative to controls. These reduced N fluxes were caused by reduced carbon (C) availability in burned soils.

Effects of wildfires and prescribed fires on gross inorganic N fluxes in riparian soils were compared using  $^{15}\text{N}$  isotope pool dilution in mixed soils incubated in the lab. Three watersheds burned by wildfires that occurred in summer 2003 and three watersheds burned by prescribed fires conducted in spring 2004 were chosen. All the watersheds burned by wildfires and prescribed fires were paired with control watersheds. Microbial  $\text{NO}_3^-$  uptake rates were reduced significantly in soils burned by both wildfires and prescribed fires compared to their controls. There was no fire effect on gross nitrification rates in either fire types. The wildfires reduced gross  $\text{NH}_4^+$  fluxes relative to controls, on the other hand, there was no such effect observed in soils burned by prescribed fires. Prescribed burns may not impact on soil N dynamics in the same magnitude as wildfires.

An effect of ash, a product of combusted organic matter and plant biomass, on N availability for understory vegetation post-fire was investigated at the Danskin Creek watershed where a wildfire burned a part of the watershed in August, 2002. Ash from burned and organic matter, a major source of ash, from adjacent unburned area were analyzed for their N properties. Ash loads were manipulated at three levels (i.e. double ash, control and no ash) two weeks after the fire. Foliage samples of understory vegetation were collected from the ash-manipulated plots in the following year to analyze N content and  $\delta^{15}\text{N}$ . Ash had lower N content, lower C:N ratio and higher  $\delta^{15}\text{N}$  than organic matter. The results of inferential statistics using linear mixed-effect ANOVA showed positive correlation between ash levels and foliar N content, and negative correlation between ash levels and foliar  $\delta^{15}\text{N}$ . Ash can be a significant N source for understory vegetation post-fire.

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## CHAPTER 1

### INTRODUCTION TO THE DISSERTATION

#### *Forest fires in the Inland Northwest, USA*

Forest fires are one of the most important natural disturbances in coniferous forests of the Inland Northwest, USA (Hessburg and Agee 2003). The region's prolonged hot, dry summer and lightning in thunderstorms promote periodic forest fires. The forest fires in the region are historically characterized as mixed-severity fires (Hessburg and Agee 2003). The fire severity ranges from low-intensity surface fires to stand-replacing fires (Hessburg and Agee 2003). The mixed-severity fires in forests influence species diversity (Arno et al. 1985, Gallant et al. 2003), landscape diversity (Romme 1982) and biogeochemical cycles (Boerner 1982), thus strongly influencing the landscape of the region.

This historical fire-regime, however, has been changed for the past century because of the fire suppression and prevention along with the policies for land uses such as logging and grazing (Hessburg and Agee 2003). The policy has led to biomass accumulation in some forests, which increases susceptibility of catastrophic fires (Arno and Allison-Bunnell 2002). To reduce the susceptibility of catastrophic fires, prescribed burns have been practiced extensively in the region.

#### *Fire effects on Nitrogen biogeochemistry*

Forest fires play an important role in biogeochemistry. Plants, including overstory conifers and understory vegetation, sequester carbon (C) through photosynthesis, which accumulates in forms of plant biomass, organic matter (OM) on forest floors and in

mineral soils between fires. Forest fires oxidize the accumulated C to CO<sub>2</sub> and other products of incomplete combustion, and release them back to the atmosphere in relatively short period of time compared to C sequestration by plants. The amount of C loss through forest fires depends on fire severity. In a high severity fire, up to 95% of C in OM was lost through combustion (Baird et al. 1999), but in low intensity fires, less C is consumed.

Nitrogen (N) is also significantly affected by forest fires. N can be lost through volatilization (Hosking 1938, White et al. 1973). For example, significant amounts of N can be lost from OM on the forest floor, which is a major source of available N for plants and microbes (DeBano 1995). The N loss from OM is correlated with degrees of combustion of OM (Raison et al. 1984), ranging from 10% in a low intensity fire (Covington and Sackett 1984) up to 97% in an intense fire (Grier 1975). N can be also lost from forest ecosystems through leaching post fire (DeLuca and Zouhar 2000). Contradictory to the loss of N, inorganic N (i.e. NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup>) in soils often increases after forest fires (Wan et al. 2001). NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup> are N forms that are readily available for plants and soil microbes. NH<sub>4</sub><sup>+</sup> tends to increase just after fires, stay elevated for approximately one year, and then decrease to background levels (Wan et al. 2001). NO<sub>3</sub><sup>-</sup> tends to increase following increased NH<sub>4</sub><sup>+</sup>, and the elevated soil NO<sub>3</sub><sup>-</sup> level lasts up to several years (Wan et al. 2001).

The increased inorganic N pools post-fire are, however, not simple for interpretation because a pool size is a function of demand and supply (Fig. 1) and N cycling pathways are complex (Fig. 2). Similar-sized pools can result from low, moderate or high supply of N if supply is balanced by demand (Fig. 1abc). There are three possible explanations of the increased pool sizes of the inorganic N in soil post-fire, increased

production rate (Fig. 1d), decreased consumption rate (Fig. 1e), and the combination of increased production and decreased consumption rates (Fig. 1f). Therefore, it is necessary to measure gross flux rates to assess the causes of increased inorganic N pool sizes post fire, and assess the effects of forest fires on N dynamics in soils.

There are many possible causes of changed flux rates that could explain the increases in the inorganic pool sizes post-fire (Table 1). Supply rates of  $\text{NH}_4^+$  can be increased by conversion of organic N to  $\text{NH}_4^+$  by heat (Covington and Sackett 1992), ash deposition (Grogan et al. 2000) and stimulated ammonification in favorable conditions in burned soils (Ahlgren 1974). Demand for  $\text{NH}_4^+$  can be decreased by diminished plant uptake (Wright and Bailey 1982) and microbial uptake due to fire-caused mortality. Forest fires can also create favorable environments to stimulate nitrification. These favorable conditions include increased temperature (Ahlgren 1974), removal of inhibitory chemicals (White 1986), increased substrate for autotrophic nitrification (i.e.  $\text{NH}_4^+$ ), and increased pH by ash (Fowells and Stephenson 1934). Potential causes of decreased demand of  $\text{NO}_3^-$  include decreased  $\text{NO}_3^-$  uptake by plants (Wright and Bailey 1982) and soil microbes (Kaye and Hart 1998). Because of so many factors can influence inorganic N fluxes, it is challenging to assess the direct causes and relative contribution for increased inorganic N pools post-fire.

#### *Importance of assessing fire effects on N dynamics in forest ecosystems*

The regional climate, characterized by cool, moist winters and hot, dry summers, governs the productivity of coniferous forests. The low temperature in winter makes plants dormant and low water availability in soil in late summer limits the growth of

plants. During the growing season between winter and late summer when temperature and water availability are relatively moderate for plant growth, N often limits net primary productivity of coniferous forests in the region (Moore et al. 1991).

One reason for the N limitation in the region is the relatively low N input to the forest ecosystems. Atmospheric N inputs are relatively low compared to eastern U.S. and European forests, ranging from 0.5 to 1.5 kg/ha/yr (National Atmospheric Deposition Program 2007). N input by symbiotic and asymbiotic N fixation is also relatively low in the dry inland forests (Jurgensen et al. 1991). In one of the few studies available, Fahey et al. (1985) reported 0.1 N kg/ha/yr input by symbiotic N fixation in a southeastern Wyoming lodgepole pine (*Pinus contorta* Dougl. Ex Loud.) stand. Asymbiotic N fixation, which is associated with decay of organic matter on the forest floor, is less than 0.5 N kg/ha/yr in the region (Jurgensen et al. 1987). The low N input to the forest ecosystems and N limitation for forest productivity are reflected in low inorganic N concentrations in stream water of headwater ecosystems (Davis and Minshall 1999). These low input and output of N in forest ecosystems, together with observed N limitation for net primary productivity, implies conservative N use by biota of the forest ecosystems with minimum anthropogenic N input (Perakis & Hedin 2002).

In forest ecosystems with conservative N use, fires can have large impacts by removing N through direct combustion and subsequent leaching. Therefore, it is important to know the mechanisms responsible for fires impact on N dynamics in the forest ecosystems and how the biota in the forest ecosystems responds to the impact post fire. The knowledge of the fundamental mechanisms will help us understand how the biota in the N limited ecosystems has adapted to periodic N losses by forest fires and low N

inputs. This knowledge will also help us to predict how the forest ecosystems will respond to changing environments. For example, if the current trends of climate change proceeds, the intensity and frequency of wildfires will increase (Westerling et al. 2006), which, in turn, can lead to further N loss from the ecosystems and, therefore, potentially magnify N limitations for plants in the forests. Another example is increasing atmospheric CO<sub>2</sub> levels, one of the major causes for the climate change. The elevated CO<sub>2</sub> levels can exacerbate N limitation for plants (i.e. progressive N limitation, Luo et al. 2004). The climate change and elevated CO<sub>2</sub> levels together may intensify N limitation in the forest ecosystems and change ecological processes tied to N dynamics.

Another possibility that can alter ecological processes in the forests is prescribed burns practiced extensively as a management tool in the region. The primary purpose of prescribed burns is to reduce the fuel abundance. Another goal is to reintroduce ecological processes associated with historical wildfires. Prescribed burns, however, may not fully mimic wildfires due to their timing (typically early spring and late fall) and lower intensity relative to the historical wildfires.

### *Scope of this dissertation*

In this dissertation, I present three studies about fire effects on N dynamics in forest ecosystems of central Idaho, USA (Fig. 3). Chapter 2 is titled “Wildfire effects on soil gross nitrogen fluxes in coniferous forests of central Idaho, USA.” I studied fire effects on gross fluxes of inorganic N in mineral soils two years after three different wildfires that occurred in summer 2003. The three wildfires are Canyon Creek Fire (CA), Hall Fire (HA) and South Fork Salmon Fire (SF) (Fig. 3). To measure the gross flux of

inorganic N in the soil, I employed  $^{15}\text{N}$  isotope pool dilution methods in intact soils cores in situ. In addition, I examined some important factors (e.g. temperature during incubation in situ, C availability) that could control the gross flux of inorganic N in mineral soils.

Chapter 3 is titled “Fire effects on gross inorganic N fluxes in riparian soils in coniferous forests of central Idaho, USA: Wildfires vs. prescribed burns.” I investigated fire effects on gross fluxes of inorganic N in mineral soil from riparian forests. In addition, I compared the difference between wildfires and prescribed burns in their effects on N dynamics in mineral soils. Soil samples were collected from riparian forests burned by three wildfires used for the study mentioned above, and three prescribed burns implemented in spring 2004. The three prescribed burns are Danskin Creek Fire (DA), Parks Fire (PA) and Sixbit Fire (SI) (Fig. 3). All the burned soils were paired with control soils collected from comparable unburned riparian forests close to the burned forests. I used  $^{15}\text{N}$  isotope pool dilution methods in homogenized soil incubated in the lab.

Chapter 4 is titled “Wildfire effects on nitrogen dynamics and nitrogen stable isotopes in a coniferous headwater ecosystem in Idaho, USA: A case study.” I studied if ash deposition increased available N for plants post-fire by manipulating ash loads. This study was conducted in the Danskin Creek watershed burned by a wildfire in August 2002 (this wildfire at Danskin Creek is different from the Danskin Creek Fire, one of the prescribed burns mentioned in the chapter 3. They are, however, located in close proximity). I examined the difference in N properties between ash and organic matter on the forest floor, a major source of ash. I analyzed foliar N contents and  $\delta^{15}\text{N}$  of understory vegetation collected from ash-manipulated plots to investigate if ash

manipulation changed N availability for regenerating and resprouting understory vegetation.

I close this dissertation with chapter 5, “Final remarks.” I present a brief summary and conclusion of my studies and discuss the future directions for research.

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Table 1. Possible causes of increased supply rates and decreased demand rates of inorganic N in forest soils.

Inorganic N form	Causes to increase supply rate	Causes to decrease demand rate
NH <sub>4</sub> <sup>+</sup>	<ul style="list-style-type: none"> <li>• Pyrolysis of organic N (Covington and Sackett 1992)</li> <li>• N from ash (Grenon et al. 2000)</li> <li>• Stimulated ammonification (Ahlgren 1974)</li> </ul>	<ul style="list-style-type: none"> <li>• Decreased microbial uptake</li> <li>• Decreased plant uptake (Wright and Bailey 1982)</li> </ul>
NO <sub>3</sub> <sup>-</sup>	<p>Increased nitrification due to:</p> <ul style="list-style-type: none"> <li>• Increased pH (Fowells and Stephenson 1934)</li> <li>• Removal of inhibitory chemicals (White 1986)</li> <li>• Increased substrate for autotrophic nitrification (i.e. NH<sub>4</sub><sup>+</sup>)</li> <li>• Favorable environment (e.g. temperature, Ahlgren 1974)</li> </ul>	<ul style="list-style-type: none"> <li>• Decreased microbial uptake (Kaye and Hart 1998)</li> <li>• Decreased plant uptake (Wright and Bailey 1982)</li> </ul>

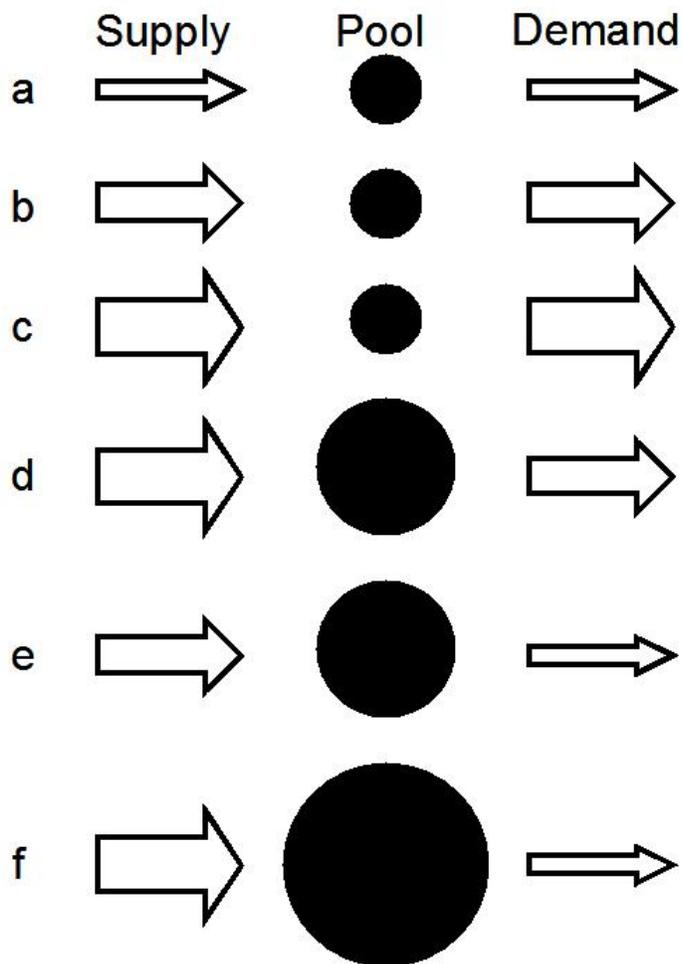


Fig. 1. The schematic relationship among inorganic N pool sizes, supply and demand rates. The sizes of circles reflect the relative sizes of N pools and the arrows reflect the relative flux rates. The combinations of different rates in supply and demand determine the pool sizes at a given time, (a) small pool with low flux rates, (b) small pool with medium flux rates, (c) small pool with high flux rates, (d) medium pool with high supply and medium demand rates, (e) medium pool with a medium supply and low demand rates, and (f) large pool with high supply and low demand rates.

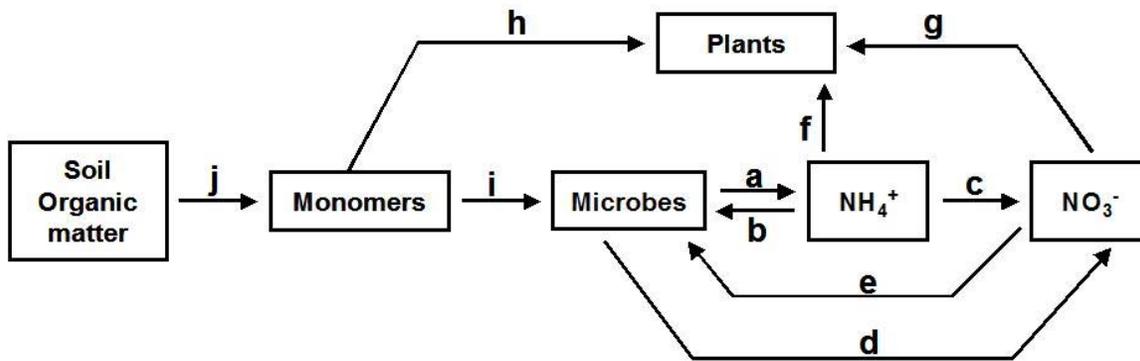


Fig. 2. N cycling model in a forest ecosystem. Boxes and arrows represent N pools and fluxes, respectively. (a) ammonification, (b) microbial  $\text{NH}_4^+$  uptake, (c) autotrophic nitrification, (d) heterotrophic nitrification, (e) microbial  $\text{NO}_3^-$  uptake, (f) plant  $\text{NH}_4^+$  uptake, (g) plant  $\text{NO}_3^-$  uptake, (h) plant organic N uptake, (i) microbial uptake of organic N (relatively small organic molecules), and (j) depolymerization. This figure is adapted and modified from Schimel and Bennett (2004) and Cookson et al. (2006).

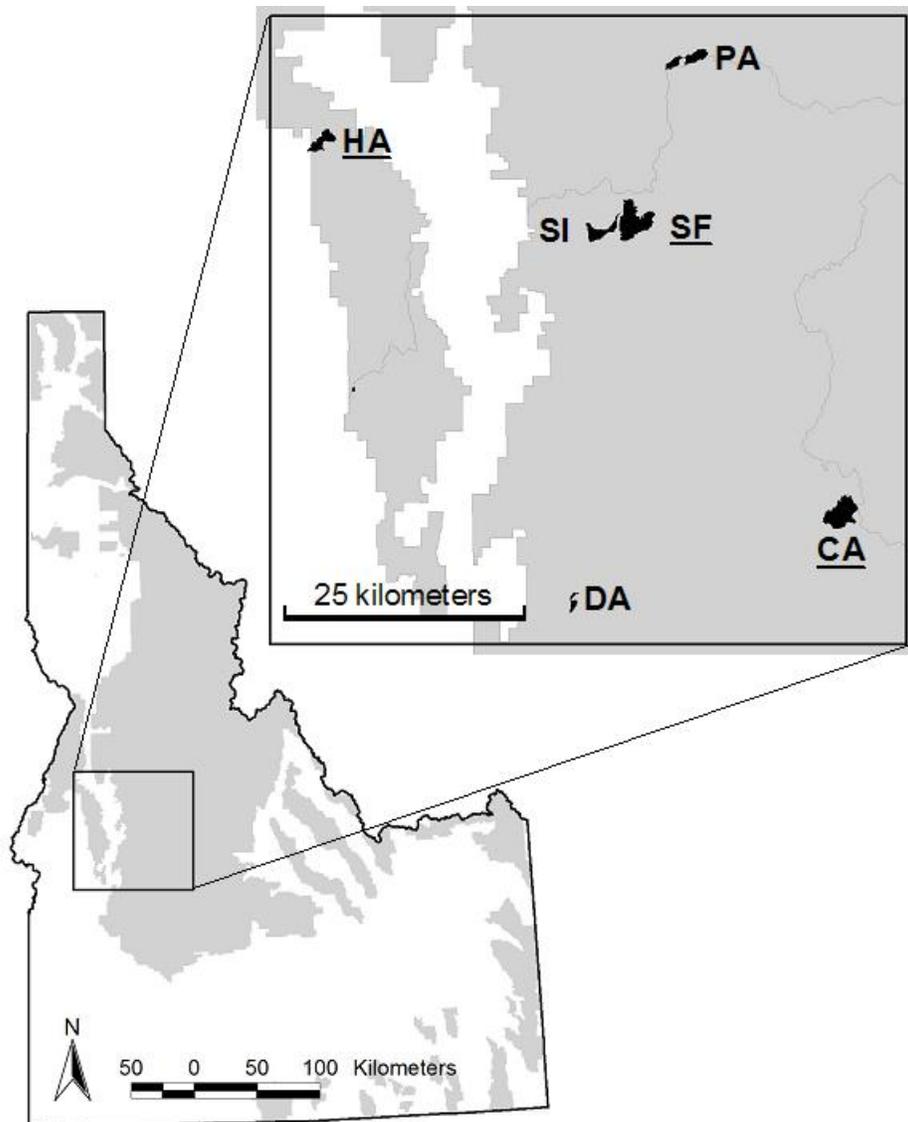


Fig. 3. Map showing the study sites in forests of central Idaho, USA. The gray areas are the National Forests. CA, HA, SF, DA, PA and SI represent Canyon Creek Fire, Hall Fire, South Fork Salmon Fire, Danskin Fire, Parks Fire and Sixbit Fire, respectively. The underlined letters are wildfires (CA, HA and SF), and the others (DA, PA and SI) are prescribed burns.

## CHAPTER 2

### WILDFIRE EFFECTS ON SOIL GROSS NITROGEN FLUXES IN CONIFEROUS FORESTS OF CENTRAL IDAHO, USA

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#### Abstract

Forest fires often increase soil nitrate ( $\text{NO}_3^-$ ) content for several years. The complex and dynamic nature of inorganic nitrogen (N) fluxes in the plant-microbe-soil complex make it challenging to determine the cause of this increased soil  $\text{NO}_3^-$ . We investigated gross inorganic N fluxes in mineral soil two years after three wild fires in central Idaho coniferous forests to determine the causes of the elevated soil  $\text{NO}_3^-$ . We also measured key factors that could affect the gross N fluxes, including temperature during soil incubation *in situ*, soil water contents, pH and available C. We found that there were no significant differences ( $P = 0.461$ ) in  $\text{NO}_3^-$  production rates between burned and control soils. However,  $\text{NO}_3^-$  consumption rates were significantly higher ( $P = 0.012$ ) in control soils than burned soils. The decoupling of supply and demand of  $\text{NO}_3^-$  in burned soils almost certainly caused elevated  $\text{NO}_3^-$  contents relative to controls. Among the measured key factors, available C was the most significant predictor for  $\text{NO}_3^-$  consumption rates. In addition, there were no significant differences ( $P = 0.547$ ) in  $\text{NH}_4^+$  contents between burned and controls soils. The  $\text{NH}_4^+$  fluxes in burned soils were, however, significantly lower ( $P = 0.028$  for ammonification rates, and  $P = 0.001$  for microbial uptake rates) than the controls and the fluxes were positively correlated with available C. We conclude that

availability of C is the main factor that regulates inorganic N dynamics in soils burned by forest fires in coniferous forests of central Idaho.

