AN ABSTRACT OF THE THESIS OF

Vicente J. Monleon-Moscardo for the degree of Master of Science in Forest Science presented on November 4, 1993.

Title: Long-term Effects of Prescribed Fire on Nitrogen Availability in Ponderosa Pine Stands in Central Oregon.

Signature redacted for privacy.

Abstract approved: ______________________
Kermit Cromack, Jr.

The effects of prescribed burning on the rates of recent litter decomposition, nitrogen and phosphorus release from litter, soil total and inorganic nitrogen pools, and net nitrogen mineralization were determined in ponderosa pine sites that had been burned 0.3, 5 or 12 years earlier. Prescribed burning decreased litter decomposition rates significantly ($p > 0.1$), in the sites burned 0.3 and 12 years previously, although the differences in litter decomposition rates between burned and control plots were small. Nitrogen and P release from recent litter was significantly higher in the plots burned 5 years previously, but there were no significant differences in the plots burned 0.3 or 12 years earlier. Soil inorganic N concentration significantly increased shortly after prescribed burning, but declined thereafter to reach the levels of the control plots at the end of the next growing season. Both inorganic and total soil N pools in soil were significantly lower in the plots burned 5 years previously, and there were no differences in any of the N pools measured for the sites burned 12

years earlier. Prescribed burning did not significantly affect annual net nitrogen mineralization 0.3 years after burning, but net N mineralization decreased significantly in the 5 and 12 year burned plots. The decrease in net nitrogen mineralization is probably caused by a decrease in substrate quantity 5 years after burning, and by changes in substrate quality 12 years after burning. A long-term decrease in net N mineralization in the N-poor ponderosa pine stands of Central Oregon may result in a decrease in long-term site productivity and may explain the observed pattern of long-term decrease in stand growth following prescribed burning.

Long-term Effects of Prescribed Fire on Nitrogen Availability in Ponderosa Pine Stands in Central Oregon

by

Vicente J. Monleon-Moscardo

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Completed November 4, 1993
Commencement June, 1994

APPROVED:

Signature redacted for privacy.

Associate Professor of Forest Science in charge of major

Signature redacted for privacy.

Head of the Department of Forest Science

Signature redacted for privacy.

Dean of Graduate School

Date thesis is presented November 4, 1993

Typed by Vicente J. Monleon-Moscardo

ACKNOWLEDGEMENTS

There were many people and institutions that played an important role in this project, for which I am grateful. I would like to take this opportunity to acknowledge some of them. My advisor, Kermit Cromack Jr., was always ready to help and advise. The Silviculture Lab in Bend, allowed me to use the plots which they had established and maintained. Joan Landsberg from Bend was especially helpful. Carol Glassman taught me many soil analytical procedures and carried out part of the chemical analyses. Tom Sabin provided important statistical advice. Finally, many friends provided the necessary support to carry out all this work: Carolina, Chris, Carlos, Matthew, Erik, Jose, Laura, Patricia, and many, many others. To all of them, my most sincere thanks.

My program at Oregon State University was funded through a scholarship from the Ministry of Agriculture of Spain.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LONG-TERM EFFECTS OF PRESCRIBED FIRE ON NITROGEN AVAILABILITY IN PONDEROSA PINE STANDS IN CENTRAL OREGON

I. INTRODUCTION

Historically, ponderosa pine (*Pinus ponderosa*) forests had a regime of frequent, low intensity ground fires (Kilgore, 1981) which kept the stands open and park-like, free of litter, woody debris and underbrush (Languille *et al.*, 1903; Munger, 1917). Fire frequency decreased with the arrival of the European settlers in Central Oregon in the late 1800s, due to an increase in livestock grazing, decrease fires started by Native Americans, and extensive timber harvesting. Since about 1919, an active policy of fire suppression has virtually eliminated all fire from these forests (Bork, 1985).

Fire suppression has caused important changes in forest structure and composition, and has resulted in some undesirable conditions. As early as 1943, Weaver noted that the exclusion of fire resulted in overstocked, even-aged stands, with stagnated growth, decreased tree vigor, and increased susceptibility to insects and pests. He also noted changes in species composition towards fire-sensitive true firs (*Abies* spp.), Douglas-fir (*Pseudotsuga menziesii*), and incense cedar (*Calocedrus decurrens*); and a greatly increased risk of destructive wildfire. Finally, he suggested that a controlled fire that mimics the natural regime can be used to alleviate these deleterious effects (Weaver, 1943).

Currently, forest managers are increasingly using low intensity prescribed underburning in ponderosa pine forests, mainly to reduce fuel loads and fire hazard. However, even though prescribed burning can have many beneficial applications, its effect on the productivity of second growth, managed ponderosa pine stands is not clear. Cochran and Hopkins (1991) observed that current growth of ponderosa pine stands was higher than the growth predicted from yield tables developed shortly after fire exclusion. They attributed the faster growth under fire suppression to an increase of soil productivity in the absence of fire. On the other hand, other authors have speculated that fire suppression results in reduced productivity, through stagnation of decomposition and nutrient cycling. It has been suggested that nutrients accumulate in the litter and become less available for plant uptake, and that fire releases these nutrients (Biswell, 1972; Covington and Sackett, 1984, 1990).

Recent experimental studies in managed ponderosa pine stands in the Pacific Northwest show a decrease in tree growth following prescribed burning that may last for 12 years or more (Grier, 1989; Landsberg, 1992). The causes of this relatively long term decrease in growth are not known. Fire can affect tree growth and survival directly, through cell and tissue damage, or indirectly, through changes in nutrient availability or pathogen susceptibility (Chambers *et al.*, 1986). Direct effects of fire are not likely responsible for the observed long term decrease in tree growth. First, crown scorch is usually very low (Landsberg and Cochran, 1980), equivalent to a light pruning, and not enough to reduce growth (Landsberg, 1992). Second, although burning decreases fine root biomass (Grier, 1989), a healthy tree should be able to replace the lost roots quickly (Chambers *et al.*, 1986; Waring and Schlesinger, 1985). Third, heat damage to cambial tissue is probably negligible, given the low intensity of the fires and the thick, dense bark of ponderosa pine (Martin, 1963). The latter is supported by the very low tree mortality following prescribed burning (Landsberg, 1992), and by the lack of fire scars on the trees.

The observed long-term decrease in growth can likely be attributed to indirect effects of fire in the environment, especially changes in the nutrient economy of the stand. Ponderosa pine growth in Central Oregon is severely limited by nitrogen (Cochran, 1978, 1979), and foliar N concentration is usually below the critical deficiency level (Landsberg *et al.*, 1984). Four years after prescribed burning, fire did not affect foliar N concentration but decreased total foliar N content between 14 and 33 %, a much higher reduction than the initial foliage loss due to crown scorching (Landsberg *et al.*, 1984). This result suggests that fire caused an increase in N stress in these already stressed ecosystems.

The short-term effects of prescribed burning in the N economy of ponderosa pine stands are well known. Prescribed burning consumes part of the forest floor, and N is lost in proportion to the amount of forest floor consumed (Raison *et al.*, 1985). In Central Oregon, N losses can be as high as 500 kg ha^{-1}, although they often are about half that amount (Shea, 1993; Landsberg, 1992; Nissley *et al.*, 1980). However, a small part of the N in the forest floor is converted to ammonium, resulting in an increase in plant available N in the soil following burning (Covington and Sackett, 1986, 1992; Kovacic *et al.*, 1986; White, 1986a). Also, usually there is an increase in nitrification rates (White, 1986a) and nitrate concentration (Covington and Sackett, 1992, Kovacic *et al.*, 1986), attributed to the consumption of volatile inhibitors of nitrification by fire (White, 1986a,b). This explanation has been disputed, and the increased nitrification has been attributed to high levels of available NH_4^+ for the nitrifier population (Bremner and McCarty, 1988).

The initial increase in available N following fire is always short-lived, and after some months inorganic N concentrations return to pre-burn levels. Then, the availability of N to the plants is determined by the rates of decomposition and N mineralization (Schlesinger, 1985). However, there are few studies that address the long-term effects of burning on N mineralization and availability, and none in ponderosa pine ecosystems. Prescribed burning consumes an important portion of the forest floor, accumulated over decades of fire suppression, and thus may decrease the quantity and quality of N available for mineralization and also may change the soil biological activity and microclimate. In the nutrient-poor soils of Central Oregon, this may result in a decrease in site fertility and tree growth.

The general objective of this study is to determine the long-term (up to 12 years) effects of prescribed burning on N availability in ponderosa pine stands in Central Oregon. The first part of the study addresses the effects of fire on decomposition and nutrient dynamics in the recently fallen litter. The second part addresses the effects of fire on N fluxes in the soil, and on the pools of inorganic and total N. These parameters were measured during one year on sites that have been experimentally burned 0.3, 5, or 12 years before the beginning of the study. We hypothesize that fire will increase N availability immediately following the fire, but it will be decreased later on, coinciding with the observed decrease in tree growth. Twelve years after the fire, nutrient availability may be similar to before burning.

II. LONG-TERM EFFECTS OF PRESCRIBED UNDERBURNING ON LITTER DECOMPOSITION AND NUTRIENT RELEASE IN PONDEROSA PINE STANDS IN CENTRAL OREGON

ABSTRACT

The effects of low intensity prescribed underburning on the rates of litter decomposition and N and P release were studied using a litter-bag technique for an 18 month period in sites burned 0.3, 5, or 12 years earlier. Litter decomposition rates were low, between 0.15 and 0.28 $year^{-1}$, and were significantly ($p<0.1$) reduced by prescribed fire on the sites burned 0.3 and 12 years earlier. However, the reduction in decomposition rates was small, from 0.22 to 0.19 on the sites burned 12 years earlier, and from 0.172 to 0.167 on the sites burned 0.3 years earlier. Nitrogen tended to be immobilized in the decomposing litter, while P was rapidly released, suggesting that these ecosystems are limited by N, but not by P. Nitrogen showed a distinctive seasonal pattern of net immobilization during winter, and a net release during summer. Prescribed burning significantly increased the release of N and P from the litter on the sites burned 5 years earlier, which may indicate changes in microbial activity in the forest floor. However, there were no significant differences in nutrient dynamics on the remaining sites.

INTRODUCTION

Before European settlement in the late 1800s, ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) forests of Central Oregon had a fire regime of low intensity, frequent surface fires, but fire has been virtually eliminated for the last 70-80 years (Bork, 1985). The effective elimination of several fire cycles has led to an accumulation of organic matter and nutrients on the forest floor, which has been suggested to result in stagnated nutrient cycles and decreased productivity (Biswell, 1972; Covington and Sackett, 1990, 1984). However, Cochran and Hopkins (1991) found increased tree growth after fire suppression, which they attributed to increased soil fertility in the absence of fire.

Currently, forest managers are increasingly using low intensity prescribed underburning, mimicking the historic regime, to reduce fuel loads and fire hazard. However, prescribed fire causes a decrease in tree growth that may last for more than 12 years (Grier, 1989; Landsberg, 1992). The reasons for this reduction in growth are not known, but previous studies suggest that fire may have increased N stress in these N poor sites (Landsberg *et al.*, 1984). Thus, additional research on the possible effects of fire suppression and the reintroduction of fire to nutrient cycling in these ecosystems is needed.

The decomposition of litter is an important process in forest nutrient cycling. It is a very complex process, influenced by climate, substrate quality, biological activity, availability of exogenous nutrients, and other factors (Swift *et al.*, 1979). Fire consumes part of the forest floor, accumulated over decades of fire suppression, and can modify the rates of litter decomposition and nutrient release. These changes in litter dynamics may influence the patterns of nutrient availability and long-term site productivity. The objective of this study was to determine the effect of moderate intensity prescribed underburning on ponderosa pine needle litter decomposition and nutrient dynamics on sites that had been burned 0.3, 5, and 12 years earlier.

MATERIALS AND METHODS

Study sites

The study was conducted at five locations on the Deschutes National Forest near Bend, in Central Oregon (Table II.1). The climate is continental and dry, with hot, dry summers and cold, wet winters. Mean annual precipitation in Bend is 29.3 cm, and mean monthly temperature ranges between -0.7°C in January and 17.3°C in July. However, climate at the study sites is cooler and wetter than in Bend, with annual precipitation varying from 65 cm at Annabelle to 43 cm at Far East. Most of the precipitation falls in winter as snow, which remains on the ground for 4-5 months. The first winter of this study was exceptionally dry and warm. Total precipitation between December, 1991, and March, 1992, was 35 % of the historic average, but rainfall was higher than normal during the following summer. Monthly temperatures for this period were about 2°C warmer than average. The second winter, on the other hand, was exceptionally cold and moist.

The elevation of the sites ranges from 1200 to 1550 m, and the terrain is flat or with a gentle slope. The soils are sandy-loam Xeric Vitricriands, formed on a mantle of Mt. Mazama volcanic pumice and ash deposited approximately 7000 years ago. This ash layer extends to a depth of 0.4-1.0 m, overlying older buried material. The area is covered with even-aged ponderosa pine, naturally regenerated from logging in the 1920s, and grown during a period of fire exclusion. The sites were thinned in the early 1960s, and the residues left in place.

Treatments and experimental design

At each site, two treatments were applied: prescribed burning and no-burn controls. The burn treatment was an operational prescribed underburning carried out in the spring that consumed untreated slash and other ground fuels. The fires were of low intensity (around 300 kW m^{-1} fire line intensity), and consumed between 40 and 60% of the forest floor (Landsberg, 1992; Shea, 1993). All the sites were established by the USDA-Forest Service Silviculture Lab in Bend. The plots at Lava Butte were burned in 1979, and at Annabelle in 1986, 12 years and 5 years before the beginning of the study, respectively. At these sites, the experimental design was completely randomized, with 2 replicates of each treatment at each site. The plots at Far East, Sugar Cast and Swede Ridge were burned in 1991, four months before the beginning of the study, following a randomized block design with 3 replicates of each treatment. However, when this study was initiated, the control plot at Swede Ridge could not be reached because of a snow storm, and therefore was not included in this study. The plot size was 25 x 25 m, and each plot was surrounded by a buffer strip at least 10 m wide. Hereafter, the sites burned in 1979, 1985, and 1991 will be referred as year-12, year-5 and year-0, respectively.

Litter decomposition and nutrient release

Litter decomposition and nutrient release were determined using the litter-bag method (Bocock *et al.*, 1960). Senescent ponderosa pine needles were collected from an unburned area in the Annabelle site by shaking the trees and collecting needles on a drop cloth. The needles used at year-12 and year-5 sites were collected in October 1991, and the needles used at year-0 sites were collected in November, 1991, at the same location. Five grams of air-dried needles were placed in 20 x 20 cm, 2 mm mesh nylon bags. In November, 1991, five 3-bag clusters were placed in each plot, on the surface of the forest floor, at 5 m intervals along a diagonal transect. Every 25th bag was selected to determine the initial litter moisture and nutrient content.

In April 1992, November 1992, and May, 1993 one litter-bag was removed from each cluster, a total of 5 bags per plot. The litter was dried at 70°C for 48 h, and weighed. The dried material was ground in a Wiley mill to pass a 40 mesh (450 μm screen), and 1 g of material from each bag was combined to yield one composite sample per plot. Subsamples were taken to determine ash content (450°C for 5 h), and total N and P. Total N and P were determined colorimetrically with an automatic analyzer (Alpkem, R.F.A.), following standard micro-Kjeldahl digestion. The results are expressed as the proportion of initial mass or nutrient remaining after the field exposure (ash-free dry mass basis). Litter decomposition rate (k) was calculated following the exponential decay model (Olson, 1963), as the slope of a regression line fitted to the logtransformed data with the restriction that the intercept had to be 0 (no mass loss at time 0). To calculate C:N and C:P ratios, total C was assumed to be 50 % of the ash-free needle dry mass.

Statistical analyses

The effects of fire on the variables of interest were analyzed separately for each burning date. Because different sites were burned each time, the independent variables "time since burn" and "site" are confounded, and each burning date should be considered an independent study.

Mass loss and the proportion of N and P remaining were analyzed separately using split-plot analysis of variance, with treatment as the main plot and time as the subplot (Steel and Torrie, 1980). This analysis was preferred to a factorial analysis of variance with litter bag incubation time as a factor (Wieder and Lang, 1982) because samples taken over time from the same plot are not independent. Litter decomposition rates were analyzed using analysis of variance. The SAS statistical package was used for all the statistical analyses (SAS Institute Inc. 1985). Differences were considered significant, and p-values reported, when $p<0.1$.

RESULTS

Although the intention was to have a homogeneous initial substrate for all the sites, the initial N and P concentrations of needles collected in October and November, 1991, were different. The needles collected in October had N and P concentrations of 4.85 and 0.90 mg g^{-1}, respectively, while those collected in November had N and P concentrations of 6.02 and 0.96 mg g^{-1}. Only the difference in N concentration was statistically significant ($p<0.01$, t-test, $n=8$). The difference in nutrient content in the initial substrate did not affect the comparison between burned and unburned treatments at a given burning date, because the same substrate was used in sites burned at the same time. However, it should be considered when comparing sites.

Mass loss

Needle mass in the litter bags significantly decreased at all sites and with all treatments over time, in a roughly linear fashion. After 18 months, between 80.0 % and 64.7 % of the original mass remained (Figs II.1-II.3), and k-values ranged from 0.15 to 0.28 $year^{-1}$ (Table II.2). Mass losses and k-values were highest in Annabelle, followed by Lava Butte and then the remaining sites.

