The Effects of Fire on Nitrogen Cycling Processes Within Bandelier National Monument, NM

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Abstract.—Nitrogen is often the nutrient limiting production in conifer forests. Fire acts as a mineralizing agent, releasing nutrients in available forms. However, nitrogen is lost during fires, which can further deplete this limiting nutrient. Without fire, nitrogen becomes tied up in partially decomposed litter (needles and woody debris). The problems faced by managers of these forest systems are how and when to use fire from a nutrient perspective. A chronosequence of fire intervals in ponderosa pine forests (Pinus ponderosa) was studied to determine (1) if nitrogen cycling processes (mineralization and nitrification) decrease and (2) if concentrations of organics that inhibit these processes increase along the fire chronosequence. Patterns were not statistically significant, but fairly clear trends occurred. Nitrogen mineralization and nitrification patterns were higher in sites recently burned (within two years) and were lowest in sites without fire since the 1890's. The patterns at intermediate age sites varied, perhaps because of differential usage by elk and variable amounts of needle scorch which resulted in differential needle litterfall after fire. Within a site, concentrations of certain monoterpenes were consistently negatively correlated with rates of nitrification and mineralization. In these systems, fire promotes more rapid cycling of nitrogen, in part through combustion of monoterpene inhibitors.

INTRODUCTION

Within the nutrient cycling literature, there is considerable controversy about the role of fire in ecosystems. At the center of the controversy is the fact that fire causes a net loss of nitrogen while most other nutrients are released in available mineral forms (Raison 1979). Nitrogen loss occurs through volatilization and with particulates in smoke during combustion. Those on one side of the controversy argue that frequent fires would create severe nitrogen limitation within the ecosystem (Vitousek and Howarth 1991), leading to replacement of existing vegetation. However, in many ecosystems with high historical fire frequencies, net nitrogen mineralization and production actually declines in the absence of fire. This has led those on the other side of the controversy to believe that fire is necessary to keep nitrogen cycling within the ecosystem and maintain productivity (White 1991a). Thus, the role of fire in ecosystems is not well understood from a nitrogen cycling perspective.

In general, soils of ponderosa pine ecosystems are fairly low in nutrients and have low rates of nitrogen mineralization (Vitousek et al. 1982). In a ponderosa pine (Pinus ponderosa) stand near Bear Springs in the southern part of the Jemez Mountains, two separate prescribed burns increased rates of nitrogen mineralization and nitrification in the residual forest floor and mineral soil horizons (White 1986a, White 1991a). The low pre-burn rates of nitrogen mineralization and nitrification were attributed in part to high concentrations of monoterpenes.
monoterpenes (found in "turpentine") within needle litter and the forest floor (White 1991a, 1991b). Monoterpenes are highly flammable and are mostly consumed during fires (White 1991a). These results suggest that frequent, low-intensity fires consume flammable monoterpenes, which in the absence of fire act to inhibit nitrogen mineralization and nitrification. Higher rates of nitrogen cycling are promoted by fire, but nitrogen losses during frequent, low-intensity fires must be replenished to be long-term sustainable. One way to replenish losses is to increase nitrogen fixation rates (see Loftin and White, This Volume). However, studies of changes in nitrogen fixation after fires have not identified increases substantial enough to offset losses from frequent fire, so the controversy continues (Vitousek and Howarth 1991).

The purpose of this article is to investigate the relationship between time since last fire, rates of nitrogen cycling, and the amount of monoterpenes in the forest floor and mineral soils of ponderosa pine. Nitrogen cycling characteristics and monoterpene content of soils were determined for sites within Bandelier National Monument with known durations since the last fire. The theoretical approach and earlier experimental results that form the foundation for this research and terminology used in ecosystem nutrient cycling will be presented first.

**The Nitrogen Cycle**

The supply of nitrogen often limits production in terrestrial ecosystems (Vitousek and Howarth 1991). Inputs of nitrogen to terrestrial ecosystems are from precipitation, air-borne particles trapped by the vegetation and soil (dry deposition and impaction), and through gaseous fixation (N-fixation; Figure 1). N-fixation occurs through free-living organisms (i.e., cyanobacteria and lichens) and symbiotically with plants and their root-associated microorganisms. On an annual basis, inputs of nitrogen are thought to be small relative to the amount obtained from the soil.

To a large extent, the supply of nitrogen for plant growth in terrestrial ecosystems is determined by the rate at which organic-bound soil nitrogen is released in inorganic form - a process termed nitrogen mineralization (Fig. 1). The first inorganic form of nitrogen is ammonia (NH₃), which readily converts to ammonium (NH₄⁺) in the soil solution. Ammonium (or ammonia) can be converted to nitrate (NO₃⁻) through the two-step process of nitrification. Through the nitrification process, a portion of the ammonium-nitrogen can be lost to the atmosphere as nitrous oxide. Both ammonium and nitrate are assimilated by the soil microbial community and by higher plants. If demand for inorganic nitrogen by the microbial community is high, then concentrations of inorganic nitrogen within the soil may decline, which is termed 'immobilization.' Only when the demand by the microbial population is satisfied can concentrations of inorganic nitrogen increase within the soil, representing net mineralization.