*Key words*; forest fires, soil, gross N fluxes,  $^{15}\text{N}$  pool dilution, coniferous forests, available C

## **Introduction**

Forest fires are a natural disturbance ubiquitous to many parts of the world including the inland Pacific Northwest (Agee 1993). Forest fires influence the structure and composition of forests (Gallant et al. 2003), landscape diversity (Romme 1982) and biogeochemical cycles (Woodmansee and Wallach 1981, Chorover et al. 1994, Boerner 1982, Raison 1979). With fires, significant amounts of nitrogen (N) can be lost through combustion of forest floor organic matter and above ground biomass (Grier 1975, Raison et al. 1984, Caldwell et al. 2002) and subsequent leaching (Minshall et al. 1997).

One phenomenon often observed post-fire is increased inorganic N ( $\text{NH}_4^+$  and  $\text{NO}_3^-$ ) in soils, which is readily available for plants and soil microbes (Covington and Sackett 1992). Soil  $\text{NH}_4^+$  contents typically increase soon after the fire and then decreases to pre-fire levels within a year (Wan et al. 2001). In contrast, soil  $\text{NO}_3^-$  contents increase more gradually, peaking between 0.5 and 1 year after the fire, and gradually decrease to pre-fire levels within several years (Wan et al. 2001). The prolonged elevated  $\text{NO}_3^-$  concentrations can lead to additional N losses through leaching (Minshall et al. 1997, Woodmansee and Wallach 1981).

Although increased soil inorganic N has been widely reported, the underlying mechanisms are not well understood due to the dynamic nature of soil inorganic N. To assess the mechanisms for post-fire increases in inorganic soil N pools, the relationship between supply and demand of inorganic N (i.e. gross flux rates) need to be measured. For increased  $\text{NO}_3^-$  contents in burned soils, demand factors include reduced N uptake by fire-killed plants (Wright and Bailey 1982) and decreased uptake by soil microbes (Kaye and Hart 1998). N supply is potentially enhanced by favorable environmental conditions for nitrification such as increased temperature (Ahlgren 1974), increased pH (Fowells and Stephenson 1934) and increased substrate (i.e.  $\text{NH}_4^+$ , Stock and Lewis 1986, Covington and Sackett 1992). The relative importance among these factors is not well understood and these factors can interact in the plant-microbes-soils complex.

It is important to understand the fundamental processes that lead to the observed increased inorganic N contents post-fire and following N loss through leaching, because N is often a limiting nutrient for forest productivity (Vitousek and Howarth 1991). Nitrogen is often the most limiting nutrient for conifers in the inland Northwest (Moore et al. 1991). In addition, there is evidence that the intensity and frequency of wildfire will increase if the current trends of climate change in the inland Northwest proceed (Westerling et al. 2006). Accurately predicting the effects of shifting wildfire regimes on N pools and dynamics will require models that are based on a mechanistic understanding of the complex interactions that regulate these pools.

We investigated gross fluxes of inorganic N in mineral soils two years after wildfires in coniferous forests of central Idaho. In addition, several key factors affecting inorganic N fluxes were investigated to determine the relative importance among them.

We also measured net ammonification and nitrification rates in intact soil cores incubated in situ and transferred reciprocally and incubated for one month during the growing season. The purpose of net inorganic N flux measurements was to investigate the relative importance between soil characteristics affected by the fires and environments altered by the fires for soil N dynamics.

## **Materials and Methods**

### *Study sites*

The three study sites are located in coniferous forests of central Idaho (Fig. 1, Table 1). The regional climate is characterized by warm dry summers and cool moist winters. The coniferous forests of central Idaho are historically characterized by mixed-severity fire regime with varying fire intensities from frequent, low-intensity fires to high severity fires (Hessburg and Agee 2003). Three coniferous forests burned by three different wildfires in summer 2003 were selected for this study. The year 2003 was a typical fire year in terms of area burned. In 2003, 85,943 wildland fires (i.e. any non-structure fire that occurs in the wildland) burned approximately 2 million ha nationwide, which was slightly above 10-year average (National Interagency Fire Center 2007). Since it was not possible to collect pre-fire data, we carefully chose our burned sites and paired them with comparable unburned control sites. The criteria for site selection were, 1) severely burned stands with all the dominant conifers killed and organic matter consumed on the forest floor, 2) large enough to set up 30 m by 30 m plots, 3) having control stands with no fire effects in the vicinity (ranging from 70 m to 280 m, Table 1),

with similar topographic features such as slope and aspect, and 4) unaffected by application of N-containing fire retardant.

#### *Inorganic N flux measurements*

Field experiments to measure gross inorganic N fluxes were conducted in late June or early July 2005. We used  $^{15}\text{N}$  pool dilution methods with intact cores to measure gross N fluxes in mineral soils as described in Davidson et al. (1991), Hart et al. (1994a), and Stark (2000). Briefly, to measure five gross N fluxes (a through e in Fig. 2), we used both  $^{15}\text{NH}_4^+$  and  $^{15}\text{NO}_3^-$  in combination with acetylene to inhibit autotrophic nitrification (Stark and Hart 1997). We obtained five intact cores of mineral soil (5 cm diameter and 10 cm deep) within  $0.16\text{ m}^2$  at six randomly selected locations at each site. Larger diameter cores (10 cm diameter and 10 cm deep) surrounding inner cores were used to obtain soils to estimate background inorganic N and water content. All the cores were processed in the shade under a tarp and transported in white cotton bags to avoid effects from direct sun light. Two of the cores were injected with  $(^{15}\text{NH}_4)_2\text{SO}_4$  or  $\text{K}^{15}\text{NO}_3$  (99 atom %  $^{15}\text{N}$ ) and immediately extracted with 2 mol/L potassium chloride (KCl) to assess extraction efficiencies for each N species. The third core was injected with  $(^{15}\text{NH}_4)\text{SO}_4$ . The fourth and fifth cores were injected with  $\text{K}^{15}\text{NO}_3$ , and one of them was placed in a 1 L canning jar with a lid containing a septum, and atomic grade acetylene was injected directly into the core (approximately 10 kpa). Cores 3 to 5 were buried back to the original locations for 24 hours. Following incubation, the soils were extracted with 2 mol/L KCl in pre-weighed specimen cups. The amount of  $^{15}\text{N}$  injected was based on the previously measured background inorganic soil N content at each site. To overcome the

variability of  $\text{NH}_4^+$  contents between inner and outer cores, we chose an 150% increase in N content based on the previously collected data for  $\text{NH}_4^+$  (600 to 700  $\mu\text{g N}$  in 10 mL added tracer solution). To obtain enough  $\text{NO}_3^-$ -N for post-incubation isotopic analyses, 400 to 500  $\mu\text{g}$  of  $\text{NO}_3^-$ -N in 10 mL tracer solution were injected to each core. Temperature data loggers (Thermochron iButton®) were buried at 5 cm depth next to the incubated cores to measure temperature during the field incubation.

The extracted soil samples were brought back in coolers to the lab, mechanically shaken for one hour, filtered (pre-leached Whatman No. 1), and stored frozen before analyses. Rocks larger than 4 mm were removed by sieving to calculate soil chemical and water contents based on soil mass (Paul et al. 1999). Soil water contents were determined by drying soil samples at 105°C for 48 hours. Nitrogen contents ( $\text{NH}_4^+$ -N and  $\text{NO}_3^-$ -N) in KCl extracts were determined using a Lachat AE Low Injection Autoanalyzer (Lachat Instruments, Inc., Milwaukee, Wisconsin, USA). Diffusion methods were used to process the labeled N pools for  $^{15}\text{N}$  analyses (Stark and Hart 1996).  $^{15}\text{N}$  levels were determined by a continuous flow mass spectrometer (Europa Integra, Cheshire, UK) in UC Davis Stable Isotope Facility. Gross rates of ammonification (a in Fig. 2),  $\text{NH}_4^+$  consumption (b plus c in Fig. 2), heterotrophic nitrification (d in Fig. 2; nitrification in acetylene applied soils), total nitrification (c in Fig. 2; nitrification in soils without acetylene), and microbial  $\text{NO}_3^-$  uptake (e in Fig. 2) were calculated based on the equations in Kirkham and Bartholomew (1954), and the flux rates of five processes of our interest (i.e. gross rates of ammonification, microbial  $\text{NH}_4^+$  uptake, autotrophic nitrification, heterotrophic nitrification and microbial  $\text{NO}_3^-$  uptake represented as processes a, b, c, d and e, respectively in Fig. 2) were derived. Gross production rates, rather than gross

consumption rates, were used to calculate mean residence time. This is because the  $^{15}\text{N}$  pool dilution methods can overestimate consumption rates by increasing the labeled N pools (Hart et al. 1994). To calculate  $\text{NO}_3^-$  mean residence time for soils with the  $\text{NO}_3^-$  pool sizes under detection limit (i.e. less than 0.025 mg N/L in soil KCl extracts), the pool sizes were calculated using half the value of the detection limit (i.e. 0.0125 mg N/L in soil KCl extracts).

Net ammonification, nitrification and mineralization were measured using soil incubation in situ in closed-top PVC cylinders (Hart et al. 1994a). Our purpose for the net N flux measurement was to investigate the relative importance of environmental properties associated with fires (e.g. increased temperature in burned plots) against the soil properties affected by fire (e.g. substrate availability for microbial activities in soils). Accordingly, in addition to soils incubated at original locations, we incubated soil cores transferred between burned and control plots within sites. Briefly, at each site, six randomly selected locations at each plot, two mineral soil cores to 10 cm in depth were obtained in PVC cylinders (5 cm diameter and 10 cm deep). After both ends of the cylinders were wrapped by gas-permeable polyethylene films, one was buried at the original location, and the other was transferred to the other treatment plot (burned vs. control) and buried at the corresponding location. The initial inorganic N contents were measured in the same manner as for gross N flux measurements described above. They were incubated for approximately one month at the beginning of the growing season, from late May to late June. The net ammonification, nitrification and mineralization rates were calculated based on the difference in  $\text{NH}_4^+$ ,  $\text{NO}_3^-$ , and total inorganic N ( $\text{NH}_4^+$  plus

NO<sub>3</sub><sup>-</sup>) contents between at the beginning and the end of the incubation periods, respectively.

#### *Analyses for soil properties*

To measure soil carbon (C), pH, soil water content, total N and C:N ratio, samples from the outer core were brought back to the lab on ice in coolers and stored at 4 °C until they were processed. Soil samples were sieved with a 4-mm screen prior to the following measurements (Paul et al. 1999). Short-term respiration potential (C mineralization rate) was used to measure available C as described in Robertson et al. (1999). Briefly, a portion of the sieved soil samples from the five outer cores within the 0.16 m<sup>2</sup> plots were combined and soil water content at field capacity was determined using a pressure plate at -10 kPa. Soil samples (50 g) were adjusted to 50% of the field capacity using deionized water, and incubated in 1-L canning jars at 25°C for 24 hours. Mineralized CO<sub>2</sub> in the air-tight canning jars was trapped in 1 mL of 1.0 mol/L NaOH solution in 10 mL vials, precipitated with BaCl<sub>2</sub>, and excess NaOH was measured by titration with 0.10 mol/L HCl and phenolphthalein to quantify the trapped CO<sub>2</sub>. Mineral soil pH in water was measured following procedures in Thomas (1996). Ten grams of soil samples and 10 mL deionized water were mixed and stirred in beakers, and pH was measured with an Accuet Basic pH meter (Fisher Scientific, Pittsburgh, PA, USA). Nitrogen and C contents were measured by NC 2500 elemental analyzer (CE Instrument, Milan, Italy) connected with a Finnigan MAT DELTA plus isotope ratio mass spectrometer (Bremen, Germany) in the Idaho Stable Isotope Lab (Moscow, Idaho, USA). Microbial biomass N was measured by the chloroform fumigation extraction method (Brookes et al 1985). Fifteen g of soil

sample was extracted with 45 mL of 0.5 mol/L  $K_2SO_4$  and the other 15 g of soil subsample was fumigated with chloroform for 5 days, and extracted with 45 mL of 0.5 mol/L of  $K_2SO_4$ . The alkaline persulfate digest method (Cabrera and Beare 1993) was used to oxidize N to  $NO_3^-$  in  $K_2SO_4$  extracts.  $NO_3^-$  contents in the digested extracts were measured by Alpkem Autoanalyzer FS-3000 (OI Analytical, College Station, Texas, USA) at School of Biological Sciences of Washington State University (Pullman, Washington, USA).

### *Statistical analysis*

Linear mixed-effects ANOVA was employed for statistical analyses in R (Ihaka and Gentleman 1996). Since one of our objectives is to make inferences for coniferous forests of inland Northwest with three replicated sites, we used site (CA, HA and SF, Figure 1, Table 1) as a random effect for all the statistical analyses. Other independent variables were treated as fixed effects. For each analysis, we assessed normality of error effects, and appropriate transformations were applied when necessary.

We note that our study unit is plot (i.e. 30 m by 30 m plot), therefore we have three replications. Because of this small sample size, we took two different approaches for statistical analyses. To analyze the differences between burned and control soils in soil properties and gross N fluxes, values within plots were averaged and analyzed in mixed effects ANOVA. In these cases, we employed  $p = 0.10$  or less for statistical significance considering the relatively small sample size.

Another approach was taken to assess the contribution of the key factors to the five measured gross N fluxes. In these cases, we treated subsamples within plots as

sampling units in mixed effects ANOVA. This approach is taken to prevent the loss of information in the correlated variables within plots. Because of this approach, the statistical results from this approach are partially inferential (Oksanen 2001). This approach was also taken to analyze net N flux rates.

The following procedures were used to assess the contribution of the key factors to the five gross N fluxes. For each of five measured inorganic N flux rates (i.e. ammonification, microbial  $\text{NH}_4^+$  uptake, autotrophic nitrification, heterotrophic nitrification and microbial  $\text{NO}_3^-$  uptake), a combination of some of the following factors were used as fixed effects. The combination of factors selected for the model was based on a priori knowledge of soil N transformations as follows. The first four factors (available C, temperature, pH and soil water content) are all generally considered important for enzymatic activities for soil microbes (Paul and Clark 1996), thus were used for all the statistical analyses. Total N and C:N ratio of mineral soils were added to models for ammonification and heterotrophic nitrification because Total N and C:N are important attributes of substrates (i.e. organic N) for these processes. The pool size of  $\text{NH}_4^+$ , which is the substrate for autotrophic nitrification, was added to a model for autotrophic nitrification. Akaike information criterion was used to evaluate the quality of mixed-effects models when assessing the relative importance among the key factors for N flux rates (Burnham and Anderson 1998).

## Results

Two years following wildfire there was no difference in  $\text{NH}_4^+$  content between burned and control soils (Fig. 3a, Table 2). In contrast,  $\text{NO}_3^-$  which was undetectable in

unburned soils, was readily detected in burned soils (Figure 3b and Table 2) and microbial biomass N decreased in burned soils relative to unburned soils (Fig. 3c, Table 2). Despite the lack of fire effects on  $\text{NH}_4^+$  content two years post-fire, both ammonification and microbial  $\text{NH}_4^+$  uptake were significantly larger in control soils than burned soils (Fig. 4, Table 3). These  $\text{NH}_4^+$  contents and flux rates are contrasting to those of  $\text{NO}_3^-$ . There was no significant difference in nitrification rates (autotrophic, heterotrophic and total nitrification) between burned and control soils (Fig. 5a, Table 3). However, microbial  $\text{NO}_3^-$  uptake rates were significantly larger in control soils than burned soils (Fig. 5b, Table 3). In addition, rates of total nitrification and microbial uptake were similar in burned soils (i.e. close to 1:1 line, Fig. 5c), conversely, microbial  $\text{NO}_3^-$  uptake rates were higher than total nitrification rates (i.e. above 1:1 line, Fig. 5c) in unburned soils. There was no such distinctive difference between burned and control soils for  $\text{NH}_4^+$  fluxes (Fig. 4c).

The mean residence times calculated based on the pool sizes and production rates were also contrasting between  $\text{NH}_4^+$  and  $\text{NO}_3^-$ . There was no significant difference between control and burned soils for  $\text{NH}_4^+$  mean residence time (Fig. 6a, Table 3), ranging from 2.1 days (control, SF) to 20.6 days (control, CA). However, there was a significant difference in  $\text{NO}_3^-$  mean residence time;  $\text{NO}_3^-$  turned over approximately 50% faster in control soils than burned soils (Fig. 6b, Table 3). In addition,  $\text{NO}_3^-$  mean residence time in soils, either burned or control, were shorter than the shortest  $\text{NH}_4^+$  mean residence time (the unit for  $\text{NO}_3^-$  mean residence time is hours, and shortest  $\text{NH}_4^+$  mean residence time is 2.1 days, or 50.4 hours in control soils of SF, Fig. 6).

The potential key factors affecting inorganic flux rates are shown in Fig. 7 and Table 2. Available C, measured as C mineralized under controlled conditions, was significantly higher for control soils relative to burned soils (Fig. 7a, Table 2). Soil temperature at 5 cm in depth during the period of gross N flux measurements was significantly higher in burned soils than control soils (Fig. 7b, Table 2). There was no consistency in soil pH (Fig. 7c, Table 2). Control soils had higher soil water contents than burned soils (Fig. 7d, Table 2). Total N content of mineral soil was higher in control sites than burned sites (Fig. 7e, Table 2). There was no difference in C:N of mineral soils between burned and control soils (Fig. 7f, Table 2).

Each of the five measured inorganic N flux rates (i.e. ammonification, microbial  $\text{NH}_4^+$  uptake, autotrophic nitrification, heterotrophic nitrification and microbial  $\text{NO}_3^-$  uptake) was influenced by different key factors. For ammonification, available C and pH were significant factors (Table 4). For microbial  $\text{NH}_4^+$  uptake, available C was the only significant factor (Table 4). None of the factors was significant for autotrophic nitrification (Table 4), and pH was the only significant factor for heterotrophic nitrification (Table 4). For microbial  $\text{NO}_3^-$  uptake, available C and temperature were significant factors, and surprisingly, the coefficient for temperature was negative (Table 4).

Net ammonification, nitrification and mineralization rates are shown in Fig. 8. Treatment effect was significant for net ammonification and nitrification rates, but transfer and the interaction effects were not significant (Fig. 8ab, Table 5). Either treatment or transfer effects were not significant for net mineralization rates (Fig. 8c, Table 5).

## Discussion

Our results clearly show the effects of fire on mineral soil N dynamics and they illustrate the importance of measuring soil gross N flux rates when interpreting and modeling inorganic N pool sizes. We conducted our experiments two years post-fire when  $\text{NH}_4^+$  content in burned soils had declined to background levels, but when  $\text{NO}_3^-$  contents were still increased as observed in many studies (Wan 2001, Smithwick et al. 2005). The similar soil  $\text{NH}_4^+$  content between treatments could lead to the conclusion that  $\text{NH}_4^+$  dynamics in burned soils were no longer impacted by fire. However, we found that gross ammonification and microbial  $\text{NH}_4^+$  uptake rates in burned soils were still significantly reduced compared to control soils, and the balance between these fluxes partially contributed to the observed  $\text{NH}_4^+$  pool sizes. Thus, while the  $\text{NH}_4^+$  content was similar, the reasons for the  $\text{NH}_4^+$  pool sizes on burned and unburned sites were due to a different set of processes.

Gross  $\text{NO}_3^-$  fluxes established that increased  $\text{NO}_3^-$  contents were caused by reduced microbial  $\text{NO}_3^-$  uptake rates and not by increased nitrification rates. The ratios between nitrification and microbial  $\text{NO}_3^-$  uptake rates in burned soils were close to 1:1 (Fig. 5c). The slight difference between the supply and demand rates of  $\text{NO}_3^-$  can explain the detectable, yet small, sizes of  $\text{NO}_3^-$  pools (Fig. 3b). In contrast, unburned soils have microbial uptake rates that exceed nitrification rates leading to undetectable levels of soil  $\text{NO}_3^-$ . This supports previous evidence that microbial activity is a key factor in soil  $\text{NO}_3^-$  content (Kaye and Hart 1998).

It has been assumed that disturbances, including logging and fire, increase nitrification, increases soil  $\text{NO}_3^-$  content, and thus lead to N loss through  $\text{NO}_3^-$  leaching (e.g. Likens et al. 1969, Christensen 1973, Covington and Sackett 1986, White 1986). In these studies, however, gross nitrification rates were not measured. The increased  $\text{NO}_3^-$  pool sizes in soils and subsequent  $\text{NO}_3^-$  leaching in those studies might be caused partially by decreased microbial  $\text{NO}_3^-$  uptake rates as observed in this study and by Kaye and Hart (1998). However, the observations in this study and by Kaye and Hart (1998) were based on one-time measurement for 24 hours. It is necessary to measure gross  $\text{NO}_3^-$  fluxes multiple times within and among years in different regions to verify the universal causes, if any, for increased  $\text{NO}_3^-$  pool sizes and subsequent  $\text{NO}_3^-$  leaching.

There was a marked difference in mean residence time between the two inorganic N species.  $\text{NH}_4^+$  had relatively long residence time ranging from 2.1 to 20.6 days (Fig. 6a). Conversely,  $\text{NO}_3^-$  had a much shorter mean residence time ranging from 1.5 to 9 hours, even in burned soils (Fig. 6b). The mean residence time of  $\text{NO}_3^-$  in unburned soils is shorter for two reasons. The actual  $\text{NO}_3^-$  pool sizes in most of the control soils was under the detection limit of 0.025ppm therefore we used 0.0125ppm as an estimated value. However the actual value could be smaller than the estimated  $\text{NO}_3^-$  pool size used to calculate the mean residence time. In addition, the gross microbial  $\text{NO}_3^-$  uptake rates in control soils were higher than nitrification rates (Fig. 5c), implying that microbes take up  $\text{NO}_3^-$  as soon as  $\text{NO}_3^-$  is produced. The observed fast turnover rates of  $\text{NO}_3^-$  in conifer forest soils are consistent with the observations by Stark and Hart (1997).

In assessing the relative importance of key factors for inorganic N flux rates, we found that available C is a significant factor for three out of four microbial processes

involving C as an energy source (ammonification, microbial  $\text{NH}_4^+$  uptake and microbial  $\text{NO}_3^-$  uptake rates, Table 4). These findings support the tight coupling of available C and inorganic N flux rates in microcosm studies (Schimel 1986, Hart et al. 1994b, Luxhøi et al. 2006). Available C was also a significant predictor of microbial biomass N ( $F_{1, 33} = 12.4610$ ,  $P = 0.0013$ , with site as a random factor in a mixed effect ANOVA). The significant correlation between available C and these N fluxes and microbial biomass N pools suggests a strong down-regulation in N fluxes due to carbon availability for the inorganic N cycle in soils (Fig. 2).