Prescribed underburning significantly decreased needle mass loss and k-values ($p=0.02$) at year-12, and k-values at year-0 ($p=0.02$). At year-12, the interaction between time of exposure and mass loss was also significant

($p=0.02$), indicating that the effect of treatment on mass loss was not consistent through time. Mass loss was slightly faster in the burned plots during the first 6 months, but this situation reversed afterwards (Fig. II.1).

Nutrient dynamics

Nitrogen content in the decaying needles showed a similar pattern at all sites and with all treatments (Fig. II.1-II.3). During the first 6 months, corresponding to the first winter, N was immobilized, and the total amount of N in the litter either increased or remained nearly the same as the initial quantity. During the summer, there was a net N release, so that after one year of exposure, needles contained between 83 and 99 % of the original amount of N. However, during the next winter, N was strongly immobilized, increasing to between 100 and 120 % of the original amount after 18 months of exposure. Since the loss of mass was faster than the loss of N, the concentration of N in the decaying litter increased, and the C/N ratio decreased, especially during the winter months (Table II.3).

Prescribed burning caused a statistically significant change in N loss only in the year-5 burn ($p=0.036$), where N was lost more rapidly from the litter in the burned plots (Fig. II.2). After one year, 91 % and 83 % of the original litter N remained in the control and burned plots, respectively. At the remaining sites, there was no clear pattern of N loss between burned and control plots.

The pattern of P loss was different from that of N (Fig. II.1-II.3). At all sites and with all treatments, P was released very rapidly during the first 6 months, and at a slower rate afterwards. After one year of incubation, the proportion of P remaining stabilized at around half of the initial amount at all the sites. As a result of this rapid initial release, the concentration of P in the decaying litter decreased strongly, and the C/P ratio nearly doubled after one year of exposure, to decrease later (Table II.3).

Prescribed burning caused a statistically significant change in P loss only in the year-5 burn ($p=0.097$), where P was lost more rapidly on the burned plots. After a year, 47% of the original P remained on the control plots, compared to 41% on the burned plots.

DISCUSSION

Mass loss

Litter in the unburned plots tended to decay faster than in the control plots, even 12 years after the burn. However, although the difference between treatments was statistically significant at year-0 and year-12, its actual magnitude was low and its biological significance difficult to interpret. After 18 months, the decomposition rate (k) was 10.8 % higher in the unburned plots than in the controls at year-12, and 6.6 % at year-0. This difference translates into a half-life of 3.22 years in the unburned plots, compared to 3.57 years in the burned plots at year-12, and 4.03 compared to 4.15 at year-0. Previous studies that have examined litter decomposition shortly after a fire, equivalent to year-0 in this study, showed contrasting results, from negligible, non-significant effects (Grigal and McColl, 1977; O'Connell and Menage, 1983; Stark, 1977; Viereck and Dyrness, 1979) to mass loss reductions between 10-48 % on the burned sites (Raison *et al.*, 1986, 1983; Springett, 1976).

Litter mass loss and k-values varied widely between sites, and this seems to correlate well with the different climatic conditions of the sites. Litter decomposition is known to depend on macroclimate (Meentemeyer, 1978), and on our sites the highest k-value, 0.28 $year^{-1}$, was at Annabelle, where precipitation is around 65 cm and which is situated in the more mesic mixed conifer community type. The remaining sites are in the ponderosa pine community type, where precipitation ranges between 43 and 50 cm, and k-values varied between 0.15 and 0.22 $year^{-1}$. On the other hand, initial C:N ratio does not seem to correlate with higher decomposition rates. Litter at year-0 sites, which had the litter with the highest initial C:N ratio, tended to decompose more slowly than that at the remaining sites.

Litter decomposition rates observed in this study were low compared to other ecosystems in the Pacific Northwest. For example, on the west side of the Cascade Range, k-values of 0.82, 0.63, 0.45, and 0.45 $year^{-1}$ for red alder, Douglas-fir, western hemlock, and Pacific silver-fir, respectively, have been reported (Edmonds, 1980), and in a high-elevation mountain hemlock forest, k-values varied between 0.36 and 0.42 $year^{-1}$ (Cromack *et al.*, 1991). However, the decomposition rates and mass loss found in this study are similar to those reported for ponderosa pine ecosystems throughout its range (Table II.4). Hart *et al.* (1992) reported the lowest litter mass loss after one year, which they attributed to the temporal separation of warm temperature and moist conditions in their Mediterranean-type climate site. Litter mass loss is greater on our sites, even though the climatic pattern is similar, and temperatures and annual precipitation much lower. The faster decomposition on our sites may be due to the presence of a snowpack, since in continental climates most of the litter mass loss occurs under the snow (Fahey, 1983; Stark, 1977). During the first winter, litter mass loss varied between 6.6 and 15 %, excluding the data from the Far East site (3.1 % loss), and during the second winter between 7.3 and 12.3 %.

These winter values are equivalent to the mass loss observed after a full year by Hart *et al.* (1992).

Nutrient dynamics

Nitrogen and P release from litter followed distinctly different patterns. Compared with mass loss, N accumulated in the litter, while P was rapidly released. This pattern suggests that litter decomposition is limited by N and not by P, the same nutrient response that has been observed for ponderosa pine growth in Central Oregon (Cochran, 1978).

Nitrogen dynamics were highly seasonal, showing net N accumulation during the winter and net N release during the summer at all sites. However, mass loss did not vary substantially between seasons, which suggests that microbial activity was similar. Changes in the exogenous availability of N may explain the seasonal changes in N dynamics. The concentration of inorganic N in upper centimeters of the soil tended to be higher during winter (Chapter III, this thesis), and N may have been imported into the decomposing litter through fungal translocation (Hart and Firestone, 1991). During summer, plant uptake increases and the concentration of inorganic N in the soil decreases, reducing the amount of N available for translocation. During this time, leaching and breakdown of the litter may dominate, resulting in a net release of N.

The dynamics of N and P in litter observed in this study were similar to those reported from other ponderosa pine ecosystems (Table II.4), even though there was a wide range in litter quality, as shown by initial C:N ratios ranging from 65 to 122 and C:P ratios from 522 to 1217. When compared with other studies, the release of both N and P tends to be faster at our sites, especially at Annabelle. The faster release of P can be explained by the lower initial C:P and N:P ratios (Gholz *et al.*, 1985). However, the same explanation cannot be applied to N release, because initial C:N ratios at our sites were high. In this study, there was a net release of N at a C:N ratio from 75 to 103, but N was immobilized afterwards to reach a C:N ratio from 61 to 75. The critical C:N ratio at which net N release started in other ponderosa pine ecosystems varied from 60 to 80 in California (Hart *et al.*, 1992) and from 37 to 40 in Arizona (Klemmedson *et al.*, 1985).

Five years after the burning, fire caused a significant increase in the amount of N and P released from current litter, even though decomposition was slower in the burned plots. The dynamics of N and P in litter are controlled by microbial processes (Swift *et al.*, 1979), suggesting that fire changed the microbial activity in the litter layer. The greater amount of N and P retained in the litter in the unburned plots, together with the higher decomposition rate, suggests that nutrients were immobilized in a higher microbial biomass. Changes in microbial activity may have been caused by a decrease in exogenous available N, especially during winter (Chapter III, this thesis). Other factors, such as changes in nutrient deposition through atmospheric precipitation or throughfall, or changes in nutrient leaching, are not likely to vary between the plots, given their close proximity and the presence of a full canopy on all of them.

Fire did not cause any clear differences in the nutrient dynamics on the sites burned the same year and 12 years before the beginning of the study. In the year-12 site, fire effects may have disappeared or been greatly reduced, since the response in the control and burned plots is hardly distinguishable (Fig. II.1). In the time-0 sites, a possible effect of fire may not have been detected due to a high variability, both between treatments and among sites.

The effects of prescribed fire on total nutrient release from recent litter will depend upon how fire changes both the total amount of nutrients in litter-fall and the rate of nutrient release from the litter. This study shows that, five years after the fire, the rate of N and P release from recent litter is higher in burned areas. However, fire may also change the total amount of nutrients in the litterfall. At Lava Butte, four years after prescribed burning, fire did not change needle N concentration, but it reduced total needle mass from 10.76 Mg Ha^{-1} to 9.64 Mg Ha^{-1}, and consequently decreased the total amount of N in the foliage (Landsberg *et al.*, 1984). A simple decomposition and nutrient turnover model was constructed (Table II.5), with assumptions that fire did not change the ratio of needle fall to total needle mass or the retranslocation of nutrients before shedding the leaves. Results show that the total amount of P released after one year of decomposition is not affected by burning, but the amount of N released is almost doubled in the burned plots.

Total plant N availability from the forest floor will depend also on the behavior of the older litter and duff. Prescribed fire reduces the total mass of the forest floor to approximately 50 %, and the recovery to pre-burn levels may take a long time. For example, in Arizona, the forest floor did not recover to its original depth even 22 years after prescribed fire (Ffolliot and Guertin, 1989). Unless the rates of N release from older litter and duff are greatly increased, the total N supply from the forest floor will be reduced. Since ponderosa pine stand growth is severely limited by N (Cochran, 1978; Powers *et al.*, 1988), decreased N supply may affect stand productivity and may explain the decrease in tree growth observed following fire (Grier, 1989; Landsberg, 1992).

Table II.1. Site characteristics.

Site	Burn date	Elev. (m)	Location	Annual[1] precip. (cm)	Basal[2] area (m^2/ha)	Stand[2] density (tree/ha)	Age[2] (yr)
Lava Butte	1979	1425	43°54' N 121°19' W	46	36	583	60
Annabelle	1986	1210	44°14' N 121°38' W	65	31	572	75
Far East	1991	1540	43°15' N 121°08' W	43	24	481	60
Sugar Cast	1991	1400	43°52' N 121°22' W	47	32	706	55
Swede Ridge	1991	1520	44°01' N 121°30' W	50	33	782	45

[1] Estimated from an annual precipitation isoline map for the Deschutes National Forest (Larsen, 1976).
[2] Lava Butte and Annabelle data from Landsberg (1992). Far East, Sugar Cast and Swede Ridge data from Shea (1993).

Table II.2. Decomposition rates (k, $year^{-1}$) of ponderosa pine needle litter decomposing for 18 months. Standard error in parentheses.

	Time since fire (yr)	Treatment Control	Burned
Lava Butte	12	0.215 (0.003)	0.194 (0.001)
Annabelle	5	0.277 (0.017)	0.258 (0.003)
Far East	0	0.157	0.146
Sugar Cast	0	0.188	0.178
Swede Ridge	0	-----	0.178
Average year-1	0	0.172 (0.015)	0.167 (0.010)

Table II.3. Changes in the C:N and C:P ratios for ponderosa pine needle litter decomposing for 18 months. Ratios calculated assuming that 50% of the ash-free litter mass is carbon. Standard error in parentheses.

Burn date	1979		1986		1991	
Treatment	Control	Burn	Control	Burn	Control	Burn
C:N ratio						
Initial	103	103	103	103	83	83
6 months	92 (5.4)	92 (0.3)	85 (1.0)	91 (1.1)	70 (1.2)	72 (1.2)
12 months	94 (0.9)	93 (4.9)	87 (1.5)	98 (2.3)	74 (3.3)	73 (3.0)
18 months	63 (2.4)	65 (0.5)	63 (3.6)	71 (4.4)	58 (1.7)	54 (1.0)
C:P ratio						
Initial	554	554	554	554	522	522
6 months	858 (33)	864 (61)	798 (32)	953 (16)	706 (106)	686 (18)
12 months	1074 (50)	989 (75)	904 (17)	1062 (37)	887 (40)	857 (15)
18 months	749 (3)	731 (11)	720 (73)	837 (86)	746 (71)	728 (16)

Table II.4. Decomposition rates and nutrient dynamics of ponderosa pine needles after one year of decomposition in Arizona, California and Oregon.

	Klemmedson et al., 1985	Klemmedson 1992[1]	Hart et al. 1992	This study
Location	Arizona	Arizona	California	Oregon
% Mass loss	18-25[3]	17[3]	6.8-14.5	12.7-22.7
k ($year^{-1}$)	0.20-0.29[4]	0.19[4]	0.08-0.16	0.13-0.28
Initial N concentration[2]	6.6	4.0	5.71-8.14	4.9-6.0
Initial C:N	73.7	121.8	64.9-89.3	83-103
% N remaining after 1 year	95-105[3]	92[3]	100[3]	83-99
Initial P concentration[2]	0.6	0.4	0.47[3]	0.9-0.96
Initial C:P	815	1217	1060	522-554
% P remaining after 1 year	68-75[3]	58[3]	65-75[3]	41-52

[1] Litter-bags containing ponderosa pine needles only
[2] g kg^{-1} litter
[3] Calculated interpolating from figures
[4] Calculated from mass loss after one year, assuming an exponential decay model (Olson, 1963).

Table II.5. Rates of net nutrient release after a year of needle decomposition in burned and unburned plots, 5 years after the burn.

		Nutrient in[1] needle fall ($kg\ ha^{-1}\ year^{-1}$)	Net release ($kg\ ha^{-1}\ year^{-1}$)
N	Unburned	9.92	0.85
	Burned	8.88	1.54
P	Unburned	1.84	0.97
	Burned	1.65	0.97

[1] Assuming that litterfall is 19 % (Klemmedson *et al.*, 1990) of the total needle mass four years after prescribed underburning in Lava Butte (Landsberg *et al.*, 1984). Concentrations of nutrients in the needle fall are from this study.

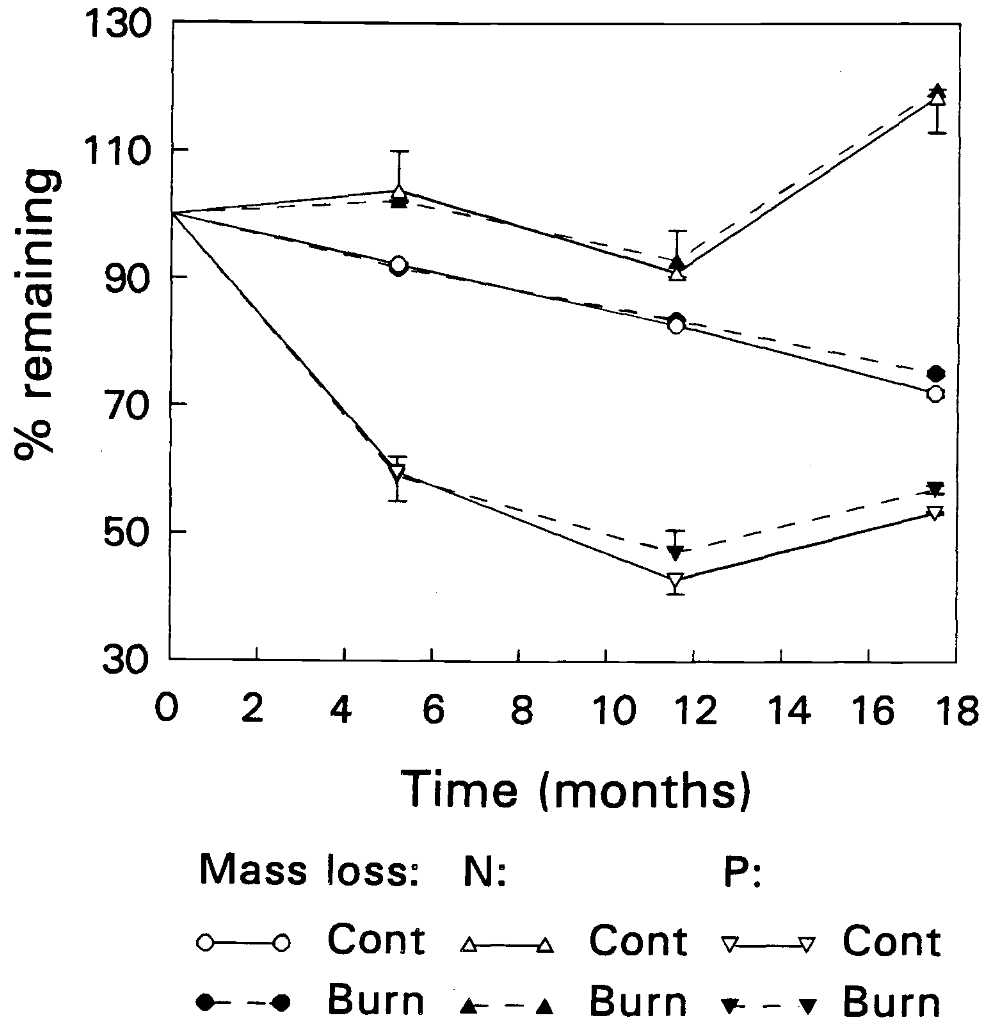

Fig. II.1. Percent original mass, N and P remaining in ponderosa pine needle litter decomposing from November, 1991 to May, 1993 in burned and control plots at year-12. Error bars denote standard errors (n=2 composite samples of 5 litter bags).

