Forest Ecology and Management, 54 (1992) 175–191
Elsevier Science Publishers B.V., Amsterdam

Soil mineral nitrogen changes following prescribed burning in ponderosa pine

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(Accepted 7 November 1991)

ABSTRACT

Covington, W.W. and Sackett, S.S., 1992. Soil mineral nitrogen changes following prescribed burning in ponderosa pine. *For. Ecol. Manage.*, 54: 175–191.

In a ponderosa pine (*Pinus ponderosa* Laws.) forest near Flagstaff, AZ, USA, there was a striking pattern in forest characteristics, consisting of substands of old-growth trees (28–120 cm diameter at breast height (dbh) and 200–500 years old) and of saplings (1.5–10 cm dbh and 60–70 years old) in a matrix of pole-sized trees (10–28 cm dbh and 60–100 years old). Tree size and forest floor mass decreased from old-growth to pole to sapling substands, but soluble N (as KCl extractable inorganic N) in the mineral soil did not vary substantially among substands before prescribed burning.

Prescribed burning had little immediate impact on the overstory but substantially decreased the forest floor mass, with the greatest absolute and relative decreases being in the old-growth substands. Immediately after burning, ammonium-nitrogen (NH_4–N) increased from 2.3 to 45.1 mg kg^{-1} in the old-growth substands, from 1.3 to 26.7 mg kg^{-1} in the pole substands, and from 1.3 to 8.3 mg kg^{-1} in the sapling substands. These differences in NH_4–N among the substand types are directly correlated with differences in the initial forest floor weight and the amount of forest floor burned. Nitrate-nitrogen (NO_3–N) was not changed immediately after burning.

By 1 year after burning, NH_4–N had declined substantially with only the old-growth substands being significantly higher than controls (30.0 versus 2.56 mg kg^{-1}). Much of this decline showed up as an increase in NO_3–N, particularly for the old-growth substands where NO_3–N was 18.6 mg kg^{-1} on burned plots compared with 0.03 mg kg^{-1} on controls.

These results support the conclusion that while increases in NH_4–N are an immediate effect of burning (most likely from NH_4–N produced by pyrolysis of forest floor material), nitrate increases, which occur later, are most likely caused by nitrification of the high NH_4–N produced immediately after burning.

A preliminary budgetary analysis for the mineral soil showed an immediate increase in inorganic N of 34.3 kg ha^{-1} in old-growth substands, 14.7 kg ha^{-1} in pole substands, and 4.0 kg ha^{-1} in sapling substands. Because these increases appear to have been transferred directly to the mineral soil from the forest floor, previous studies which have not accounted for this phenomenon may have somewhat overestimated N volatization losses from burning.

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INTRODUCTION

Frequent low intensity natural fires have shaped ecological patterns and processes in southwestern ponderosa pine ecosystems for millennia (e.g. Weaver, 1951; Cooper, 1960; Biswell et al., 1973; Pyne, 1984). However, fire exclusion over the past century has caused major changes in the fire regime and hence in the ecological processes of these ecosystems (Kilgore, 1981).

Before settlement, ponderosa pine forests in northern Arizona had a natural fire regime interval of 2–5 years (Dieterich, 1980). Beginning in the mid-1870s, heavy livestock grazing decreased herbaceous fuel continuity and broke the continuity of the forest floor. This, coupled with active fire suppression from the early 1900s, resulted in the absence of natural fires from these ecosystems for over 100 years.

There can be no doubt that fire exclusion has radically altered both structure and function of these ecosystems. The long absence of natural fire has been blamed for everything from dangerously high fuel loads (with an associated shift from frequent, low intensity understory fires, to infrequent high intensity crown fires), to reduced productivity and stagnated nutrient cycles (Arnold, 1950; Cooper, 1960; Biswell, 1972; Weaver, 1974).

Of particular concern to this study, fire exclusion in southwestern ponderosa pine has been blamed for degrading the nitrogen (N) status of ponderosa pine forests by allowing litter to steadily accumulate, thus inhibiting the recycling of the organically bound N into forms available for plant uptake (Biswell, 1972). Because ponderosa pine ecosystem productivity, like that of many other forest types, is often severely limited by low N availability (Wagle and Beasley, 1968; Cochran, 1979; Heidmann et al., 1979; Powers, 1980), a major concern has been fire impacts on inorganic N supplies in the mineral soil.