There are two possible causes for the reduced C availability in burned soils. Soil C in mineral soil was reduced directly by intense fires (Smith 1970, Kutiel and Naveh 1987) and C supply transported belowground was reduced due to removal of aboveground biomass by fire (Bradley et al. 2000). We observed significantly reduced total C in burned soils compared to control soils and total C was significantly positively correlated with available C (data not shown; total C was not included in mixed effects ANOVA to avoid co-linearity issues). We do not know the relative contribution of these two factors (i.e. direct fire effect or reduced C supply) for reduced available C in burned soils. However, based on the growing evidences that the current photosynthate is a significant source for rhizosphere microbes (Göttlicher et al. 2006, Högberg et al. 2001, Phillips and Fahey 2005), reduced C flow from aboveground to soil could be an important influence on reduced available C in burned soils.

It is often thought that plants and soil microbes compete for N as a limiting nutrient (e.g. Jackson et al. 1989, Kaye and Hart 1997, Zak et al. 1990). However  $\text{NO}_3^-$  is tightly cycled by soil microbes and this microbial activity is supported by plant-origin C,

which prevents N loss through  $\text{NO}_3^-$  leaching. This N retention by soil microbes can sustain forest productivity since amounts of N in forests ecosystems are positively correlated with forest productivity (Prescott et al. 2000). Therefore, it can be said that plants and soil microbes are in symbiotic relationship in terms of N.

In addition to available C, temperature was negatively correlated with microbial  $\text{NO}_3^-$  uptake rates (Table 4). This negative correlation is paradoxical since increased temperature stimulates enzymatic activity including  $\text{NO}_3^-$  uptake (Paul and Clark 1996). An alternative interpretation is that increased temperature accelerated the depletion of available C in burned soils with reduced C supply from aboveground biomass, and the relative contribution of temperature to microbial  $\text{NO}_3^-$  uptake was small. Increased soil temperature in the burned area relative to the unburned soil can increase nitrification rates, which leads to high  $\text{NO}_3^-$  contents (Ahlgren 1974). However, soil temperature did not increase either autotrophic or heterotrophic nitrification rates in our study (Table 4). This observed independence of  $\text{NO}_3^-$  fluxes from temperature is consistent with the findings in a microcosm experiment by Grenon et al. (2004). Grenon et al. (2004) showed there was no significant difference between forest soils incubated at field temperature and those incubated at temperature higher than the field temperature by  $10^\circ\text{C}$  in both gross autotrophic and heterotrophic nitrification rates.

Neither ammonification nor microbial  $\text{NH}_4^+$  uptake rates were correlated with temperature (Table 4). However, it has been demonstrated that temperature affects  $\text{NH}_4^+$  flux rates (Puri and Ashman 1998, Grenon et al. 2004). In our study, the difference in C availability between burned and control soils might mask the temperature sensitivity of

$\text{NH}_4^+$  fluxes; i.e. C availability for microbes involving gross  $\text{NH}_4^+$  fluxes was more significant limiting factor than temperature for their activity.

Total N and C:N ratio of soils, attributes for substrates for ammonification and heterotrophic nitrification rates, were not significant factors for either of these fluxes (Table 4). This relationships between C:N ratio for those two fluxes were consistent with the findings of Booth et al. (2005). However, Booth et al. (2005) found that total N content was significantly correlated with ammonification and nitrification. It is possible that the wide range of N contents in their compiled data helped detect the significant correlation between N content and gross ammonification and nitrification rates. The soil N contents used in the meta-analysis by Booth et al. (2005) ranged approximately from 0.1 to 5%. In contrast, the values ranged only from 0.07 to 0.19% in this study.

Soil pH was significantly negatively correlated with ammonification and heterotrophic nitrification rates (Table 4). In contrast, autotrophic nitrification rates, which are considered to be pH sensitive (Dancer et al. 1973, Alexander 1991, Haynes 1986, but see Tarre and Green 2004), did not have any significant correlation with pH (Table 4). A meta-analysis by Booth et al. (2005), that compiled data with pH ranging from 3 to 8, show significant negative correlation between pH and nitrification rates. Further research is needed to address these observations.

It is puzzling that we did not observe significant differences in autotrophic and heterotrophic nitrification rates between burned and control soils (Fig. 5, Table 4). We observed consistently similar nitrification rates within sites (Figure 5a). The difference in C availability between burned and control soils can lead to different autotrophic: heterotrophic nitrification ratios (Penderson et al. 1999). Since C is not the energy source

for autotrophic nitrification (Wood 1986), some other factors are responsible for regulating autotrophic nitrification rates and/or autotrophic bacterial population. Allelopathy inhibiting nitrification (Rice and Pancholy 1972) is not likely because fire can remove inhibitory substances (White 1986b).  $\text{NH}_4^+$  content, the substrate size for autotrophic nitrification, was not correlated with autotrophic nitrification rates (Table 4). One possible explanation is that  $\text{NH}_4^+$  pool sizes obtained using 2 mol/L KCl were not representing available  $\text{NH}_4^+$  for autotrophic bacteria since 2 mol/L KCl can extract  $\text{NH}_4^+$  molecules bound to soil matrix (Kowalenko and Yu 1996). There might be other nutrients essential to enzymatic activities for autotrophic nitrification that regulate autotrophic nitrification rates locally. The observed significance of pH for heterotrophic nitrification rates (Table 4) also requires further research.

Statistical analyses for net ammonification and nitrification confirmed the results of gross N fluxes: environmental changes created by fires were not significantly affecting those inorganic N processes (Table 5). Rather, the properties of soils, including C availability, are the dominant factors that determine inorganic N processes. The net ammonification and nitrification rates at the South Fork (SF) site have different trends from the other two sites (Fig. 8ab). Net ammonification rates were higher in burned soils than control soils in SF site, whereas, these trends were opposite in the CA and HA sites (Fig. 8a). The SF unburned and burned sites in general had much lower net nitrification rates than CA and HA sites (Fig. 8b). In addition, the SF,  $\text{NH}_4^+$  and  $\text{NO}_3^-$  uptake rates by microbes in control soils were higher than production rates compared to the CA and HA sites. These differences in gross flux rates for a single day incubation might have cumulative effects on the one-month-long net mineralization rates. Smaller net

ammonification rates in burned soils than control soils in CA and HA sites are consistent with observation in the Greater Yellowstone ecosystem (Turner et al. 2007). They attributed their results of small net ammonification to the difference between gross ammonification and consumption rates; consumption rates were higher than production rates for up to 15 years after the fire and this trend reversed along a chronosequence for up to 350 years (Turner et al. 2007). We did not find such differences between the ammonification and  $\text{NH}_4^+$  consumption rates (Fig. 4c). The different methods for the flux measurements (mixed soils vs. intact cores) between the two studies might be a reason that the studies do not agree (Booth et al. 2006).

In conclusion, our results indicate that increased  $\text{NO}_3^-$  contents in soils after disturbances were caused by reduced microbial  $\text{NO}_3^-$  uptake capacity associated with decreased C availability (Stark and Hart 1997). Even though  $\text{NO}_3^-$  contents in soils were negligible in undisturbed coniferous forests of central Idaho,  $\text{NO}_3^-$  is produced in a similar magnitude as  $\text{NH}_4^+$ , and tightly cycled by soil microbes (Fig. 3 and 4). In soils intensely burned by forest fires, C input belowground by recovering vegetation, as energy source for soil microbes, would be a key to conserving N in the N-limited coniferous forests of central Idaho. If the ongoing climate change increases severity and frequency of wildfires in the inland Northwest (Westerling et al. 2006), more N would be lost through leaching and volatilization. Since total N in forest soils is an important factor to determine forest productivity (Prescott et al. 2000), increased N loss would intensify N limitation in these coniferous forests.

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Table 1. Site and forest characteristics of the study sites in coniferous forests of central Idaho.

	Canyon Creek Fire	Hall Fire	South Fork Salmon Fire
Abbreviation	CA	HA	SF
Symbols in Figures	●/○	▼/▽	■/□
National Forest	Boise National Forest	Payette National Forest	Boise National Forest
Time of Fires	August 11-22, 2003	August 8-11, 2003	August 10- October 15, 2003
Burned Area (ha)	2244	764	2698
Coordinates	44°11'N, 115°15'W	44°50'N, 116°20'W	44°41'N, 115°42'W
Elevation (m)	1650	1460	1590
Mean Annual Temperature (°C)*	3.8	9.1	4.8
Mean Annual Precipitation (cm)*	81.9	60.9	68.1
Slope (degree)	32	29/25	0
Aspect	West	Southwest	N/A
Distance between burned and control plots (m)	70	280	95
Habitat Type	<i>Pseudotsuga menziesii</i> / <i>Acer glabrum</i> – <i>Acer glabrum</i> phase	<i>Pseudotsuga menziesii</i> / <i>Physocarpus malvaceus</i> – <i>Pinus ponderosa</i> phase	<i>Pinus contorta</i> / <i>Vaccinium caespitosum</i>
Dominant conifer species	<i>Pseudotsuga menziesii</i> var. <i>glauca</i>	<i>Pinus ponderosa</i> var. <i>ponderosa</i> , <i>Pseudotsuga menziesii</i> var. <i>glauca</i>	<i>Pinus contorta</i> var. <i>latifolia</i>
Basal Area (m <sup>2</sup> /ha)†	31.67	33.68	10.8
LAI†	3.90	4.89	2.47
Bedrock Type	Idaho Batholith	Columbia River Basalt	Idaho Batholith
Soil Type‡	Sandy Loam	Sandy Loam	Sandy Loam/Silt Loam

Notes: \* Values of mean annual temperature and precipitation for the sites, CA, HA and SF were obtained from Deadwood Dam, Council and McCall, respectively, the closest measurement station for each site. Data from Western Regional Climate Center.

† Basal area and LAI (leaf area index) are of controls.

‡ Soil type for burned and control plots of SF are Sandy loam and silt loam, respectively.

Table 2. Results of statistical analysis to compare soil properties between burned and control soils. Independent variables are treatment (burned or control, fixed) and sites (random).

Dependent variable	<i>df</i> (Effect)	<i>df</i> (Error)	F-value	P-value
NH <sub>4</sub> <sup>+</sup> content	1	2	0.5164	0.5470
NO <sub>3</sub> <sup>-</sup> content	1	2	82.6299	<b>0.0119**</b>
Microbial Biomass N	1	2	18.2946	<b>0.0506*</b>
Available C	1	2	11.2230	<b>0.0787*</b>
Temperature	1	2	42.6130	<b>0.0227**</b>
pH	1	2	0.0441	0.8532
Soil Water Content	1	2	1.8815	0.3038
N Content of Mineral Soil	1	2	9.2245	<b>0.0935*</b>
C:N Ratio of Mineral Soil	1	2	0.0304	0.8777

*Notes:* Subsample size within burned/control plots at each site is six, except the control plot of HA. Statistically significant p-values are bolded and labeled with \*  $p < 0.10$ , \*\*  $p < 0.05$ , and \*\*\* $p < 0.01$ .

Table 3. Results of statistical analysis to compare gross inorganic N fluxes in mineral soils between burned and control plots. Independent variables are treatments (burned or control, fixed) and sites (random).

Dependent variable	<i>df</i> (Effect)	<i>df</i> (Error)	F-value	P-value
Ammonification	1	2	34.2263	<b>0.0280**</b>
Microbial NH <sub>4</sub> <sup>+</sup> Uptake	1	2	690.2870	<b>0.0014***</b>
Autotrophic Nitrification	1	2	1.3594	0.3639
Heterotrophic Nitrification	1	2	0.3025	0.6375
Total Nitrification	1	2	0.8183	0.4611
Microbial NO <sub>3</sub> <sup>-</sup> Uptake	1	2	24.2655	<b>0.0388**</b>
NH <sub>4</sub> <sup>+</sup> Mean Residence Time	1	2	1.2579	0.3786
NO <sub>3</sub> <sup>-</sup> Mean Residence Time	1	2	58.3671	<b>0.0167**</b>

*Notes:* Subsample size within burned/control plots at each site is  $N_{\text{sub}} = 6$ , except the control plot of HA ( $N_{\text{sub}} = 5$ ). Statistically significant p-values are bolded and labeled with \*  $p < 0.10$ , \*\*  $p < 0.05$ , and \*\*\* $p < 0.01$ .

Table 4. The results of statistical analysis to assess relative importance among key factors for five gross N fluxes in mineral soils using a linear mixed effects ANOVA.

Dependent Variables	Independent Variables						
	Available C	Temperature	pH	SWC	N Content	C:N Ratio	NH <sub>4</sub> <sup>+</sup> Content
Gross Ammonification	CE = 0.0006 F <sub>1, 26</sub> = 6.735 <b><u>P = 0.015*</u></b>	CE = -0.0708 F <sub>1, 26</sub> = 1.311 P = 0.263	CE = -0.1963 F <sub>1, 26</sub> = 7.875 <b><u>P = 0.009**</u></b>	CE = 0.0138 F <sub>1, 26</sub> = 0.214 P = 0.648	CE = -0.0881 F <sub>1, 26</sub> = 1.462 P = 0.238	CE = 0.0743 F <sub>1, 26</sub> = 2.255 P = 0.145	N/A
Microbial NH <sub>4</sub> <sup>+</sup> Uptake	CE = 0.0019 F <sub>1, 28</sub> = 2.170 <b><u>P = 0.002**</u></b>	CE = -0.0540 F <sub>1, 28</sub> = 0.698 P = 0.410	CE = -0.2474 F <sub>1, 28</sub> = 2.133 P = 0.155	CE = 0.0048 F <sub>1, 28</sub> = 0.118 P = 0.7337	N/A	N/A	N/A
Autotrophic Nitrification	CE = -2*10 <sup>-5</sup> F <sub>1, 27</sub> = 0.198 P = 0.660	CE = -0.0067 F <sub>1, 27</sub> = 0.144 P = 0.707	CE = -0.0175 F <sub>1, 27</sub> = 0.131 P = 0.720	CE = 0.0029 F <sub>1, 27</sub> = 0.218 P = 0.645	N/A	N/A	CE = -0.0040 F <sub>1, 26</sub> = 0.090 P = 0.767
Heterotrophic Nitrification	CE = -0.0003 F <sub>1, 26</sub> = 1.203 P = 0.283	CE = -0.0266 F <sub>1, 26</sub> = 3.029 P = 0.094	CE = 0.1017 F <sub>1, 26</sub> = 5.130 <b><u>P = 0.032*</u></b>	CE = -0.006 F <sub>1, 26</sub> = 1.304 P = 0.264	CE = 0.6922 F <sub>1, 26</sub> = 0.014 P = 0.907	CE = 0.0196 F <sub>1, 26</sub> = 0.946 P = 0.340	N/A
Microbial NO <sub>3</sub> <sup>-</sup> Uptake	CE = 0.0014 F <sub>1, 28</sub> = 7.498 <b><u>P = 0.011*</u></b>	CE = -0.1485 F <sub>1, 28</sub> = 10.525 <b><u>P = 0.003**</u></b>	CE = 0.0508 F <sub>1, 28</sub> = 0.535 P = 0.470	CE = -0.0073 F <sub>1, 28</sub> = 0.440 P = 0.513	N/A	N/A	N/A

Note: Statistically significant P values (i.e. P < 0.05) are bolded, underlined and labeled for convenience; \* P < 0.05 and \*\* P < 0.01  
CE: coefficient

Table 5. The results of statistical analyses for net ammonification, nitrification, and mineralization rates. Independent variables are treatment (fixed), transfer (fixed), interaction between treatment and transfer (fixed) and site (random).

Dependent Variables	Treatment (burned/control)	Transfer	Interaction
Net Ammonification	$F_{1, 63} = 10.795$ , <b><u>P = 0.002</u></b> **	$F_{1, 63} = 1.148$ , P = 0.288	$F_{1, 63} = 0.008$ , P = 0.928
Net Nitrification	$F_{1, 63} = 9.111$ , <b><u>P = 0.004</u></b> **	$F_{1, 63} = 0.359$ , P = 0.551	$F_{1, 63} = 1.991$ , P = 0.163
Net Mineralization	$F_{1, 63} = 0.079$ , P = 0.779	$F_{1, 63} = 0.221$ , P = 0.640	$F_{1, 63} = 1.045$ , P = 0.311

Note: Subsample size within burned/control plots and transferred samples at each site is  $N_{\text{sub}} = 6$ , except for the burned plot of CA, the control plot of HA, and the burned plot of SF ( $N_{\text{sub}} = 5$ ).

Statistically significant P values (i.e.  $P < 0.05$ ) are bolded, underlined and labeled; \*  $P < 0.05$  and \*\*  $P < 0.01$ .

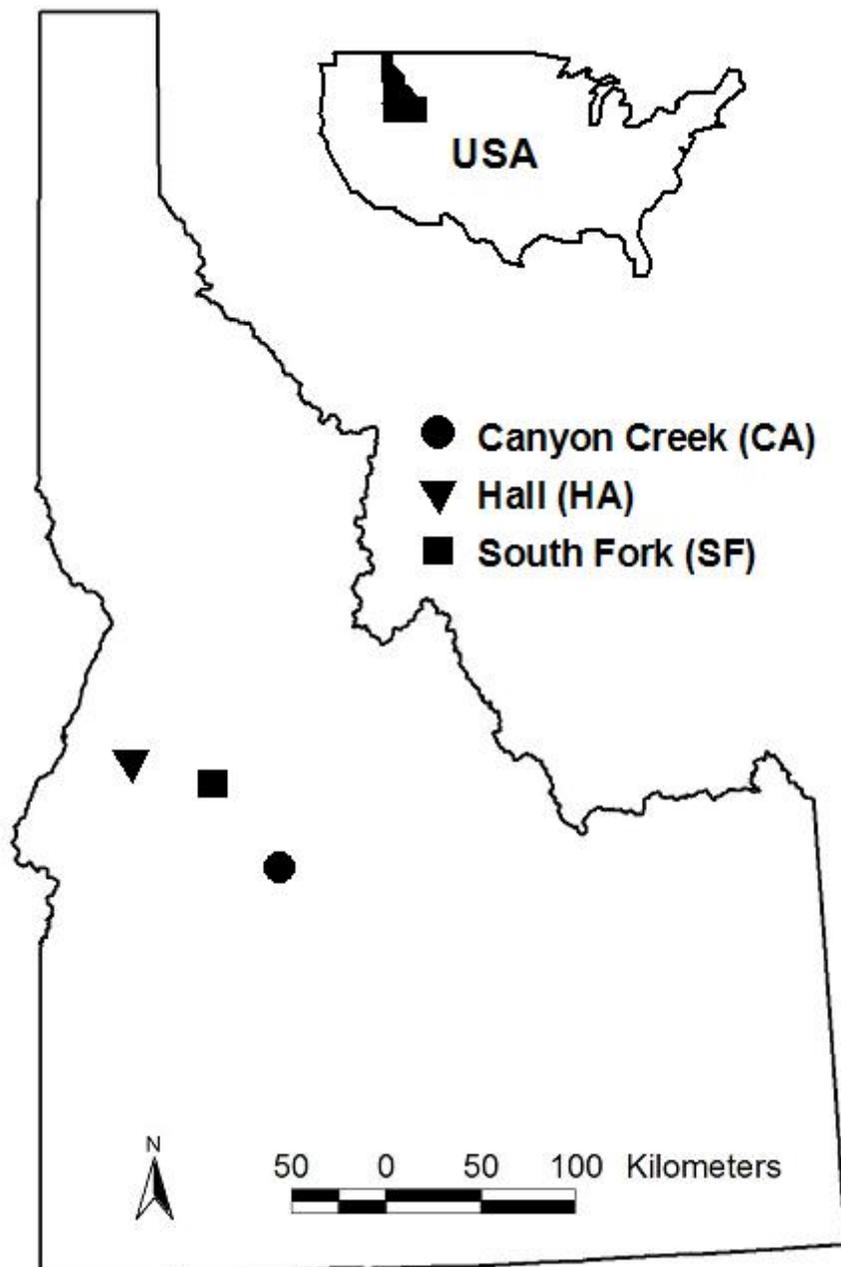


Fig. 1. Map showing study sites in coniferous forests of central Idaho, USA. The characteristics of study sites are described in Table 1.

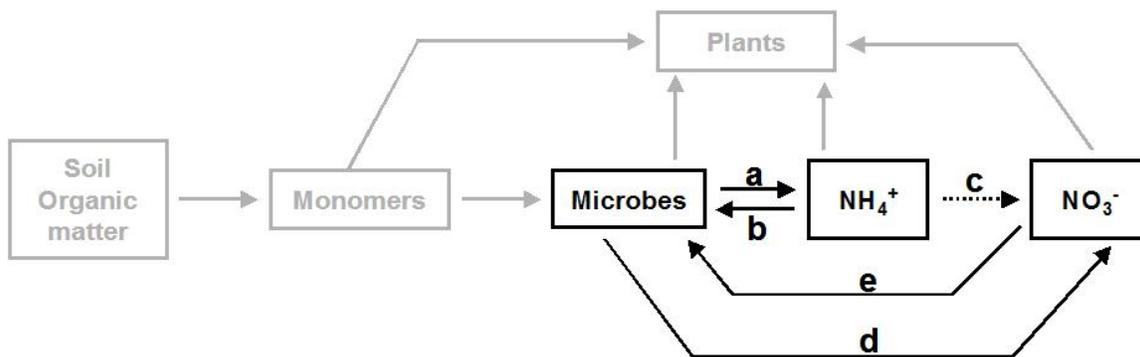


Fig. 2. Nitrogen cycling model in a forest ecosystem. Boxes and arrows represent pools and fluxes, respectively. Fluxes a: ammonification, b: microbial  $\text{NH}_4^+$  uptake, c: autotrophic nitrification, d: heterotrophic nitrification, and e: microbial  $\text{NO}_3^-$  uptake. Solid arrows are C required fluxes and a dashed for autotrophic nitrification is not required C as a energy source. Gray boxes and arrows were not measured in this study. This figure is adapted and modified from Schimel and Bennett (2004) and Cookson et al. (2006).