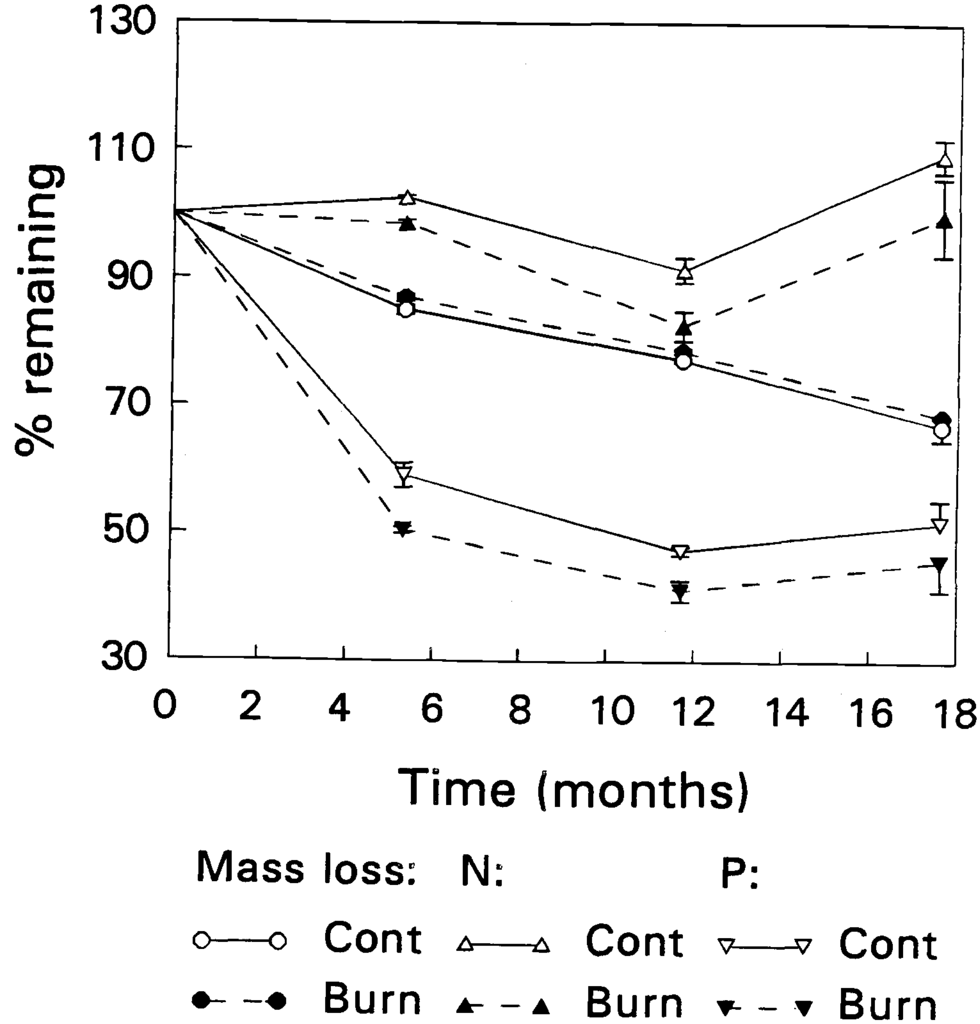

Fig. II.2. Percent original mass, N and P remaining in ponderosa pine needle litter decomposing from November, 1991 to May, 1993 in burned and control plots at year-5. Error bars denote standard errors (n=2 composite samples of 5 litter bags).

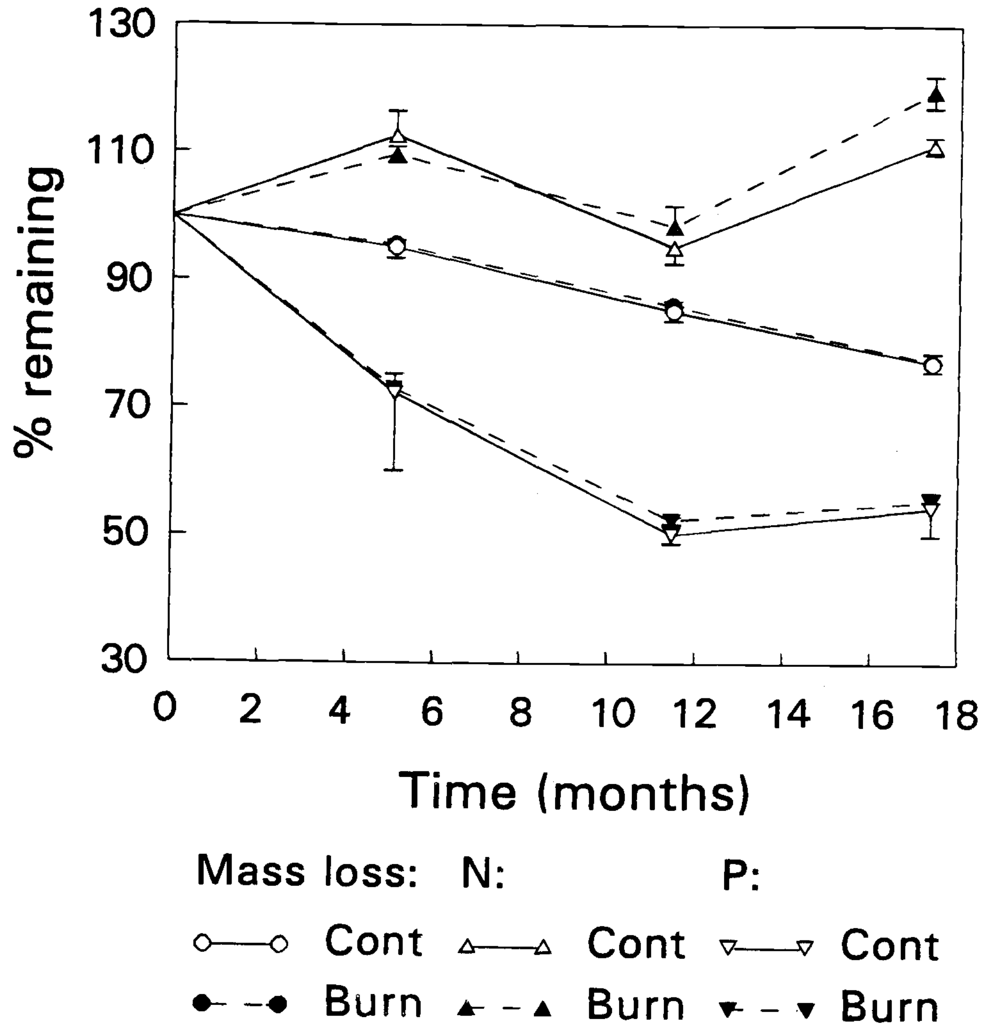

Fig. II.3. Percent original mass, N and P remaining in ponderosa pine needle litter decomposing from November, 1991 to May, 1993 in burned and control plots at year-0. Error bars denote standard errors (n=2 (control) or 3 (burned) composite samples of 5 litter bags).

LITERATURE CITED

Biswell, H.H. 1972. Fire ecology in ponderosa pine grassland. *Tall Tim. Fire Ecol. Conf. Proc.* **12**: 69-97.

Bocock, K.L., Gilbert, O.J., Capstick, C.K., Turner, D.C., Ward, J.S., and Woodman, M.J. 1960. Changes in leaf litter when placed on the surface of soils with contrasting humus types. *J. Soil Sci.* **11**: 1-9.

Bork, J. 1985. Fire history in three vegetation types on the east side of the Oregon Cascades. Unpublished Ph.D. Dissertation. Oregon State University. Corvallis, Oregon.

Cochran, P.H. 1978. Response of pole size ponderosa pine stand to nitrogen, phosphorus, and sulfur. USDA-For. Serv. PNW For. Ran. Exp. Sta. Res. Note PNW-317.

Cochran, P.H., and Hopkins, W.E. 1991. Does fire exclusion increase productivity of ponderosa pine? *In*: Management and productivity of western-montane forest soils. USDA For. Serv. Gen. Tech. Rep. INT-280. pp. 224-228.

Covington, W.W., and Sackett, D.P. 1990. Fire effects on ponderosa pine soils and their management implications. *In*: Effects of fire management on Southwestern natural resources. USDA-For. Serv. Gen. Tech. Rep. RM-191. pp.105-111.

Covington, W.W., and Sackett, D.P. 1984. The effect of a prescribed burn in southwestern ponderosa pine on organic matter and nutrients in woody debris and forest floor. *For. Sci.* **30**: 183-192.

Cromack, K. Jr., Entry, J.A., and Savage, T. 1991. The effect of disturbance by *Phellinus weirii* on decomposition and nutrient mineralization in a *Tsuga mertensiana* forest. *Biol. Fert. Soils* **11**: 245-249.

Edmonds, R.L. 1980. Litter decomposition and nutrient release in Douglas-fir, red alder, western hemlock, and Pacific silver fir ecosystems in western Washington. *Can. J. For. Res.* **10**: 327-337.

Fahey, T.J. 1983. Nutrient dynamics of aboveground detritus in lodgepole pine (*Pinus contorta* ssp. *latifolia*) ecosystems, southeastern Wyoming. *Ecol. Monog.* **53**: 51-72.

Ffolliot, P.F., and Guertin, D.P. 1989. Prescribed burning in Arizona ponderosa pine forests: A 24-year case study. 250-253.

Gholz, H.L., Perry, C.S., Cropper, W.P. Jr., and Hendry, L.C. 1985. Litterfall, decomposition, and nitrogen and phosphorus dynamics in a chronosequence of slash pine (*Pinus elliottii*) plantations. *Forest Sci.* **31**: 463-478.

Grier, C.C. 1989. Effects of prescribed springtime underburning on production and nutrient status of a young ponderosa pine stand. USDA-For. Ser. Gen. Tech. Rep. RM-191. pp. 71-76.

Grigal, D.F., and McColl, J.G. 1977. Litter decomposition following fire in northeastern Minnesota. *J. Appl. Ecol.* **14**: 531-538.

Hart, S.C., and Firestone, M.K. 1991. Forest floor-mineral soil interactions in the internal nitrogen cycle of an old growth forest. *Biogeochem.* **12**: 103-127.

Hart, S.C., Firestone, M.K., and Paul, E.A. 1992. Decomposition and nutrient dynamics of ponderosa pine needles in a Mediterranean-type climate. *Can. J. For. Res.* **22**: 306-314.

Klemmedson, J.O. 1992. Decomposition and nutrient release from mixtures of Gambel oak and ponderosa pine leaf litter. *For. Ecol. Manag.* **47**: 349-361.

Klemmedson, J.O., Meier, C.E., and Campbell, R.E. 1990. Litter fall transfers of dry matter and nutrients in ponderosa pine stands. *Can. J. For. Res.* **20**: 1105-1115.

Klemmedson, J.O., Meier, C.E., and Campbell, R.E. 1985. Needle decomposition and nutrient release in ponderosa pine ecosystems. *For. Sci.* **31**: 647-660.

Landsberg, J.D. 1992. Response of ponderosa pine forests in Central Oregon to prescribed underburning. Unpublished Ph.D. Dissertation, Oregon State University, Corvallis, Oregon.

Landsberg, J.D., Cochran, P.H., Finck, M.M., and Martin, R.E. 1984. Foliar nitrogen content and tree growth after prescribed fire in ponderosa pine. USDA-For. Serv. PNW For. Ran. Exp. Sta. Res. Note PNW-412.

Larsen, D.M. 1976. Soil resource inventory, Deschutes National Forest. Unpublished document.

Meentemeyer, V. 1978. Macroclimate and lignin control of litter decomposition rates. *Ecology* **59**: 465-472.

O'Connell, A.M., and Menage, P. 1983. Decomposition of litter from three major plant species of jarrah (*Eucalyptus marginata* Donn ex Sm.) forest in relation to site fire history and soil type. *Aust J. Ecol.* **8**: 277-286.

Olson, J.S. 1963. Energy storage and the balance of producers and consumers in ecological systems. *Ecology* **44**: 322-331.

Powers, R.F., Webster, S.R., and Cochran, P.H. 1988. Estimating the response of ponderosa pine to fertilization. USDA-For. Serv. Intermt. Res. Sta. pp. 219-225.

Raison, R.J., Woods, P.V., and Khanna, P.K. 1986. Decomposition and accumulation of litter after fire in sub-alpine eucalyptus forests. *Aust. J. Ecol.* **11**: 9-19.

Raison, R.J., Woods, P.V., and Khanna, P.K. 1983. Dynamics of fine fuels in recurrently burnt eucalyptus forests. *Aust. For.* **46**: 294-302.

SAS Institute Inc. 1985. SAS/STAT guide for personal computers, version 6. SAS Institute Inc., Cary, N.C.

Shea, R. 1993. Effects of prescribed fire and silvicultural activities on fuel mass and nitrogen redistribution in *Pinus ponderosa* ecosystems of Central Oregon. Unpublished M.S. Dissertation. Oregon State University, Corvallis, Oregon.

Springett, J.A. 1976. The effect of prescribed burning on the soil fauna and on litter decomposition in Western Australia forests. *Aust. J. Ecol.* **1**: 77-82.

Stark, N.M. 1977. Fire and nutrient cycling in a Douglas-fir/larch forest. *Ecology* **58**: 16-30.

Steel, R.G.D., and Torrie, J.H. 1980. Principles and procedures of statistics: a biometrical approach (2nd ed.). McGraw-Hill, New York.

Swift, M.J., Heal, O.W., and Anderson, J.M. 1979. Decomposition in terrestrial ecosystems. University of California Press, Berkeley.

Viereck, L.A., and Dyrness, C.T. 1979. Ecological effects of the Wickersham Dome fire near Fairbanks, Alaska. USDA Gen. Tech. Rep. PNW-90.

Wieder, R., and Lang, G.E. 1982. A critique of the analytical methods used in examining decomposition data obtained from litter bags. *Ecology* **63**: 1636-1642.

III. LONG-TERM EFFECTS OF PRESCRIBED UNDERBURNING ON NITROGEN AVAILABILITY IN PONDEROSA PINE STANDS IN CENTRAL OREGON

ABSTRACT

The effects of prescribed underburning on soil total C pools, total and inorganic N pools, and *in situ* net N mineralization were determined during a one-year study on ponderosa pine sites that had been burned 0.3, 5 or 12 years earlier. In the sites burned 0.3 years previously, prescribed burning caused a significant ($p<0.1$) increase in total C concentration and inorganic N concentration. However, inorganic N concentration declined during the one-year duration of this study to reach the levels of the control plots at the end of the next growing season. In the sites burned 5 years previously, prescribed burning significantly decreased total C and N concentrations, inorganic N concentration, and net N mineralization. At the sites burned 12 years previously, prescribed burning did not affect N and C pools, but it significantly decreased net N mineralization. The decrease in net N mineralization is likely caused by a decrease in substrate quantity 5 years after burning, and by changes in substrate quality 12 years after burning. A long-term decrease in net N mineralization in the N-poor ponderosa pine stands of Central Oregon may result in a decrease in long-term site productivity and may explain the observed pattern of long-term decrease in stand growth following prescribed burning.

INTRODUCTION

After decades of fire suppression, forest managers are increasingly using low intensity prescribed underburning in ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) forests, mainly to reduce fuel loads and fire hazard. However, prescribed burning in managed ponderosa pine stands in the Pacific Northwest results in a relatively long-term decrease in tree growth, that may last for 12 years or more (Grier, 1989; Landsberg, 1992). Ponderosa pine growth in Central Oregon is severely limited by N (Cochran, 1979, 1978), and the decrease in growth was accompanied by a 14 to 33 % reduction in foliar N content four years after burning, a much greater reduction than the initial losses caused by crown scorching (Landsberg *et al.*, 1984). In these nutrient-poor sites, prescribed burning often causes heavy losses of N (Landsberg, 1992; Nissley *et al.*, 1980; Shea, 1993), and thus may increase N stress and reduce productivity.

Prescribed burning in ponderosa pine ecosystems has the short-term effect of increasing available N (Covington and Sackett, 1992, 1986; Kovacic *et al.*, 1986; Vlamis *et al.*, 1955; White, 1986a), but the increased availability lasts only for a few months or years. After this initial pulse, the amount of N available for plant uptake and growth is determined by the rates of N mineralization, but the possible effects of fire on this process are not known. Prescribed burning can affect the long-term rates of N mineralization by decreasing the total amount of N available, by changing the quality of the remaining organic matter

(Klemmedson, 1976; Vance and Henderson, 1984), and by modifying the microclimate and biological activity of the soil.

The primary objective of this study is to determine the short- and long-term effects of prescribed burning on N mineralization and availability at experimental sites that cover a period spanning from a few months up to 12 years after burning.

MATERIALS AND METHODS

Study sites

This study was carried out on five sites located in the Deschutes National Forest near Bend (44°N, 121°W), Oregon. The sites are part of a long-term study on the effects of prescribed burning in ponderosa pine ecosystems established and maintained by personnel of the USDA-Forest Service Silviculture Laboratory in Bend, Oregon. One of the sites, Lava Butte, was burned in 1979; another site, Annabelle, in 1986; and the remaining sites, Swede Ridge, Sugar Cast, and Far East, in 1991. The sites burned in 1991 follow a gradient in productivity; site indices are 35, 31, and 25 m at 100 years (Barrett, 1978), respectively. Measurements started in September, 1991 at the aforementioned sites, 12 years, 5 years, and 4 months after the burning. Hereafter, the site burned in 1979 will be referred to as year-12, the site burned in 1985 as year-5, and the sites burned in 1991 as year-0. Stand growth was measured in both the year-5 and year-12 sites, and had decreased significantly after prescribed burning (Landsberg, 1992).