While no one has examined the immediate post-burn effects of prescribed burning on soil N for southwestern ponderosa pine ecosystems, studies in other types suggest that not all of the nitrogen in the burned fuel is volatilized. For example in both chaparral (Christensen and Muller, 1975; Dunn and DeBano, 1977) and pinyon-juniper slash (Covington et al., 1991) burns, some of the nitrogen is converted to ammonium (NH_4^+) and deposited near the soil surface. In fact, DeBano et al. (1979b) found that up to 21 kg ha^{-1} of ammonium-nitrogen (NH_4–N) were deposited in the surface soil immediately after a prescribed fire in chaparral.

Previous studies in southwestern ponderosa pine have shown that during the first few years following prescribed burns, soil nitrogen concentrations are higher on burned sites than on unburned controls (Covington and Sackett, 1986; Ryan and Covington, 1986), pine seedling establishment and growth are greater (Sackett, 1984; Ower, 1985; Haase, 1986), and herbage production (Ffolliott et al., 1977; Oswald and Covington, 1984; Andariese and Covington, 1986) and foliar nitrogen concentrations (Harris and Covington, 1983; Covington and Sackett, 1990) are higher on burned sites. However, the source of these available N increases in the mineral soil is not known. To better assess the ecological implications for the N economy and hence the long-term productivity of the site, we need to know more about changes in inorganic N in the mineral soil after burning.

The purpose of this research was to determine changes in forest floor mass and soil NH_4–N and nitrate–nitrogen (NO_3–N) before burning, immediately after burning, and for 1 year after burning in old-growth, pole, and sapling substands in a virgin ponderosa pine forest. By so doing we hoped to determine whether soil N changes immediately after burning, and whether differences might be related to differences among the substands in forest floor mass and percent of fuel consumed. If so, land managers might better predict responses to prescribed burning for substands with differing structural characteristics.

METHODS

Site description

This study was conducted at the Fort Valley Experimental Forest approximately 10 km northwest of Flagstaff, Arizona, USA, at an elevation of 2195–2255 m. The study area is gentle in topography (slopes 0–5%), with a southwest aspect. The climate is cool and subhumid with early summer drought. Mean annual precipitation is 56.7 cm and mean annual temperature is 7.5°C (Schubert, 1974). Approximately one-half of the precipitation falls as snow. The average frost-free growing season is 94 days. Soils at the study site are derived from basalt and volcanic cinders and are tentatively classified as Brolliar stony clay loam, a fine montmorillonitic, frigid Typic Argiboroll (Meurisse, 1971).

The study area was in a virgin stand of ponderosa pine, approximately 40 ha, dominated by an uneven-aged forest with trees in small, more or less even-aged groups (substands), typical of ponderosa pine in the Southwest (Cooper, 1960; Schubert, 1974; A.S. White, 1985). Figure 1 displays the spatial arrangement of these substands for an area of approximately 1 ha in the study area. Pole-sized trees, 10–28 cm diameter at breast height (dbh) and 60–100 years old, are the predominant size-class, with scattered groups of old-growth trees, 28–120 cm dbh and 200–500 years old, and dense 'doghair' thickets of sapling-sized trees, 0–10 cm dbh and 60–70 years old, comprising the balance. The site index is 82 (Minor, 1964). Except for localized fuel-wood cutting of dead trees near roads, the site had not been harvested. Dieterich (1980) determined that the last natural fire on the study area occurred in 1876; before that, fires occurred at an average interval of about 2 years.

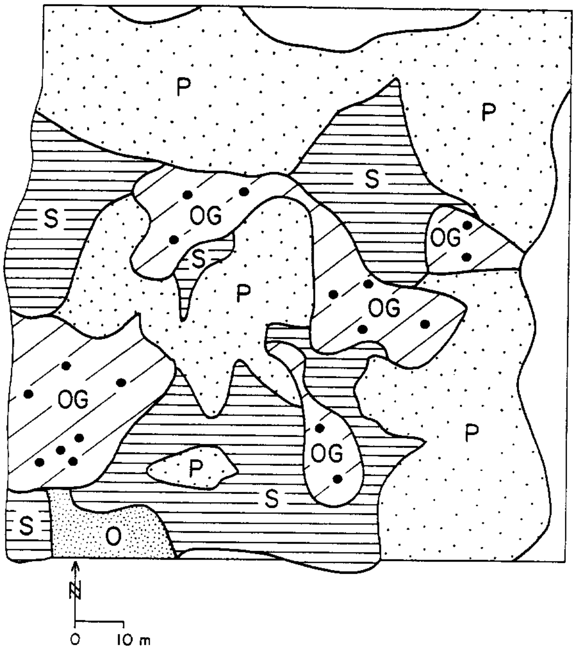

Fig. 1. Overstory map of a plot (approximately 1 ha) in the study area. Symbols are: OG, old growth; P, pole; S, sapling; O, opening. Solid circles are stems of old-growth trees.