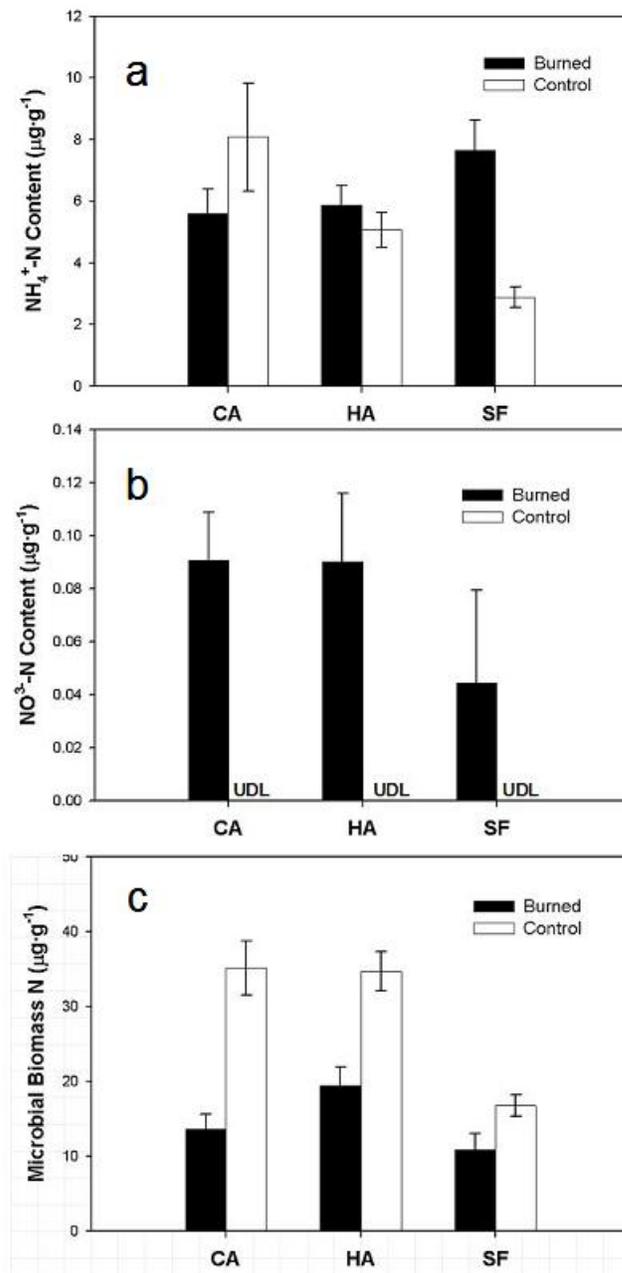


Fig. 3. Measured N pool sizes in mineral soils – (a) NH<sub>4</sub><sup>+</sup> contents, (b) NO<sub>3</sub><sup>-</sup> contents and (c) microbial biomass N for three burned and nearby unburned conifer forests in central Idaho. UDL represents under detection limit. The results of the statistical analysis are in Table 2. The error bars show standard errors within a site.

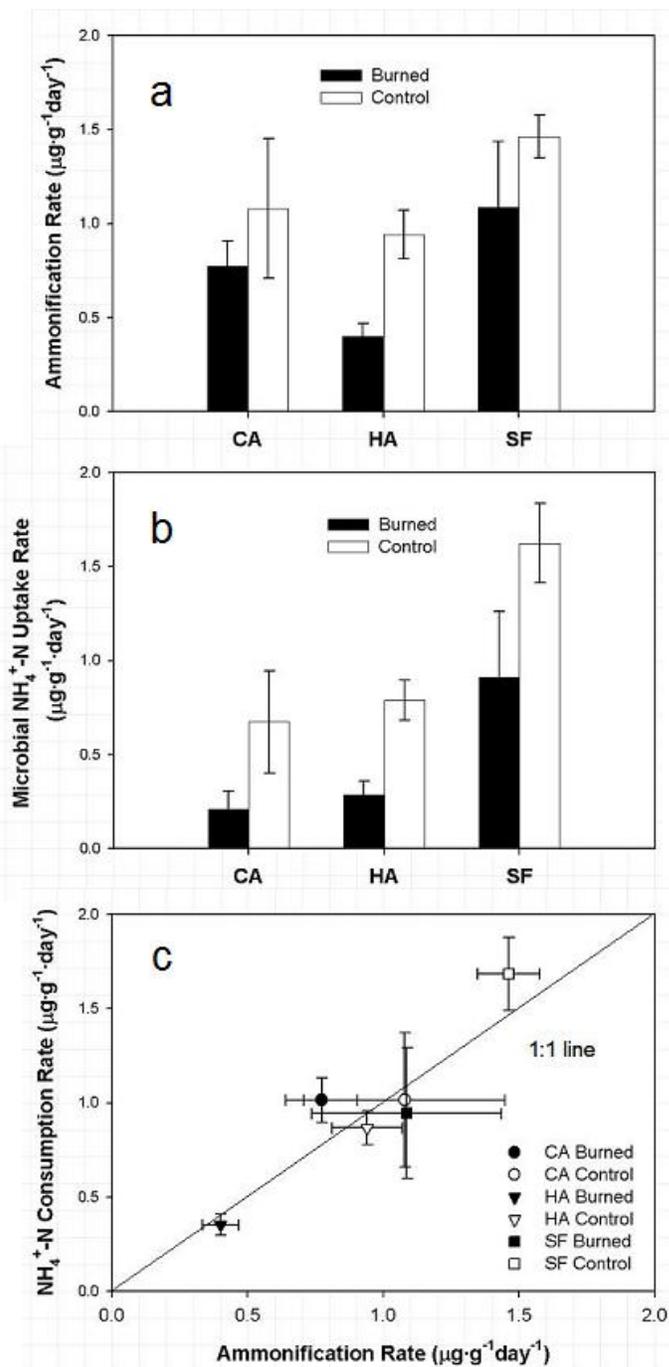


Fig. 4. Gross fluxes of  $\text{NH}_4^+$  in mineral soil – (a) ammonification rates, (b) microbial  $\text{NH}_4^+$  uptake rates, and (c) the relationship between ammonification and  $\text{NH}_4^+$  consumption rates (microbial  $\text{NH}_4^+$  uptake and autotrophic nitrification rates). The results of the statistical analyses are in Table 3. The error bars show standard errors within a site.

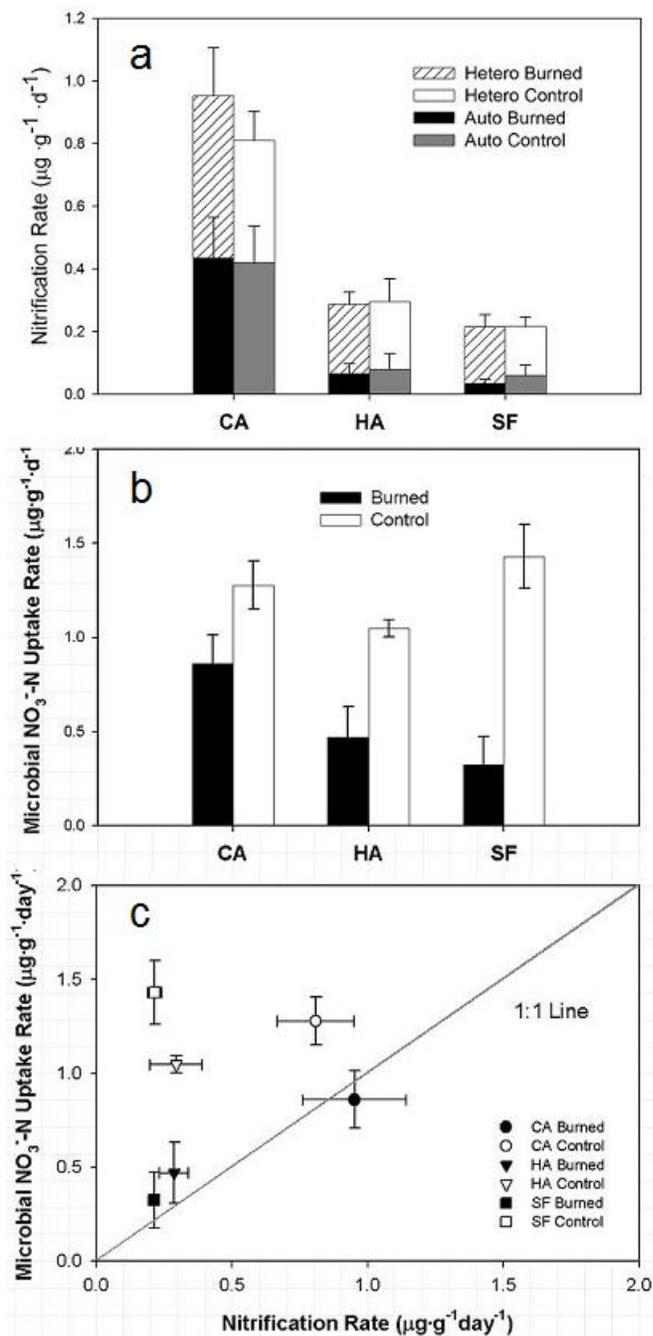


Fig. 5. Gross fluxes of  $\text{NO}_3^-$  in mineral soil – (a) nitrification rates, (b) microbial  $\text{NO}_3^-$  uptake rates, and (c) the relationship between nitrification and microbial  $\text{NO}_3^-$  uptake rates. In Fig. 4a, hetero and auto represent heterotrophic nitrification and autotrophic nitrification, respectively. The results of the statistical analysis are in Table 3. The error bars show standard errors within a site.

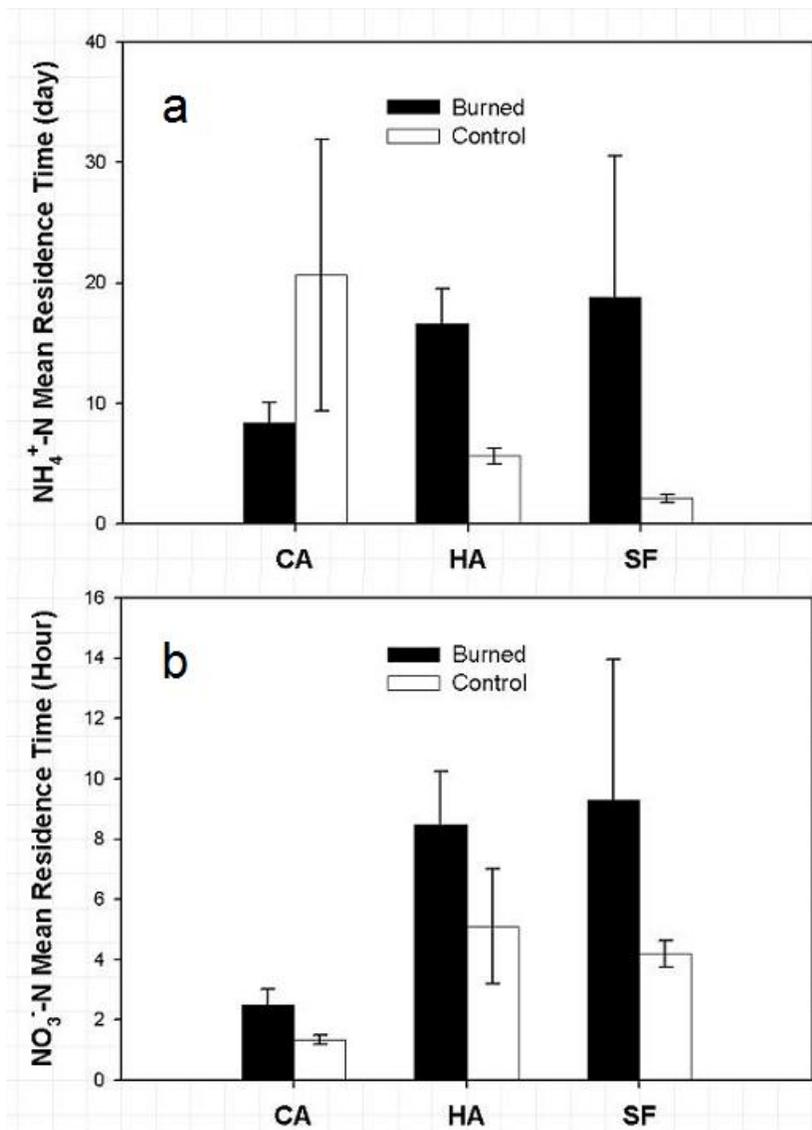


Fig. 6. Mean residence time of inorganic N in soils - (a)  $\text{NH}_4^+$  and (b)  $\text{NO}_3^-$ . Note that the units are days and hours for  $\text{NH}_4^+$  and  $\text{NO}_3^-$ , respectively. The values were calculated by dividing pool sizes by production rates. The results of the statistical analysis are in Table 3. The error bars show standard errors within a site.

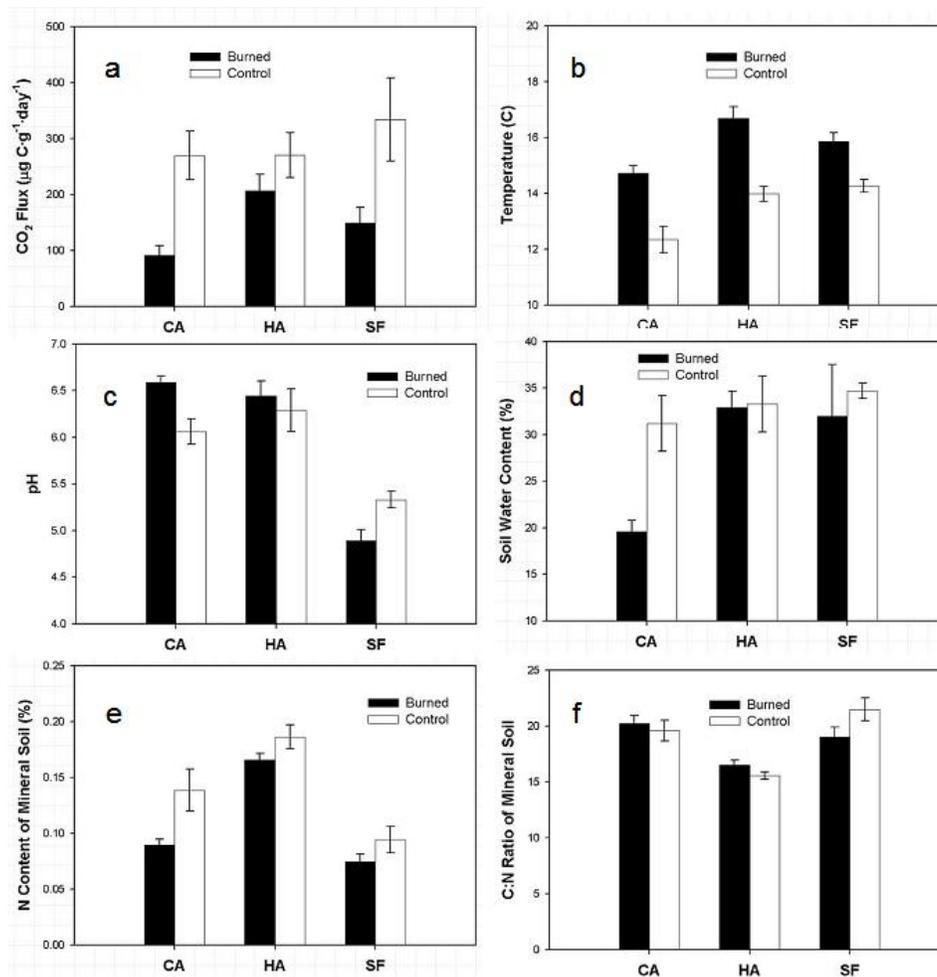


Fig. 7. Measured factors potentially important for gross inorganic N flux used as independent variables in linear mixed effect ANOVA for statistical analyses. The results of the statistical analyses for effects of fire on the measured factors above are in Table 2. The statistical results for the significance of these factors to the gross N flux rates using linear mixed-effects ANOVA are shown in Table 4. The error bars show standard errors within a site.

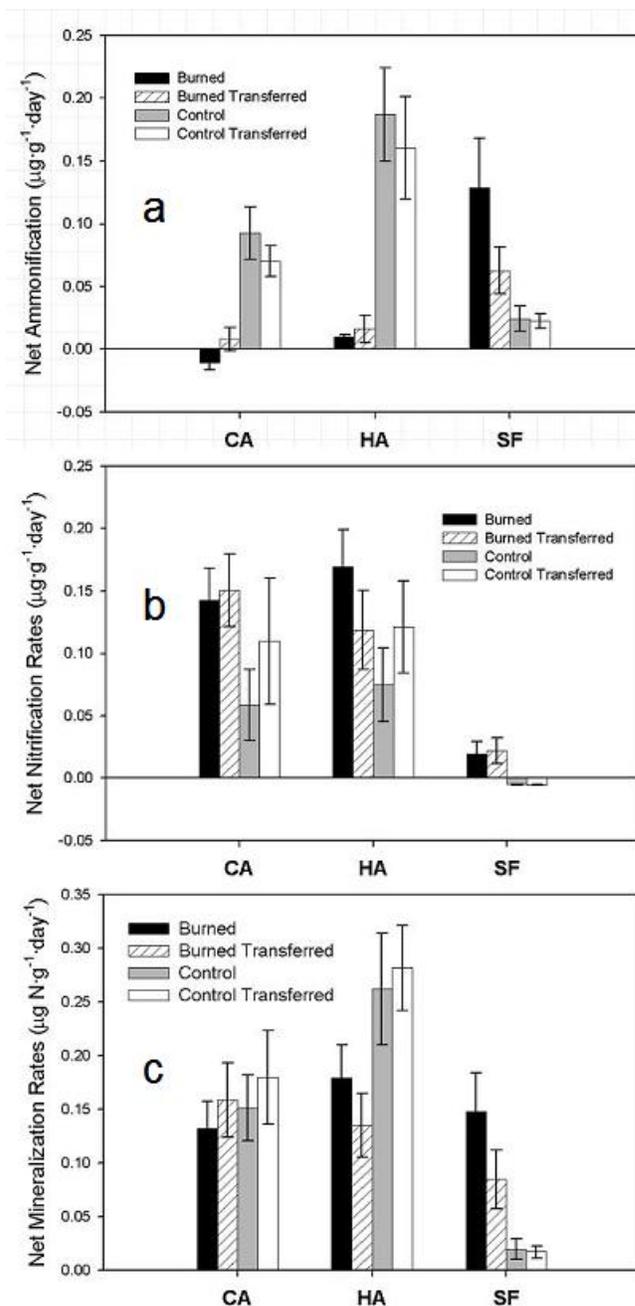


Fig. 8. Results of (a) net mineralization and (b) net nitrification rates for one month at the beginning of the growing season. Transferred soils were either burned soils incubated in control plot or control soils incubated in burned plots within each site. The results of the statistical analysis are in Table 5. The error bars show standard errors within a site.

### CHAPTER 3

#### **FIRE EFFECTS ON GROSS INORGANIC N FLUXES IN RIPARIAN SOILS IN CONIFEROUS FORESTS OF CENTRAL IDAHO, USA: WILDFIRES VS. PRESCRIBED FIRES**

Akihiro Koyama, Kathleen L. Kavanagh and Kirsten Stephan

##### **Abstract**

Riparian forests along headwater streams in the inland Northwest, USA were historically subject to wildfires. More recently, fire suppression has led to accumulation of fuels in the forests of this region. Prescribed fires have been used to reduce fuel loads, and thus, the chances of catastrophic fires. However, prescribed fires in riparian forests have not been widely practiced due to the uncertainty and lack of knowledge about their impacts on aquatic ecosystems. We investigated the effects of fires on gross fluxes of inorganic nitrogen (N) in mineral soils of riparian forests using  $^{15}\text{N}$  isotope pool dilution. We also compare the difference between wildfires and prescribed fires and their relative effects on N processes. We found elevated soil  $\text{NO}_3^-$  contents in burned soils compared to controls in both wildfires and prescribed fires ( $P < 0.10$ ). Elevated  $\text{NO}_3^-$  contents were caused by significantly reduced microbial  $\text{NO}_3^-$  uptake in burned soil ( $P < 0.05$ ). There was no significant fire effect on soil  $\text{NH}_4^+$  contents in either wildfires or prescribed fires. However, the gross  $\text{NH}_4^+$  fluxes were significantly reduced in soils burned by wildfires relative to their controls ( $P < 0.10$ ). There were no such effects on  $\text{NH}_4^+$  fluxes in soils burned by prescribed fires. We concluded that measurements of gross N fluxes are necessary to assess impacts of fires on N dynamics in soils. The differences in timing and

intensity between wildfires and prescribed fires may explain observed effects on N processes in riparian forests and aquatic systems.

*Key words:* Riparian forests; Wildfires; Prescribed fires; Nitrogen; Gross inorganic N flux;  $^{15}\text{N}$  pool dilution methods

## **Introduction**

Forest fires are one of the most important disturbances in the forests of the inland Northwest, USA (Hessburg and Agee 2003). Forest fires play an important role in species diversity during forest succession (Arno et al. 1985, Gallant et al. 2003), landscape diversity (Romme 1982), and biogeochemistry (Boerner 1982). Thus fires are important for the structure and function of the regional landscapes. Historically, coniferous forests of the region were characterized by a mixed-severity fire regime, ranging from low-intensity surface fires to stand-replacing fires (Hessburg and Agee 2003). However, this historical fire regime has been altered for the past century due to fire suppression and changing land uses including roads, logging and grazing (Hessburg and Agee 2003). In consequence, the accumulating biomass in the forests led to an increased susceptibility of catastrophic fires (Arno and Allison-Bunnell 2002). In an effort to reduce the chance of catastrophic fires, spring and fall prescribed fires have been used extensively as a management tool to decrease the fuel load. For example, prescribed fires were applied to approximately 75,000 ha of federally-owned lands in the state of Idaho alone between 2003 and 2007, and approximately eight million ha in the USA between 2000 and 2007 (National Fire Plan 2007).

Although reducing fuel loads by prescribed fires is a priority, prescribed fires also have other objectives, such as reintroducing ecological processes and functions that used to be sustained by wildfires. Such ecological processes include the biogeochemical cycling of nitrogen (N). For example, forest fires can remove significant amounts of N through combustion of forest floor organic matter and above-ground biomass (Grier 1975, Raison et al. 1984, Caldwell et al. 2002). However, inorganic N ( $\text{NH}_4^+$  and  $\text{NO}_3^-$ ) often increases in soils after fires (Covington and Sackett 1992), and some N leaches from terrestrial to aquatic systems (Hauer and Spencer 1998, Stephan et al. submitted). Therefore, it can be said that wildfires historically influenced the landscape of coniferous forests indirectly through their effects on N dynamics, because N is often a limiting nutrient to forest productivity in the inland Northwest (Moore et al. 1991). Thus, it is important to know the extent to which prescribed fires mimic wildfires in N dynamics.

In the effort to manage coniferous forests with prescribed fires, riparian forests (defined as the slope distance of one site-potential tree height of ca. 35 m) are often excluded because of the uncertainty about fire effects on aquatic ecosystems (Bisson et al. 2003), especially for native fish populations (Rieman & Clayton 1997, Dunham et al. 2003). Forest fires can have adverse influences to aquatic ecosystems. For example, severe fires can trigger erosion and sedimentation (Meyer et al. 1992, Pierce et al. 2004). This is especially the case in central Idaho forests that have granite-based bedrocks in steep terrain with relatively high erosion rates (Clayton and Megahan 1986). This region also supports fish species listed under the Endangered Species Act (ESA) such as bull trout (*Salvelinus confluentus*, U.S. Fish and Wildlife Service 2005) and Chinook salmon (*Oncorhynchus tshawytscha*, U.S. Fish and Wildlife Service 1993, Nehlsen et al. 1991).