Unlike ammonium, nitrate is negatively charged (an anion) and is mobile within the soil, which can lead to loss of nitrate from the terrestrial system to streams or ground water. Nitrate can be utilized by other microorganisms as a terminal electron acceptor, which results in the production of nitrous oxide or di-nitrogen (N₂) gas, through the process of denitrification. Di-nitrogen gas can return to the atmosphere, completing the cycle. Nitrous oxide also can escape to the atmosphere, where it can undergo reactions with other chemicals.

Both nitrate and ammonium are assimilated into plant and microbial biomass through growth.

![Figure 1.—The universal nitrogen cycle indicating pools (circles) and processes (arrows). Inputs (wet and dry deposition) and losses (leaching, erosion) are not indicated. The soil nitrogen pool (Dead org. N) is divided into three conceptual compartments (from Jansson 1981).](image-url)
Plants and microorganisms can move nitrate towards themselves through diffusion, but they must grow or move to sources of ammonium which is more tightly bound to soil particles. Nitrogen assimilated by a portion of the microbial community contributes to plant growth through mycorrhizal associations (Figure 1). A portion of the microbial and plant biomass is consumed by animals. Eventually, microorganisms, higher plants, animals and their associated wastes become part of the soil organic matter pool, a portion of which rapidly decomposes and undergoes the process of mineralization to continue the cycle. In general, monoterpenes alter rates of nitrogen cycling by slowing both the mineralization and nitrification processes (see White 1994 for a detailed review of the role of monoterpenes throughout the nitrogen cycle).

Patterns Of Nitrogen Cycling Processes Within Forest Ecosystems

Factors that regulate rates of nitrogen mineralization and nitrification for 17 forests located throughout the United States were studied by Vitousek et al. (1979, 1982). Although their main interest was to determine the potential for loss of nitrate from forest ecosystems following disturbance from clearcutting, their studies made two valuable contributions. First, they described nitrogen mineralization and nitrification patterns for sites that show a wide range in net productivity. Second, they demonstrated that patterns measured in laboratory studies mimicked those patterns displayed in field studies.

Vitousek et al. (1982) predicted that certain changes in soil inorganic nitrogen concentrations would occur in the absence of plant uptake (Figure 2; redrawn from Vitousek et al. 1982). In laboratory incubations which eliminate plant uptake (termed mineralization “potentials” because temperature and moisture are kept near optimum), these patterns are reflected in the changes in concentrations of inorganic nitrogen. After short incubation times, inorganic nitrogen levels may decline, which represents net immobilization. This period prior to net production of ammonium is termed the ‘lag phase.’ Once net production of ammonium occurs (termed ‘net mineralization’), the mineralized ammonium may be converted to nitrate (termed ‘nitrification’), which may cause a concurrent decrease in ammonium. There may be a lag in nitrification, which allows ammonium to accumulate (as shown in Figure 2), or nitrification may occur so rapidly that no increase in ammonium is apparent with only an increase in nitrate. In the field, nitrate may be transported to lower soil horizons, which can be detected in lysimeters (mechanisms for sampling soil water), or to surface streams if sufficient moisture is available.

Time for the entire response sequence (lag, mineralization, nitrification) to occur varies between sites within forest ecosystems and between different ecosystems. The range in patterns of responses for both nitrate and ammonium concentrations during incubation is shown in Figure 3. Very slow responses (C in Figure 3) included only the lag phase with a slight rise in ammonium at the end of the measurement period. A slow response includes only the portion of the predicted pattern from the disturbance to line “B” in Figure 2. Intermediate responses (B in Figure 3) had a short lag, followed by an increase in mineralization, and finally an increase in nitrification. An intermediate response corresponds to the portion of the predicted pattern from the disturbance up to line “A” in Figure 2. Very rapid responses (A in Figure 3) demonstrated an immediate increase in nitrate, corresponding to the portion of the predicted pattern beginning at line “A” in Figure 2. Very rapid responses (A in Figure 3) demonstrated an immediate increase in nitrate, corresponding to the portion of the predicted pattern beginning at line “A” in Figure 2, with the entire preceding pattern of lag and net mineralization condensed into such a short time period that it does not get measured (within the first sampling period).

The three Indiana forests studied by Vitousek et al. (1982) show responses that are typical of sites with rapid, intermediate, and slow responses (Fig-
The Indiana Maple site is a rapid response, corresponding to A of Figure 3, with an immediate increase in nitrate and a gradual decline in ammonium. The Indiana Oak site is an intermediate response, corresponding to B in Figure 3, with an increase in ammonium followed by an increase in nitrate after a short lag. The Indiana Pine site is a slow response, corresponding to C in Figure 3, with a protracted lag phase and a slight rise in ammonium at the end of the experiment.