The climate of the area is continental and dry, with hot, dry summers and cold, moist winters. Snow usually covers the sites between November and April. In Bend, mean annual precipitation is 29.3 cm, and mean monthly temperatures ranges between -0.7 °C in January and 17.3 °C in July. Temperatures at the sites are cooler, and precipitation is estimated at 65 cm for Annabelle, and between

43 and 50 cm at the remaining sites (Larsen, unpublished data, 1976). An exceptionally warm and dry winter occurred during the year of the study. Winter precipitation was 35% of the average, and mean monthly temperatures were about 2 °C warmer than average.

The soils are Xeric Vitricriands, developed in a layer of Mazama volcanic pumice and ash 0.4 to 1 m deep deposited 7000 years ago. The terrain is flat or with a moderate slope. Altitude ranges between 1210 m (Annabelle) and 1530 m (Swede Ridge and Far East). All sites are in the ponderosa pine community type, except Annabelle, which is in the more mesic mixed conifer type (Volland, 1988). This area had a pre-European settlement fire regime of low intensity surface fires with a recurrence interval between 6 and 20 years, but fire has been suppressed since the early 1900s (Bork, 1985). Currently, the area is covered by even-aged, second-growth ponderosa pine naturally regenerated after logging in the 1920s. All the sites were thinned in the 1960s and the residues left in place. At the beginning of this study, stand density ranged between 480 and 780 trees ha^{-1}, and basal area between 24 and 36 m^2/ha (Cochran and Hopkins, 1991; Landsberg, 1992).

Treatments and experimental design

At each site, two treatments were applied: spring prescribed underburning and a no-burn control. The fires were of low intensity (less than 300 kW m^{-1} fire line intensity) and consumed less than 60 % of the forest floor, typically around

40% (Landsberg, 1992; Shea, 1993). The experimental design at year-5 and year-12 sites was completely randomized, with 4 plots in each site. At year-0 sites, the experimental design was a randomized block, where each site was a block which had 2 plots (a total of six plots). Each plot was 25 x 25 m in size, and was surrounded by a buffer strip at least 10 m wide.

Soil sampling and analysis

Nitrogen fluxes were measured *in situ* during one year, using sequential incubations in minimally disturbed soil cores (Raison *et al.*, 1987). Fluxes were measured during a total of four periods that corresponded roughly to each season. Measurements started in September, 1991, and the plots were sampled again in November, April 1992 (after complete snow melt), June, and September. The control plot at Swede Ridge could not be sampled in November, and therefore incubation in this plot lasted from September until April. At the beginning of every period, 5 groups of 3 PVC tubes (30 cm long, 5 cm diameter) were driven into the soil at randomly located points within each plot. At year-0, 6 groups of tubes per plot were used. In each group, one tube was immediately removed for initial analysis of the unconfined soil, as explained below. The other two cores were left in place for field incubation, one of them capped with a plastic cup to prevent leaching, and the other left open. After the field incubation, the tubes were removed and the soil cores were carefully extracted. The undecomposed litter was discarded, the core divided into 0-5 and 5-15 cm depth layers, and bulked to yield one sample per plot, depth, and type of core (unconfined, covered, and uncovered). At the same time, a new set of cores was installed for the next incubation period. The soil samples were kept at 4 °C and carried to the laboratory. The soil samples from September and November, 1991, were frozen at -18 °C until analysis, but the samples from the other dates were processed within 3 days of sampling.

In the laboratory, large roots and gravel were discarded, and a 10 g moist field subsample was extracted with 50 ml of 2M KCl and shaken for 1 hour. The suspension was allowed to equilibrate for 12 hours and filtered. Ammonium and nitrate were determined colorimetrically in an automatic autoanalyzer (Alpkem, RFA). Only the NH_4^+ and NO_3^- concentrations from the unconfined soil were used in the discussion of fire effects on inorganic N concentration. Total soil C and N concentration were determined using a Carlo-Erba CNS analyzer in one composite sample per plot and depth. This sample was obtained by bulking equal volumes of soil from the unconfined soil cores from each plot and depth obtained from all the sampling dates. Moisture content was determined gravimetrically.

For each incubation period, N fluxes were determined for each soil depth as follows. Net N mineralization was determined by subtracting the concentration of inorganic N in the unconfined soil at the beginning of the period from the N concentration in the covered-core soil at the end of the period. Maximum N leaching (losses) was determined by subtracting the inorganic N concentration in the uncovered-core soil at the end of the period from the concentration in the covered-core soil at the end of the period. Plant N uptake was calculated by subtracting the inorganic N concentration in the unconfined soil at the end of the period and the N leaching from the concentration in the covered- core soil at the end of the period (Raison *et al.*, 1987).

Statistical analyses

In this study, the prescribed burnings were carried out at different sites each time. Therefore, the different times since burning cannot be considered as a sequence at a single site, but rather as separate studies, each analyzed separately.

The effects of prescribed burning on total C and N concentrations were tested using analysis of variance (ANOVA). Inorganic N concentrations and N fluxes, which were measured for several dates or periods in each plot, were analyzed using repeated measures ANOVA (Winer, 1971). This method provides an overall test for the effect of treatment across the dates or periods, although the effect may not be significant at a given date. The test for treatment effect is equivalent to an analysis of variance on the sum or average of the dependent variable over all sampling dates. Therefore, when the dependent variable is inorganic N concentration at each sampling date, the results of the test are interpreted as the fire effects on the average inorganic N concentration during the five sampling dates. When the dependent variable is the N flux during each incubation period, a cumulative measure, the results of the test are interpreted as the effects of fire in the cumulative yearly flux, the net annual mineralization. In addition, repeated measures ANOVA provides an overall test for the effects of the sampling date or measurement period, and their interaction with the treatment. A significant result here will indicate that the variable of interest shows a seasonal pattern. The statistical tests for effects that included the repeated measure were corrected using the Huynh and Feldt ϵ. Data were transformed when necessary. Results were considered significant when $p<0.1$, and the actual p-values are reported. All statistical analyses were carried out using the SAS statistical package (SAS Institute Inc., 1985).

RESULTS

Total carbon and nitrogen concentration

In the surface layer (0-5 cm), burning caused a significant increase in total C concentration at year-0 ($p=0.017$), but a significant decrease at year-5 ($p=0.043$) and negligible change at year-12 (Table III.1). At year-5, C concentration in the control plot surface layer was almost twice as much as in the burned plots. Total N concentration in the soil surface layer followed a similar pattern, increasing in the burned plots at year-0, although not significantly, decreasing significantly at year-5 ($p=0.031$), and showing no difference at year-12. Burning significantly increased the C:N ratio at year-0 ($p=0.033$), but it was not significantly affected by fire at year-5 and year-12. In the 5-15 cm soil depth, neither C or N concentrations nor C:N ratio were significantly affected by prescribed burning, regardless of the time since burning (Table III.2).

At year-0, the analysis of variance showed significant site differences in total C and N concentration in the surface layer ($p=0.009$ and 0.065, respectively), regardless of treatment. Total C and N concentrations at Swede Ridge, the most productive site, were 4.8 and 0.17 %, respectively. At Sugar Cast, the intermediate site, total C and N concentrations decreased to 2.9 and 0.11 %, respectively, and to 2.5 and 0.10 % at Far East, the most arid site. In the deeper 5-15 cm layer, the same trend was present, although differences were not statistically significant (data not shown).

Inorganic N concentration

At year-5 and year-12, the concentration of NO_3^- was below detection (approx. 0.0025 mg NO_3^--N kg-soil^{-1}) in most of the samples, and where detectable, it was very low compared to the concentration of NH_4 (less than 2%). Both concentrations were added and only the results for total inorganic N concentration are presented. At year-0, NO_3^- concentrations were somewhat higher than in the other sites, although they often fell below detection. Both inorganic N and NO_3^- concentrations are discussed.

In the surface layer, burning caused a significant increase in inorganic N concentration at year-0 ($p=0.014$), but a significant decrease at year-5 ($p=0.026$), and no significant change at year-12 (Fig. III.1). The sampling date factor was highly significant at all sites ($p<0.005$), which indicates that the concentration of inorganic N changed seasonally, regardless of treatment. However, at year-0 and year-5, the seasonal trend of inorganic N was different for burned and control plots (interaction between burning and sampling date significant, $p=0.1$ and 0.002, respectively). At year-0, inorganic N concentration was very high in the burned plots during the first sampling dates, a few months after the fire, and decreased thereafter to the levels of the unburned plots. At year-5, inorganic N concentration in the unburned plots was highest during winter, and decreased to the levels of the burned plots at the other seasons. At year-12, inorganic N concentration was highest in November and April at both the burned and unburned plots. In the 5-15 cm soil depth, inorganic N concentration was lower than in the surface layer, and was not significantly affected by prescribed burning (Fig. III.2), regardless of the time since fire. Nitrate concentration at year-0 was low compared with NH_4^+, and although it was several times higher in the burned plots than in the control plots across all sampling dates, the difference was not statistically significant (Fig. III.3).

Nitrogen mineralization and nitrogen fluxes

In the surface soil, prescribed burning significantly decreased annual net N mineralization at year-5 ($p=0.085$), and year-12 ($p=0.086$), but not at year-0 (Figs. III.4-III.6). At year-0, N mineralization in the burned plots tended to be lower than in the unburned plots, but very high values in Sugar Cast during winter, and especially in Far East during summer, obscured this pattern.

There was a significant difference in net N mineralization between incubation periods only at year-5 in the surface layer ($p=0.001$), where N mineralization was highest during winter (Fig. III.5). Here, the interaction between treatment and incubation period was also significant ($p=0.045$), and separate ANOVAs for each period indicate that burning significantly decreased N mineralization only during winter ($p=0.003$), the season with the highest mineralization rate. In this study, the length of the incubation periods varied greatly, and thus the net N mineralization during a given period was the result of both the actual rates of mineralization and the length of the period. To better compare net N mineralization rates during the different seasons, the rates for each period were normalized to a monthly basis, and the statistical analyses repeated. Again, only year-5 showed a significant seasonal difference, with a higher monthly mineralization rate during the winter period (Fig. III.10). Although not significant at the other sites, the tendency was for higher mineralization rates during winter and spring.

In the 5-15 cm depth layer, annual net N mineralization was not significantly affected by fire, regardless of the time since burning (Figs. III.7-III.9). At this depth, net N mineralization was very low, and often there was net immobilization. There was a tendency for immobilization during spring, and mineralization during summer at all sites (Fig. III.11). However, the monthly mineralization rates were very low, and the differences between seasons were not statistically significant.

In the surface layer, annual net nitrification was not affected by prescribed burning, regardless of the time since fire (Figs. III.4-III-6). Annual net nitrification was low, and the variability high compared with the absolute values. There were significant seasonal effects only at year-0 and year-12, where the rate of nitrification was highest during spring. In the 5-15 cm. layer, prescribed burning had a significant effect on annual net nitrification at year-5 (Figs. III.7-III.9). However, the actual values (0.0022 and 0.0008 mg-NO_3^- kg-soil^{-1} year^{-1} in the control and burned plots, respectively) are negligible, and the significance of the difference seems more an analytical artifact. Nitrification at this depth was very low in all the plots.

Estimated N losses and uptake showed inconsistent results, and are difficult to interpret. Nitrogen concentration in the uncovered soil core was extremely variable, and usually higher than in the covered soil core. Consequently, estimated N leaching usually had negative values, and therefore estimated uptake was higher than mineralization, both aberrant results with no biological meaning. Statistical analysis of these data showed no conclusive results.

DISCUSSION

A single entry prescribed burning in the nutrient-poor ponderosa pine stands of Central Oregon had lasting effects on N availability and N pools. Prescribed burning increased available N during the first several months, but this trend changed toward reduced N availability in the years that followed. In the following discussion, the short-term effects (year-0) of prescribed burning in N pools and availability, which are likely caused by direct effects of fire, are first discussed. Then, the long-term effects, 5 and 12 years following the burning, which are likely to have been caused by fire-induced changes in the environment, are addressed.

The effects of prescribed fire were appreciable only in the 0-5 cm depth soil layer, regardless of the time since burning. This discussion will refer to this surface mineral soil, unless otherwise indicated. The effects of fire in this layer are most relevant, because most of the fertility is concentrated in the first few centimeters of the young, pumice soil of Central Oregon (Geist and Cochran, 1991).

Similar aberrant estimations of N leaching and uptake have been reported in the literature (Becquer *et al.*, 1990; Whynot and Weetman, 1991). The discussion is limited to the values of net N mineralization, which are comparable to those obtained with a buried-bag incubation method (see Binkley and Hart, 1989 for a review). The high, variable levels of inorganic N in the uncovered soil core may be due to a higher soil moisture in the uncovered core than in both the covered and the bulk soil (Fig. III.12), which may result in increased mineralization. Also, it was observed that insects frequently used the uncovered PVC tubes for shelter, which may have greatly influenced the nitrogen content of the soil. The soil in the covered core did not reflect increases in moisture during the fall rainfall, and therefore mineralization may have been underestimated during this season.

Short-term effects of prescribed burning

As expected, fire mineralized part of the organic matter on the forest floor, and resulted in an increase in available N. Several months after burning, inorganic N concentration in the burned plots was approximately 3 times higher than that in the control plots, an increase within the range usually reported in the literature (Covington and Sackett, 1992, 1986; Kovacic *et al.*, 1986; White, 1986a). Covington and Sackett (1992), however, observed a 20-fold increase in inorganic N in some of their stands immediately after burning, which in some sites remained almost that high for the one year duration of their study. They attribute this very large increase to the high forest floor consumption (98.5 Mg ha^{-1}) in these stands, even though increases of the same magnitude after 7 months were observed in other stands with only 19.2 Mg ha^{-1} of forest floor consumed. Average fuel consumption in our plots was 60 Mg ha^{-1} (Shea, 1993) and yet, both the magnitude of the increase and the actual inorganic N concentration a few months after burning were several times lower than those reported by Covington and Sackett (1992).

The increase in inorganic N concentration was due primarily to an increase in NH_4^+ concentration. For the duration of this study, NO_3^- concentration was higher in the burned plots, but the variability was high and the difference not significant. However, NO_3^- concentrations were low in both burned and control plots; the average concentration in the burned plots never exceeded 0.3 mg-NO_3^--N kg-soil^{-1}.

Covington and Sackett (1992) suggested that the actual N volatilization losses after prescribed burning are often overestimated, because they are not corrected by the increase in soil inorganic N concentration after the fire, which they believe may account for a significant portion of the losses. In our sites, inorganic N concentration in the burned plots increased only about 6 mg-N kg-soil^{-1}, as measured a few months after the fire. Surface soil bulk density in the area is typically 0.75 g cm^{-3} (Landsberg, 1992). Thus, the increase in inorganic N content in the first 5 cm of soil was only 2.25 kg-N ha^{-1}, a very small amount compared with the estimated losses of 460 kg-N ha^{-1} (Shea, 1993). However, total N concentration in the burned plots increased 170 mg-N kg-soil^{-1}, which brings the total increment in soil N following the fire to 63.75 kg-N ha^{-1}, only 14% of the estimated volatilization losses.

The initial surge of inorganic N concentration in the burned plots decreased during the following months, as reported in other studies (Covington and Sackett, 1992, 1986), to reach control plot levels by the end of the next growing season. Possible mechanisms for this decrease are N losses through leaching or denitrification, microbial immobilization, and plant uptake. Losses through leaching are probably negligible, because nitrate concentration was low, and an increase in inorganic N concentration in the deeper soil layer was not observed. Denitrification is considered low in this ecosystem. However, increased biogenic emissions of oxides of nitrogen following fire have been reported (Anderson *et al.*, 1988), and denitrification rates during the winter, when soils are saturated with water and under a snowpack, may account for part of the decrease in mineral N (Sommerfeld *et al.*, 1993). Microbial immobilization is an important process reducing N losses following disturbance (Vitousek and Matson, 1985), which may have been enhanced by the increase in total C in the soil following the fire. Plant uptake will depend upon the degree of fire damage suffered by the trees, especially in the root system. Grier (1989) observed that a spring fire decreased fine root production, which he attributed to heat injury. If the spring flush of fine root growth is reduced, N uptake during the growing season following the fire may be impaired and the increase in available N not utilized.

Neither net N mineralization nor nitrification rates were significantly affected by prescribed burning. In a variety of ecosystems, fire usually causes an increase in net N mineralization for a period of months or years (Adams and Attiwill, 1986; Hobbs and Schimel, 1984; Schoch and Binkley, 1986; Singh *et al.*, 1991; White, 1986a), although decreases have also been reported (Ellis and Graley, 1983). In our study, net N mineralization was usually lower in the burned plots, but there were two outliers that obscured this pattern and resulted in a slightly higher annual mineralization rate in the burned plots. In ponderosa pine there is usually an increase in NO_3^- concentration several months after prescribed fire (Covington and Sackett, 1992, 1986), which suggests increased nitrification in the post-fire environment. White (1986a) reported greatly increased nitrification rates in laboratory incubations, but these increases did not seem to be accompanied by corresponding increases in NO_3^- in the field. Results here show similar low nitrification rates at all sites that are not affected by burning.