Historically, however, headwater and riparian forests were subject to wildfires (Everett et al. 2003, Dwire and Kauffman 2003). Fires in the riparian forests, therefore, may be an important factor to maintain complex and productive aquatic habitats (Reeves et al. 1995).

The policy of prescribed fires in riparian forests is still in its infancy. One of the recommended guidelines based on empirical knowledge is implementing prescribed fires when fuel moisture level is high in the spring without large precipitation events to follow (McMahon and deCalesta 1990). Currently, forest managers of the National Forests in the inland Northwest occasionally burn riparian forests in headwater ecosystems on an experimental basis when conditions allow cool burns (Zurstadt, C. Council Ranger District, Payette National Forest, Idaho, U.S.A. Personal communication 2007).

Forests adjacent to streams influence stream water chemistry, such as  $\text{NO}_3^-$  levels (Jones et al. 2001).  $\text{NO}_3^-$  increases in forest soils after fires, leaches down the soil profiles, and eventually to streams (Minshall et al. 1997, Stephan et al. submitted, Woodmansee and Wallach 1981). However, the mechanisms behind the increased  $\text{NO}_3^-$  in soils after forest fires are not well understood due to the dynamic nature of inorganic N fluxes and difficulty in measuring fluxes. Increased  $\text{NO}_3^-$  in soils can be caused either by increased  $\text{NO}_3^-$  supply, decreased  $\text{NO}_3^-$  demand, or combination of the two. Potential causes of increased supply includes higher  $\text{NO}_3^-$  production in favorable environments such as increased temperature (Ahlgren 1974) and increased soil pH by ash (Fowells and Stephenson 1934). Potential causes of decreased demand include decreased  $\text{NO}_3^-$  uptake by plants (Wright and Bailey 1982) and soil microbes (Kaye and Hart 1998). Thus,

measuring N production and consumption rates is required to reveal the potential mechanisms for increased soil  $\text{NO}_3^-$  contents.

Nitrogen can be one of the critical factors for riparian vegetation recovery, which, in turn, influences the recovery of aquatic biota post-fire (Minshall et al. 2001).

Therefore, it is important to assess the mechanism of fire effects on N dynamics in the riparian forests in headwater systems that cover extensive areas in the mountainous landscape (Sidle et al. 2000, Meyer and Wallace 2001). In addition, aquatic headwater systems are more sensitive to fires relative to lowland systems (Minshall et al. 1989), thus, the fire effects, are most likely to be detected in headwater aquatic systems.

In this study, we have two objectives: 1) to investigate fire effects on gross inorganic N fluxes in riparian mineral soils using the  $^{15}\text{N}$  isotope dilution, and 2) to quantify the differences between wildfires and prescribed fires in soil N processes.

## **Materials and Methods**

### *Study Site description*

Our study sites were located in coniferous forests in central Idaho (Fig. 1). We selected six sites; three burned by wildfires, and three burned by prescribed fires, with control sites paired to each burned site (Table 1). The regional climate is characterized by warm, dry summers and cool, moist winters. Depending on the elevation (1400 m - 2350 m), the mean annual air temperature ranges from 5.4 to 0.5°C and precipitation (mainly as snow) ranges from to 640-1060 mm/year (Western Regional Climate Center 2007). The three wildfires occurred in the summer of 2003, and the prescribed fires were conducted in the spring of 2004. Due to the difficulty of collecting pre-burn data, we

carefully selected the watersheds for our study so that paired burned and control sites were similar. The criteria were 1) severity of wildfires/prescribed fires of watersheds represented the relative severity of each fire type (i.e. wildfires burned relatively more severely than prescribed fires), 2) watersheds supported perennial streams (to investigate fire effects on stream ecosystems in studies associated with this research), and 3) control watersheds were similar to the paired burned watersheds in terms of aspect, elevation and dominant vegetation. Watershed areas range from 12 to 143 ha (average 62 ha), drained by small first-order perennial streams. Stream channels are confined by relatively steep hill slopes (15-41°) with only a narrow (<1m) strip of obligate riparian shrubs. At each site, we selected four plots; two plots at each side of the stream. The plots were 5–25 m upslope from the stream banks (thus inside the riparian area defined as one site tree or ca 35m), and the plots at each side of a stream were approximately 100 m apart along the stream. The plots in watersheds burned by prescribed fires were placed on patches where forest floor organic matter and most of the understory vegetation had been consumed with no overstory tree mortality.

#### *Gross N flux measurements*

Mineral soil samples were collected in October 2005 to measure gross inorganic N fluxes. Five soil cores (5 cm diameter and 10 cm deep) were taken at each plot and brought back to the lab in polyethylene bags on ice. The soil samples were sieved, roots and organic matter removed, mixed in the lab, and stored at 4°C before the experiments. To assess the initial soil water content, 30 to 50 g of each soil sample were dried at 105°C for 48 hours. To assess background inorganic N content ( $\text{NH}_4^+$ -N and  $\text{NO}_3^-$ ) 15 g

of each samples were extracted in 2 mol/L potassium chloride (KCl) solution, and filtered with pre-leached Whatman No. 1 filter papers. Inorganic N contents in KCl extracts were determined using a Lachat AE Low Injection Autoanalyzer (Lachat Instruments, Inc., Milwaukee, Wisconsin, USA).

We used the  $^{15}\text{N}$  isotope pool dilution methods to measure gross flux rates of inorganic N in the lab setting (Hart et al. 1994b). Six subsamples of the soil collected at each location were used for the measurements. They were weighed and placed in polyethylene bags. Out of the six subsamples, two subsamples, ranging from 20g to 35g depending on the background inorganic N contents, were used to assess  $\text{NH}_4^+$  fluxes. Ninety nine atom %  $^{15}\text{N}$ - $(\text{NH}_4)_2\text{SO}_4$  dissolved in deionized water was added to two of the subsamples. By adding the solution,  $\text{NH}_4^+$  and soil water content were increased by 100% and 3% relative to the background levels, respectively. One sample was immediately extracted after the  $^{15}\text{NH}_4^+$  addition in 2 mol/L KCl to assess extraction efficiency. The second one was incubated at 25°C for 12 hours in a 1 L canning jar.

For  $\text{NO}_3^-$  fluxes, 50-70  $\mu\text{g}$  of 99 atom %  $^{15}\text{N}$ - $\text{KNO}_3$  dissolved in deionized water (increased soil water content by 3%) was added to three subsamples. Since  $\text{NO}_3^-$  contents were very low or even under the detection limit (i.e. 0.025 mg/L of  $\text{NO}_3^-$ -N in KCl soil extracts), we had to add enough  $^{15}\text{N}$ - $\text{NO}_3^-$  to recover  $\text{NO}_3^-$  from soils for the subsequent analyses. One subsample was immediately extracted with 2 mol/L KCl to assess extraction efficiency. The second was incubated at 25°C for 12 hours in a 1L canning jar. The third one was placed in a canning jar with a lid containing a septum, injected with atomic grade acetylene (approximately 10 kPa) to prohibit autotrophic nitrification, and incubated at 25°C for 12 hours. Deionized water was added to final of the six samples

increasing the soil water by 3%; then the inorganic N in the sample was immediately extracted with 2 mol/L KCl to measure the initial inorganic N contents prior to incubation. The inorganic N from the incubated soil samples was extracted with 2 mol/L KCl, filtered with pre-leached Whatman No. 1 filter papers, and stored frozen at - 40°C until analyses. All the  $^{15}\text{N}$  isotope pool dilution experiments were conducted within one week after the soil collections.

We followed the diffusion methods described by Stark and Hart (1996) to analyze the  $^{15}\text{N}$  levels of labeled N in soil extracts (Stark and Hart 1996). Briefly, MgO was added to the extracts from the  $^{15}\text{NH}_4^+$  labeled soils. The  $\text{NH}_3$  released was then trapped in acidified quartz filter disks in gas-tight specimen cups. In the extracts from the  $^{15}\text{NO}_3^-$  labeled soils,  $\text{NH}_4^+$  was first removed by adding MgO to open-top specimen cups. Then,  $\text{NO}_3^-$  in the extracts were converted to  $\text{NH}_4^+$  using Devarda's alloy, and trapped in acidified quartz filter disks in the same manner described above. The  $^{15}\text{N}$  levels of the N in the quartz filter disks were determined by a continuous flow mass spectrometer (Europa Integra, Cheshire, UK) in UC Davis Stable Isotope Facility.

Gross rates of ammonification (a in Fig. 2),  $\text{NH}_4^+$  consumption (b plus c in Fig. 2), heterotrophic nitrification (d in Fig. 2; nitrification in acetylene-treated soils), autotrophic nitrification (c in Fig. 2; nitrification in soils without acetylene subtracted by heterotrophic nitrification), and microbial  $\text{NO}_3^-$  uptake (e in Fig. 2) were calculated based on the equations in Kirkham and Bartholomew (1954), and the flux rates of five processes of interest (a, b, c, d and e in Fig. 2) were derived. Net ammonification and nitrification rates were calculated by subtracting the gross consumption rates from the gross production rates.

### *Statistical analyses*

Statistical analyses were performed with R (Ihaka and Gentleman 1996). We note that the study unit is site (i.e. CA, HA, SF, PA, SI and DA. See Fig. 1 and Table 1) with paired burned and control watersheds from which soil samples were collected. Thus, our study has three replications for each fire type, wildfires and prescribed fires. Due to the small sample size and high variability, because of the nature of the soils processes measured and the heterogeneity within and among sites, we treated the individual soil samples within a site as a unit in our statistical analyses. Therefore, the statistical results to compare treatment (burned/control) are partially inferential (Oksanen 2001). We employed  $P = 0.10$  or less as an indication of statistical significance considering the variability mentioned above. A linear mixed-effects ANOVA was employed for statistical analyses. Since one of our objectives is to make inferences for coniferous forests of the inland Northwest with three replicated sites, site was a random effect in the models used. The independent variable (i.e. treatment; burned/control) was used as a fixed effect. At each analysis, we assessed normality of error effects, and appropriate transformations were applied when necessary.

## **Results**

### *Gross $NH_4^+$ fluxes*

Soil  $NH_4^+$  contents in wildfire and prescribed fire sites did not differ from the controls two years after the fires ( $P > 0.58$  in Table 2, Fig. 3a). However, gross ammonification and microbial  $NH_4^+$  uptake rates were significantly reduced in wildfires compared to their controls ( $P = 0.0539$ , and  $0.0786$ , respectively, Table 2, Fig. 4ab). Accordingly, the mean

residence time of  $\text{NH}_4^+$  in soils burned by wildfire is significantly longer than their controls ( $P = 0.026$  in Table 2, Fig. 3c). In contrast, there were no such differences in  $\text{NH}_4^+$  fluxes between soils burned by prescribed fires and their controls ( $P = 0.578$ , and  $0.914$ , respectively in Table 2, Fig. 3ab). Net ammonification rates during the 12-hour incubation were not different between burned and control soils in either wildfires or prescribed fires ( $P > 0.5093$  in Table 2, Fig. 3d). There was no significant relationship between net ammonification rates and soil  $\text{NH}_4^+$  contents ( $P = 0.191$  in Table 2, Fig. 6a).

#### *Gross $\text{NO}_3^-$ fluxes*

In contrast to the soil  $\text{NH}_4^+$  contents, riparian soils exposed to wildfires and prescribed fires, had significantly higher  $\text{NO}_3^-$  contents relative to their controls ( $P = 0.082$ , and  $0.0179$ , respectively in Table 2, Fig. 3b). There were no significant fire effects on either gross autotrophic and heterotrophic nitrification rates in either wildfires or prescribed fires ( $P > 0.426$  in Table 2, Fig. 5a). However, gross microbial  $\text{NO}_3^-$  uptake rates were significantly lower in soils exposed to wildfires and prescribed fires relative to their controls ( $P = 0.0137$  and  $0.0001$ , respectively in Table 2, Fig. 5b). Soils exposed to fire had significantly higher net nitrification rates than control soils (Fig. 5d,  $P < 0.01$  for treatment effects in Table 2).

Soils with higher net nitrification rates had higher initial  $\text{NO}_3^-$  contents (Fig. 6b). The net nitrification rates during the 12-hour incubation explained 67% of the variation in soil  $\text{NO}_3^-$  contents before the incubation ( $P = 0.001$ ,  $R^2 = 0.672$ , Fig. 5b).

## **Discussion**

#### *Gross inorganic N fluxes*

The wildfires and prescribed fires had significantly reduced rates of microbial  $\text{NO}_3^-$  uptake compared to their controls (Fig. 5b, Table 2). However, there was a clear difference between the wildfires and prescribed fires in  $\text{NH}_4^+$  fluxes, the wildfires reduced the gross  $\text{NH}_4^+$  fluxes in mineral soils compared to their controls; conversely, the prescribed fires did not show such an effect (Fig. 4ab, Table 2).

The significant differences in the net nitrification rates between the burned soils and their controls (Fig. 5d, Table 2) were influenced by the fire-caused alteration in the gross  $\text{NO}_3^-$  uptake rates (Fig. 5b, Table 2) since there was no fire effect on the gross  $\text{NO}_3^-$  production rates (Fig. 5a, Table 2). These differences in  $\text{NO}_3^-$  uptake rates, in turn, determined  $\text{NO}_3^-$  contents in soils. Therefore, the elevated  $\text{NO}_3^-$  levels in burned soils were caused by reduced microbial  $\text{NO}_3^-$  uptake rates instead of increased  $\text{NO}_3^-$  production rates in both wildfires and prescribed fires (Fig. 4ab, Table 2). This finding is consistent with Kaye and Hart (1998) and Koyama et al. (submitted), but different from a widely accepted mechanism that increased  $\text{NO}_3^-$  in soils post-fire is caused by increased nitrification (e.g. Christensen 1973, Covington and Sackett 1986, White 1986). In this study we do not know the effects of the environmental alterations by the fires (e.g. increased temperature) to the actual gross fluxes of inorganic N in situ since the experiments in this study were conducted under controlled conditions in the lab. However, the significant relationship between soil  $\text{NO}_3^-$  contents pre-incubation and net nitrification during the incubation ( $R^2 = 0.672$ ,  $P = 0.001$ , Fig. 6b) implies that the reduced microbial  $\text{NO}_3^-$  uptake rates are a major factor in determining soil  $\text{NO}_3^-$  contents. The results of this study reemphasize the importance of using gross flux measurements to interpret the causes of soil N pool sizes associated with disturbances such as fires.

The relatively low or negligible soil  $\text{NO}_3^-$  contents in all the control soils and some of the soils exposed to fire (Fig. 2b) were due to the tight cycling of  $\text{NO}_3^-$ , with mean residence time ranging from 1.4 hours (PA control) to 1.75 days (HA burned). The lack of or negligible extractable  $\text{NO}_3^-$  due to tight cycling in mineral soils in this study agrees with other studies done in western conifer forests (Stark and Hart 1997) where the demand for  $\text{NO}_3^-$  is so high that it is rarely detectable in mineral soil although nitrification rates are high.

One of the limitations in  $^{15}\text{N}$  pool dilution is that the addition of  $^{15}\text{N}$ -labeled substrates can stimulate the consumption rates (Hart et al. 1994). In such cases, the consumption to production ratio of a labeled substrate should be more than one. In this study, we observed ratios higher than one in all of the control soils (average  $2.27 \pm 0.73$  SE) and half of the burned soils ( $1.21 \pm 0.39$  SE). The high ratio of  $\text{NO}_3^-$  consumption to production rates in most of the soils imply that microbial  $\text{NO}_3^-$  uptake rates were regulated by  $\text{NO}_3^-$  production rates.

The reduced  $\text{NO}_3^-$  uptake rates in burned soil compared to control soils can explain increased  $\text{NO}_3^-$  leaching to aquatic systems after fires (e.g. Minshall et al. 1997, Williams and Melack 1997, Hauer and Spencer 1998, Stephan et al. submitted). Even though we observed reduced microbial  $\text{NO}_3^-$  uptake rates in soils burned by prescribed fires as well as by wildfires,  $\text{NO}_3^-$  in stream water is lower in the watersheds burned by the prescribed fires than the wildfires (Stephan et al. submitted) because the fire intensity and proportions of burned areas were lower in the prescribed fire sites relative to the wildfire sites (Stephan et al. submitted).

In contrast to the similarity in fire effects on gross  $\text{NO}_3^-$  fluxes between wildfires and prescribed fires compared to their controls, we observed differences in  $\text{NH}_4^+$  fluxes between the two fire types. In soils burned by wildfires, gross fluxes of  $\text{NH}_4^+$  were still significantly lower than control soils, despite the  $\text{NH}_4^+$  pool sizes not varying (Fig. 2a, Fig. 3ab). No such fire effect was observed in prescribed fires (Fig. 3ab). Since only a fraction of soil microbial population is involved in gross N transformation (Puri and Ashman 1998), the wildfires and prescribed fires might have different effects on soil microbes responsible for  $\text{NH}_4^+$  and  $\text{NO}_3^-$  fluxes. Possible sources for such different effects include different timings (i.e. prescribed fires were in early spring vs. wildfires were in summer) and different severity (prescribed fires were in low severity vs. wildfires were in high severity).

We have observed a casual relationship between fire and gross fluxes of inorganic N in soils. However, we did not assess the direct mechanisms causing the alterations in gross N fluxes due to fire. Reduced gross ammonification rates in soils burned by wildfires (Fig. 3a) could be due to changed microbial structures (Smithwick et al. 2005). Another cause could be reduced carbon availability to ammonifiers (Hart et al. 1994a). Since rhizosphere carbon supplied by live vegetation is an important energy source for soil microbes (Högberg et al. 2001, Högberg and Högberg 2002, Phillips and Fahey 2005),  $\text{NH}_4^+$  fluxes could be reduced due to the decreased carbon supply for microbes in soils burned by wildfires (Koyama et al. submitted). This potential reduction of carbon supply could also explain reduced microbial  $\text{NO}_3^-$  uptake in soils burned by wildfires and prescribed fires (Fig. 4b, Hart et al. 1994a).

In contrast to the significant correlation between net nitrification and  $\text{NO}_3^-$  content pre-incubation, there was no such relationship for  $\text{NH}_4^+$  (Fig. 5a). This could be due the methods used for  $\text{NH}_4^+$  extraction. Two mol/L KCl can extract  $\text{NH}_4^+$  bound to negatively charged soil particles which is normally unavailable for either microbes or plants (Kowalenko and Yu 1996). It is possible that  $\text{NH}_4^+$  in soils was cycled as tightly as  $\text{NO}_3^-$ . Average  $\text{NH}_4^+$  production and consumption rates ( $4.19 \pm 0.61 \text{ SE}$  and  $4.00 \pm 0.58 \text{ SE}$ ), respectively) were more than five times higher than average  $\text{NO}_3^-$  production and consumption rates ( $0.66 \pm 0.10 \text{ SE}$  and  $0.73 \pm 0.11 \text{ SE}$ , respectively). In addition, the relatively large soil  $\text{NH}_4^+$  pools we observed contradict the finding that nitrogen is a limiting nutrient for conifers in the region (Moore et al. 1991) and that  $\text{NH}_4^+$  is a preferable form of nitrogen for conifers (Van Den Driessche 1971, Smirnov et al. 1984). Extraction with different media, such as deionized water, may be more appropriate to estimate the  $\text{NH}_4^+$  pool sizes available for plants and microbes.

## Conclusions

Increased soil  $\text{NO}_3^-$  content in riparian soils burned by either wildfires or prescribed fires was caused by reduced microbial  $\text{NO}_3^-$  uptake rates. This reduced ability of microbes to assimilate  $\text{NO}_3^-$  is most likely a major cause for increased  $\text{NO}_3^-$  concentration in stream water post-fire, especially severe wildfires. A difference between wildfires and prescribed fires was found in gross  $\text{NH}_4^+$  fluxes; wildfires reduced both ammonification and microbial  $\text{NH}_4^+$  uptake rates compared to their controls, but this change was not observed in prescribed fires. Prescribed fires in riparian forests can mimic wildfires to some degree such as reduced fuel load, however, some underlying processes,

such as N dynamics in terrestrial and aquatic ecosystems, may be lacking. More research is needed to understand the complex natural processes associated with fires in riparian forests and aquatic systems and the degree to which prescribed fire can be used to mimic wildfires.

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Table 1. Characteristics of study sites; three wildfires and three prescribed burns in central Idaho.

Names of fires/burns	Canyon Creek Fire	Hall Fire	South Fork Salmon Fire	Danskin Creek Burn	Parks-Eiguren Burn	Sixbit Burn
Abbreviation	CA	HA	SF	DA	PA	SI
Fire Type	Wildfire	Wildfire	Wildfire	Prescribed fires	Prescribed fires	Prescribed fires
National Forest	Boise NF	Payette NF	Boise NF	Boise NF	Payette NF	Boise NF
Time of Fire/burn	Aug 2003	Aug 2003	Aug – Oct 2003	Apr 2004	May 2004	May 2004
Location*	115°14'W, 44°12'N	116°21'W, 44°50'N	115°44'W, 44°42'N	115°49'W, 44°5'N	115°34'W, 44°58'N	115°44'W, 44°41'N
Elevation (m, B/C)†	2100/2190	1420/1400	1940/ 1770	1410/ 1540	1880/ 1840	1960/ 1790
Aspect of watershed (B/C)†	NW/ W	W/W	W/SW	W-SW/NW	S-SE/S-SW	SE/S
Area of watershed (ha, B/C)†	115/ 38	143/ 81	82/ 48	53/ 13	89/ 35	33/12
Distance between burned and control sites (m)	6800	600	9500	1600	8500	5500
Dominant conifer species (B/C)†‡	PM, PP / AL	PM / PM	PM / PM, PP	PM, PP/ PM, PP	PM, PP / PM	PM, PP / PM
Bedrock Type	Idaho Batholith Granitics	Columbia River Basalt	Idaho Batholith Granitics	Idaho Batholith Granitics	Idaho Batholith Granitics	Idaho Batholith Granitics

Notes: \* Location for sites burned by wildfires/ prescribed burns. † B/C refers to burned/control. ‡ Abbreviation for dominant species are; AL – *Abies lasiocarpa* (Hook.) Nutt; PM – *Pseudotsuga menziesii* (Mirbel) Franco; PP - *Pinus ponderosa* Dougl.

Table 2. The results of statistical analyses using linear mixed-effects ANOVA to test effects of burning on soil properties and processes. For each dependent variable, treatment (burned/control, fixed) and site (random) were used as independent variables.