Vitousek et al. (1979, 1982) also studied ponderosa pine, mixed conifer, aspen, and spruce-fir sites located in the Tesuque Watersheds, New Mexico. That ponderosa pine stand showed a slow response in laboratory mineralization potential experiments (Figure 5), similar to the Indiana Pine site (Figure 4). Nitrogen mineralization potentials

Figure 3.—Potential patterns for ammonium and nitrate concentrations in a soil following disturbance or during laboratory incubations for determination of mineralization and nitrification potentials. Patterns range from rapid (A), through intermediate (B), to slow (C).

Figure 4.—Changes in inorganic nitrogen during laboratory incubation of mineral soil samples from the Indiana Maple, Oak, and Pine forests reported in Vitousek et al. (1982, redrawn with permission).
of soils from a ponderosa pine stand in the Jemez Mountains also showed either net immobilization or low mineralization (pre-burn in Figure 6), typical of sites with slow responses (White 1986a).

For most sites studied by Vitousek et al. (1979, 1982), the rate of response was correlated to "site quality" (estimated potential productivity of the site), with lower quality sites having the slowest responses and highest quality sites with rapid responses; the Indiana Maple site was the highest quality site, oak intermediate, and pine the lowest quality site. Based upon these patterns, the ponderosa pine site is a low quality site. Conversely, if ponderosa pine displayed mineralization patterns like that of Indiana Maple, one could conclude that ponderosa pine occurs on high quality sites. The studies of Vitousek et al. (1979, 1982) tend to leave the impression that these patterns are inherent characteristics of each system that are unlikely to change. However, these patterns are known to change seasonally, annually (Gosz and White 1986), and following prescribed fire (White 1986a). To truly manage forests for long-term health and sustainability, managers need to understand the dynamics in patterns of these processes and the effects that various management practices have on nutrient cycling patterns.

Factors Controlling Nitrogen Mineralization and Nitrification

White and Gosz (1987) investigated the factors controlling nitrogen mineralization and nitrification in the New Mexico forest sites reported in Vitousek et al. (1979, 1982). They added potentially limiting nutrients (nitrogen, phosphorus, and/or micronutrients) to forest floor and mineral soil from the ponderosa pine site of Vitousek et al. (1982) in attempts to alter the mineralization patterns in laboratory incubations. A positive response to nutrient additions would shorten the lag in min-
eralization or nitrification and increase production of inorganic N. They found the mineralization pattern to be very resistant to change. White and Gosz (1987) concluded that nitrogen mineralization in the New Mexico Ponderosa Pine site was limited by (1) organic quality factors (which includes inhibition by an organic inhibitor) or by (2) the availability of a combination of limiting nutrients (including combinations of N, P, and/or micronutrients).

Given the low rates of net mineralization and nitrification and the resistance to amendments designed to increase these rates in laboratory studies (White and Gosz 1987), high concentrations of ammonium and nitrate in the field were not expected in a ponderosa pine site. However, high concentrations of ammonium and nitrate were reported in a single field collection from both trenched and control plots in the New Mexico Ponderosa Pine site of Vitousek et al. (reported in Gosz and White 1986). In September of 1977, concentrations of ammonium and nitrate in the forest floor (organic soil horizons) of both trenched and control plots were approximately 20 and 0 mg N/kg, respectively. Both ammonium and nitrate concentrations increased to approximately 80 mg N/kg soil (a total of about 160 mg N/kg soil) in the October 1977 collection, but returned to the September 1977 levels by the next collection (February 1978).

The obvious question is how did such dramatic and rapid changes in soil inorganic nitrogen occur? Between the collection with low inorganic nitrogen concentrations (Sept. 1977) and the next collection with high concentrations of ammonium and nitrate (Oct. 1977), exceptionally hot, dry conditions forced complete closure of the forest to the public because of extreme fire danger. The high ammonium and nitrate concentrations (indicating rapid mineralization and nitrification) were measured in forest floor collections taken after rains had moistened the forest floor and reduced the fire danger. This suggested that the hot, dry conditions altered some critical controlling factor, which allowed rapid mineralization and nitrification to occur in the forest floor. Higher than normal precipitation and an early freeze after the Oct. 1977 collection prevented further collection at the New Mexico Ponderosa Pine site until later that winter. Low concentrations of ammonium and nitrate in Feb. 1978 indicate limited mineralization and nitrification. Since needle-cast (senescence of older needles) occurred during the interim period, it is likely that the controlling factor was contributed in litterfall and/or throughfall. If the controlling factor was an organic inhibitor, the inhibitor had to (a)

be denatured and/or removed (perhaps volatilized) during heating and drying of the forest litter, (b) contributed through litterfall and/or throughfall, and (c) persist within frozen soils.