Long-term effects of prescribed burning

Five and twelve years after the fire, net N mineralization on the burned plots was significantly lower than on the control plots, indicating a decrease in the ability of the burned sites to supply N for plant uptake. However, although net N mineralization per unit weight of soil was decreased by burning, net N mineralization per unit of total soil N was not significantly affected n the site burned 5 years earlier (8.4 and 7.5 mg-N g-total-N^{-1} $year^{-1}$ on the control and burned plots, respectively), while it decreased on the plots burned 12 years earlier (12.6 and 4.2 mg-N kg-total-N^{-1} $year^{-1}$ at the control and burned plots, respectively, $p=0.04$). Differences in net N mineralization expressed as a proportion of total soil N indicate differences in organic matter quality, if soil temperature and moisture remain similar (Frazer *et al.*, 1990; Nadelhoffer *et al.*, 1983; Powers, 1990). Soil moisture content was approximately the same in burned and control plots (data not shown), and soil temperature was not likely to have changed substantially, because all sites had a complete tree canopy and litter cover. Therefore, the lower net mineralization rate in the burned plots at year-5 was likely to have been caused by a decrease in the quantity of the available substrate, while at year-12 it was likely to have been caused by changes in the quality of the substrate. Similar results were observed after repeated prescribed burning in an oak savanna (Vance and Henderson, 1984), and a loblolly pine plantation (Bell and Binkey, 1989).

Total N and C concentration tended to increase at the sites recently burned, but decreased at the sites burned 5 years earlier, and returned to control levels in the sites burned 12 years earlier. This pattern is difficult to explain. A decrease in total N during the first 5 years would indicate increased mineralization, which was not observed. At year-5, total N concentration at the burned plots was 570 mg-N kg-soil^{-1} (214 kg-N ha^{-1}) lower than at the control plots, a figure much higher than the estimated net N mineralization rates of 8 to 17 mg-N kg-soil^{-1} year^{-1}. The effects of prescribed burning on mineral soil total N are very variable; it has been reported to cause increases, decreases and no changes (see Raison, 1979; Wells *et al.*, 1979 for a review). It is possible that burning had a different initial effect at each of these sites, depending on the conditions of the fire. In fact, prescribed burning at year-0 increased total N concentration at two sites, Far East and Sugar Cast, but not at the third one, Swede Ridge.

The possible increase in total N concentration between 5 and 12 years could be caused by reduced mineralization, or increased N inputs through N fixation or litter decomposition. However, none of these processes seems to be able to generate such a high quantity of N. First, as noted before, the estimated difference in net mineralization rate between burned and control plots is relatively small compared to the difference in total N between treatments. Second, there were no N fixers in the study plots, which were almost completely free of understory. Third, N release from recent litter was higher in the burned plots, but the increase was estimated to be only 0.7 kg-N ha^{-1} $year^{-1}$ (Chapter II, this thesis). These rates indicate that the time necessary to reach the total N values in the control at the year-5 site may be much longer that the 12 years required at the year-12 sites.

In conclusion, prescribed burning increased available N initially, but the situation reversed afterwards to decreased N availability, even 12 years after the fire. This decrease in site fertility may explain the observed long-term growth decreases after prescribed burning, and should be taken into consideration when prescribing fires in ponderosa pine forest in Central Oregon.

Table III.1. Total soil carbon and nitrogen concentration (%), and C:N ratio in the 0-5 cm depth layer. Standard error in parentheses.

	Total C		Total N		C:N ratio	
Site	Control	Burned	Control	Burned	Control	Burned
Year-0	2.91 (0.77)	3.92 (0.66)	0.122 (0.026)	0.139 (0.015)	23.4 (1.6)	27.8 (1.6)
Year-5	5.57 (0.59)	3.11 (0.20)	0.182 (0.005)	0.125 (0.009)	30.5 (2.4)	24.9 (0.2)
Year-12	3.35 (0.39)	3.54 (0.39)	0.135 (0.015)	0.130 (0.001)	24.9 (0.2)	27.4 (3.1)

Table III.2. Total soil carbon and nitrogen concentration (%), and C:N ratio in the 5-15 cm depth layer. Standard error in parentheses.

	Total C		Total N		C:N ratio	
Site	Control	Burned	Control	Burned	Control	Burned
Year-0	1.49 (0.23)	1.58 (0.17)	0.078 (0.010)	0.072 (0.003)	19.0 (1.7)	21.9 (1.5)
Year-5	1.85 (0.31)	1.41 (0.10)	0.070 (0.004)	0.067 (0.004)	26.9 (5.8)	21.6 (0.4)
Year-12	1.26 (0.02)	1.29 (0.14)	0.075 (0.002)	0.075 (0.009)	16.9 (0.7)	14.6 (0.1)

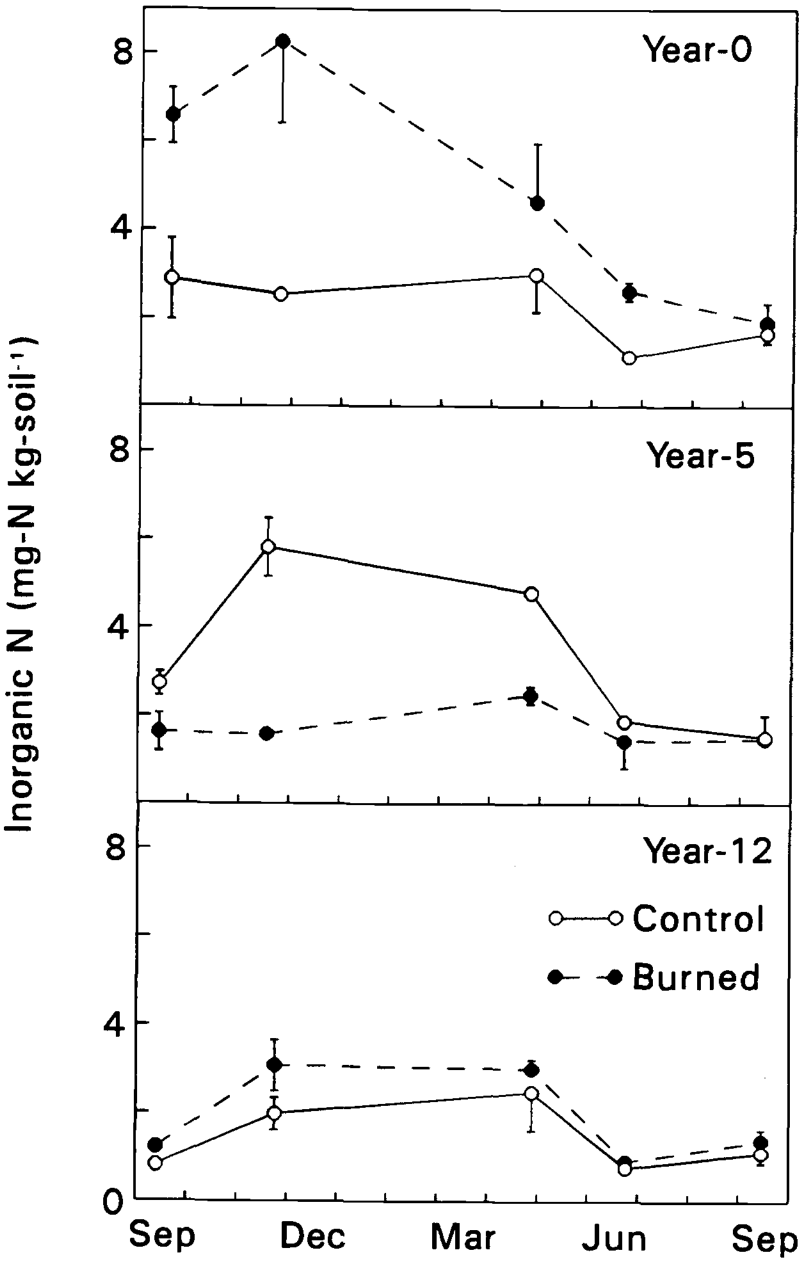

Fig. III.1. Inorganic N concentration in the 0-5 cm depth soil layer in burned and control plots. Error bars denote standard errors.

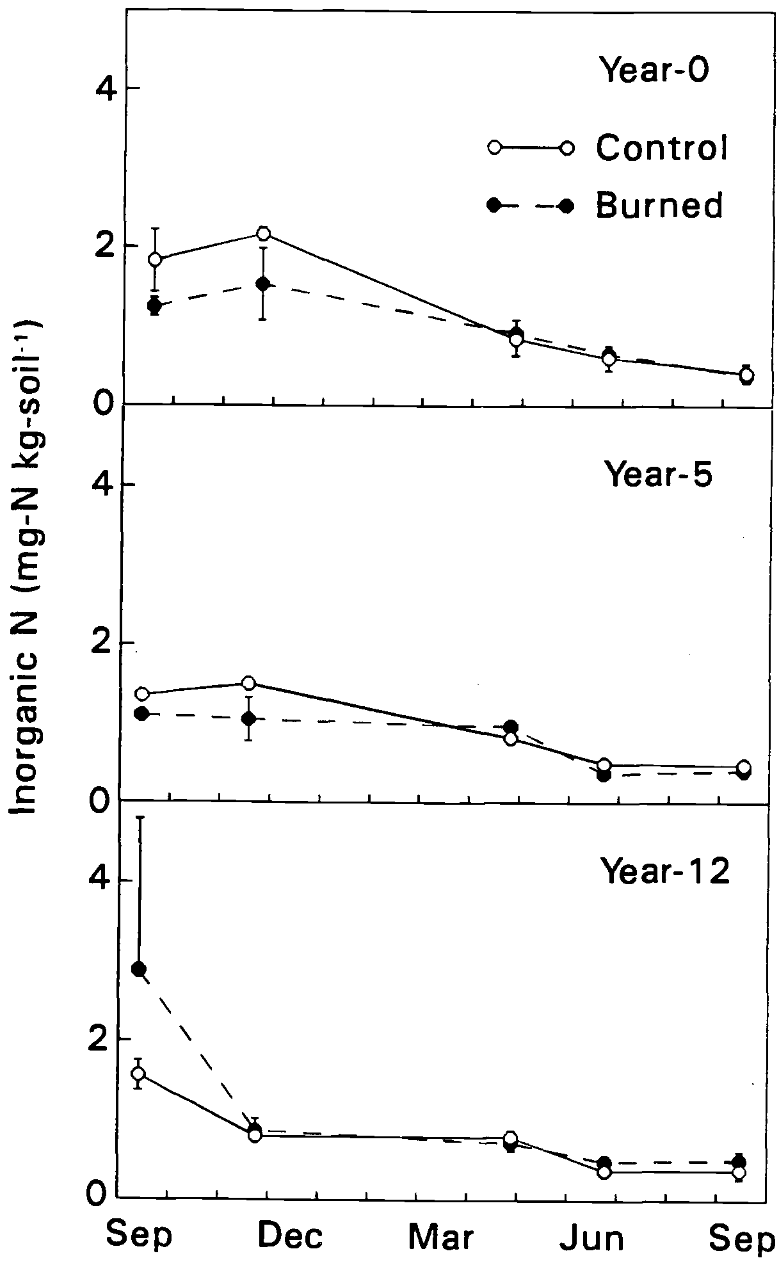

Fig. III.2. Inorganic N concentration in the 5-15 cm depth soil layer in burned and control plots. Error bars denote standard errors.

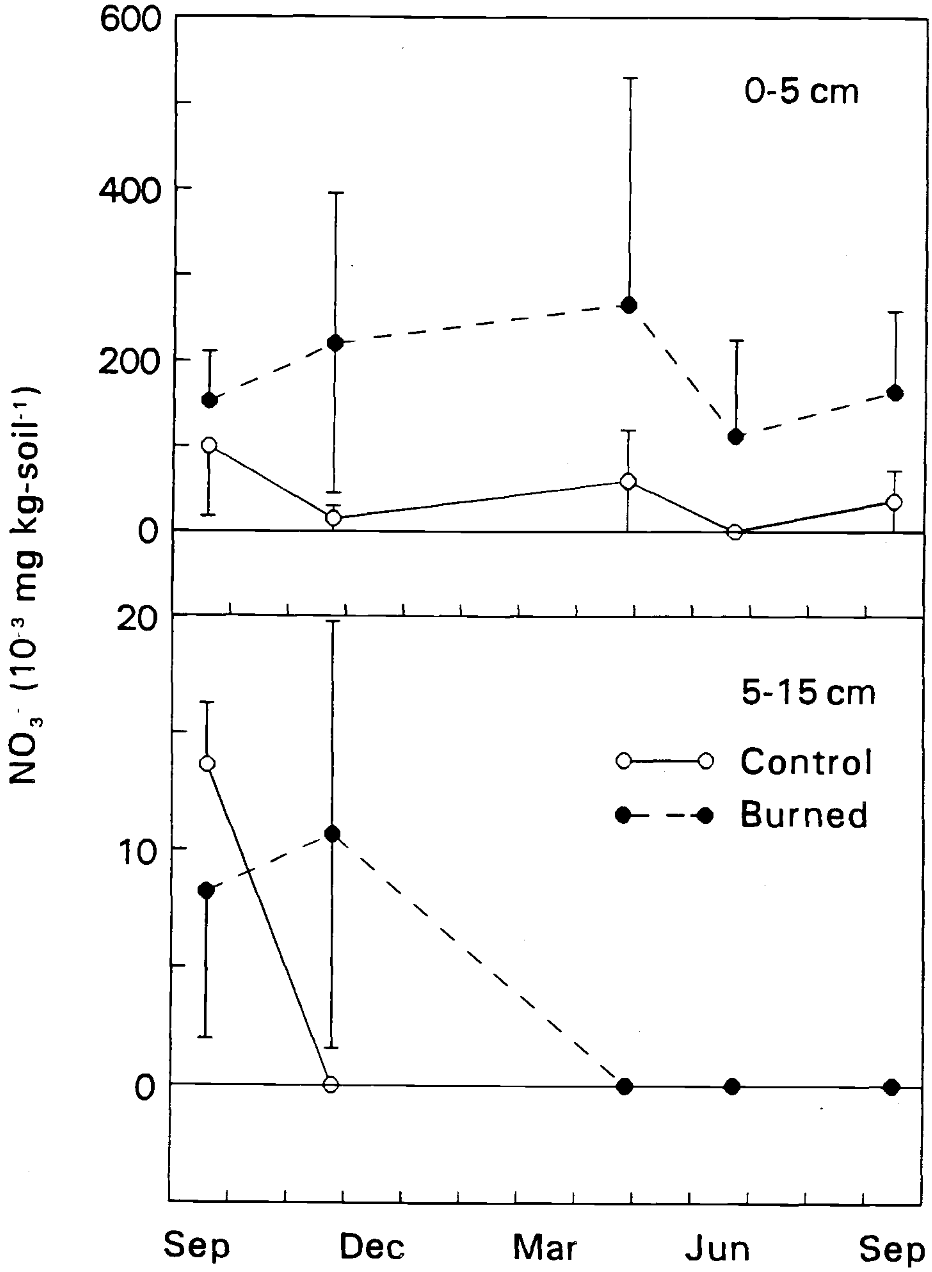

Fig. III.3. Nitrate (NO_3^-) concentration in the 0-5 and 5-15 cm depth soil layer in burned and control plots at year-0. Error bars denote standard errors.

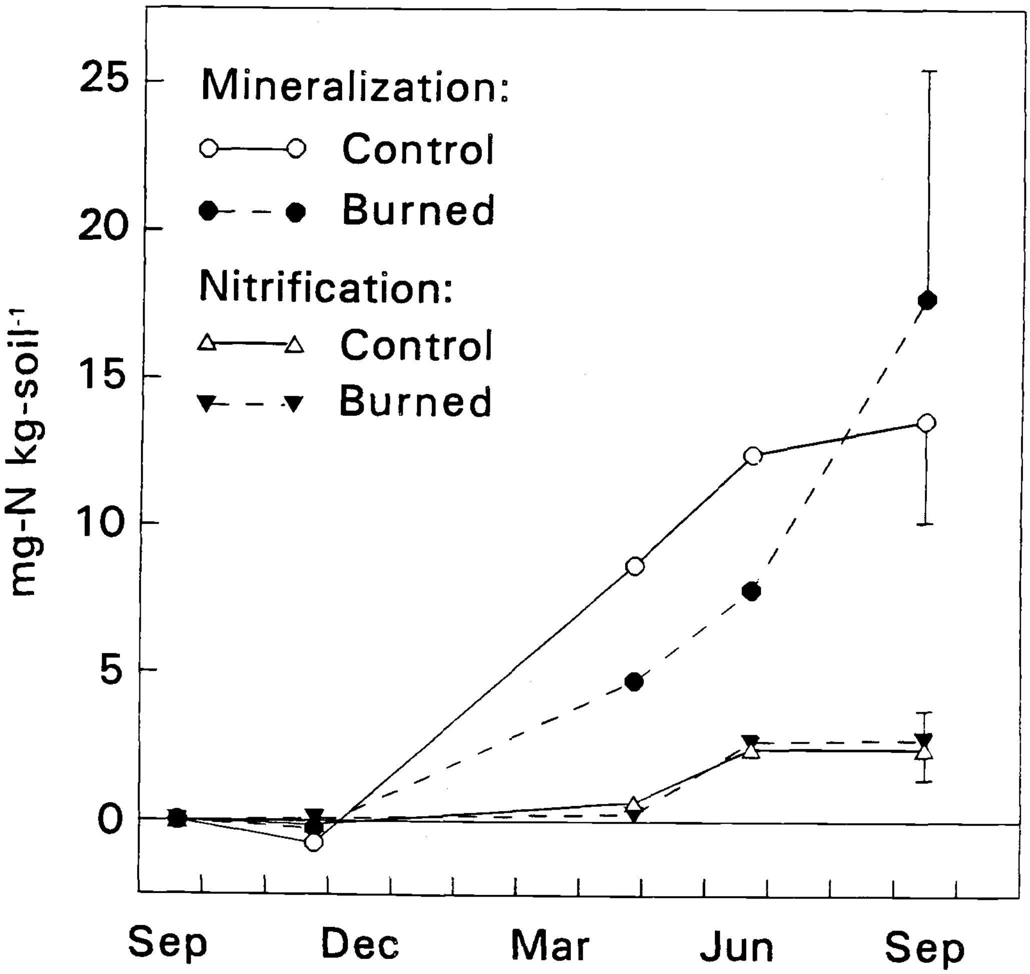

Fig. III.4. Cumulative net N mineralization and nitrification in the 0-5 cm depth soil layer in burned and control plots at year-0. Error bars denote standard error of the annual cumulative values.

