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Clear cutting and burning affect nitrogen supply, phosphorus fractions and seedling growth in soils from a Wyoming lodgepole pine forest

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Abstract

Timber harvesting, with and without prescribed slash fire, and wild fire are common disturbances in pine forests of western North America. These disturbances can alter soil nitrogen (N) pools and N supply to colonizing vegetation, but their influence remains poorly understood for many forests. We investigated the effects of clear cut harvesting and fire on KCl extractable N pools, net N mineralization rates, phosphorus (P) fractions, seedling N uptake, and seedling growth in mineral soils sampled from a lodgepole pine forest in southern Wyoming. At a site where wild fire burned through a harvested stand of lodgepole pine and the adjacent intact forest, we analyzed mineral soils from the following four treatments: unburned clear cut, burnt clear cut, unburned forest, and burnt forest. Soils from unburned and burnt clear cut treatments had higher concentrations of KCl extractable N and higher net N mineralization rates, and produced larger pine seedlings in bioassays than soils from unburned and burnt intact forest treatments. Further, while seedlings grown in soils from the unburned and burnt forest treatments responded strongly to N fertilization, seedlings grown in clear-cut soils did not respond to fertilization. Taken together, these results suggest that harvesting had increased soil N supply. In comparing clear cut treatments, soils from the unburned clear cut had smaller extractable N and P pools, and lower net N mineralization rates, but produced larger pine seedlings than soils from the burnt clear cut.

Keywords: Fire; Nutrients; Seedling growth; Lodgepole pine; Soil nitrogen; Soil phosphorus

1. Introduction

Nitrogen (N) availability commonly limits productivity of lodgepole pine (*Pinus contorta* ssp. *latifolia* [Engelm. ex Wats.] Critchfield) in western North America (Yang, 1985; Weetman et al., 1988, 1992; Preston and Mead, 1994). It has been observed that lodgepole pine growth in southern Wyoming increases after N fertilization (Binkley et al., 1995). Fahey et al. (1985) suggested that N is limiting to the growth of these trees because rates of N-fixation and N deposition are very low compared with other forest types.

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Further, stand-replacing wild fires can cause large losses of N from these forests by releasing to the atmosphere N contained in living plants, detritus, and surface soils (Fahey et al., 1985). Harvesting practices may also affect the N capital and long-term productivity of managed forests (Waring and Schlesinger, 1985; Binkley, 1986). Few studies, however, have investigated the impacts of wild fire, clear cut harvesting, and residue management on soil N availability and seedling growth (DeByle, 1980; Lopushinsky et al., 1992).

In Fox Park, Wyoming, we encountered a natural experiment that allowed comparison of harvesting and burning treatments within a topographically and edaphically homogenous site. A wildfire burned through half of a 10 ha clear-cut and extended into the adjacent stand of lodgepole pine. The objective of our study was to compare N supply and seedling growth in soils sampled from a burnt and unburned clear cut harvest and burnt and unburned standing lodgepole pine forest. To investigate the individual and combined effects of clear-cut harvest and fire on soil N availability, we used a combination of laboratory soil incubations and a greenhouse seedling bioassay. Because soil P is also influenced by slash burning (Giardina et al., 2000; Romanya et al., 1994) and P can limit plant productivity in western forests (Binkley, 1986), we examined the influence of harvesting and fire on various soil P fractions.

2. Methods

2.1. Site description

Mineral soils for laboratory analyses and a greenhouse bioassay were collected from a 15 ha site near Fox Park in the Medicine Bow National Forest of Wyoming (41°04′N, 106°10′W). Soils are classified as loamy Typic Cryoboralfs. Our research site is dominated by lodgepole pine and is characterized by long, cold winters and cool, dry summers. Fox Park annually receives ~600 mm of precipitation with ~70% coming as snow. From 1948 to 1979, maximum air temperatures for June, July, and August averaged 18.5, 22.4, 21.1°C, respectively, while minimum temperatures averaged 0.6, 2.9 and 2.1°C. Elevation for the study site is 2800 m. Slopes of less than 3% characterize the entire site and surrounding area. Forest understory in the area of the study consists almost entirely of *Vaccinium* spp.