Dependent Variable	Wildfires	Prescribed burns
NH <sub>4</sub> <sup>+</sup> Content	F <sub>1, 19</sub> = 0.1482, P = 0.7045	F <sub>1, 20</sub> = 0.3031, P = 0.5881
NO <sub>3</sub> <sup>-</sup> Content	F <sub>1, 19</sub> = 3.3665, <b>P = 0.0822</b> †	F <sub>1, 20</sub> = 6.6578, <b>P = 0.0179</b> *
Ammonification Rate	F <sub>1, 19</sub> = 4.2240, <b>P = 0.0539</b> †	F <sub>1, 20</sub> = 0.3195, P = 0.5782
Microbial NH <sub>4</sub> <sup>+</sup> Uptake Rate	F <sub>1, 19</sub> = 3.4571, <b>P = 0.0786</b> †	F <sub>1, 20</sub> = 0.0120, P = 0.914
NH <sub>4</sub> <sup>+</sup> Mean Residence Time	F <sub>1, 19</sub> = 5.326, <b>P = 0.026</b> *	F <sub>1, 20</sub> = 0.1556, P = 0.6974
Net Ammonification	F <sub>1, 19</sub> = 0.1032, P = 0.7515	F <sub>1, 20</sub> = 0.4515, P = 0.5093
Autotrophic Nitrification Rate	F <sub>1, 19</sub> = 0.4318, P = 0.5190	F <sub>1, 20</sub> = 0.6609, P = 0.4258
Heterotrophic Nitrification Rate	F <sub>1, 19</sub> = 0.3476, P = 0.5624	F <sub>1, 20</sub> = 0.2902, P = 0.5960
Microbial NO <sub>3</sub> <sup>-</sup> Uptake Rate	F <sub>1, 19</sub> = 7.3785, <b>P = 0.0137</b> *	F <sub>1, 20</sub> = 19.4700, <b>P = 0.0001</b> ***
NO <sub>3</sub> <sup>-</sup> Mean Residence Time	F <sub>1, 19</sub> = 2.7901, P = 0.1112	F <sub>1, 20</sub> = 7.6615, <b>P = 0.0119</b> *
Net Nitrification	F <sub>1, 19</sub> = 8.0516, <b>P &lt; 0.0105</b> *	F <sub>1, 20</sub> = 12.2350, <b>P = 0.0023</b> **

Note: Statistically significant P values (i.e. P < 0.1) are bolded and labeled; † P < 0.100, \* P < 0.05, \*\* P < 0.01, and \*\*\* P < 0.001

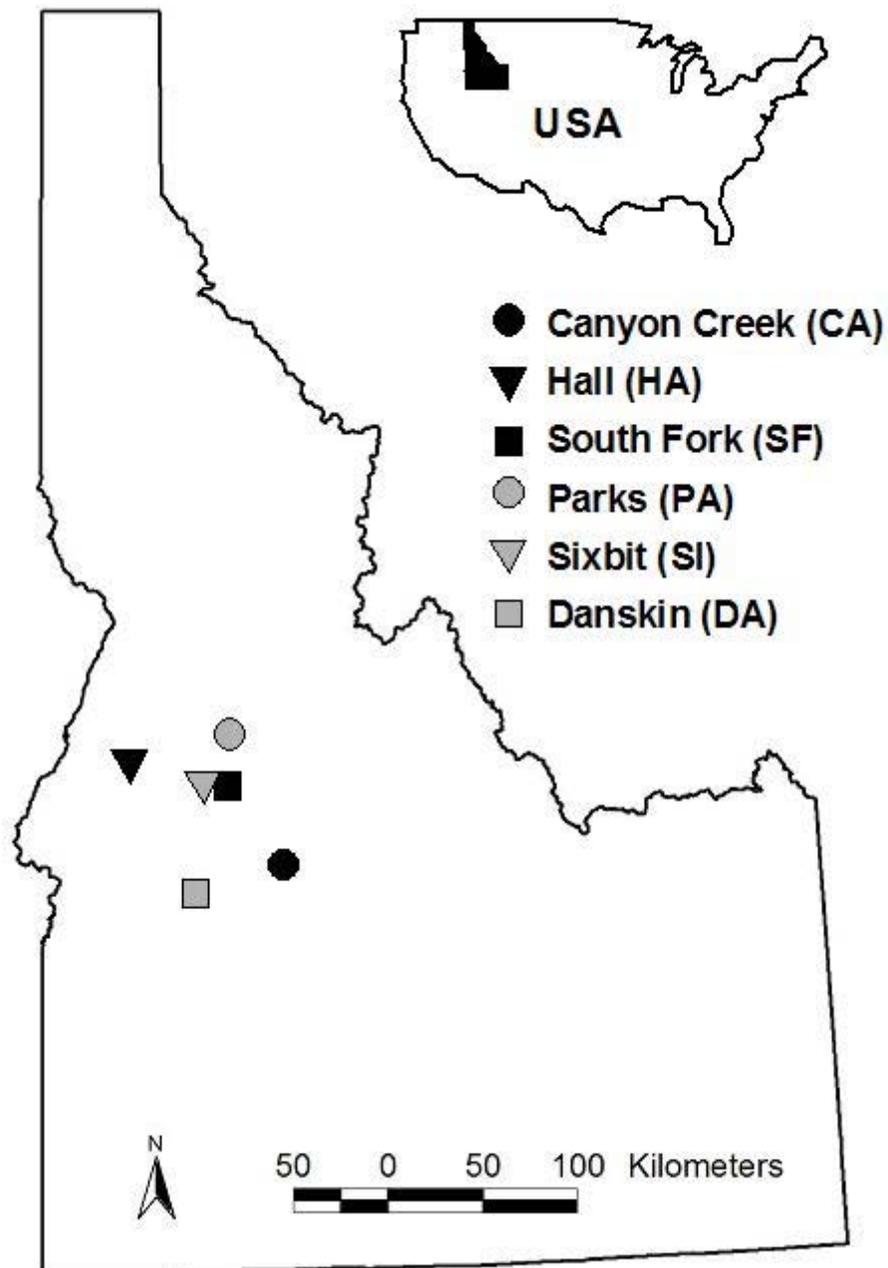


Fig. 1. Map showing study sites in coniferous forests of central Idaho. Black legends represent wildfires and gray symbols represent prescribed burns. The characteristics of each site are described in Table 1.

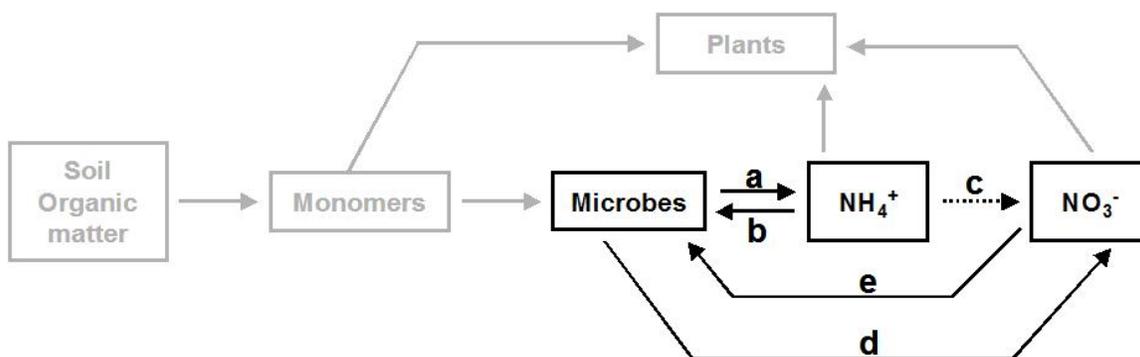


Fig. 2. Nitrogen cycling model in a forest ecosystem. Boxes and arrows represent pools and fluxes, respectively. Fluxes a: ammonification, b: microbial  $\text{NH}_4^+$  uptake, c: autotrophic nitrification, d: heterotrophic nitrification, and e: microbial  $\text{NO}_3^-$  uptake. Solid arrows are C required fluxes and a dashed for autotrophic nitrification is not required C as an energy source. Gray boxes and arrows were not measured in this study. This figure is adapted and modified from Schimel and Bennett (2004) and Cookson et al. (2006).

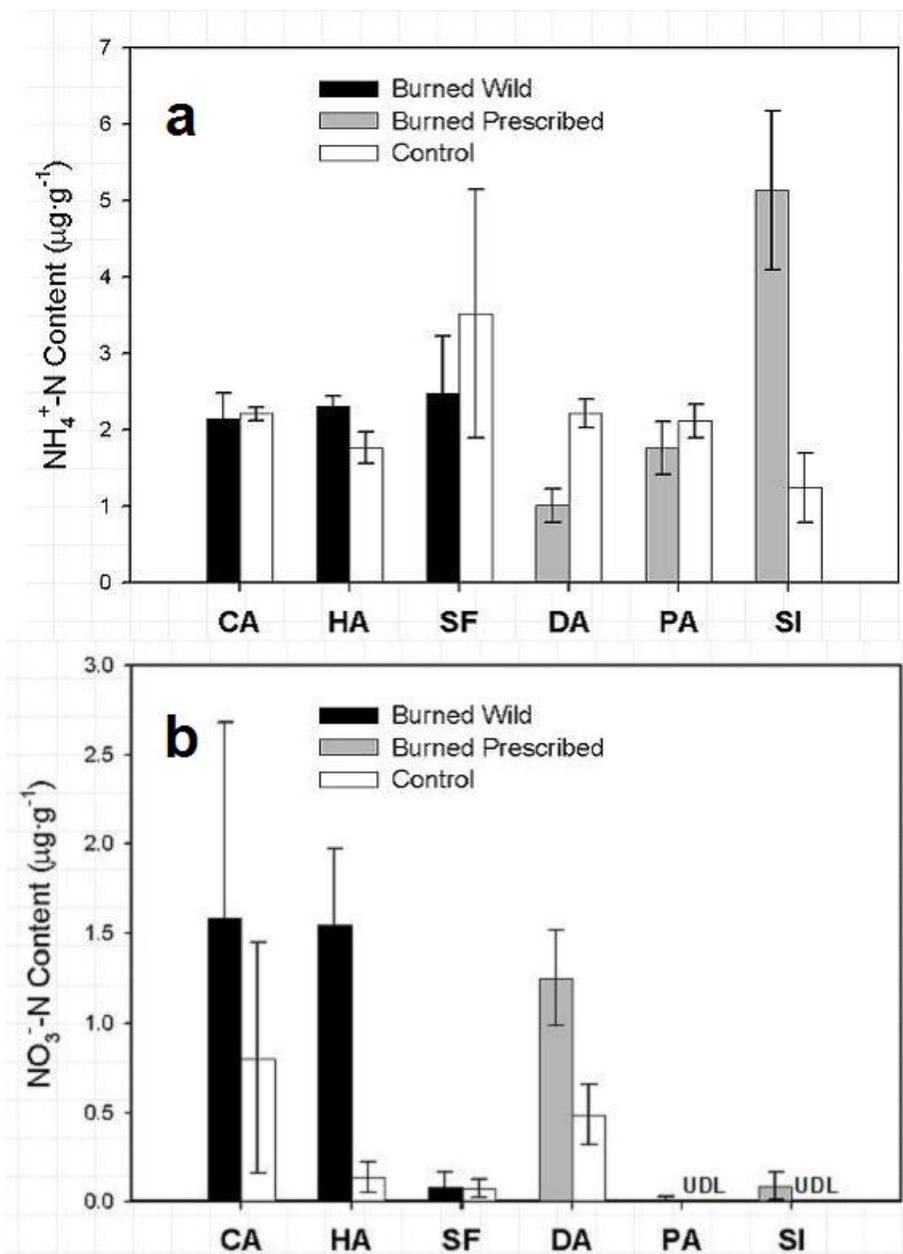


Fig. 3. Inorganic N contents in mineral soils from riparian conifer forests of central Idaho two years following fires and adjacent controls: (a) NH<sub>4</sub><sup>+</sup>-N content, and (b) NO<sub>3</sub><sup>-</sup>-N content. The results of statistical analyses are shown in Table 2. The black, gray and white columns represent wildfires, prescribed fires and paired controls, respectively. UDL refers to under detection limit (i.e. N-NO<sub>3</sub><sup>-</sup> contents in soil extracts were less than 0.025 mg/L). The error bars show standard errors within a site.

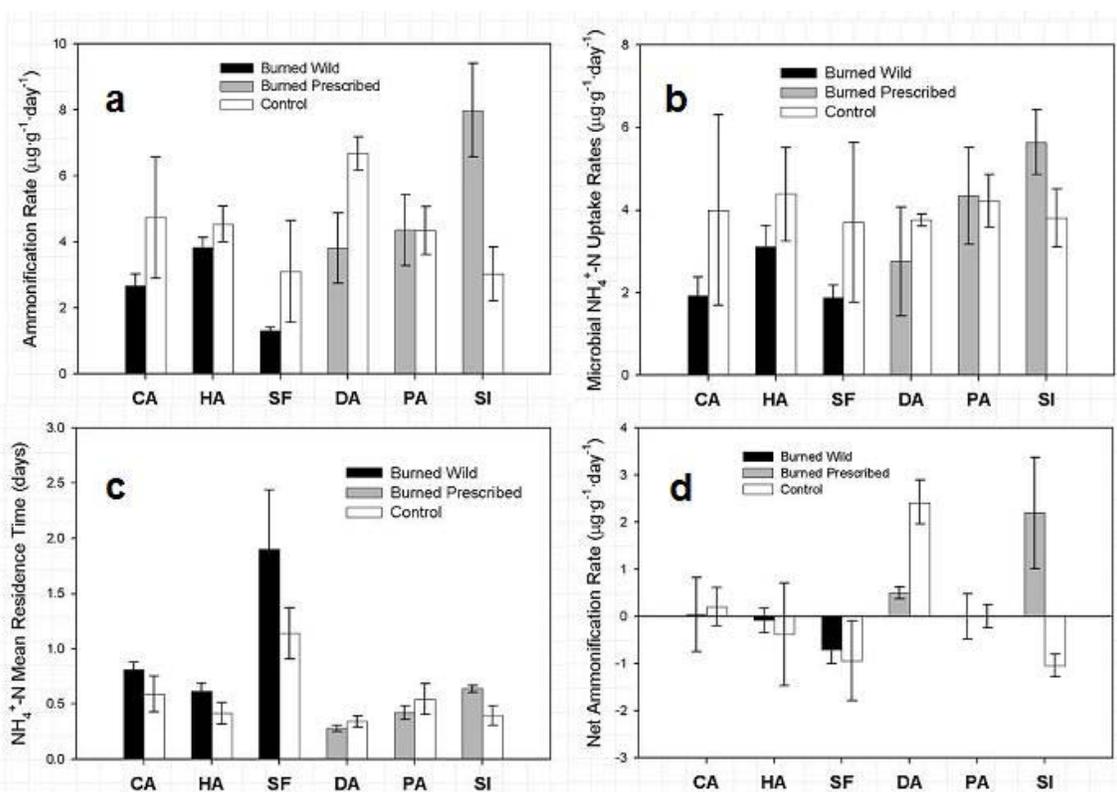


Fig. 4.  $\text{NH}_4^+$  fluxes in mineral soils from riparian conifer forests of central Idaho two years following fires and adjacent controls: (a) gross ammonification rates, (b) gross microbial  $\text{NH}_4^+$ -N uptake rates, (c)  $\text{NH}_4^+$  mean residence time, and (d) net ammonification rates. The results of statistical analyses are shown in Table 2. The black, gray and white columns represent wildfires, prescribed fires and controls, respectively. The error bars show standard errors within a site.

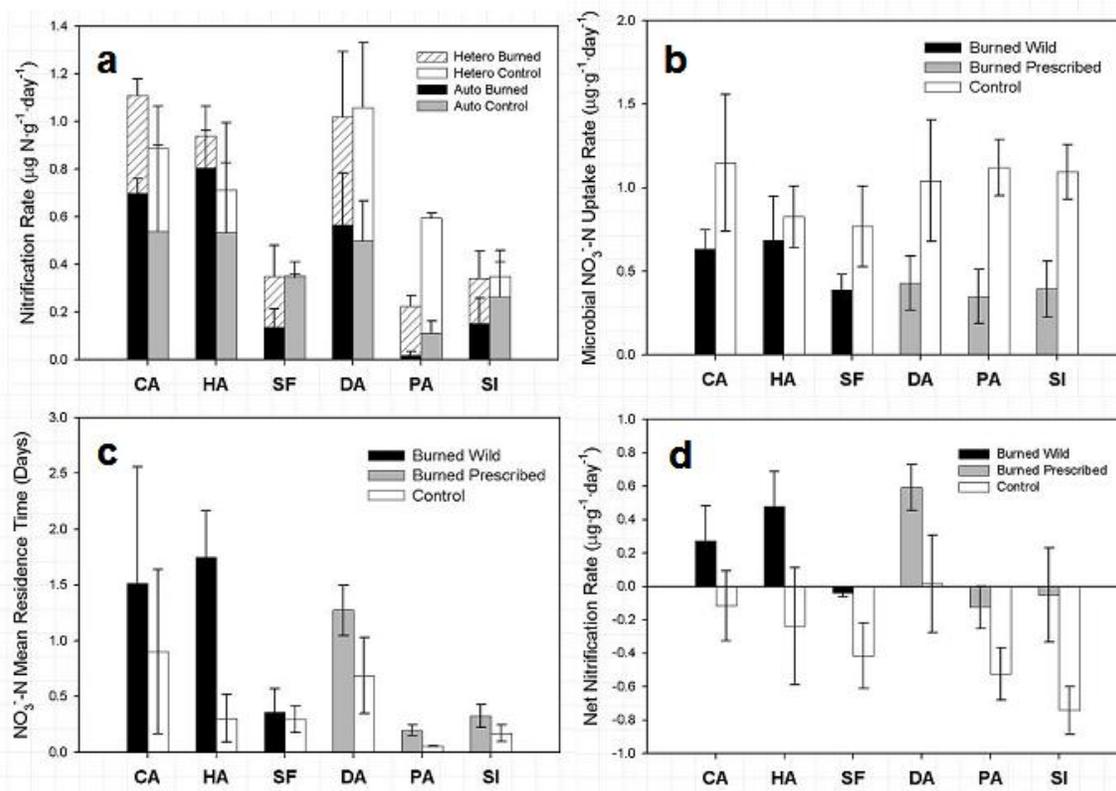


Fig. 5.  $\text{NO}_3^-$  fluxes in mineral soils from riparian conifer forests of central Idaho two years following fires and adjacent controls. (a) gross nitrification rates, (b) gross microbial  $\text{NO}_3^-$ -N uptake rates, (c) mean residence time, and (d) net nitrification rates. The results of statistical analyses are shown in Table 2. The error bars show standard errors within a site.

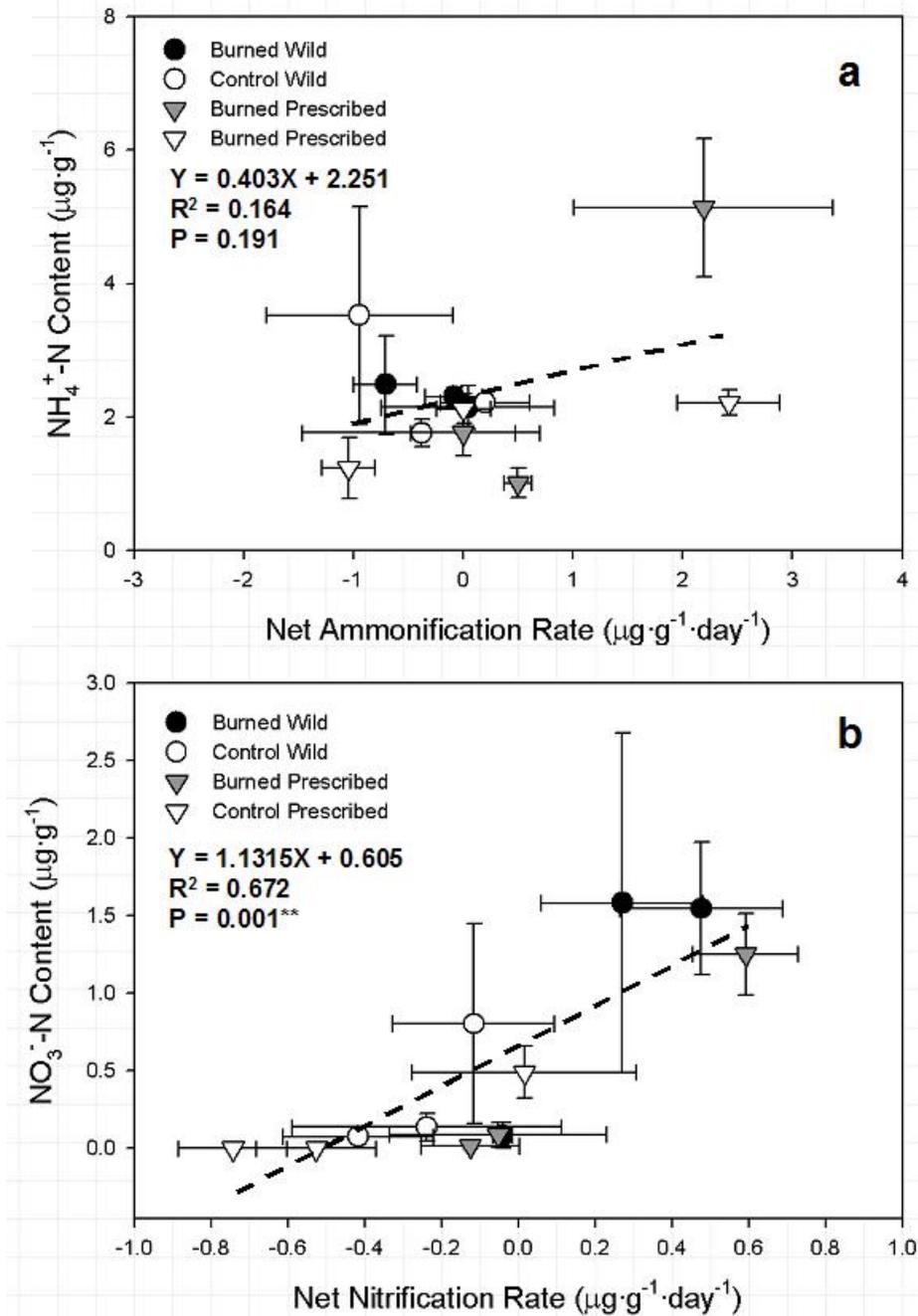


Fig. 6. Relationship between net flux rates and contents of (a)  $\text{NH}_4^+$  and (b)  $\text{NO}_3^-$  in soils from riparian conifer forests of central Idaho two years following fires and adjacent controls. Burned Wild, Control Wild, Burned Prescribed and Control Prescribed refer to burned in wildfires, controls for wildfires, burned by prescribed fires and controls for prescribed burns, respectively. The linear regression lines calculated based on mean values (dotted lines) and their equations,  $R^2$  values and P values are also shown. The error bars show standard errors within a site.