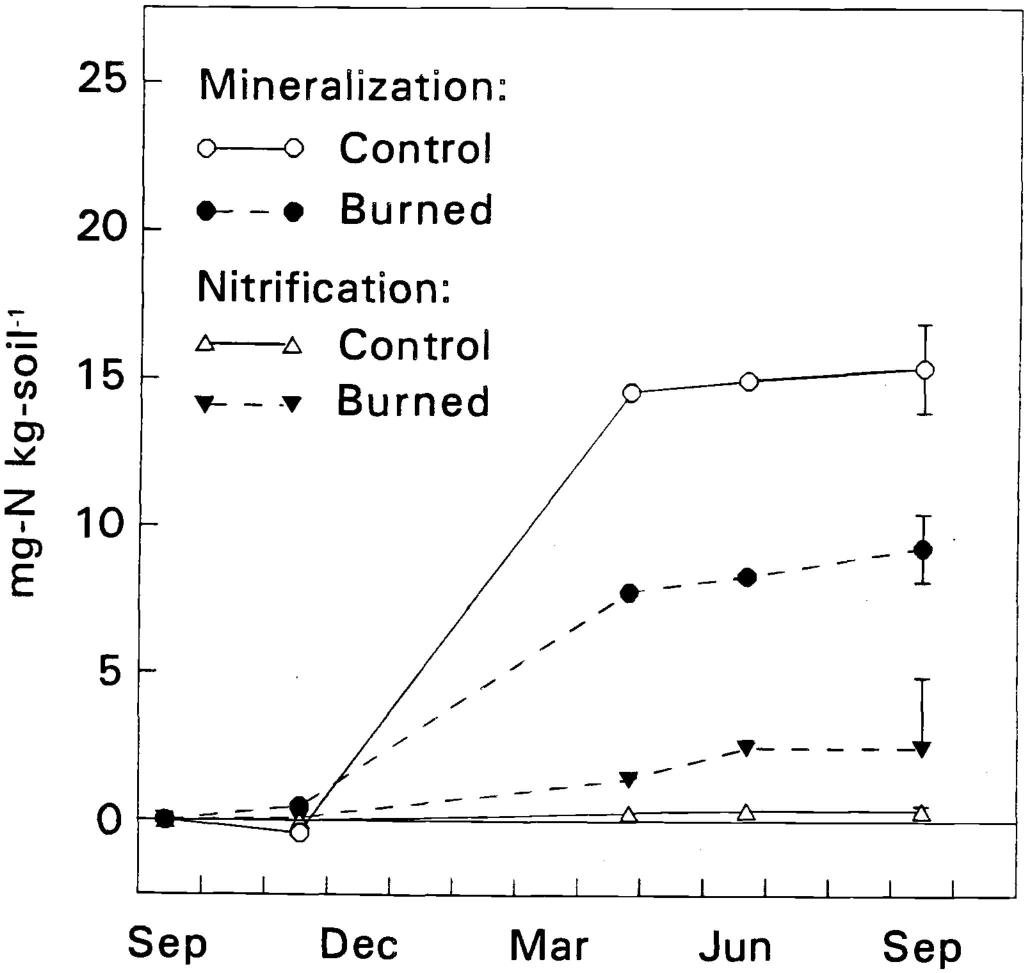

Fig. III.5. Cumulative net N mineralization and nitrification in the 0-5 cm depth soil layer in burned and control plots at year-5. Error bars denote standard error of the annual cumulative values.

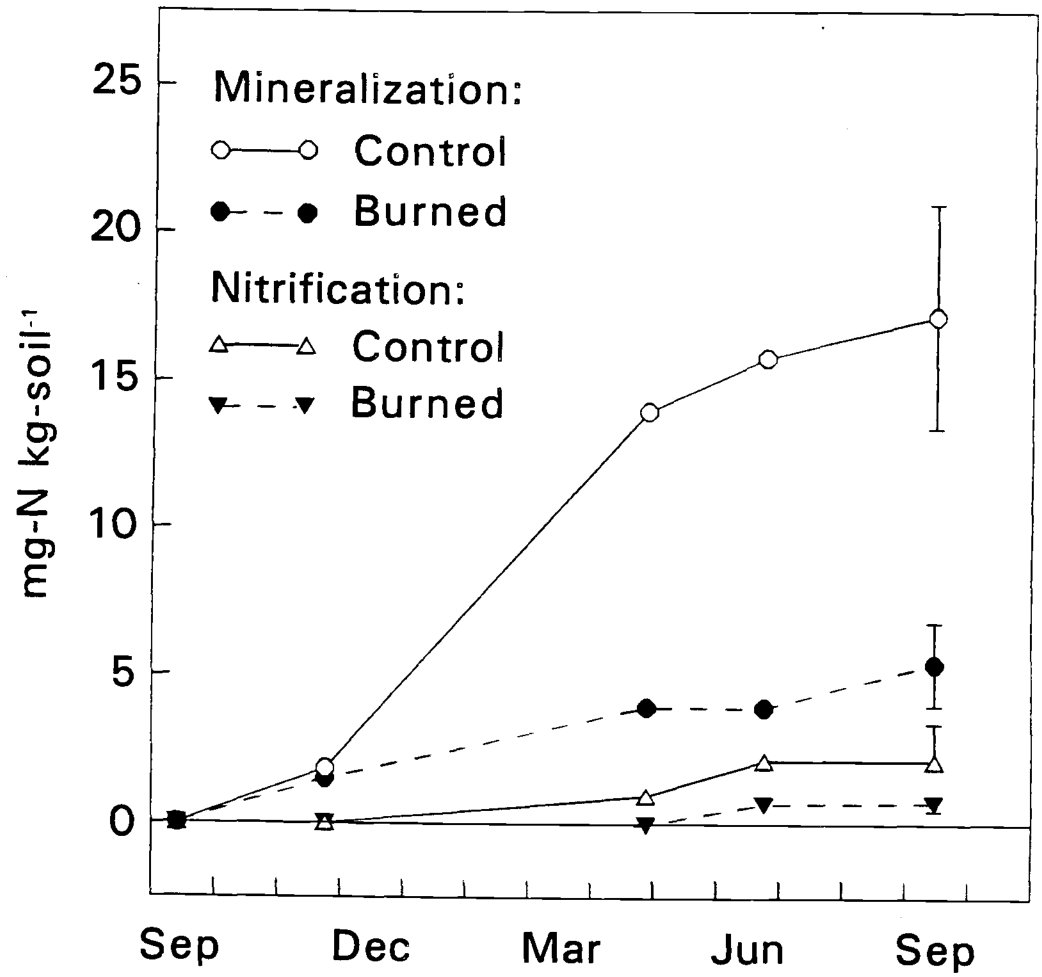

Fig. III.6. Cumulative net N mineralization and nitrification in the 0-5 cm depth soil layer in burned and control plots at year-12. Error bars denote standard error of the annual cumulative values.

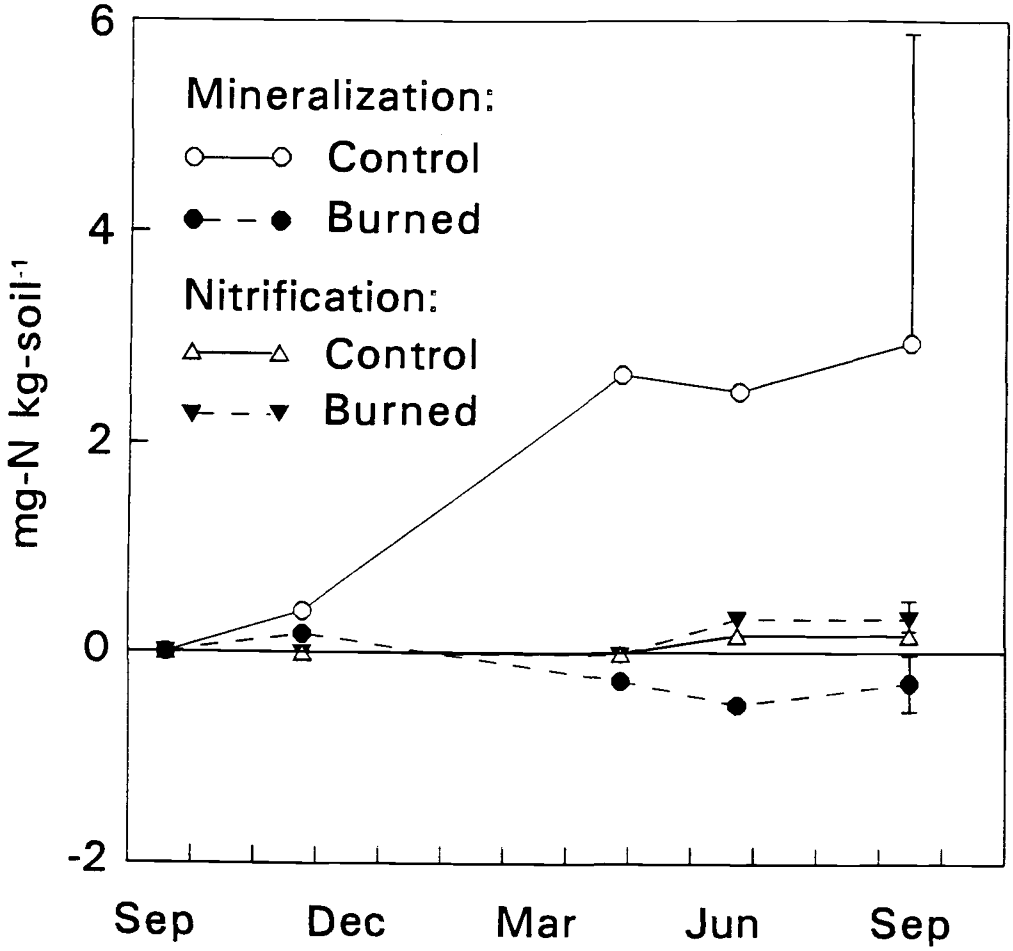

Fig. III.7. Cumulative net N mineralization and nitrification in the 5-15 cm depth soil layer in burned and control plots at year-0. Error bars denote standard error of the annual cumulative values.

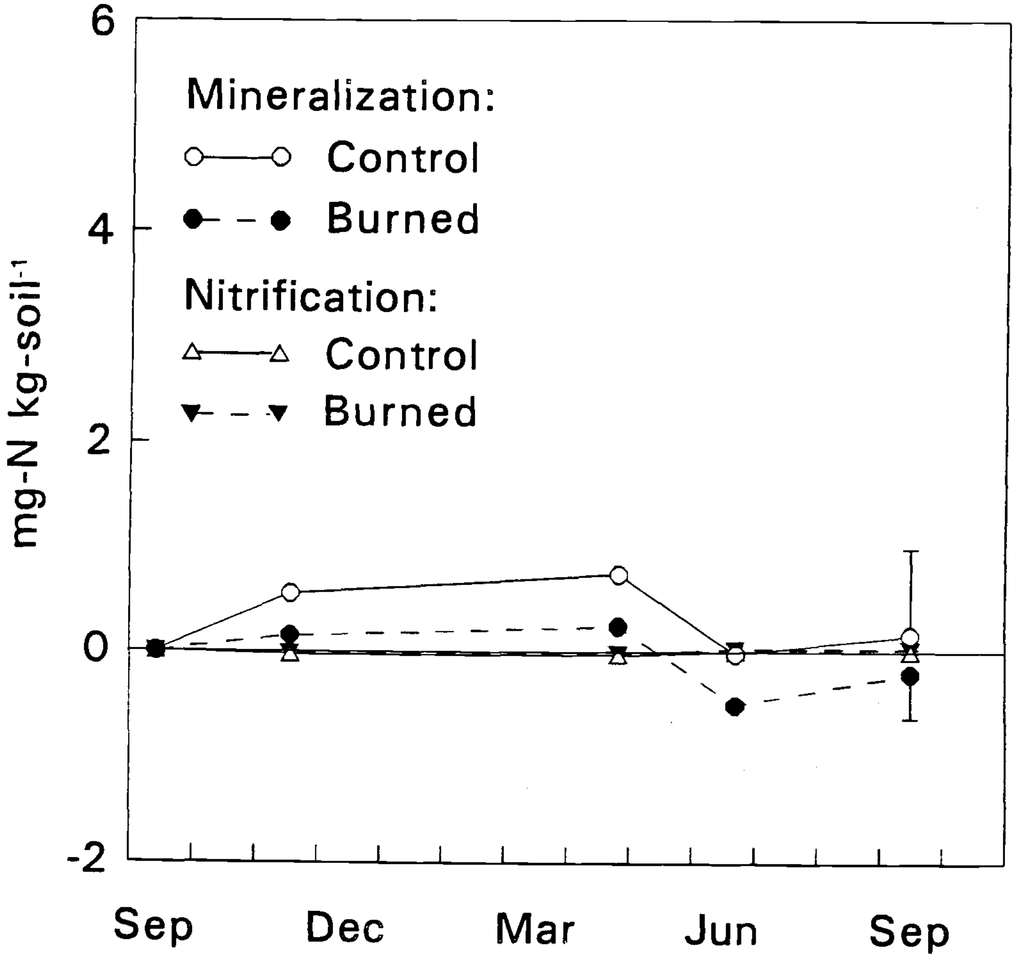

Fig. III.8. Cumulative net N mineralization and nitrification in the 5-15 cm depth soil layer in burned and control plots at year-5. Error bars denote standard error of the annual cumulative values.

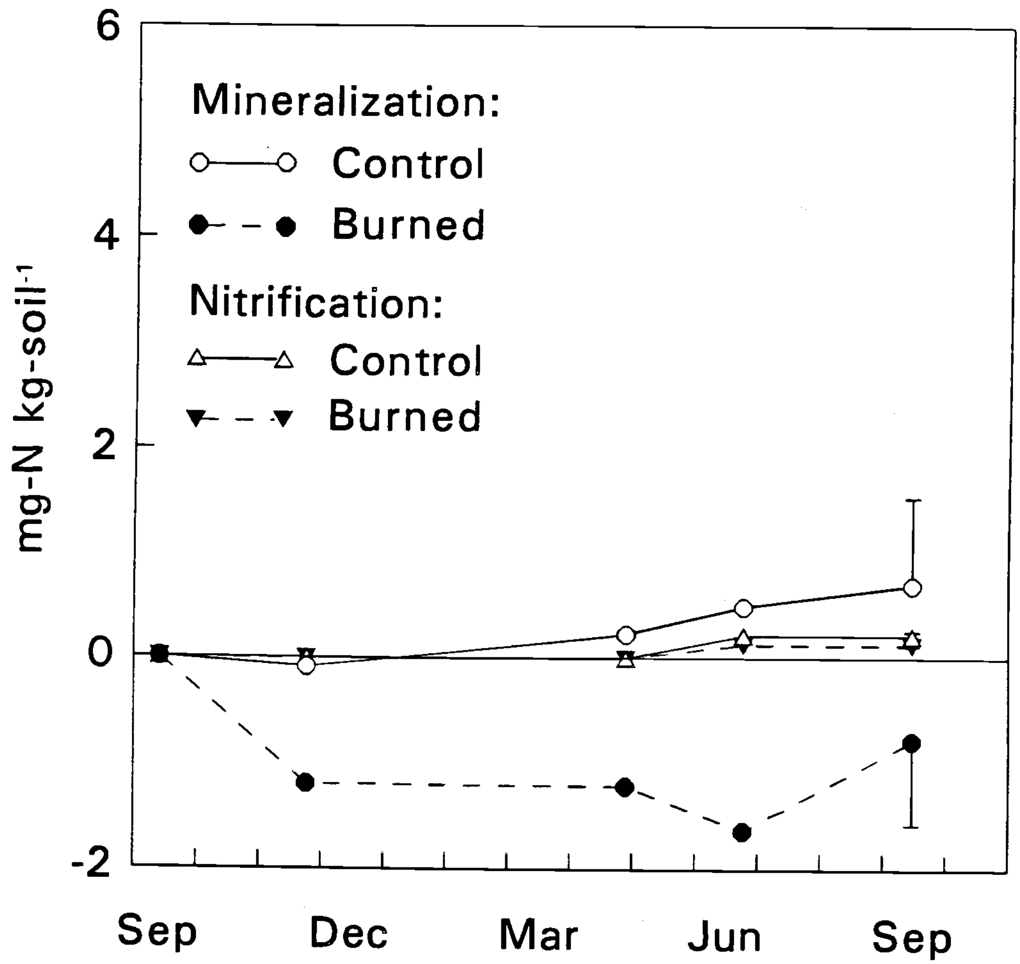

Fig. III.9. Cumulative net N mineralization and nitrification in the 5-15 cm depth soil layer in burned and control plots at year-12. Error bars denote standard error of the annual cumulative values.