Experimental design

Within the 40 ha study area, three replicate plots (0.3–0.7 ha) each of sapling pole, and old-growth substands were established for control and burn treatments. Treatments were randomly assigned to available plots. Plots were sampled immediately before and immediately after fall burning, in the spring after burning, and in the fall 1 year after burning. All samples were collected from beneath the canopy projection within the substands (the few small grassy openings between substands were omitted from this analysis). For each sampling date all samples were collected within a 4–5 day period with no intervening precipitation.

Fire description

The plots were burned on 18 and 19 October from 13:30 h to 18:00 h. May and June were dry months, as is typical. The first summer precipitation occurred on 8 July. By 11 October, the date of the last precipitation (0.38 cm) prior to burning, 23.6 cm of summer precipitation had fallen on the site. Burning conditions are presented in Table 1. Moisture content of woody material up to 2.54 cm diameter ranged from 7.7 to 8.7%.

TABLE 1

Range of fire characteristics, fuel moisture, and weather parameters during prescribed burning 18 and 19 October 1982

	Moisture content (%)			Rate of spread ($m\ min^{-1}$)		Ambient temperature (°C)	Relative humidity (%)	Wind speed ($km\ h^{-1}$)
	L layer	F layer	H layer	Backfire	Headfire			
Old growth	7–10	4	12–20	0.15–0.3	1.2	11–14	15–20	0–5.0
Poles	10	7–9	13–20	0.15–0.2	1.5–2.9	14–17	15–22	0–4.5
Saplings	8–10	7–10	13–18	0.2–0.4	3.1–3.6	16–19	19–24	0–3.0

Light winds were steady from the southwest with speeds from 0 to 5 km h^{-1} measured 1.4 m above the ground in the stand. Backing fires were used for the most part, but some strip headfires were also used. Backing fire rates of spread were typically consistent at 0.15–0.4 m min^{-1}. We applied strip headfires at 4.5- to 9-m intervals; thus they never reached a steady-state rate of spread. Strip headfire rates of spread ranged from 1.2 to 3.6 m min^{-1}. Flame lengths for backing fires were from 7 to 23 cm, whereas headfires had flame lengths from 50 to 250 cm.

Forest floor sampling

Two procedures were used to sample the forest floor. For pole and sapling substands the forest floor was sampled using a square (0.09 m^2) frame. All material inside the frame less than 2.54 cm in diameter was excavated to the mineral soil. Since there was some contamination of this material by mineral soil, organic matter content was determined by loss on ignition at 500°C, so that results could be presented on an ash-free, combustible weight basis. Preliminary sampling showed that forest floor variability increased from sapling to pole to old-growth substands; therefore, we varied sampling intensity with substand type with the goal of achieving a standard error of the estimate for each type within 5–10% of the mean. Thus, 86 samples each were taken in control and treated plots in the sapling type; in the pole type, 100 samples were taken in each.

Sample points were systematically spaced within a $1 \times 1\ m^2$ grid on each plot. Variation in forest floor weight in the old-growth substands was so great than an unrealistically high number of samples would have to have been taken. Therefore, for old-growth substands we used a double sampling method. First we developed regression equations relating forest floor mass (kg ha^{-1}) to forest floor depth (cm) for unburned forest floor ($r^2=0.80$, standard error of the estimate$=67.1$) and for burned forest floor ($r^2=0.90$, standard error of the estimate$=170.5$), by which we could calculate forest floor organic matter content from forest floor depth. Then we measured forest floor depth at 870 randomly located points in control plots and 191 in the burned plots (where variation was less) and used the regression equations to calculate forest floor weight for each plot. This double sampling procedure precludes calculation of standard error terms. All forest floor weight data are presented on an ash-free, combustible weight basis.