I collected all samples of forest floor and soils from that ponderosa pine site. Before closure during the September 1977 collection, the “turpentine” aroma of a pine forest was very strong. I remember this clearly because I have an allergy to turpentine in “oil-based” paints, and I suffered from allergic symptoms during that collection. While collecting precipitation samples the following month when rain lessened the fire danger, I noted the lack of “turpentine” aroma and had no allergic symptoms. It was as if the turpentines were “volatilized” from the needles on the forest floor during the hot, dry conditions. Turpentine is a mixture of various monoterpenes, which are highly volatile, with smaller amounts of sesquiterpenes, which are less volatile. Since monoterpenes have physical characteristics that are consistent with those of a potential organic inhibitor (highly volatile, in relatively high concentration in litterfall and throughfall, and freezing is a means of preserving monoterpenes in living tissues), this observation suggested the potential role of monoterpenes in the processes of nitrogen mineralization and nitrification. Since those first observations, considerable progress has been made investigating the role of monoterpenes in nitrogen cycling processes (White 1986a, 1986b, 1988, 1991a, 1991b), which is reviewed in White (1994). In ponderosa pine forest systems, monoterpenes act to limit the rate of nitrogen mineralization (production of ammonium) and nearly halt the rate of nitrification, which results in very low rates of inorganic nitrogen cycling in these systems.

Fire and Monoterpenes: Their Role as Flammable Compounds

Mutch (1970) hypothesized that fire-adapted tree species produced compounds that enhanced the probability of fire at more frequent intervals. His hypothesis was based upon comparisons of the amount of extractable plant material in species with differing fire frequencies. Ponderosa pine had the highest amount of extractable compounds and had a high fire frequency (or short fire interval). Since 1970, improvements in analytical techniques and the availability of instruments (principally in gas chromatographs and associated techniques) have led to the understanding that monoterpenes are a major portion of the extractable plant material referred to by Mutch.
Monoterpenes are highly flammable compounds and can reach parts-per-thousands concentration in ponderosa pine litter, and conifer litter in general. Monoterpenes are de-gassed early in the combustion process, and heat from their combustion provides the energy for direct pyrolysis of the solids to occur (Chandler et al. 1983). Thus, higher monoterpenes concentrations would increase the probability of ignition and increase the ability to carry a fire, which could lead to shorter fire intervals in these systems.

The apparent sequence of events that link monoterpenes, soil nitrogen cycling processes and fire are as follows: low monoterpenes concentrations and high rates of mineralization and nitrification in soil and the litter that remains after a fire, followed by a buildup of monoterpenes and a decline in mineralization and nitrification rates, which inevitably leads to a high fire potential because of the buildup of these flammable monoterpenes. A question left unanswered is: how much time is needed between fires before mineralization and nitrification processes are inhibited and the higher probability of fire? By sampling soils and litters from sites with increasing time since fire, aspects of this question may be addressed. Sites within Bandelier National Monument were of particular interest because documentation existed on fire history and the dominant soils in the Monument are derived from the same parent material as the soils near Bear Springs sampled in earlier studies by White (1986a, 1991a).

Hypotheses.-The specific hypotheses to be tested by this research were:

1. Monoterpenes in the soil organic horizons will increase along a fire chronosequence.

2. Soil mineralization and/or nitrification will decrease along the same fire chronosequence.

METHODS

Site Selection

A total of 6 sites were sampled (Figure 7), including: (1) a site south of Lummis Canyon (Lummis), which was sampled before and four times following a prescribed burn; (2) a site east of Corral Hill (Corral Hill); (3) a site near the back gate (Back Gate); (4) a site on Escobas Mesa (Foxx) near sites established by Teralene Foxx (Foxx 1984); and two sites outside of the area burned by the La Mesa Fire, (5) a cluster of three plots below highway NM 4 in salamander habitat (Salamander) and (6) a site on Sawyerm Mesa (Sawyer Mesa). The elevations and interval since the last fire at all sites are listed in Table 1. All sites occur on Bandelier tuff parent material, which is the same parent material at the Bear Springs site reported by White (1986a, 1986b, 1991a), except for the Salamander site which is on Tschicoma Formation (Smith et al. 1970). Sites varied in other respects, ranging from lower elevation stands of ponderosa pine interdigitating with piñon and juniper woodlands (Lummis and Corral Hill sites), to a mid-elevation ponderosa pine stand with nearly closed canopy conditions (Back Gate), with the Foxx site approximately intermediate in elevation and ponderosa pine overstory density. The Salamander and Sawyer Mesa sites are in upper ponderosa pine/lower mixed conifer habitat with ponderosa pine, limber pine (Pinus flexilis), Douglas-fir (Pseudotsuga menziesii), and white fir (Abies concolor), with Rocky Mountain maple (Acer glabrum) and aspen (Populus tremuloides) the major deciduous species. The Salamander site, which is scheduled for treatment with prescribed fire in fall 1995 (C. Allen, personal communication), is more mesic than the Sawyer Mesa site, which is on an exposed ridge. A variable that may have particular influence on nitrogen cycling processes at some or all of these sites is use by elk and deer. Nearly the entire area is used by elk and deer, but use of the more remote sites by elk (Lummis and Foxx sites in particular, and to a lesser degree Corral Hill) appeared greater than at the Back Gate site. Areas with obvious elk disturbance (i.e., droppings) were not sampled, but the potential for unrecognized impacts from elk at time of sampling to altered patterns of nitrogen mineralization/nitrification was high (e.g. through urination).