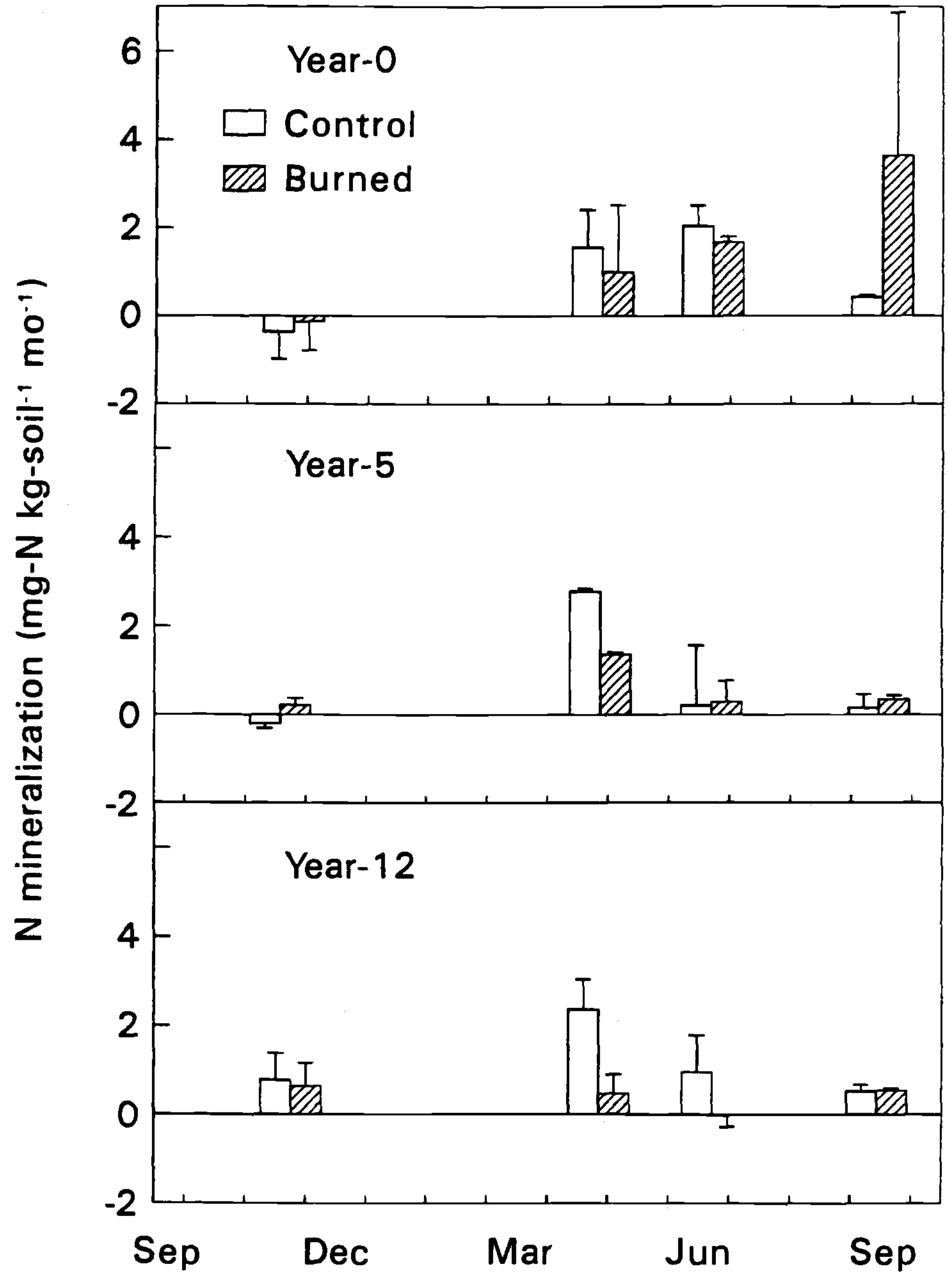

Fig. III.10. Monthly rates of net N mineralization in the 0-5 cm depth soil layer in burned and control plots. The bars are located at the end of each sequential incubation period. Error bars denote standard errors.

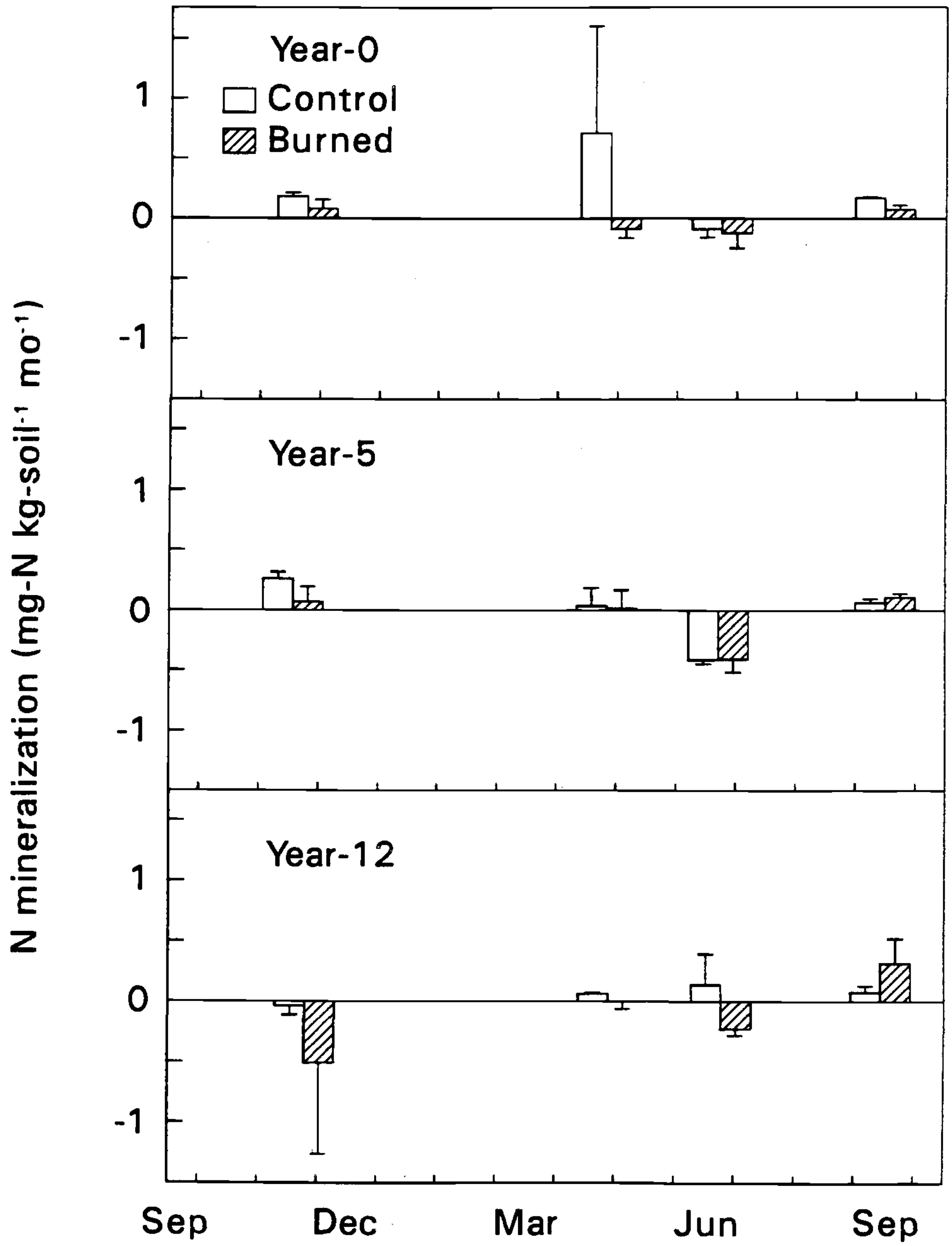

Fig. III.11. Monthly rates of net N mineralization in the 5-15 cm depth soil layer in burned and control plots. The bars are located at the end of each sequential incubation period. Error bars denote standard errors.

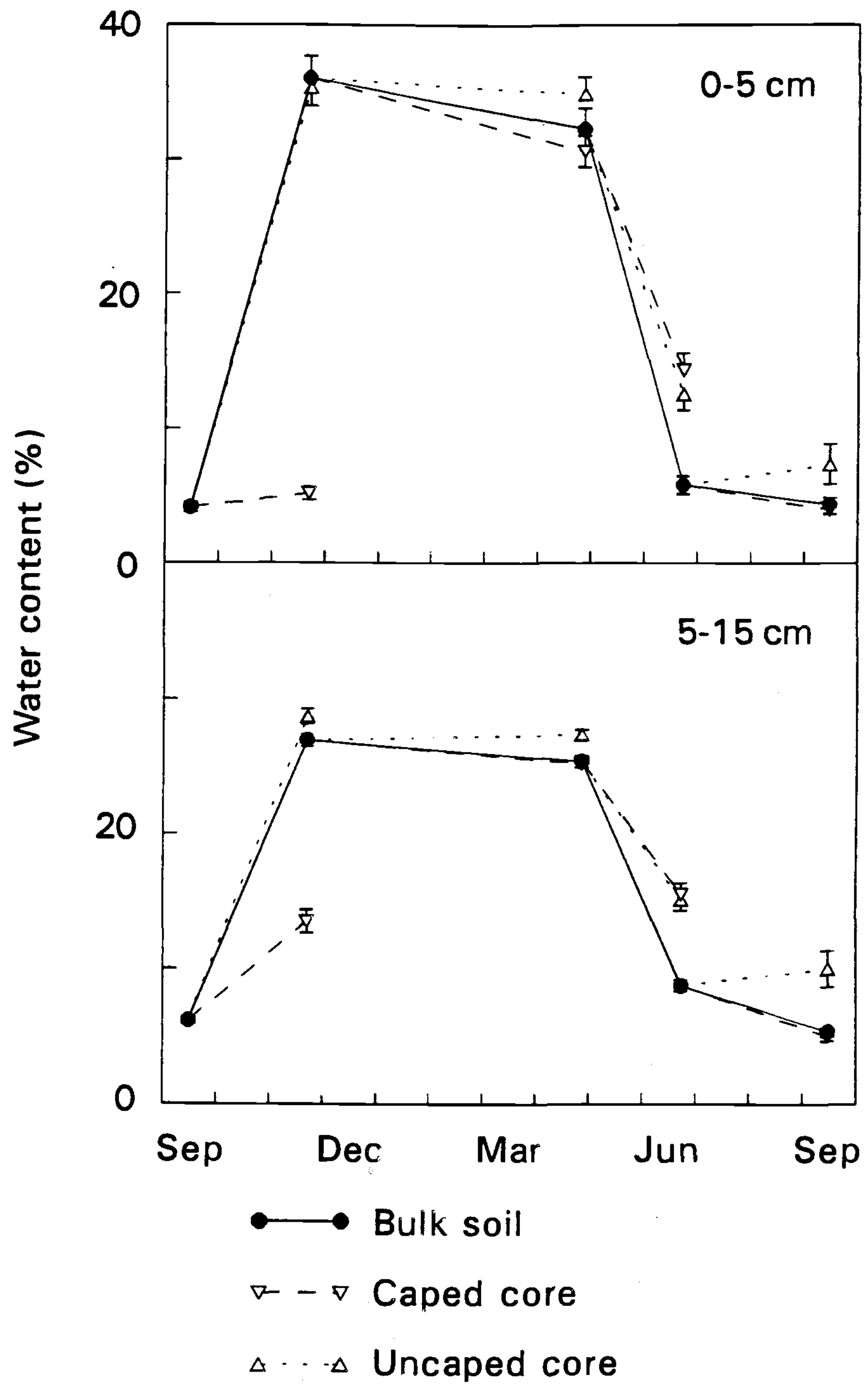

Fig. III.12. Water content in the bulked soil and in the capped and uncapped soil cores at the end of the field incubation. Error bars denote standard errors.

LITERATURE CITED

Adams, M.A., and Attiwill, P.M. 1986. Nutrient cycling and nitrogen mineralization in eucalyptus forests of southeastern Australia. II. Indices of nitrogen mineralization. *Plant Soil* **92**: 341-362.

Anderson, I.C., Levine, J.S., Poth, M.A., and Riggan, P.J. 1988. Enhanced biogenic emissions of nitric oxide and nitrous oxide following surface biomass burning. *J. Geophys. Res.* **93**: 3893-3898.

Barrett, J.W. 1978. Height growth and site index curves for managed even-aged stands of ponderosa pine in the Pacific Northwest. USDA-For. Serv. Res. Pap. PNW-232.

Becquer, T., Merlet, D., Boudot, J.P., Rouiller, J., and Gras. F. 1990. Nitrification and nitrate uptake: Leaching balance in a declined forest ecosystem in eastern France. *Plant Soil* **125**: 95-107.

Bell, R.L., and Binkley, D. 1989. Soil nitrogen mineralization and immobilization in response to periodic prescribed fire in a loblolly pine plantation. *Can. J. For. Res.* **19**: 816-820.

Binkley, D., and Hart, S.C. 1989. The components of nitrogen availability assessments in forests soils. *Adv. Soil Sci.* **10**: 57-112.

Bork, J.L. 1985. Fire history in three vegetation types on the East side of the Oregon Cascades. Unpublished Ph.D. Dissertation. Oregon State University, Corvallis, Oregon.

Cochran, P.H. 1979. Response of thinned ponderosa pine to fertilization. USDA-For. Serv. Res. Note PNW-339.

Cochran, P.H. 1978. Response of pole size ponderosa pine stand to nitrogen, phosphorus, and sulfur. USDA-For. Serv. Res. Note PNW-317.

Cochran, P.H., and Hopkins, W.E. 1991. Does fire exclusion increase productivity of ponderosa pine? *In*: Management and productivity of western-montane forest soils. USDA For. Serv. Gen. Tech. Rep. INT-280. pp. 224-228.

Covington, W.W., and Sackett, D.P. 1992. Soil mineral nitrogen changes following prescribed burning in ponderosa pine. *For. Ecol. Manag.* **54**: 175-191.

Covington, W.W., and Sackett, D.P. 1986. Effect of periodic burning on soil nitrogen concentration in ponderosa pine. *Soil Sci. Soc. Am. J.* **50**: 452-457.

Ellis, R.C., and Graley, A.M. 1983. Gains and losses in soil nutrients associated with harvesting and burning eucalypt rainforest. *Plant Soil* **74**: 437-450.

Frazer, D.W., McColl, J.G., and Powers, R.F. 1990. Soil nitrogen mineralization in a clearcutting chronosequence in a northern California conifer forest. *Soil Sci. Soc. Am. J.* **54**: 1145-1152.

Geist, J.M., and Cochran, P.H. 1991. Influences of volcanic ash and pumice deposition on productivity of western interior forest soils. *In*: Management and productivity of western-montane forest soils. USDA For. Serv. Gen. Tech. Rep. INT-280. pp. 82-88.

Grier, C.C. 1989. Effects of prescribed springtime underburning on production and nutrient status of a young ponderosa pine stand. USDA-For. Ser. Gen. Tech. Rep. RM-191. pp. 71-76.

Hobbs, N.T., and Schimel, D.S. 1984. Fire effects on nitrogen mineralization and fixation in mountain shrub and grassland communities. *J. Range Manag.* **37**: 402-405.

Klemmedson, J.O. 1976. Effect of thinning and slash burning on nitrogen and carbon in ecosystems of young dense ponderosa pine. *For. Sci.* **22**: 45-53.

Kovacic, D.A., Swift, D.M., Ellis, J.E., and Hakonson, T.E. 1986. Immediate effects of prescribed burning on mineral soil nitrogen in ponderosa pine in New Mexico. *Soil Sci.* **141**: 71-76.

Landsberg, J.D. 1992. Response of ponderosa pine forests in Central Oregon to prescribed underburning. Unpublished Ph.D. Dissertation, Oregon State University, Corvallis, Oregon.

Landsberg, J.D., Cochran, P.H., Finck, M.M., and Martin, R.E. 1984. Foliar nitrogen content and tree growth after prescribed fire in ponderosa pine. USDA-For. Serv. Res. Note PNW-412.

Larsen, D.M. 1976. Soil resource inventory. Deschutes National Forest. Unpublished document.

Nadelhoffer, K.J., Aber, J.D., and Melillo, J.M. 1983. Leaf-litter production and soil organic matter dynamics along a nitrogen-availability gradient in southern Wisconsin. *Can. J. For. Res.* **13**: 12-21.

Nissley, S.D., Zasoski, R.J., and Martin, R.E. 1980. Nutrient changes after prescribed surface burning of Oregon ponderosa pine stands. *In*: Proceedings Sixth Conference on Fire and Forest Meteorology. Soc. Am.For. Washington, D.C. pp. 214-219.

Powers, R.F. 1990. Nitrogen mineralization along an altitudinal gradient: interactions of soil temperature, moisture, and substrate quality. *For Ecol. Manag.* **30**: 19-29.

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

Raison, R.J., Connell, M.J., and Khanna, P.K. 1987. Methodology for studying fluxes of soil mineral-N *in situ. Soil Biol. Biochem.* **19**: 521-530.

SAS Institute Inc. 1985. SAS/STAT guide for personal computers, version 6. SAS Institute Inc., Cary, N.C.

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

Shea, R.W. 1993. Effects of prescribed fire and silvicultural activities on fuel mass and nitrogen redistribution in *Pinus ponderosa* ecosystems of Central Oregon. Unpublished M.S. Dissertation. Oregon State University, Corvallis, Oregon.