Soil sampling and analysis

Control and burn plots for each of the three substand types were sampled at 0–5 and 5–15 cm depths with a 2.5-cm diameter soil sampling tube. Because we were interested in characterizing the substand types as a whole, we composited samples in the field before extracting them (Peterson and Calvin, 1965). Using compositing optimization equations (Falck, 1973), we determined that the optimal compositing ratio would be 30 individual samples composited into two composite samples from each plot. To meet the data structure requirements for an analysis of variance repeated measures model we averaged the two samples from each plot. Since there were three replicates of each treatment per substand type, this gave a sample size of three for each treatment–substand combination.

Soils were sieved (2 mm) immediately in the field and a 10–20 g subsample for NH_4–N and NO_3–N analysis was added to a preweighed bottle containing 100 ml of 2 N KCl extractant (acidified with HCl to pH 2.5). The extractant contained 1 ppm phenyl mercuric acetate as a preservative. Because the soils at our study site are typically very dry in the fall, no pretreatment was necessary before sieving. Within 24 h a subsample of the extractant was carefully removed so as to eliminate sediment or floating organic matter from the sample to be analyzed (to reduce effects of storage on NH_4–N and NO_3–N concentrations). Field weight of the soil was determined by a second weighing of the tared bottle, and its dry weight was determined from another sample taken in the field at the same time as the extracted sample and dried in a forced-air oven at 105 °C until weight loss ceased.

Chemical analysis

Within 2 days of sampling, NH_4–N and NO_3–N in the KCl extract were determined colorimetrically using a Technicon AutoAnalyzer. Samples were stored at 1 °C until analysis. AutoAnalyzer methods were: NO_3–N, Technicon Industrial Method No. 100-70W; NH_4–N, Technicon Industrial Method No. 98-70W/A (Anonymous, 1974).

Statistical analysis

For each substand type we used analysis of variance program BMDP2V (Dixon, 1985) to test for significant ($P<0.05$) differences. Since variance increased with increasing mean (determined with program BMDP7D), we transformed the data to natural logarithms to better approximate homogeneity of variance. Because the data are not normally distributed, standard errors are asymmetric. For this reason, as well as to keep the tables as uncluttered as possible, standard errors are not reported. However, the standard errors of the transformed data were generally within 5–10% of their respective means.

First, to determine whether control and treated plots could be treated as homologous, we compared control to those to be burned. To determine the immediate effects of burning on soil N we compared treatment plot measures before burning to those immediately after burning. Finally, to determine temporal changes among dates we used a repeated measures analysis of variance design with the same plots being measured repeatedly, i.e. before burning, immediately after burning, spring after burning, and fall after burning. To determine the relationship between forest floor consumption and preburn forest floor mass as well as the relation between soil ammonium concentration and amount of forest floor consumed, we conducted regression analysis using BMDP1R (Dixon, 1985).

RESULTS

Preburn characteristics of substands

Before burning, the old-growth, pole, and sapling substands varied widely in tree size and density as well as forest floor mass. However, inorganic N concentrations in the mineral soil were fairly uniform among types.

Tree size and density

Old-growth substands had the greatest basal area (35 m^2 ha^{-1}) and the largest trees (average dbh of 63 cm), but the lowest number per hectare (120 ha^{-1}); pole substands were intermediate for these characteristics (31 m^2 ha^{-1}, average dbh of 15 cm, 1730 trees ha^{-1}. Sapling substands had the lowest basal area (15 m^2 ha^{-1}) and the smallest trees (an average of only 4.5 cm dbh), but the most per hectare (10 070 trees ha^{-1}). There were trees in each substand that did not fall within the diameter class designation for a particular plot (i.e. some saplings were present in the pole substands and some poles were present in the sapling substands).

Forest floor

Average forest floor organic matter varied drastically among substand types with the old-growth substands being the greatest, pole intermediate, and sapling the least (Table 2). Within substand variation was least in the sapling and greatest in the old-growth substands. In sapling substands, weights of material less than 2.5 cm diameter for individual plots ranged from about 24 Mg ha^{-1} to more than 28 Mg ha^{-1}. Pole substands ranged from 30 Mg ha^{-1} to more than 47 Mg ha^{-1}. In old-growth substands, the variation in forest floor weights was even more drastic where weights ranged from 72 Mg ha^{-1} to almost 128 Mg ha^{-1}.

Inorganic N

Before burning, inorganic N concentrations were generally less than 2 mg of N kg^{-1} of soil for all three substand types (Tables 3 and 4). NH_4–N and NO_3–N concentrations were similar in pole and sapling substands. Although old-growth substands appeared to be somewhat higher in both NH_4–N and NO_3–N, these differences were not significant.