Table 1.—Names for sites sampled in this study, elevations, and time since last fire.

<table>
<thead>
<tr>
<th>Site #</th>
<th>Site Name</th>
<th>Elevation (m)</th>
<th>Time since last fire</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Lummis</td>
<td>2000</td>
<td>15 years</td>
</tr>
<tr>
<td></td>
<td>Pre-burn</td>
<td></td>
<td>1 day</td>
</tr>
<tr>
<td></td>
<td>Post-Burn</td>
<td></td>
<td>5 months</td>
</tr>
<tr>
<td></td>
<td>5 month</td>
<td></td>
<td>12 months</td>
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<tr>
<td></td>
<td>12 month</td>
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<td>17 months</td>
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<tr>
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</tr>
<tr>
<td>2</td>
<td>Corral Hill</td>
<td>2000</td>
<td>1.5 years</td>
</tr>
<tr>
<td>3</td>
<td>Foxx</td>
<td>2245</td>
<td>15 years</td>
</tr>
<tr>
<td>4</td>
<td>Back Gate</td>
<td>2325</td>
<td>7 years</td>
</tr>
<tr>
<td>5</td>
<td>Salamander</td>
<td>2720</td>
<td>94 years*</td>
</tr>
<tr>
<td>6</td>
<td>Sawyer Mesa</td>
<td>2670</td>
<td>99 years*</td>
</tr>
</tbody>
</table>

* Based on fire scars collected at nearby sites. (Allen 1989)
Sample Collection

The Back Gate was sampled on 15 May 1992, as was the Lummis site (1 day post-burn) following the prescribed fire on 14 May 1992. Corral Hill, Lummis pre-burn, Foxx, and Sawyer Mesa sites were sampled on 6 May 1992. These samples (collected in May 1992) were analyzed for monoterpane content of the organic horizon and nitrogen mineralization potentials for the mineral soils. Mineral soil was resampled on 2 October 1992, 28 May 1993, and 12 October 1993 at the Lummis site and analyzed for nitrogen mineralization and nitrification potentials only. Samples were taken from 4 points within each site. Effort was made to take samples from microsites representative of the range observed rather than the average at each site. Separate samples of the organic horizon and 0- to 10-cm depth mineral soil horizon were collected at each point. The organic horizons were sampled by harvesting all organic horizons beneath a 200 cm² template (White 1991a). The organic horizon was separated into an L (fresh litter) and a F-H (fermentation and humus) horizon for the Foxx site and the pre-burn collection at Lummis (data later summed to get organic horizon totals). The entire organic horizon was collected at all other sites. Mineral soil was collected with a 7.8-cm diameter tube driven to a depth of 10 cm.

At the Sawyer site, samples were taken from areas where the overstory was dominated by (1) limber pine, (2) Douglas-fir, (3) aspen, and (4) ponderosa pine, although litter of other species were also present in the samples. Also, samples of freshly fallen needles of ponderosa pine, limber pine, and Douglas fir were collected for monoterpane analyses (2 samples for each species). A sample of scorched ponderosa pine needles from a prescribed burn were collected on top of the mesa along the trail to Corral Hill for monoterpane analyses. Samples of freshly fallen needles were collected within 1 m of the soil samples at Corral Hill and analyzed for monoterpenes.
The sampling design at the Salamander site differed from that at other sites. Samples were taken adjacent to three previously established arthropod pitfall transects, each 50 m long, on 9 September 1993. Two of the transects are adjacent to each other below NM 4, the other transect is also below NM 4 about one kilometer away. A total of six samples were taken from each of the transects (18 total samples). The entire forest floor was harvested from beneath a 200 cm\(^2\) template (White 1991a). The dry mass of each forest floor sample was measured to determine pre-burn organic matter content; monoterpenes were not analyzed on these samples. The underlying soil was collected in a 7.8-cm diameter tube driven to a depth of 10 cm and analyzed for nitrogen mineralization potentials.

### Analytical Methods

Methods detailed in White (1991a) were used to analyze all samples. The May 1992 samples of organic horizons and needles were analyzed for monoterpene content by gas-liquid chromatography following extraction in ether. All mineral soil samples were analyzed for nitrogen mineralization/nitrification potentials by aerobic incubation and subsequent extraction with KCl. The KCl extracts were analyzed for ammonium and nitrate with a Technicon AutoAnalyzer.

### Statistical Analyses

All statistical analyses were performed with StatView SE© (BrainPower, Inc.). Correlation coefficients were generated by correlating nitrification rates with forest floor monoterpene concentrations. These coefficients were then analyzed by chi-square method to determine if randomly distributed.