Singh, R.S., Raghubanshi, A.S., and Singh, J.S. 1991. Nitrogen-mineralization in dry tropical savanna: effects of burning and grazing. *Soil Biol. Biochem.* **23**: 269-273.

Sommerfeld, R.A., Mosier, A.R., and Musselman, R.C. 1993. CO_2, CH_4 and N_2O flux through a Wyoming snowpack and implications for global budgets. *Nature* **361**: 140-142.

Vance, E.D., and Henderson, G.S. 1984. Soil nitrogen availability following long-term burning in an oak-hickory forest. *Soil Sci. Soc. Am. J.* **48**: 184-190.

Vitousek, P., and Matson, P. 1985. Disturbance, nitrogen availability, and nitrogen losses in an intensively managed loblolly pine plantation. *Ecology* **66**: 1360-1376.

Vlamis, J., Biswell, H.H., and Schultz, A.M. 1955. Effects of prescribed burning on soil fertility in second-growth ponderosa pine. *J. For.* **53**: 905-909.

Volland, L.A. 1988. Plant associations of the central Oregon pumice zone. USDA-For. Serv. R-6-Ecol-104-1985. Portland, OR.

Wells, C.G., Campbell, R.E., DeBano, L.F., Lewis, C.E., Fredriksen, R.L., Franklyn, C.C., Froelich, R.C., and Dunn, P.H. 1979. Effects of fire on soil. A state-of-knowledge review. USDA-For. Serv. Gen. Tech. Rep. WO-7.

White, C.S. 1986a. Effects of prescribed fire on rates of decomposition and nitrogen mineralization in a ponderosa pine ecosystem. *Biol. Fert. Soil* **2**: 87-95.

Whynot, T. W., and Weetman, G.F. 1991. Repeated fertilization effects on nitrogen fluxes measured by sequential coring. *Soil Sci. Soc. Am. J.* **55**: 1101-1111.

Winer, B.J. 1971. Statistical principles in experimental design. 2nd ed. McGraw-Hill, New York.

IV. BIBLIOGRAPHY

Adams, M.A., and Attiwill, P.M. 1986. Nutrient cycling and nitrogen mineralization in eucalyptus forests of south eastern Australia. II. Indices of nitrogen mineralization. *Plant Soil* **92**: 341-362.

Anderson, I.C., Levine, J.S., Poth, M.A., and Riggan, P.J. 1988. Enhanced biogenic emissions of nitric oxide and nitrous oxide following surface biomass burning. *J. Geophys. Res.* **93**: 3893-3898.

Barrett, J.W. 1978. Height growth and site index curves for managed even-aged stands of ponderosa pine in the Pacific Northwest. USDA-For. Serv. Res. Pap. PNW-232.

Becquer, T., Merlet, D., Boudot, J.P., Rouiller, J., and Gras, F. 1990. Nitrification and nitrate uptake: Leaching balance in a declined forest ecosystem in eastern France. *Plant Soil* **125**: 95-107.

Bell, R.L., and Binkley, D. 1989. Soil nitrogen mineralization and immobilization in response to periodic prescribed fire in a loblolly pine plantation. *Can. J. For. Res.* **19**: 816-820.

Binkley, D., and Hart, S.C. 1989. The components of nitrogen availability assessments in forests soils. *Adv. Soil Sci.* **10**: 57-112.

Biswell, H.H. 1972. Fire ecology in ponderosa pine grassland. *Tall Tim. Fire Ecol. Conf. Proc.* **12**: 69-97.

Bocock, K.L., Gilbert, O.J., Capstick, C.K., Turner, D.C., Ward, J.S., and Woodman, M.J. 1960. Changes in leaf litter when placed on the surface of soils with contrasting humus types. *J. Soil Sci.* **11**: 1-9.

Bork, J.L. 1985. Fire history in three vegetation types on the East side of the Oregon Cascades. Unpublished Ph.D. Dissertation. Oregon State University, Corvallis, Oregon.

Bremner, J.M., and McCarty, G.W. 1988. Effects of terpenoids on nitrification in soil. *Soil Sci. Soc. Am. J.* **52**: 1630-1633.

Chambers, J.L., Dougherty, P.M., and Hennessey, T.C. 1986. Fire: its effects on growth and physiological processes in conifer forests. *In*: Hennessey, T.C., Dougherty, P.M., Dossuth, S.V., and Johnson, J.D. (eds.). Stress physiology and forest productivity. Kluwer Academic Pub. Dordrecht. pp. 171-189.

Cochran, P.H. 1979. Response of thinned ponderosa pine to fertilization. USDA-For. Serv. Res. Note PNW-339.

Cochran, P.H. 1978. Response of pole size ponderosa pine stand to nitrogen, phosphorus, and sulfur. USDA-For. Serv. Res. Note PNW-317.

Cochran, P.H., and Hopkins, W.E. 1991. Does fire exclusion increase productivity of ponderosa pine? *In*: Management and productivity of western-montane forest soils. USDA For. Serv. Gen. Tech. Rep. INT-280. pp. 224-228.

Covington, W.W., and Sackett, D.P. 1992. Soil mineral nitrogen changes following prescribed burning in ponderosa pine. *For. Ecol. Manag.* **54**: 175-191.

Covington, W.W., and Sackett, D.P. 1990. Fire effects on ponderosa pine soils and their management implications. *In*: Effects of fire management of Southwestern natural resources. USDA-For. Serv. Gen. Tech. Rep. RM-191. pp.105-111.

Covington, W.W., and Sackett, D.P. 1986. Effect of periodic burning on soil nitrogen concentration in ponderosa pine. *Soil Sci. Soc. Am. J.* **50**: 452-457.

Covington, W.W., and Sackett, D.P. 1984. The effect of a prescribed burn in a southwestern ponderosa pine on organic matter and nutrients in woody debris and forest floor. *For. Sci.* **30**: 183-192.

Cromack, K. Jr., Entry, J.A., and Savage, T. 1991. The effect of disturbance by *Phellinus weirii* on decomposition and nutrient mineralization in a *Tsuga mertensiana* forest. *Biol. Fert. Soils* **11**: 245-249.

Edmonds, R.L. 1980. Litter decomposition and nutrient release in Douglas-fir, red alder, western hemlock, and Pacific silver fir ecosystems in western Washington. *Can. J. For. Res.* **10**: 327-337.

Ellis, R.C., and Graley, A.M. 1983. Gains and losses in soil nutrients associated with harvesting and burning eucalypt rainforest. *Plant Soil* **74**: 437-450.

Fahey, T.J. 1983. Nutrient dynamics of aboveground detritus in lodgepole pine (*Pinus contorta* ssp. *latifolia*) ecosystems, southeastern Wyoming. *Ecol. Monog.* **53**: 51-72.

Ffolliot, P.F., and Guertin, D.P. 1989. Prescribed burning in Arizona ponderosa pine forests: A 24-year case study. USDA-For. Serv. Gen. Tech. Rep. RM-191. pp.250-253.

Frazer, D.W., McColl, J.G., and Powers, R.F. 1990. Soil nitrogen mineralization in a clearcutting chronosequence in a northern California conifer forest. *Soil Sci. Soc. Am. J.* **54**: 1145-1152.

Geist, J.M., and Cochran, P.H. 1991. Influences of volcanic ash and pumice deposition on productivity of western interior forest soils. *In*: Management and productivity of western-montane forest soils. USDA For. Serv. Gen. Tech. Rep. INT-280. pp. 82-88.

Gholz, H.L., Perry, C.S., Cropper, W.P. Jr., and Hendry, L.C. 1985. Litterfall, decomposition, and nitrogen and phosphorus dynamics in a chronosequence of slash pine (*Pinus elliottii*) plantations. *Forest Sci.* **31**: 463-478.

Grier, C.C. 1989. Effects of prescribed springtime underburning on production and nutrient status of a young ponderosa pine stand. USDA-For. Ser. Gen. Tech. Rep. RM-191. pp. 71-76.

Grigal, D.F., and Mccoll, J.G. 1977. Litter decomposition following fire in northeastern Minnesota. *J. Appl. Ecol.* **14**: 531-538.

Hart, S.C., and Firestone, M.K. 1991. Forest floor-mineral soil interactions in the internal nitrogen cycle of an old growth forest. *Biogeochemistry* **12**: 103-127.

Hart, S.C., Firestone, M.K., and Paul, E.A. 1992. Decomposition and nutrient dynamics of ponderosa pine needles in a Mediterranean-type climate. *Can. J. For. Res.* **22**: 306-314.

Hobbs, N.T., and Schimel, D.S. 1984. Fire effects on nitrogen mineralization and fixation in mountain shrub and grassland communities. *J. Range Manag.* **37**: 402-405.

Kilgore, B.M. 1981. Fire in ecosystem distribution and structure: western forests and scrublands. *In:* H.A. Mooney, T.M. Bonnicksen, N.L. Christensen, J.E. Lotan, and W.A. Reiners (eds.). Fire regimes and ecosystem properties. USDA-For. Serv. Gen. Tech. Rep. WO-26. pp. 58-89.

Klemmedson, J.O. 1992. Decomposition and nutrient release from mixtures of Gambel oak and ponderosa pine leaf litter. *For. Ecol. Manag.* **47**: 349-361.

Klemmedson, J.O. 1976. Effect of thinning and slash burning on nitrogen and carbon in ecosystems of young, dense ponderosa pine. *For. Sci.* **22**: 45-53.

Klemmedson, J.O., Meier, C.E., and Campbell, R.E. 1990. Litter fall transfers of dry matter and nutrients in ponderosa pine stands. *Can. J. For. Res.* **20**: 1105-1115.

Klemmedson, J.O., Meier, C.E., and Campbell, R.E. 1985. Needle decomposition and nutrient release in ponderosa pine ecosystems. *For. Sci.* **31**: 647-660.

Kovacic, D.A., Swift, D.M., Ellis, J.E., and Hakonson, T.E. 1986. Immediate effects of prescribed burning on mineral soil nitrogen in ponderosa pine in New Mexico. *Soil Sci.* **141**: 71-76.

Landsberg, J.D. 1992. Response of ponderosa pine forests in Central Oregon to prescribed underburning. Unpublished Ph.D. Dissertation, Oregon State University, Corvallis, Oregon.

Landsberg, J.D., and Cochran, P.H. 1980. Prescribed burning effects on foliar nitrogen content in ponderosa pine. *In*: Proceedings of the Sixth Conference on Fire and Forest Meteorology. Soc. Am. For. Washington, D.C. pp. 209-213.

Landsberg, J.D., Cochran, P.H., Finck, M.M., and Martin, R.E. 1984. Foliar nitrogen content and tree growth after prescribed fire in ponderosa pine. USDA-For. Serv. Res. Note PNW-412.

Langille, H.D., Plummer, F.G., Dobwell, A., Rixon, T.F., and Lieberg, J.B. 1903. Forest conditions in the Cascade Range forest reserve, Oregon. U.S. Geological Survey Professional Paper, 9. Washington, D.C.

Larsen, D.M. 1976. Soil resource inventory, Deschutes National Forest. Unpublished document.

Martin, R.E. 1963. A basic approach to fire injury of tree stems. *Tall Tim. Fire Ecol. Conf. Proc.* **2**: 151-162.

Meentemeyer, V. 1978. Macroclimate and lignin control of litter decomposition rates. *Ecology* **59**: 465-472.

Munger, T.L. 1917. Western yellow pine in Oregon. USDA Bulletin 418. Washington, D.C.

Nadelhoffer, K.J., Aber, J.D., and Melillo, J.M. 1983. Leaf-litter production and soil organic matter dynamics along a nitrogen-availability gradient in southern Wisconsin. *Can. J. For. Res.* **13**: 12-21.

Nissley, S.D., Zasoski, R.J., and Martin, R.E. 1980. Nutrient changes after prescribed surface burning of Oregon ponderosa pine stands. *In:* Proceedings Sixth Conference on Fire and Forest Meteorology. Soc. Am. For. Washington, D.C. pp. 214-219.

O'Connell, A.M., and Menage, P. 1983. Decomposition of litter from three major plant species of jarrah (*Eucalyptus marginata* Donn ex Sm.) forest in relation to site fire history and soil type. *Aust J. Ecol.* **8**: 277-286.

Olson, J.S. 1963. Energy storage and the balance of producers and consumers in ecological systems. *Ecology* **44**: 322-331.

Powers, R.F. 1990. Nitrogen mineralization along an altitudinal gradient: interactions of soil temperature, moisture, and substrate quality. *For Ecol. Manag.* **30**: 19-29.

Powers, R.F., Webster, S.R., and Cochran, P.H. 1988. Estimating the response of ponderosa pine to fertilization. USDA-For. Serv. Intermt. Res. Sta. pp. 219-225.

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

Raison, R.J., Connell, M.J., and Khanna, P.K. 1987. Methodology for studying fluxes of soil mineral-N *in situ. Soil Biol. Biochem.* **19**: 521-530.

Raison, R.J., Khanna, P.K., and Woods, P.V. 1985. Mechanisms of element transfer to the atmosphere during vegetation fires. *Can. J. For. Res.* **15**: 132-140.

Raison, R.J., Woods, P.V., and Khanna, P.K. 1986. Decomposition and accumulation of litter after fire in sub-alpine eucalyptus forests. *Aust. J. Ecol.* **11**: 9-19.

Raison, R.J., Woods, P.V., and Khanna, P.K. 1983. Dynamics of fine fuels in recurrently burnt eucalyptus forests. *Aust. For.* **46**: 294-302.

SAS Institute Inc. 1985. SAS/STAT guide for personal computers, version 6. SAS Institute Inc., Cary, N.C.

Schlesinger, W.H., 1985. Decomposition of chaparral shrub foliage. *Ecology* **66**: 1353-1359.

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

Shea, R.W. 1993. Effects of prescribed fire and silvicultural activities on fuel mass and nitrogen redistribution in *Pinus ponderosa* ecosystems of Central Oregon. Unpublished M.S. Dissertation. Oregon State University, Corvallis, Oregon.

Singh, R.S., Raghubanshi, A.S., and Singh, J.S. 1991. Nitrogen-mineralization in dry tropical savanna: effects of burning and grazing. *Soil Biol. Biochem.* **23**: 269-273.

Sommerfeld, R.A., Mosier, A.R., and Musselman, R.C. 1993. CO_2, CH_4 and N_2O flux through a Wyoming snowpack and implications for global budgets. *Nature* **361**: 140-142.

Springett, J.A. 1976. The effect of prescribed burning on the soil fauna and on litter decomposition in Western Australia forests. *Aust. J. Ecol.* **1**: 77-82.

Stark, N.M. 1977. Fire and nutrient cycling in a Douglas-fir/larch forest. *Ecology* **58**: 16-30.

Steel, R.G.D., and Torrie, J.H. 1980. Principles and procedures of statistics: a biometrical approach (2nd ed.). McGraw-Hill, New York.

Swift, M.J., Heal, O.W., and Anderson, J.M. 1979. Decomposition in terrestrial ecosystems. University of California Press, Berkeley.

Vance, E.D., and Henderson, G.S. 1984. Soil nitrogen availability following long-term burning in an oak-hickory forest. *Soil Sci. Soc. Am. J.* **48**: 184-190.

Viereck, L.A., and Dyrness, C.T. 1979. Ecological effects of the Wickersham Dome fire near Fairbanks, Alaska. USDA Gen. Tech. Rep. PNW-90.

Vitousek, P., and Matson, P. 1985. Disturbance, nitrogen availability, and nitrogen losses in an intensively managed loblolly pine plantation. *Ecology* **66**: 1360-1376.

Vlamis, J., Biswell, H.H., and Schultz, A.M. 1955. Effects of prescribed burning on soil fertility in second-growth ponderosa pine. *J. For.* **53**: 905-909.

Volland, L.A. 1988. Plant associations of the central Oregon pumice zone. USDA-For. Serv. R-6-Ecol-104-1985. Portland, OR.

Waring, R.H., and Schlesinger, W.H. 1985. Forest ecosystems concepts and management. Academic Press, Inc. Orlando, FL.

Weaver, H. 1943. Fire as an ecological and silvicultural factor in the ponderosa pine region of the Pacific slope. *J. For.* **41**: 7-15.

Wells, C.G., Campbell, R.E., DeBano, L.F., Lewis, C.E., Fredriksen, R.L., Franklyn, C.C., Froelich, R.C., and Dunn, P.H. 1979. Effects of fire on soil. A state-of-knowledge review. USDA-For. Serv. Gen. Tech. Rep. WO-7.

White, C.S. 1986a. Effects of prescribed fire on rates of decomposition and nitrogen mineralization in a ponderosa pine ecosystem. *Biol. Fert. Soil* **2**: 87-95.

White, C.S. 1986b. Volatile and water-soluble inhibitors of nitrogen mineralization and nitrification in a ponderosa pine ecosystem. *Biol. Fert. Soil* **2**: 97-104.

Whynot, T. W., and Weetman, G.F. 1991. Repeated fertilization effects on nitrogen fluxes measured by sequential coring. *Soil Sci. Soc. Am. J.* **55**: 1101-1111.

Wieder, R., and Lang, G.E. 1982. A critique of the analytical methods used in examining decomposition data obtained from litter bags. *Ecology* **63**: 1636-1642.

Winer, B.J. 1971. Statistical principles in experimental design. 2nd ed. McGraw-Hill, New York.