## CHAPTER 4

### WILDFIRE EFFECTS ON NITROGEN DYNAMICS AND NITROGEN STABLE ISOTOPES IN A CONIFEROUS HEADWATER ECOSYSTEM IN IDAHO, USA: A CASE STUDY

Akihiro Koyama, Kathleen L. Kavanagh and Kirsten Stephan

#### **Abstract**

Ash, a product in forest fires through combustion of organic matter (OM) and vegetation, can play a role in nitrogen (N) dynamics in forest ecosystems. We investigated effects of ash on nitrogen (N) dynamics in mineral soil and plants after a 2002 wildfire in a headwater coniferous forest of Boise National Forest, ID, USA. We created plots with three levels of ash loads; no ash (plots where ash was removed from the surface), double ash (plots where ash was added from no ash plots) and control (no manipulation). We hypothesized that ash increased N availability to plants regenerating after the fire. We also set up four sites in adjacent unburned area for comparison. Ash had less N content ( $P < 0.001$ ), higher  $\delta^{15}\text{N}$  ( $P < 0.001$ ) and lower C:N ratio ( $P = 0.004$ ) than OM. There was no difference in total mineral soil N content between burned and unburned plots. Linear mixed effects ANOVA for statistical analysis show positive correlation between foliar N content and ash levels, and negative correlation between foliar  $\delta^{15}\text{N}$  and ash levels. The results indicate that ash can be a significant N source for understory plants after fires.

*Key words:* Ash; Wildfire; Nitrogen; Understory vegetation; Stable nitrogen isotopes

## Introduction

Forest fires are a major natural disturbance in a large part of the world including the inland Pacific Northwest (Agee 1993). Coniferous forests of central Idaho are historically characterized by mixed-severity fire regime with varying fire intensities from frequent, low-intensity fires to relatively infrequent, high severity fires (Hessburg and Agee 2003). One notable aspect of forest fires is their role in biogeochemical cycles. Significant amounts of elements that accumulate in vegetation and organic matter (OM) on the forest floor can be lost through combustion (Grier 1975, Vitousek and Howarth 1991). Nitrogen (N) is easily lost, especially in high intensity wildfires because the element's sensitivity to the heat (Hosking 1938, White et al. 1973). In addition to the N loss during fires, N can also be lost through leaching following fires (DeLuca and Zouhar 2000). Despite N losses through combustion and leaching, readily available inorganic N for plants (i.e.  $\text{NH}_4^+$  and  $\text{NO}_3^-$ ) increases in soils after fire (Wan et al. 2001). Several factors associated with forest fires are associated with the elevated inorganic N contents in soil. These include heating (Choromanska and DeLuca 2002), enhanced mineralization (Klopateck et al. 1990), reduced uptake by vegetation (Vitousek and Melillo 1979) and microbes (Kaye and Hart 1998), and ash deposition (Grogan et al. 2000). It is difficult, however, to estimate the contribution of each factor to increased inorganic N contents, because these factors are often confounded with each other.

Among these factors, the effects of ash on N dynamics has been overlooked and only a few studies have been conducted (e.g. Grogan et al. 2000, Marion et al. 1991, Raison et al. 1985). Even though OM on the forest floor can lose significant amounts of N, during a fire, the remaining ash can retain some N (Raison et al. 1985). The loss of N

from the OM is proportional to the total weight loss of OM (Raison et al. 1985) and increasing fire severity reduces the inorganic N contents in ash (Marion et al. 1991). These changes in N quantity and quality through fire can change the N availability to plants and soil microbes. For example, the C:N ratio of OM, an important index for N mineralization (Enriquez et al. 1993), can be altered by combustion and heat in fires. Inhibitory chemicals such as polyphenols, which suppress the microbial activities in soil (Hättenschwiler and Vitousek 2000), can be reduced by heat (White 1986). Ash can also have indirect effects on N cycling by raising the pH of mineral soils (Fritze et al. 1994).

We investigated ash effects on N availability for plants by manipulating ash loads immediately after a wildfire. We hypothesized that ash would increase N availability to plants regenerating after the fire. Specifically, we hypothesized that foliar N concentrations of regenerating plants would be positively correlated with ash loads. We also investigated foliar  $\delta^{15}\text{N}$  levels of regenerating plants to get insights of ash effects on N processes in the mineral soil. Other measurements included N contents and  $\delta^{15}\text{N}$  levels of OM in unburned sites and ash collected from burned sites to see the difference in N properties between ash and OM, the major source of ash. We note that this is a case study. Therefore, all the statistics used to analyze data in this paper are inferential statistics (Oksanen 2001).

## **Materials and methods**

### *Study site*

This study was conducted in the Danskin Creek watershed in the Boise National Forest, Idaho, USA (44°6'N, 115°49'W, Fig. 1). The average annual precipitation and

mean temperature are 636mm and 8C°, respectively (Western Regional Climate Center 2007) with the majority of the precipitation in the form of snow. The soil and bedrock types are sandy loam and Idaho Batholith, respectively. Douglas-fir (*Pseudotsuga menziesii* (Mirb. Franco)) and ponderosa pine (*Pinus ponderosa* (Dougl. ex Laws)) are the dominant tree species.

A part of the watershed was burned by a wildfire in August 2002. Two weeks after the fire, we selected four sites along the Danskin Creek where mature conifers were not killed, but understory vegetation and OM on forest floor were well consumed by the fire. We did not observe any evidence of the red stains associated with the application of fire retardant at the four sites selected. We avoided areas with fire retardant since it contains large amounts of inorganic N (Larson et al. 1999). At each site, we set up three 1.5 by 1.5 m plots for ash-level manipulation, creating three treatment levels: double ash (DA), control (C) and no ash (NA). We also selected four sites from an adjacent unburned area comparable to sites in burned area in terms of plant species and topographic characteristics (Fig. 1).

#### *Sample collection and analyses*

Ash was collected from burned sites, OM from unburned sites, and mineral soils to the depth of 10 cm from burned and unburned sites in August 2002 to measure N content, C:N ratio and  $\delta^{15}\text{N}$  value. Mineral soil samples to 10 cm depth were also collected from burned and unburned sites in May, July and September 2003 to quantify inorganic N content and pH. Soil samples were transported to the lab on ice, and stored at 4°C up to 10 days until processed. Soil samples were sieved (2mm) and roots and OM

were removed with forceps. To measure inorganic N ( $\text{NH}_4^+$  and  $\text{NO}_3^-$ ) content, 15 g of mineral soil samples were extracted in 50 mL of 2 M potassium chloride (KCl) solution. The soil samples and KCl solution were mixed in specimen cups, mechanically shaken for one hour, filtered with no. 42 Whatman filter papers, and stored frozen before analysis. Dissolved  $\text{NH}_4^+$  and  $\text{NO}_3^-$  were measured with an Alpkem Autoanalyzer (OI Analytical, College Station, Texas, USA) at the Rocky Mountain Research Station, Moscow, Idaho, USA. Mineral soil pH was measured following Thomas (1996); 10 grams of soil samples and double deionized water were mixed and stirred in specimen cups, and an Accumet Basic pH meter (Fisher Scientific, Pittsburgh, PA, USA) was used. Ash, OM and foliage samples were transported to the lab on ice and dried at 70°C for 24 hours. N and C contents,  $\delta^{15}\text{N}$  values were measured by NC 2500 elemental analyzer (CE Instrument, Milan, Italy) connected with a Finnigan MAT DELTA plus isotope ratio mass spectrometer (Bremen, Germany) at the Idaho Stable Isotope Lab (Moscow, Idaho, USA).

Plants resprouting and regenerating in ash-manipulated plots were collected in July 2003 from burned sites, and the same species were collected on unburned sites to quantify foliar N content and  $\delta^{15}\text{N}$  values. The plant species collected include *Epilobium ciliatum* Raf. (EC), *Rubus parviflorus* Nutt. (RP), *Symphoricarpos albus* (L.) Blake (SA), *Spiraea betulifolia* Pallas (SB), and *Spiraea pyramidata* Greene (SP). We also collected current year sun foliage samples from three to six individual dominant *Pseudotsuga menziesii* per site in October 2002 and July 2003. Trees sampled in burned sites were those that survived the fire and were not damaged. The *P. menziesii* foliage samples were processed and analyzed in the same manner described above.

### *Statistical Analyses*

Statistical analyses were performed with R (Ihaka and Gentleman 1996). A one-way ANOVA was used to detect the fire effects on N contents, C:N ratios and  $\delta^{15}\text{N}$  of mineral soils and OM/ash samples collected in August 2002. A repeated measurement ANOVA was employed to detect the effects of ash treatments and time on mineral soil pH,  $\text{NH}_4^+$  and  $\text{NO}_3^-$  contents. In cases where significant treatment effects were found, Tukey's Honestly Significant Differences tests were performed to compare the differences among treatments at each sampling time. A linear mixed effects ANOVA was used for analyses to detect the effects of ash treatments and understory plant species on foliar N contents and  $\delta^{15}\text{N}$  values. The independent variables in the models are ash levels (fixed), species (fixed) and sites (random). The effects of fire and time on foliar N contents and  $\delta^{15}\text{N}$  of *P. menziesii* were analyzed by a repeated measurement ANOVA. Since the root systems of *P. menziesii* covered a significantly larger area than the ash plots, we compared foliar N contents and  $\delta^{15}\text{N}$  levels only between burned and unburned sites with no ash manipulation.

### **Results**

We observed significant differences between the N properties in ash and OM (Fig. 2). OM contained 1.7 times more N than ash (Fig. 2a, 1.7% and 0.69%, respectively,  $P < 0.001$ ). Interestingly, ash had lower C:N ratio than OM (Fig. 2b, 16.1 and 25.4, respectively,  $P = 0.004$ ). Ash had higher  $\delta^{15}\text{N}$  values than OM (Fig. 2c, 2.6‰ and -1.8‰, respectively,  $P < 0.001$ ). Mineral soil samples from burned and unburned

sites were not significantly different in N concentrations, C:N ratios and  $\delta^{15}\text{N}$  (Fig. 2a, b and c).

There were significant effects of ash treatments ( $P < 0.001$ ) and time ( $P < 0.001$ ) on the mineral soil pH. Soil pH levels of double ash and control plots were higher than unburned sites in September (Table 1). Soil pH levels of three treatments in burned area had similar trend; pH levels declined in July and increased in September (Table 1). This trend contrasts with pH levels of unburned soils that decreased throughout the season (Table 1).

Significant effects of ash treatments ( $P < 0.001$ ), time ( $P < 0.001$ ) and interaction between ash treatment and time ( $P = 0.008$ ) were found on  $\text{NH}_4^+$  content in mineral soils.  $\text{NH}_4^+$  content in unburned soils were low throughout the season (Table 1). In contrast,  $\text{NH}_4^+$  content in all burned area plots increased from May to July, and maintained these values through September (Table 1). The  $\text{NH}_4^+$  content in all the ash treatment plots was significantly higher than unburned sites in July and September (Table 1) There was no significant difference in  $\text{NO}_3^-$  content among the three ash treatments ( $P = 0.383$ ) and with sampling time ( $P = 0.533$ ).

Ash level had a significant effect on foliar N content of understory vegetation (Fig. 3a, Table 2). Foliage N content tended to be higher with increasing ash levels for most of the understory species. However, this relationship between ash levels and foliar N contents were also dependent on species; species effect was significant ( $P < 0.0001$ , Table 2), and there was a significant interaction effect between ash levels and understory species ( $P = 0.0007$ , Table 2). Foliar N contents in unburned areas were lower than in burned area (Fig. 3a). Ash levels also had significant effects on foliar  $\delta^{15}\text{N}$  of understory

vegetation (Fig. 3b, Table 2). Among the three ash treatments, increasing ash levels tended to have decreasing foliar  $\delta^{15}\text{N}$  values (Fig. 3b). There was a significant species effect on foliar  $\delta^{15}\text{N}$  values ( $P = 0.0243$ , Table 2). In contrast to foliar N contents, there was no interaction between ash levels and understory species on foliar  $\delta^{15}\text{N}$  values ( $P = 0.6598$ , Table 2).

The foliar N content of *P. menziesii*, was not different between burned and unburned areas, and between sampling time ( $P = 0.9648$ , Fig. 4a, Table 3). There was no effect of burning on foliar  $\delta^{15}\text{N}$  values of *P. menziesii*, but the values changed significantly between the two samplings times ( $P = 0.0015$ , Fig. 3b, Table 3).

## Discussion

Foliar N concentrations of regenerating plants were positively correlated with ash loads, however there was a species effect. The response of understory species to increasing ash levels varied. The trend that increasing ash load elevated foliar N contents was evident in PR, SA and SB. However, EC and SP did not show such a trend (i.e. there was a significant interaction between treatment and plant species,  $P = 0.0007$ , Table 2, Fig. 3a). In addition, ash levels had a significant effect on foliar  $\delta^{15}\text{N}$  values ( $P = 0.0025$ , Table 2, Fig. 3b). In contrast to the ash effects on foliar N contents, however, there was no interaction effect between ash levels and plant species on foliar  $\delta^{15}\text{N}$  values ( $P = 0.6598$ , Table 2).

Species differences in plant foliar  $^{15}\text{N}$  have been linked with differences in source N (Pate et al. 1993; Kielland et al. 1998), N availability (Michelsen et al. 1998), and mycorrhizal associations (Hobbie et al. 2000). In addition, phenology of each species,

micro-environments for each individual plant, and interactions among these factors, all would contribute to foliar  $\delta^{15}\text{N}$  values (Evans 2001, Robinson 2001). Therefore, it is not surprising to find a wide range of foliar  $\delta^{15}\text{N}$  values among understory species in the region (Chambers et al. 2004). Given those many sources of variability, it's surprising that ash levels had statistically significant effects on foliar  $\delta^{15}\text{N}$  values. One explanation of the observed trend in foliar  $\delta^{15}\text{N}$  is that N in ash increased N availability in soil compared to relatively small demand by regenerating plants that the plants preferentially took up lighter N (i.e.  $^{14}\text{N}$ ) over heavier N (i.e.  $^{15}\text{N}$ ). Högberg et al. (1999) reported that *Pinus sylvestris* seedlings fractionated against  $^{15}\text{N}$  when N supply was relatively high compared to N demand. Interestingly, the foliar  $\delta^{15}\text{N}$  values in double ash plots were relatively close to those in unburned plots, even though their foliar N contents were most different (PR, SA and SB in Fig. 3). The foliar  $\delta^{15}\text{N}$  values in unburned plots under N limited condition most likely reflected  $^{15}\text{N}$  levels of sources of N (Högberg 1997). These observed  $^{15}\text{N}$  values need to be interpreted with caution because foliar  $^{15}\text{N}$  values integrate many factors (Evans 2001, Robinson 2001).

We did not observe any difference in foliage N content (Fig. 4a, Table 3) and  $\delta^{15}\text{N}$  value of *P. menziesii* between burned and unburned treatments (Fig. 4b, Table 4). The contrasting results in foliage N content could happen because the dominant *P. menziesii* trees sampled had significantly larger biomass compared to the understory plants, thus the increased available N after the fire was diluted (Buchman et al. 1996). This interpretation is also consistent with results by Chambers et al. (2004); relatively large biomass of dominant conifers diluted the fertilizer labeled with  $^{15}\text{N}$ . On the other hand, foliar  $\delta^{15}\text{N}$  of understory vegetation reflected the labeled fertilizer. There were

significant differences in foliar  $\delta^{15}\text{N}$  values of *P. menziesii* (Fig. 4b, Table 3) between the two sampling occasions. Foliar  $\delta^{15}\text{N}$  values can significantly change seasonally (e.g. Shearer et al. 1983, Evans and Ehleringer 1994). However, the inter-seasonal change can also depend on species (Billings et al. 2002) and N availability (Kielland et al. 1998). The difference in this study may be caused due to an inter-seasonal variation (i.e. post-growing vs. during growing season) in addition to inter-annual variations (i.e. 2002 vs. 2003).

The N content, C:N ratio and  $\delta^{15}\text{N}$  value of OM and ash are consistent with Saito et al. (2007). When OM and mineral soils were combusted in a muffle furnace with high enough temperature (400°C) and long enough duration (15 to 60 minutes),  $\delta^{15}\text{N}$  levels increased and C:N ratios decreased significantly (Saito et al. 2007). Some portion of the ash collected in our study should be from the combusted understory vegetation, thus we have uncertainty in directly comparing OM and ash for their N properties. However, considering the relatively low foliage  $\delta^{15}\text{N}$  of understory vegetation (average = -0.9 ‰, SE = 0.4, n=23, Fig. 3b), and relatively small N stock in understory vegetation compared to OM in coniferous forests (Cole and Rapp 1981), we are confident in our comparison. We did not observe the difference in these N properties in mineral soil between burned and unburned areas (Fig. 2abc). These results are not surprising because surface fires do not increase the temperature of the mineral soil enough to volatilize N even in intense fires (e.g. less than 200°C at 2.5 cm in depth: DeBano et al. 1979, 60°C at 5 cm in depth: Gara et al. 1985, negligible increase at 2.5 cm in depth: Giovannini and Lucchesi 1997).

The C:N ratio of OM is an important index for N mineralization; OM with lower ratios release more available N (Enriquez et al. 1993). Based on the difference in C:N

ratios between OM and ash, N in ash is more readily available for plants. Ash is primarily water soluble minerals (i.e. Ca, Mg and K; Raison et al. 1985) bound to anions, mostly hydroxide ( $\text{OH}^-$ ) and carbonate ( $\text{CO}_3^-$ ) (Etiégni and Campbell 1991). Ash could contain N in forms of  $\text{NO}_3^-$  and  $\text{NH}_4^+$  (Marion et al. 1991). We do not know, however, the other forms of N in ash, which leaves uncertainty in how readily N in ash is available for plants. Based on our data of enhanced foliar N contents with increasing ash loads (Fig. 3a), N in ash was probably easily mineralized.

Increasing pH in burned soils (Table 1) is consistent with the generally accepted effects of fire on soils (Raison 1979, Certini 2005). Heating soil can increase pH by organic acid denaturation if temperature exceeds  $400^\circ\text{C}$  (Giovanni and Lucchesi 1997, Certini 2005). Ash, which has high mineral contents with hydroxide and carbonate, also increases soil pH (Ulery et al. 1993). The increased soil pH in burned soils in our study could be caused by both heating and ash deposition because the pH levels were not significantly different among the three ash treatments in September. At the same time, mineral soils from double ash and control plots had significantly higher pH than unburned plots (Table 1).

Numerous studies reported that  $\text{NH}_4^+$  content in burned soils immediately increases after fires, and then declined to background levels in one year, followed by a gradual increase in  $\text{NO}_3^-$  content (Wan 2001, Smithwick et al. 2005). We also observed increased  $\text{NH}_4^+$  contents in burned soils compared to unburned soils (Table 1). It was intriguing that there was no significant difference in  $\text{NH}_4^+$  content in May, followed by sharp, significant increase in all three ash treatment plots compared to unburned sites (Table 1). The consistently high  $\text{NH}_4^+$  contents in three ash-manipulated plots in July and

September implies that ash is not the only cause to increase  $\text{NH}_4^+$  content in burned soils. There could be other factors associated with fire that cause elevated  $\text{NH}_4^+$  contents in soils. We did not find significant differences in  $\text{NO}_3^-$  content among ash treatments and unburned soils at three sampling occasions (Table 1). We might have collected these data before the gradual increase in soil  $\text{NO}_3^-$  content often observed (Wan et al. 2001).

Forest fires with mixed-severity create landscape heterogeneity (Turner and Romme 1994). Fires also create heterogeneity at finer scales due to local factors affecting combustion such as topography, biomass, moisture and wind (Hobbs and Atkins 1988). Ash can be an additional factor that creates local heterogeneity by its N properties. Ash distribution in fires is heterogeneous by nature (Rice 1993) and ash can be redistributed by winds and rains post-fire (Grogan et al. 2000). N availability affects understory species diversity (Hutchinson et al. 2004), productivity (Grogan et al. 2000) and herbivory (Mattson 1980). The ash patches can create gradients in local N availability, which, in turn, can result in heterogeneous vegetation mosaic after fires.

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Table 1. Mineral soil characteristics (pH, NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup> contents) measured the first growing season following a wildfire. There were three ash manipulation treatments (double ash, control and no ash) in burned sites and unburned sites in central Idaho.

Mineral soil characteristics	Treatments			
	Double Ash	Control	No Ash	Unburned
pH May	7.16 (0.27)	6.65 (0.18)	6.51 (0.25)	6.47 (0.05)
pH July	6.53 (0.14)	5.90 (0.21)	6.12 (0.19)	5.96 (0.11)
pH September	6.92 (0.02) a	6.66 (0.24) a	6.37 (0.21) ab	5.79 (0.20) b
NH <sub>4</sub> <sup>+</sup> May	37.63 (33.92)	5.61 (3.43)	8.67 (5.42)	6.22 (2.69)
NH <sub>4</sub> <sup>+</sup> July	50.48 (19.37) a	44.24 (15.27) a	43.19 (3.37) a	2.52 (0.46) b
NH <sub>4</sub> <sup>+</sup> September	42.36 (16.07) a	38.69 (9.61) a	32.07 (6.60) a	1.70 (0.18) b
NO <sub>3</sub> <sup>-</sup> May	14.99 (6.78)	10.01 (2.27)	25.48 (12.12)	1.78 (0.88)
NO <sub>3</sub> <sup>-</sup> July	11.03 (7.52)	7.37 (3.56)	6.72 (2.52)	5.05 (2.47)
NO <sub>3</sub> <sup>-</sup> September	17.69 (7.99)	8.95 (3.57)	13.48 (5.13)	5.82 (2.04)

Different letters in the same row mean statistically significant difference ( $P < 0.10$ ) among treatments. In cases without letters, there was no statistically significant difference among treatments

Table 2. The results of statistical analysis with a linear mixed effects ANOVA. The dependent variable is foliar  $\delta^{15}\text{N}$ .

Dependent variable	Independent variables		
	Treatment	Plant species	Interaction
Foliar N content	$F_{2,31} = 5.478$ $P = 0.0078$	$F_{4,41} = 19.724$ $P < 0.0001$	$F_{8,41} = 4.399$ $P = 0.0007$
Foliar $\delta^{15}\text{N}$	$F_{2,41} = 6.937$ $P = 0.0025$	$F_{4,41} = 3.138$ $P = 0.0243$	$F_{8,41} = 0.735$ $P = 0.6598$

Table 3. The results of statistical analysis with linear mixed effects ANAOVA. The dependent variable is foliar N contents and  $\delta^{15}\text{N}$  of *P. menziesii*.