Post-burn characteristics of substands

Burning had little immediate impact on tree density, although there was some localized mortality from torching of crowns in one of the pole plots where fire reached into the crown of two 0.04 ha areas. However, forest floor mass was, of course, radically altered. Both the absolute and relative forest floor losses were greatest in the old-growth, intermediate in the pole, and least in the sapling substands (Table 2). Inorganic N concentrations in the mineral soil increased substantially following burning.

TABLE 2

Forest floor characteristics and amount consumed by the fire

	Combustible weight (Mg ha^{-1})	Consumption	
		Amount (Mg ha^{-1})	Percent of total
Burn plots			
Old growth	123.4	98.5	79.8
Poles	35.9	19.2	53.5
Saplings	27.1	9.3	34.3
Control plots			
Old growth	90.8	–	–
Poles	39.9	–	–
Saplings	25.8	–	–

TABLE 3

Mean concentrations of NH_4-H and NO_3-N in ponderosa pine soils (0–5 cm depth). Means within a substand type with different superscripts differ at $P<0.05$ using Scheffe's test

Substand type	Year 1			Year 2			
	October			May		October	
	Control	Pre-burn	Burned	Control	Burned	Control	Burned
NH_4-N (mg kg^{-1})							
Old growth	1.92^a	2.33^a	45.10^b	1.83^a	32.70^b	2.56^a	30.0^b
Pole	0.74^a	1.34^a	26.72^b	1.22^a	18.63^b	1.62^a	2.66^a
Sapling	0.76^a	1.29^a	8.28^b	1.06^a	7.50^b	1.60^a	1.62^a
NO_3-N (mg kg^{-1})							
Old growth	0.033^a	0.176^a	0.109^a	0.022^a	0.567^b	0.029^a	18.6^b
Pole	0.010^a	0.003^a	0.060^b	0.016^a	0.438^b	0.008^a	0.509^b
Sapling	0.013^a	0.008^b	0.023^a	0.019^a	0.138^a	0.018^a	0.027^a

TABLE 4

Mean concentrations of NH_4-N and NO_3-N in ponderosa pine soils (5–15 cm depth). Means within a substand type with different superscripts differ at $P<0.05$ using Scheffe's test

Substand type	Year 1			Year 2			
	October			May		October	
	Control	Pre-burn	Burned	Control	Burned	Control	Burned
NH_4-N (mg kg^{-1})							
Old growth	0.78^a	1.06^a	13.82^b	0.90^a	14.48^b	1.26^a	3.59^b
Pole	0.58^a	0.86^a	3.15^b	0.83^a	4.14^b	1.17^a	1.15^a
Sapling	0.64^a	0.81^a	1.38^b	1.08^a	2.09^b	1.13^a	0.95^a
NO_3-N (mg kg^{-1})							
Old growth	0.015^a	0.027^a	0.065^a	0.011^a	0.528^b	0.008^a	6.96^b
Pole	0.002^a	0.010^b	0.029^c	0.020^a	0.091^b	0.007^a	0.074^b
Sapling	0.005^a	0.011^b	0.012^b	0.013^a	0.042^b	0.010^a	0.009^a

The diverse nature of forest floor and canopy conditions among sapling, pole, and old-growth substands caused major differences in both fire behavior and forest floor consumption. Flaming combustion consumed virtually all L layer material on all plots regardless of substand type. As fire passed over any given spot, whether glowing combustion started depended on the amount of F plus H layer material present; the greater the F plus H layer (as in old-growth substands) the more likely glowing combustion. In sapling substands an average of 9.3 Mg ha^{-1} (34.3%) of the total forest floor mass was consumed; however, small localized areas burned to mineral soil — usually around the base of trees to a distance of only 5–8 cm from the stem or where larger woody fuels were consumed. In pole substands, a similar response was noted except that the area burned around each stem was as much as 15–25 cm; an average of 19.2 Mg ha^{-1} (53.5%) was consumed in these substands. On old-growth sites, the entire forest floor was consumed out to the drip lines of the trees. An average of 98.5 Mg ha^{-1} (79.8%) was consumed in the old-growth substands.