### RESULTS

#### Mineralization Patterns

The mineralization pattern for the Lummis pre-burn samples showed a fairly rapid rise in nitrification (Figure 8), even though the site had not burned since the La Mesa Fire (15 years). The relatively rapid rise in nitrate is characteristic of higher quality sites and is not characteristic of sites with heavy fuel loads. One day after the prescribed burn, the shape of the nitrification pattern was not significantly changed (Figure 8), but the amount of ammonium was substantially increased. Five months after the fire, both the rate of nitrate production (indicated by a steeper rise in nitrate) and initial ammonium levels were greater than pre-burn samples (Figure 8). The most rapid rate of nitrate production occurred in the 1 year post-burn collection (Figure 8), although total concentrations were lower than 1-day and 5 month post-burn collections. The 17-month collection started to show slight immobilization and a lag period before rapid mineralization and nitrification occurred (Figure 8).

Mineralization pattern at the Corral Hill site (1.5 years after a prescribed burn) also showed high rates of nitrification (Figure 9), very similar to the pattern at the Lummis site 12 month post-burn. This pattern is characteristic of high quality sites, similar to the pattern shown by the Indiana Maple site (Figure 4).

The Back Gate site (7 years since last burn) had relatively low rates of ammonium production and very low rates of nitrification (Figure 9), similar to the ponderosa pine reported in Vitousek et al. (1979, 1982). These patterns are typical of slow mineralization responses of low quality sites (Figures 3 and 4).

The Foxx site (15 years since last burn, La Mesa Fire) had a mineralization pattern more like an intermediate response with an initial lag before significant nitrate production occurred (Figure 9), much like the Indiana Oak site (Figure 4).

The mineralization pattern at the Sawyer site (Figure 9) reflected the influence of the single sample beneath the aspens, which showed a pattern very similar to the aspen site in the Tesuque Watersheds. The three samples taken beneath the conifers showed lags in mineralization with little or no nitrification, similar to Back Gate or the Salamander sites (Figure 9). Thus, the rise in nitrate (and ammonium) for the site as a whole is due to the higher production in the single aspen sample.

Mineralization patterns at the Salamander site (94 years since last fire) are the lowest of all sites (mean of all sites shown in Figure 9). Fourteen of the 18 sites showed net immobilization throughout the incubation period and only slight nitrification, with net mineralization and net nitrate production only in four samples. These patterns are characteristic of very poor quality sites, even though this is the most mesic site sampled in this study.

### Monoterpene Concentrations

The amount of variation encountered in the monoterpene concentrations of the forest floor
samples was high, both within and between sites (as shown by large standard error bars). There was a general trend with increasing forest floor mass and fire interval (Figure 10); however, that trend is

Figure 8.—Changes in inorganic nitrogen (ammonium open squares, nitrate closed circles) during laboratory incubation of mineral soil samples from the Lummis site before and with time after a prescribed burn (burned 14 May 1992).
largely a function of the first and last sites in the chronology. Similarly, the general trend in increasing monoterpeno concentrations was due to the first and last sites in the chronology. If the first and last sites of the chronology are excluded, no real pattern appeared for the intermediate sites for all monoterpenes and their sum (Figure 10). Also, there was not statistically significant relationship between mineralization or nitrification potentials and total monoterpenes when all samples from all

Figure 9.—Changes in inorganic nitrogen (ammonium open squares, nitrate closed circles) during laboratory incubation of mineral soil samples from the sites in and near Bandelier National Monument, NM. Sites are arranged from top left to right bottom with respect to increasing length of fire interval (see Table 1).
Figure 10.—The amount of forest floor mass (a), a-pinene (b), b-pinene (c), the sum of a-pinene and monoterpenes with carbon-carbon double bonds (d), and sum of all monoterpenes (e) present at each site (mean of four samples with standard errors). Sites are arranged with increasing time since fire from left to right. Sites with years since fire in parentheses are: 1 = Lummis 1 day Post-Burn (0); 2 = Corral Hill (1.5); 3 = Back Gate (7); 4 = Lummis Pre-Burn (15); 5 = Foxx (15); and 6 = Sawyer Mesa (99).
sites are included in this analysis. However, there was a consistent and strong negative relationship between monoterpenes and nitrification potentials within individual sites, as shown by the negative correlation coefficients (Table 2). Using a Chi-square test, the probability of obtaining consistently negative correlations between two random and unrelated variables is less than 1 in 10,000 (P<0.0001).