Dependent variable	Independent variables		
	Burned/Unburned	Sampling time	Interaction
Foliar N content	F1, 6 = 0.305 P = 0.6011	F1, 45 = 0.0857 P = 0.7711	F1, 45 = 1.2519 P = 0.2691
Foliar $\delta^{15}\text{N}$	F1, 6 = 0.00211 P = 0.9648	F1, 45 = 11.363 P = 0.0015	F1, 45 = 1.747 P = 0.193

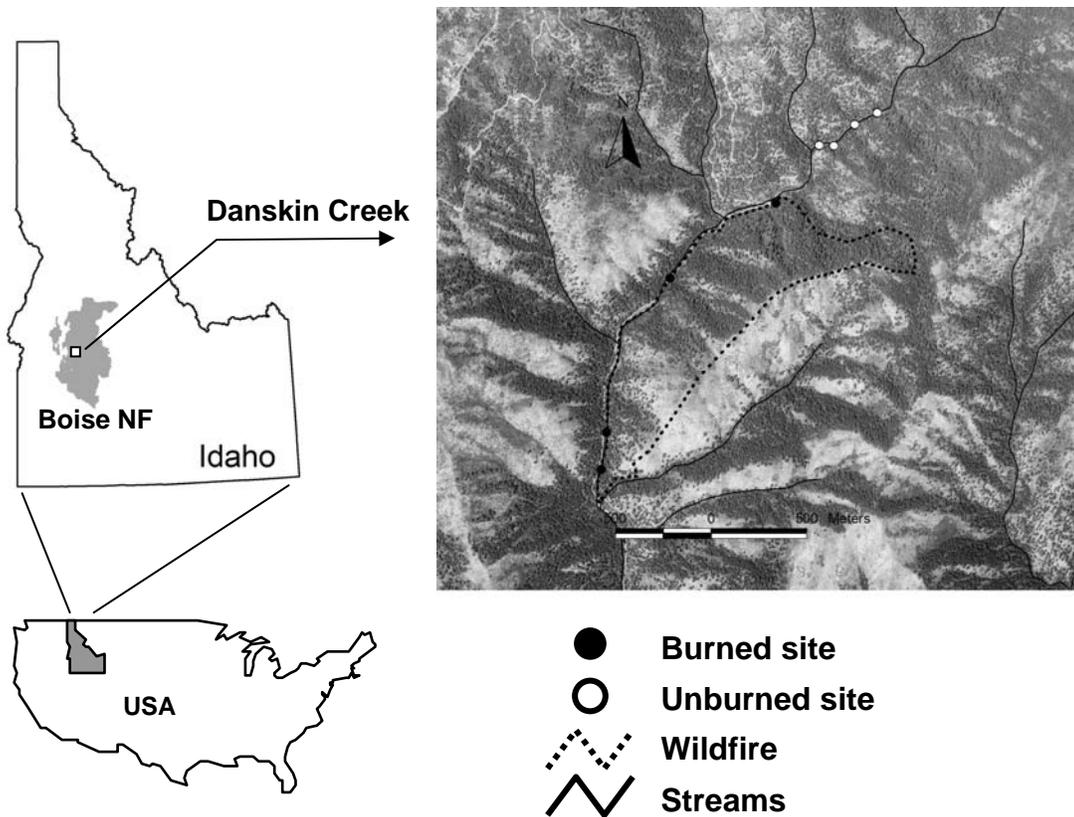


Fig. 1. Maps showing the location of study sites in Danskin Creek Watershed, a headwater stream in Boise National Forest of Idaho, USA. The area within the dotted line was burned by a wildfire in August 2002. The black and white circles show burned sites and unburned sites, respectively.

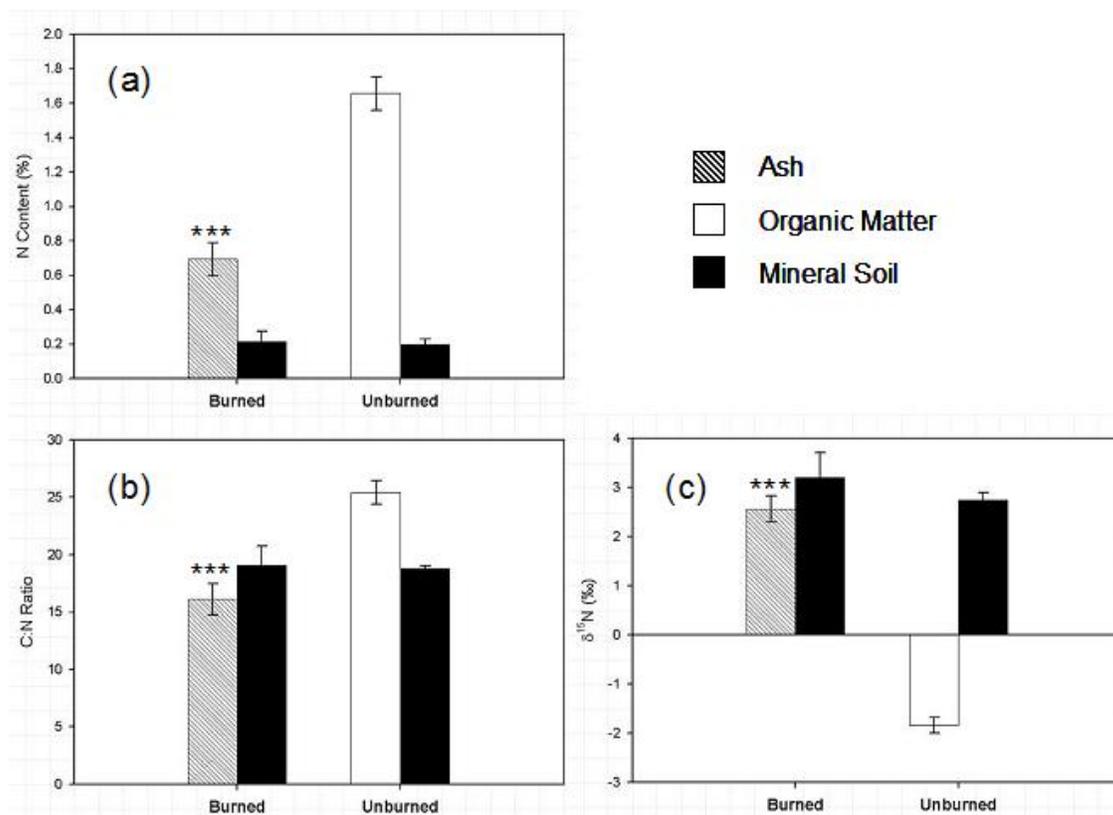


Fig. 2. Nitrogen properties of ash, organic matter and mineral soils (a) N content, (b) C:N ratios and (c)  $\delta^{15}\text{N}$  values of ash, organic matter and mineral soils collected two weeks after the fire central Idaho in August 2002. Ash was collected from each burned site and organic matters from each unburned site. Each value is average of four samples. Error bars represent standard errors. \*\*\* denotes significant difference at  $P < 0.001$  level was found between the ash from burned and the OM unburned sites.

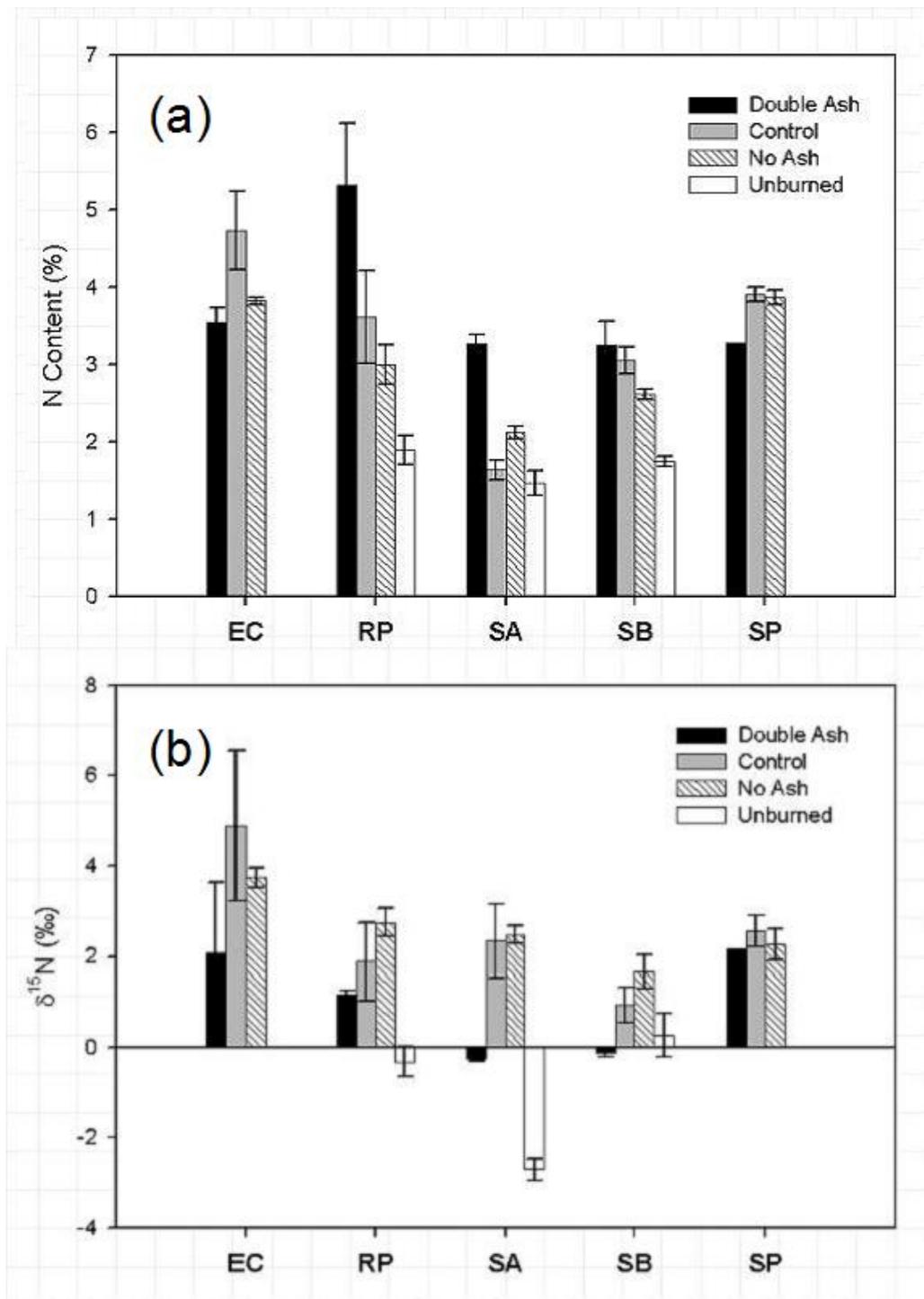


Fig. 3. (a) Foliar N contents and (b)  $\delta^{15}\text{N}$  values of understory vegetation collected from ash manipulation plots and unburned sites in July 2003, in central Idaho, one year after the fire. Species abbreviations: EC (*Epilobium ciliatum*), RP (*Rubus parviflorus*), SA (*Symphoricarpos albus*), SB (*Spiraea betulifolia*) and SP (*Spiraea pyramidata*).

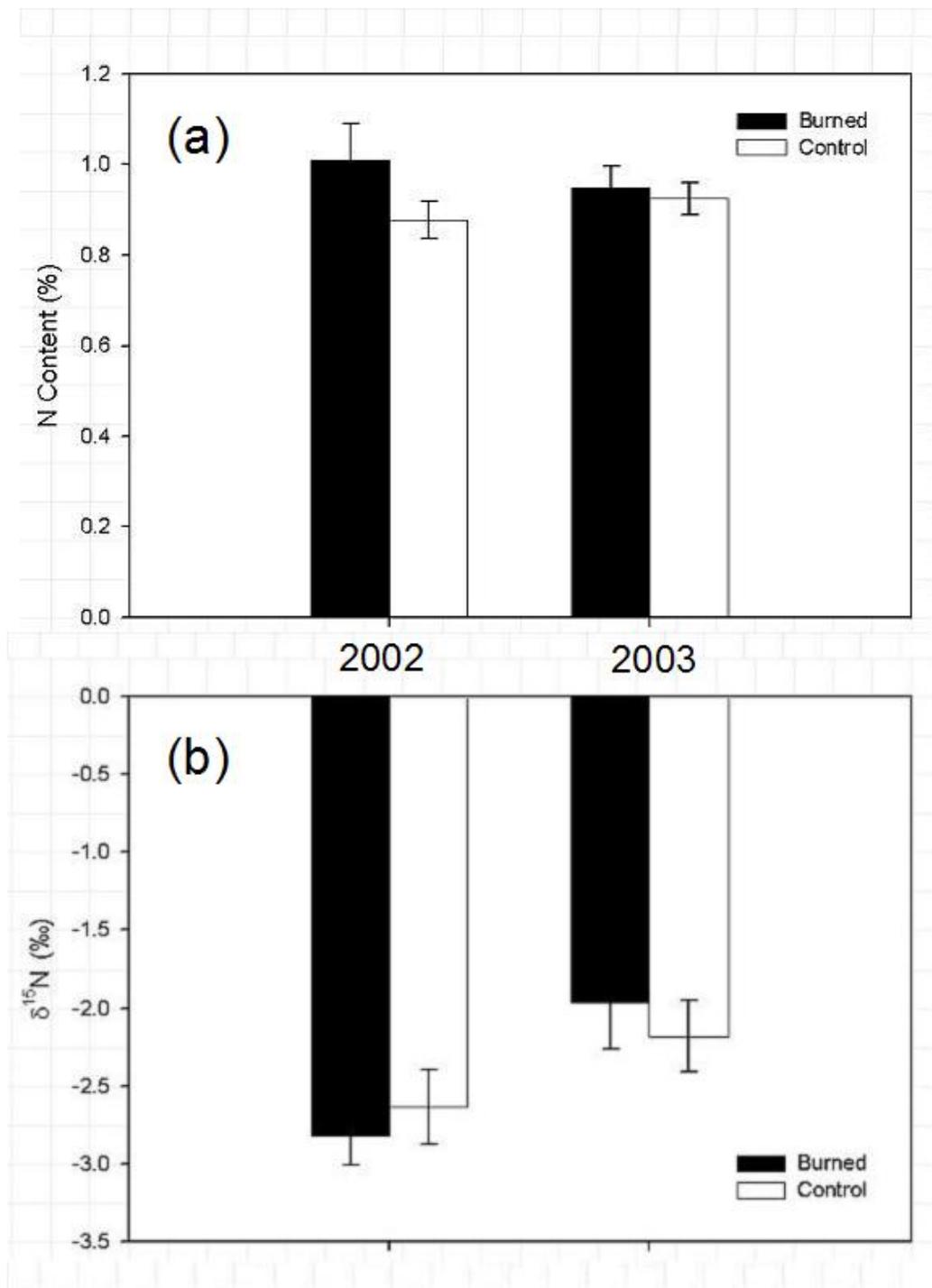


Fig. 4. (a) Foliar N content and (b)  $\delta^{15}\text{N}$  values of *P. menziesii* collected in October 2002, two months after the fire and in July 2003, one year after the fire. Error bars represent standard errors.

## CHAPTER 5

### CLOSING REMARKS

#### Summary and conclusion

This research investigated two aspects of nitrogen (N) dynamics influenced by forest fires. One is how fires affected gross fluxes of inorganic N (i.e.  $\text{NH}_4^+$  and  $\text{NO}_3^-$ ) in mineral soils using  $^{15}\text{N}$  isotope pool dilution (chapter 2 and 3), and the other is if ash was a significant factor to increase N availability for plants after a wildfire (the ash study, chapter 4). In studying fire effects on gross inorganic N fluxes, we conducted two studies with different interests. In one study, the focus was to quantify effects of severe wildfire on gross inorganic N fluxes in soils, and to investigate the relative importance of several key factors that could control gross inorganic N fluxes in soils (the upslope study, chapter 2). In the other study, the focus was to compare wildfires and prescribed fires in their impacts on gross fluxes of inorganic N in riparian soils (the riparian study, chapter 3). All three studies were conducted in coniferous forests of central Idaho, USA.

In the upslope study, three sites burned by three different wildfires in summer 2003 were used for the experiments. Gross inorganic N fluxes were measured using  $^{15}\text{N}$  isotope pool dilution in intact cores in late June or early July of 2005, two years after the fires. We found that gross nitrification rates were not affected by fires, but microbial  $\text{NO}_3^-$  uptake rates were significantly reduced relative to controls. This reduced microbial  $\text{NO}_3^-$  uptake rates resulted in increased  $\text{NO}_3^-$  pool sizes in burned soil relative to control soils. Despite there was no significant difference in  $\text{NH}_4^+$  pool sizes between burned and control soils, both ammonification rates and microbial  $\text{NH}_4^+$  uptake rates were significantly reduced in burned soils compared to control soils. The gross fluxes

significantly reduced by fires (microbial  $\text{NO}_3^-$  uptake, ammonification and microbial  $\text{NH}_4^+$  uptake rates) were caused by reduced carbon (C) availability in soils. This study emphasized the importance of gross flux measurements to assess the impacts of fires on N dynamics in soils.

In the riparian study, three watersheds burned by the three wildfires (same as in the upslope study), and three watershed burned by three prescribed burns were chosen for comparison. The prescribed burns were conducted in spring 2004. The burned watersheds by both wildfires and prescribed fires were paired with unburned watersheds as controls. Gross inorganic N fluxes were measured by  $^{15}\text{N}$  isotope pool dilution in mineral soils collected from riparian areas in the watersheds. Wildfires and prescribed fires had similar effects on gross nitrification rates in soils. Microbial  $\text{NO}_3^-$  uptake rates were reduced significantly in soils burned both wildfires and prescribed burns compared to their controls. There was no fire effect on nitrification rates in either fire types. There was a significant difference in gross  $\text{NH}_4^+$  fluxes in soils between wildfires and prescribed fires. In soils burned by wildfires, ammonification and microbial  $\text{NH}_4^+$  uptake rates were significantly reduced compared to their controls. On the other hand, there was no such difference between soils burned by prescribed burns and their controls. We concluded that prescribed burns may not impact on soil N dynamics in the same magnitude as wildfires.

In the ash study, we investigated if ash, a product of combusted organic matter and plant biomass, was a significant source of N for regenerating and resprouting understory vegetation in an area burned by a wildfire in August, 2002. Ash was analyzed for its N properties including N content, C:N ratio and  $\delta^{15}\text{N}$ . Organic matter, a major

source of ash, was collected from adjacent unburned areas and analyzed for its N properties for comparison. Ash load levels were manipulated at three levels (i.e. double ash, control and no ash) just after the fire, and foliage samples of understory vegetation were collected from the ash-manipulated plots in the following year to analyze N content and  $\delta^{15}\text{N}$ . There were significant differences in N properties between ash and organic matter. Ash had lower N content, lower C:N ratio and higher  $\delta^{15}\text{N}$ . The results of inferential statistics using linear mixed-effect ANOVA showed positive correlation between ash levels and foliar N content, and negative correlation between ash levels and foliar  $\delta^{15}\text{N}$ . I concluded that ash can be a significant N source for understory vegetation post-fire.

### **Recommendation for future research**

In the upslope study, the experimental plots at the burned sites were set up on areas with all the dominant conifers killed by fires. These plots with 100% mortality rates were at the extreme end of mixed-severity fire regime of the region. It would be ideal that gross fluxes of inorganic N and the key factors be measured at areas burned in lower severity with dominant conifers survived. These measurements would address if the survived dominant conifers are significant C sources for soil microbial organisms involved in N transformations. Recent studies have shown that current photosynthate is an important energy source for rhizosphere microbes (Göttlicher et al. 2006, Högberg et al. 2001, Phillips and Fahey 2005). Measurements of  $\delta^{13}\text{C}$  levels of important soil properties (e.g. microbial biomass C, soil respired  $\text{CO}_2$ , photosynthate in phloem) are

promising methods to investigate the relationship between soil microbial activity and current photosynthate.

The most serious limitation of the upslope study is that the experiments were conducted at one time at the beginning of the growing season (late June or early July) two years after the fires. It would be ideal that the experiments are conducted multiple times within and among years, even for decades along forests' recovery post-fire. The inland Northwest has seasonal environmental gradients, thus different environmental factors can control activities of soil microbes and vegetation along seasons. For example, low temperature during winters and low moisture availability at the mid and late summers can be more important factors for gross inorganic N fluxes than available C which was found the most important in this study. Measurements in multiple years would reveal how long it takes for forests to recover from impacts from fires in N-limited ecosystems.

Another limitation of the upslope study, and also of the riparian study, is its relatively small replication ( $N = 3$  for both studies). Increasing replications can compensate two shortcomings of those studies to some extent. One is a high variability inherent to soils. A combination of high variability and small sample size tends to lead to an erroneous statistical conclusion (i.e. type II error; null hypothesis is false for a population, but it's accepted based on samples, Moore and McCabe 1999). Larger sample sizes can increase statistical power to reject null hypotheses. For example, in upslope and riparian studies, I employed  $P = 0.10$  or less for statistical significance to test differences in gross inorganic N fluxes and soil properties between burned and control soils due to the low power to reject null hypotheses. However, it would be better to employ  $P = 0.05$  or less for statistical significance, which is more widely accepted.

The other shortcoming is the fact that it was impossible to collect pre-burn data in upslope and riparian studies. Even though control sites were carefully chosen so that they were comparable to burned sites in topographic and biotic characteristics, there is still some room that the differences found between burned and control soils were due to their inherent site variability, not due to effects of fires. Increased sample size decrease the room for this argument.

Experiments of the ash study were conducted in an area burned by one fire, thus the study has no replication. Similar experiments in multiple fires will be ideal to draw conclusions on ash effects on N availability for plants. In manipulating ash levels (i.e. double ahs, control and no ash), the amounts of ash in ash-manipulated plots were not quantified, which might add variability among sites. It was ideal to control ash levels quantitatively. In addition, regeneration of understory vegetation post-fire in ash-manipulated plots were poor, thus we could not collect plant samples in a balanced manner. It is better to seed several native species in ash-manipulated plots and to place cages to prevent grazing for subsequent sampling and analyses.

Lastly, more studies about fire effects on gross inorganic fluxes should be conducted. Our studies (i.e. the upslope study and riparian study) were conducted in coniferous forests of central Idaho, USA. As far as we know, there are only two studies that investigated fire effects on gross inorganic N fluxes in soil. One is by Kaye and Hart (1998) in a ponderosa pine-bunch grass ecosystem in Arizona, USA and the other is by Smithwick et al. (2005) and Turner et al. (2007) in Yellowstone National Park, Wyoming, USA. However, forest fires are a natural disturbance ubiquitous to many parts of the world (Agee 1993). More measurements of gross inorganic N fluxes in burned and

control soils will give us better understanding about fire effects on N dynamics in soils. The quantification of fire effects on gross inorganic N fluxes will also help us model how N dynamics will be altered in an expected future scenario with higher fire intensity and frequency in changing environments (Westerling et al. 2006). Since N is often a limiting nutrient in many parts of the world (Vitousek and Howarth 1991), understanding of fire effects on those processes will help us manage ecosystems in the future.

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