Regression analysis to determine the relation between preburn forest floor weight, humus weight, and fuel consumption showed the relation of percentage forest floor consumed to initial forest floor weight ($r^2=0.89$) and to humus layer weight ($r^2=0.78$) were both highly significant ($P<0.01$). However, like the relation of forest floor depth to forest floor weight (Sackett, 1979), the actual predictive power of the consumption relationship is probably site specific.

Burning caused immediate changes for NH_4–N concentrations, but had no major immediate impact on NO_3–N. The greatest post-burn NH_4–N concentrations were in the 0–5 cm depth of the old-growth substands (45.1 mg kg^{-1}), intermediate in the pole (26.7 mg kg^{-1}), and least in the sapling (8.3 mg kg^{-1}) (Table 3). This same pattern was apparent in the 5–15 cm depth, although the increases in NH_4–N concentrations were not so striking (Table 4). Although there were a few immediate post-burn differences in nitrate concentrations (Tables 3 and 4), concentrations were still quite low, less than 0.1 mg kg^{-1}.

Fuel loads and proportion of forest floor burned were highest in the old-growth, intermediate in the pole, and least in the sapling substands (Table 2), and NH_4–N concentrations followed a similar pattern (Tables 3 and 4), supporting our hypothesis that differences in post-burn NH_4–N concentrations were due to differences in fuel consumption. We tested this relationship with regression analysis, relating post-burn soil NH_4–N concentration (mg kg^{-1}) to fuel consumption (Mg ha^{-1}) for each plot. The result was a highly significant ($P<0.01$) regression with an r^2 of 0.82.

In May after burning, NH_4–N concentrations remained at approximately the same level that they had been immediately after burning (Tables 3 and 4). However, NO_3–N concentrations had changed markedly (Tables 3 and 4) particularly in the 0–5 cm depth. The greatest NO_3–N concentrations in May were in the old-growth substands. Again, pole substands were intermediate and sapling substands least in their response. However, NO_3–N concentrations were still quite low, the highest being 0.57 mg kg^{-1} in the burned old-growth substands.

One year after burning, NH_4–N concentrations had declined somewhat, although they were still higher than controls for the old-growth type (Tables 3 and 4). Nitrate–N concentrations were higher than controls in both old-growth

TABLE 5

Budgetary changes in inorganic (NH_4-N+NO_3-N) nitrogen in ponderosa pine soils (0–15 cm depth)

Substand type	Year 1		Year 2			
	October		May		October	
	Control	Burned	Control	Burned	Control	Burned
NH_4-N (kg ha^{-1})						
Old growth	1.7	35.9	1.9	31.4	2.6	19.6
Pole	1.0	15.6	1.5	13.1	2.1	2.5
Sapling	1.0	5.0	1.7	5.8	0.8	2.1
NO_3-N (kg ha^{-1})						
Old growth	0.02	0.12	0.02	0.86	0.02	16.2
Pole	0.01	0.06	0.03	0.30	0.01	0.3
Sapling	0.01	0.01	0.02	0.11	0.02	0.3
Total NH_4-N+NO_3-N (kg ha^{-1})						
Old growth	1.7	36.0	1.9	32.3	2.6	35.8
Pole	1.0	15.7	1.5	13.4	2.1	2.8
Sapling	1.0	5.0	1.7	5.9	0.8	2.4

and pole, with the greatest difference being in the old-growth, where concentrations were 18.6 mg kg^{-1} in the 0–5 cm depth, the largest NO_3–N concentration we observed.

To estimate budgetary changes in NH_4–N and NO_3–N, we multiplied the concentrations in Table 3 by 0.45×10^6 kg ha^{-1} and those in Table 4 by 1.13×10^6 kg ha^{-1}, the weight of the less than 2 mm component of the 0–5 and 5–15 cm depths of the mineral soil, calculated from the previously cited soil report for the area by Meurisse (1971). Then we summed the 0–5 and 5–15 cm depths. The results (Table 5), show substantial increases in inorganic N, most of which was NH_4–N, immediately after burning. The greatest increase (34.2 kg ha^{-1}) occurred in old-growth substands. There was no meaningful change in inorganic N between October (immediately after burning) and May. However, by the next October (1 year after burning), there had been a striking decrease in NH_4–N for all three substand types. In old-growth substands NH_4–N declined by 11.8 kg ha^{-1}, while pole and sapling substands showed decreases of 10.6 and 3.7 kg ha^{-1}, respectively. For old-growth substands this decrease of 11.8 kg ha^{-1} of NH_4–N was offset by an increase of 16.2 kg ha^{-1} of NO_3–N. No such counterbalancing was observed for pole and sapling substands.