In 1992, we sampled soils and forest floor material from a 15 ha area that had been part of large, uniform stand of ~100 years old lodgepole pine. In 1987, a 10 ha unit within this larger stand had been clear-cut harvested. Logging slash was left in place and untreated following harvesting. In the fall of 1991, a wild fire burned through the southern half of the 10 ha clear-cut and 3 ha of adjacent uncut forest. The resulting natural experiment allowed for comparisons of burnt and unburned clear cut, and burnt and unburned forest. Skid trails prevented the wild fire from spreading across the entire clear cut. The relatively low quantities of fuel and cool October temperatures prevented the fire from spreading further into the adjacent forest. The terrain was virtually flat throughout the study area and the four treatments differed only with regard to burn or harvest treatment. While we are aware of the potential confounds from pre-treatment soil variation, we believe that the close proximity of the treatments (<150 m from plot center to plot center) and their high degree of topographic and original stand uniformity warranted investigating this unique natural experiment.

The two burn treatments closely resemble broadcast burn and wild fire disturbances encountered in lodgepole pine forests of the central Rocky Mountain region, USA. The burn consumed >95% of the residual logging slash in the clear cut (Fig. 1) and most of the downed woody debris in the adjacent forest, as well as 85 to 89% of the forest floor (Table 1). In the forest, the fire remained on the ground, with trees variably charred to 2 m above the ground; tree mortality was near 100%, but declined towards the perimeter of the fire. Ten by 50 m measurement plots were established in the center of the four treatments from which information was collected on stem number, basal area, stand age (largest five trees), and mean and maximum diameter at 25 cm. Decaying boles from the previous forest generation were the only forest floor materials left on the burnt clear cut, and were mapped for a 15 m×20 m area in the center of this treatment. In the unburned forest, the forest floor (the O horizon or LFH layer) overlying mineral soil was composed of a 4 to 6 cm deep mat of fresh litter, organic material in various stages of decomposition,

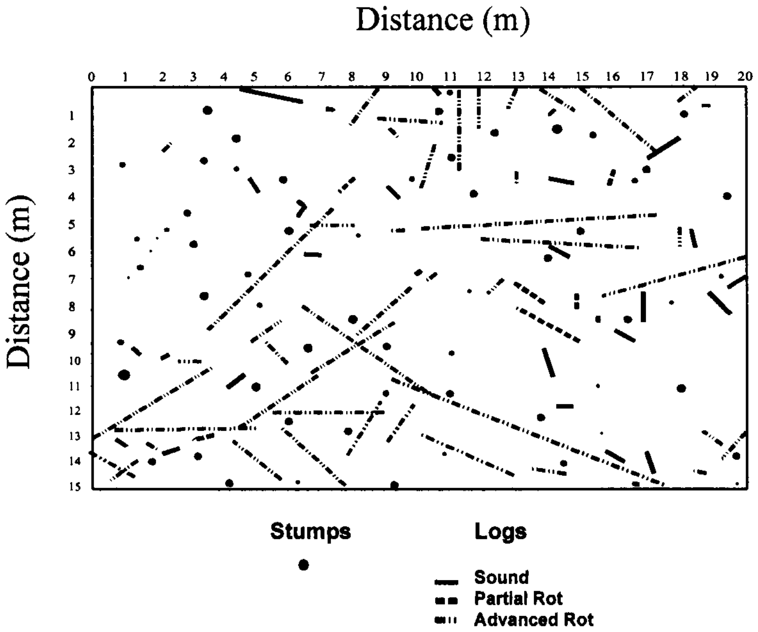

Fig. 1. Distribution of downed lodgepole pine boles in the clear cut treatment.

roots, and fungal hyphae. Fresh litter consisted of needles, fine branch material, and scattered coarse material. The unburned clear cut was also covered with logging debris.

2.2. *Vegetation and soil sampling and analysis*

Samples of forest floor material and 0–10 cm depth mineral soil were collected in September of 1992 along 150 m transects that crossed through the center of each of the four treatments. Forest floor, when present, was collected within a 0.1 m^2 quadrat to mineral soil, at 5 m intervals along each of the transects (n=30). Three samples of mineral soil were collected every 15 m along each transect and composited for a total of 10 composite samples per transect; prior to sampling mineral soil, overlying forest floor material was removed. Soil and forest floor samples were maintained in coolers or under refrigeration at 4°C until analyses were conducted 14 days later. Moisture content of soil was determined by drying samples for 24 h at 105°C; forest floor samples were dried at 65°C until no change was observed. Moisture content is presented on a dry weight basis.