DISCUSSION

White (1991b) proposed a conceptual model for the effects of increasing monoterpane concentrations on the inorganic nitrogen content of a soil. The model also may mimic the effects of fire on soil inorganic nitrogen because natural dynamics of monoterpenes in soils should follow the fire cycle. After fire, monoterpenes are in low concentration and net mineralization and nitrification are high (White 1991a). With time since fire, monoterpenes increase, lowering net mineralization (by increasing immobilization) and inhibiting nitrification by inhibiting the enzyme initially involved in the conversion of ammonium to nitrate (ammonium mono-oxygenase). Eventually, monoterpenes accumulate to the point that nitrogen cycling processes are greatly reduced, while their elevated concentrations concurrently increase the probability of another fire. The occurrence of low net nitrogen mineralization and net nitrification rates might indicate when a fire could be beneficial from a nutrient cycling perspective, regardless of the apparent fuel loads.

The results presented here only partially support this conceptual model. Mineralization and nitrification rates were among the highest at sites with recent burns (post-burn Lummis and Corral Hill, Figure 9), whereas sites with the longest fire intervals (Sawyer and Salamander site, Figure 9) have the lowest rates of mineralization and nitrification (when aspen is excluded from the Sawyer site), which supports the model. However, the two sites with 15 year fire intervals (Foxx and Lummis pre-burn, Figure 9) had intermediate, but relatively high rates of nitrification, particularly the Lummis site. Explanations for deviation from the predicted model may include differences in microclimate that result in greater loss of monoterpenes from these sites and/or the use of these areas by elk. The Foxx and Lummis sites are fairly remote and are used rather heavily by elk during the winter months. Usage by elk would increase the nitrogen inputs to these forest stands through urine and feces. In laboratory experiments, forest floor samples from a spruce-fir forest in the Tesuque Watersheds only produced nitrate following the addition of urea (White and Gosz 1987). Fairly long-term inputs of nitrogen from elk may partially eliminate the normal condition of nitrogen limitation within ponderosa pine ecosystems and allow higher rates of mineralization and nitrification.

The Back Gate site, which was last burned 7 years before sampling, showed steadily increasing net mineralization but almost no nitrification (Figure 9). This site only gets migratory usage by elk and deer because of its proximity to the highway and a campground, so the influence of elk and deer on the mineralization and nitrification pattern is expected to be relatively slight. Based on fire scars on trees in that area, the historic mean fire interval for that ponderosa pine stand was approximately 7 years (estimated at 7.3 average; Allen 1989). Thus,

Table 2. Correlation coefficients for comparison of relative nitrification rate and listed factors (Factors) at the indicated sites (n=4). Correlation coefficients can range between 1 and -1. The probability of the frequency of inverse correlation obtained by completely unrelated factors is P<0.0001 for all sites. Sum All Sites is the summation of all correlation coefficients for all sites; highly negative numbers would indicate the strongest negative relationship across all sites.

<table>
<thead>
<tr>
<th>Factor</th>
<th>Lummis Pre-Burn</th>
<th>Corral Hill</th>
<th>Foxx</th>
<th>Back Gate</th>
<th>Sawyer Mesa</th>
<th>Sum All Sites</th>
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<td>-.748</td>
<td>.933</td>
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<tr>
<td>a-Pinene</td>
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<td>-.827</td>
<td>-.497</td>
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<td>b-Pinene</td>
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<td>-.115</td>
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<td>Myrcene</td>
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<td>-.441</td>
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<tr>
<td>a-Pinene + C=C bonds</td>
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<td>-.100</td>
<td>-.604</td>
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the pattern of little or no nitrification may occur at or near the time of historic fires. Perhaps the lack of nitrification can be used as a cue for when fires could be used for management of areas without known fire histories.

Response to Prescribed Fire

In previous studies, both the forest floor and mineral soil showed an increase in response pattern following prescribed fire (White 1986a, 1991b), although the response was faster and greater in the forest floor. In the present study, it was uncertain if the fire would consume the entire forest floor, leaving nothing for post-burn samples. Thus, only the mineral soil was analyzed in this study.

Regrettably, the area scheduled for prescribed burning at the time of this study, the Lummis site, was affected by elk use. The expected low rates of mineralization and nitrification did not occur (Figure 8), so there was not much room for fire to improve rates. One day after the prescribed burn, ammonium concentrations were increased (shown by higher initial concentrations) and the nitrification pattern was nearly the same as pre-burn. About five months after the fire, ammonium concentrations remained higher and rate of nitrate production was increased. This pattern of increased ammonium and a delay before nitrification rates can increase was also shown on two occasions at a site on the southern part of the Jemez Mountains (White 1986a, 1991b). The response to fire appeared to peak at about 12 months after the fire and slightly declined after 17 months (short lag in mineralization present, Figure 8). Similarly, a year and half after fire at the Corral Hill site (Figure 9), mineralization and nitrification patterns are typical of high quality sites. Assuming that these results are not purely an artifact of elk usage, these results suggest that (1) the results of previous burns at the Bear Springs site (White 1986a, 1991) were not site-specific, at least with respect to the direction of change with fire (positive) and (2) the effect of fire lasts through at least a full growing season following a fall burn (based upon Corral Hill results).