DISCUSSION

Characteristics of our study area are within the range reported for uncut ponderosa pine stands in the Southwest in tree density and size as well as site index (Schubert, 1974). Our data are also within the ranges for southwestern ponderosa pine ecosystems reported in the literature for forest floor mass (Ffolliott et al., 1968; Welch and Klemmedson, 1975; Klemmedson, 1976; Sackett, 1979) and inorganic N concentrations for our control plots (Wollum, 1970; C.S. White, 1985; Covington and Sackett, 1986; Ryan and Covington, 1986).

Our results are: (1) that old-growth, pole, and sapling substands vary widely in fire effects on the forest floor and inorganic N; (2) that NH_4–N increases are proportional to the amount of forest floor burned; (3) that NO_3–N increases lag behind NH_4–N increases.

Nitrogen concentrations

Before burning, there were major differences in tree size and density as well as forest floor mass (Table 2) among old-growth, pole, and sapling substands, creating a strong spatial heterogeneity (Fig. 1). However, there were no substantial differences in inorganic N concentrations (Tables 3 and 4).

Although burning did cause some obvious tree mortality in one of the pole substands and one of the sapling substands, its most striking immediate impact was in reducing forest floor mass and increasing soil NH_4–N.

Burning immediately established a gradient of very high NH_4–N in old-growth, intermediate in pole, and lowest in sapling substands (Tables 3 and 4), in proportion to the amount of forest floor consumed. We are unaware of any literature demonstrating this relationship between NH_4–N response and forest floor consumption.

Although NO_3–N concentration was not immediately changed by burning (Tables 3 and 4), NO_3–N had begun to increase slightly by the first spring after burning, with the greatest increases being in the old-growth and the least in the sapling substands. Nonetheless, concentrations were still quite low (less than 1 mg kg^{-1}) in the spring following burning. Ammonium-N was unchanged from immediate post-burn concentrations.

Between the spring and fall sampling dates there was a decline in NH_4–N concentrations in old-growth substands with an offsetting increase in NO_3–N (Tables 3 and 4), to as much as 18.6 mg kg^{-1} in the old-growth substand. A concentration of 18.6 mg kg^{-1} for NO_3–N is among the highest reported in the literature for unfertilized stands, but is consistent with the high NH_4–N of the burned old-growth substands.

These immediate increases in NH_4–N are due to abiotic factors, most likely the transfer of NH_4–N from the forest floor into the mineral soil. That ammonium can be produced during a fire through pyrolysis of organic nitrogen compounds has been shown by others (Christensen, 1973; DeBano et al., 1979a; Dunn et al., 1979; Mroz et al., 1980). However, these increases have generally been no more than two to three-fold over preburn levels. Our results indicate increases of as much as 20-fold immediately after burning. Because the magnitude of our observed ammonium increase was positively correlated with preburn fuel load and amount of fuel consumption, and since our forest floor mass was much higher than that reported by the aforementioned authors, we infer that our ammonium response was higher than previously observed because our fuel loads and amounts consumed were higher. The positive correlation of ammonium with fuel consumption further supports the inference that the source of the increase is forest floor organic N that has been pyrolyzed.

In the spring and fall following burning, soil ammonium declined for all substands. This suggests some combination of leaching loss, conversion to NO_3–N, immobilization by plant uptake or microbial activities, or denitrification. For the old-growth substands, the increase in nitrate between the spring and fall sample dates almost exactly offsets the decrease in NH_4–N (Table 5). Thus nitrification of NH_4–N to NO_3–N is the probable cause of the decline in NH_4–N in the old-growth substands.

However, this is not the case for either the pole or the sapling substands, where NH_4–N decreases but NO_3–N remains quite low. Which other mechanism might be involved is in question. However, higher N concentrations in understory vegetation (Harris and Covington, 1983), as well as in pine needles and needle fall (Covington and Sackett, 1990), 1 year after a nearby prescribed burn in ponderosa pine suggest that at least some of this decline could be explained by increased uptake by the vegetation.

In addition to our results for old-growth substands there is other evidence in the literature for increased nitrification following prescribed burning in ponderosa pine. Using a laboratory incubation method, C.S. White (1985) found substantial increases in nitrification 6 months after prescribed burning in ponderosa pine in New Mexico. Higher nitrification in situ might be caused by warmer soil temperatures and higher soil moisture conditions after burning (Milne, 1979; Ryan and Covington, 1986), as well as fire-caused decreases in allelopathy. The feasibility of the last mechanism is suggested by the results of Lodhi and Killingbeck (1980), who found nitrification inhibiting allelopathy in both the forest floor and the mineral soil of ponderosa pine stands. C.S. White's (1985) laboratory results provide evidence for the role of fire in denaturing these allelopathic agents.

Nitrogen budgeting

Budgetary analysis suggests an immediate increase in inorganic N of 34.2 kg ha^{-1} in old-growth substands, 14.6 kg ha^{-1} in pole substands, and 4.0 kg ha^{-1} in sapling substands (Table 5). This 34.2 kg ha^{-1} increase in the old-growth substands is the greatest increase in inorganic N from prescribed burning reported for any forest type. In fact, the only report for immediate increases of this magnitude for prescribed burning in any vegetation type is the increase of 24 kg ha^{-1} observed by DeBano et al. (1979a) in chaparral soils.

Our estimates of increases in the inorganic N content of the mineral soil allow for a more complete analysis of N volatization losses from burning. Klemmedson et al. (1962) found a N loss of 139.7 kg ha^{-1} from the forest floor after prescribed burning in a California ponderosa pine forest. They concluded that this N was lost from the ecosystem through volatization to the atmosphere. Similarly Klemmedson (1976), working at two sites within 10 km of ours, estimated a loss of 58–91 kg ha^{-1} of N from slash and forest floor burning. He inferred that the unaccounted for N was lost to volatization.

Our results suggest that these may be overestimates. We observed that as much as 34 kg ha^{-1} of the apparent N loss may be transferred immediately from the forest floor to the mineral soil as NH_4–N.

Implications for productivity

The increases of inorganic N after burning probably contribute to the increased seedling establishment of both herbaceous vegetation (Vose and White, 1987) and ponderosa pine (Sackett, 1984), as well as higher herbaceous production and greater foliar N concentrations (Harris and Covington, 1983; Oswald and Covington, 1984; Andariese and Covington, 1986; Covington and Sackett, 1990) and increased pine seedling growth (Ower, 1985) on prescribed burned ponderosa pine sites. This mechanism is supported in part by results from Harris and Covington (1983) who found the greatest increases in foliar N in their old-growth substands with less in pole and sapling, consistent with our observed pattern for inorganic N in the soil. A feedback mechanism for recovery after burning is suggested by our results. The most intense fires and the greatest understory (Vose and White, 1987) and overstory mortality typically occur in the old-growth patches where fuels are the heaviest (W.W. Covington, personal observation, 1990). However, it is in these patches that inorganic N is the highest after burning. This nutrient enrichment, much like a natural fertilization, should enhance re-vegetation and recovery of the severely burned sites. In fact, re-vegetation of severely burned old-growth substands is rapid (Vose and White, 1987); furthermore, growth rates of individual plants can be exceptional. For example, Sackett (1984) reported 6-year-old ponderosa pine seedling heights of up to 60 cm on nearby prescribed burned plots in contrast with a normal height of 15–20 cm for 6-year-old ponderosa pine seedlings on similar unburned sites.

Implications for fire management

The foregoing discussion establishes that the effects of burning on forest floor mass, soil N, and understory production vary widely among the three substand types. Thus, burning prescriptions for ponderosa pine which fail to account for this spatial variability in both pretreatment conditions and post-treatment response ignore a fundamental ecological characteristic of this type and are, therefore, likely to produce unforeseen consequences. It seems to us that this might be especially important in decisions regarding reintroducing natural fires, managing wilderness, or maintaining old growth.

For stands which, because of harvesting or wildfire, do not have this spatial heterogeneity, the land manager can now better predict the consequences of prescribed burning on soil N; however, caution should be exercised in extending the results we observed especially for the old-growth and sapling substands (which were of small area) to larger areas (e.g. hundreds of hectares).

ACKNOWLEDGMENTS

T.G. Huntsberger of the Bilby Research Center at Northern Arizona University conducted the chemical analyses. S.W. Andariese of the School of Forestry assisted in the statistical analysis. This research was supported by the US Dep. Agric. Forest Service through the Rocky Mountain Forest and Range Experiment Station and the State of Arizona through Northern Arizona University.

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