The duration of effect of fire on soil processes is important, because needle cast from needles scorched by fire is very high after prescribed fires in these systems in which fires have been suppressed for about a century (see Touchan et al., This Volume). This major pulse of needles and monoterpenes after the first use of fire may shorten the duration of fire effects on N cycling processes. Thus, areas with long periods since the last fire may need to have a follow up fire shortly after the first prescribed burn to consume the typically heavy litterfall of scorched needles. With more frequent fires, fewer needles remain on low branches and fire intensities should be less, thus the degree of scorch should be less and subsequent needle cast would be reduced.

Chronosequence and Monoterpenes

The pattern of increasing monoterpenic content in the forest floor along the chronosequence was weak at best. However, the strong negative relationship between monoterpenes and nitrification within each site (Table 2) is strong support of the proposed mechanism of inhibition (White 1988, 1994). The predicted response to monoterpenes and fire was based upon work at a single site (or within-site patterns; White 1986a, 1986b, 1991a, 1991b). The results from this study show that the pattern extends to five additional sites. The pattern of high monoterpane/low mineralization and nitrification is obscured by between-site differences, because samples from other sites had lower absolute amounts of monoterpenes yet nitrification appeared to be completely inhibited. Thus, the results of the present study show that the pattern is very consistent within a site, but indicate that differences between sites mask this pattern along the chronosequence.

I feel these results are especially strong in light of the number of uncontrolled (or unmeasured) site factors that could influence the pattern. Other major factors include stand density or basal area, annual litterfall, site overstory production, and microclimate. An additional site factor that could alter the relationship between monoterpenes and nitrification along the chronosequence is the variable amount of needle cast following fires at each site. The scorched but unburned needles have high monoterpane concentrations (Figure 11). The amount of scorching-induced needlecast could vary with canopy cover and height, time since last fire, fuel loads, and many other factors. These scorched needles add to normal litterfall, but the amount of needle scorch should diminish as the height of the canopy increases after the first few uses of fire within the stand.

CONCLUSIONS

HYPOTHESIS 1. Monoterpenes in the soil organic horizons will increase along a fire chronosequence.
Monoterpene concentrations were low in sites with recent fire and very high in sites with long periods since a fire, but the trend is not clear in the intermediate sites (Figure 10). Factors that could ‘cloud’ the overall predicted pattern include:

1. Differential use of the sites by elk, which add nitrogen in the form of feces and urea, stimulating both the decomposition of the carbon-rich monoterpene and increasing mineralization/nitrification rates;

2. Following prescribed fires, needles scorched during the fire still contain high concentrations of monoterpenes and are dropped soon afterward. The amount of needle cast could vary with canopy cover and height, time since last fire, fuel loads, and many other factors. This needle cast adds to normal litterfall, but should diminish as the height of the canopy increases after the first few fires.

3. Other site factors (basal area, site productivity, aspect, elevation, actual evapotranspiration, etc.).

HYPOTHESIS 2. Soil mineralization and/or nitrification will decrease along the same fire chronosequence.

Again, the sites at the tails of the chronosequence fit the predicted pattern well, but the intermediate sites do not have a clear pattern (Figure 9). The two sites that differ the most from predicted are the
Fox site and the Lummis pre-burn site, both of which have higher mineralization and nitrification rates than predicted by fire interval. Both sites had evidence of heavy elk use, which may contribute to the higher rates of mineralization and nitrification (White and Gosz 1987).

There are four major conclusions that can be drawn from this study:

(1) It is clear at these sites that monoterpenes are effective regulators of nitrification within each site (Table 2). Differences between sites alter the relationship, making it difficult to extrapolate results from one site to another with respect to the effect of a specific monoterpane concentration;

(2) Elk may be having major effects on nutrient cycling patterns within Bandelier National Monument. Elk alter the distribution of nutrients within a site, removing nutrients from areas relatively rich in nitrogen (areas with grass, herbs, and species with symbiotic nitrogen fixation) and depositing nutrients in areas relatively low in available nitrogen (within stands of ponderosa pine);

(3) Inhibition of nitrification may be a sensitive indicator of when management with prescribed fire may be beneficial from a nutrient cycling perspective; and

(4) The two sites outside of the area burned by the La Mesa Fire show very slow rates of nitrogen mineralization and nitrification, characteristics of poor quality sites although these probably have the potential to be the highest quality sites in this study. These results strongly indicate that low-intensity fire would improve rates of nutrient cycling at these sites. Scheduled prescribed burns at the Salamander habitat site will provide the opportunity to test this prediction.

ACKNOWLEDGMENTS

I thank Craig Allen for his willingness to support this research, help in site selection, organizing this symposium, and for editorial comments that improved this paper. Colleen Wyss provided valuable technical assistance through analysis of monoterpenes. Samuel Loftin provide valuable field sampling assistance. I thank the National Park Service and USDA Forest Service for financial support of this project. Partial financial support for my research was provided by the National Science Foundation and the Sevilleta Long-Term Ecological Research program (Pub. #56).