Table 1
Properties of the stand and soil for each of the four treatments[a]

Treatment	Basal area (m^2 ha^{-1})	Stem density (trees ha^{-1})	Diameter at 25 cm (cm)		Age of dominants (year)		Soil bulk density (Mg m^{-3})	Forest floor mass (Mg ha^{-1})
			Mean	Max	Mean	Max		
Unburned forest	55.4	3240	14.3	27.1	109	111	1.1	25
Unburned clear-cut	51.6	2300	16.5	26.0	102	105	1.0	35
Burnt forest	62.6	3300	15.1	26.5	104	110	0.9	3
Burnt clear-cut	50.2	2420	15.9	26.0	101	108	1.1	4

[a] Mean basal area and mean stem density are for centrally located 10 m×50 m areas. Mean soil bulk density and forest floor mass were sampled along 150 m transects. (n=5 for age of dominant stems, n=3 for bulk density, and n=10 for forest floor).

Bulk density was determined on intact soil cores (Blake and Hartge, 1986); three cores per treatment were taken 25 m apart along each transect.

Soil pH was measured in deionized water and in a 0.01M calcium chloride solution (1:1 air-dried soil to solution), after shaking solutions for 1 h on a reciprocating shaker. Aerobic incubations of mineral soil were used to measure net N mineralization and nitrification rates (Hart et al., 1994). The incubations were carried out on fresh mineral soil after handpicking coarse material and roots. 10 g fresh weight of each soil were incubated in plastic containers with loose fitting caps at 20°C for 30 days. Throughout the incubation, soil moisture was maintained at field capacity by periodic adjustments with deionized water. Field capacity was predetermined as the moisture content remaining in soils that were wetted and drained freely for 24 h. Soil NO_3^- and NH_4^+ were extracted with 2M potassium chloride (KCl) from a set of sub-samples prior to the incubation and on incubated sub-samples. NO_3^- and NH_4^+ in the extracts were analyzed on a Lachat Instruments injection flow auto analyzer (Lachat Instruments, Inc., Milwaukee, WI) according to Lachat Instruments *QuikChem* Methods 107-06-2-A (1990) and 107-04-1-B (1992). Net N transformations were calculated as follows (Hart et al., 1994): net mineralization$=(NH_4\text{-}N+NO_3\text{-}N)t_{30d}-(NH_4\text{-}N+NO_3\text{-}N)t_0$ and net nitrification$=(NO_3\text{-}N)t_{30d}-(NO_3\text{-}N)t_0$.

Sub-samples of the 10 soils from each of the treatments were analyzed for P using a modified fractionation method (Hedley et al., 1982). Phosphorus was sequentially extracted from 1 g of air dried soil as follows: (a) soil solution inorganic P (Pi) was extracted with an Ionics brand anion exchange resin (Type 103-QZL-386, Ionics, Inc. Boston, MA); (b) readily solubilized Pi and easily mineralized organic P (nucleic acids, lipids, some organic matter) were extracted with a 0.5M sodium bicarbonate solution adjusted to a pH of 8.5; (c) moderately to non-plant-available Pi and Po (P bound to iron and aluminum surfaces, stabilized as soil organic matter, or immobilized within microbes) were extracted with a 0.2M sodium hydroxide (NaOH) solution; (d) mineral bound P (calcium mineral or occluded sesquioxide Pi) was extracted by 1M hydrochloric acid (HCl) solution. Total (organic+inorganic) P in the bicarbonate and NaOH extracts were determined after acidified ammonium persulfate digestion at 120°C in an autoclave. Because the HCl fraction rarely contains measurable quantities of Po, it was not digested (Hedley et al., 1982; Giardina et al., 2000). All extracts were neutralized, diluted, and analyzed according to Lachat Instruments *QuikChem* Method 10-115-01-1-B (1992).

2.3. *Bioassay experiment*

For the bioassay experiment, additional 0–10 cm depth mineral soils were sampled every 30 m along each of the four transects. For each of the four treatments, the five soil samples were bulked into a single sample, twice sieved to 6 mm to remove roots and rocks, and thoroughly mixed with perlite (1:1). Approximately 125 g of the soil–perlite mixture was placed into plastic pots that were perforated on the bottom to allow water, but not soil, to drain freely. Twenty pots were prepared per soil type (unburned clear cut, burnt clear cut, burnt forest, and unburned forest). In each pot, two lodgepole pine seeds were placed in each of three 1 cm deep depressions, covered with soil, and placed in a greenhouse that was maintained at ~22°C. All pots contained germinating seeds after the first month. After 60 days, the seedlings were thinned to one per pot. The bioassay pots were watered with 40 ml deionized water, twice a week for the 8-month length of the bioassay. Ten of the 20 pots per treatment were watered monthly with 40 ml of a dilute nutrient solution so that by the end of the bioassay each fertilized pot had received 150 mg N, 125 mg K, 0.86 mg sulfur, 0.65 mg magnesium and 5.25 mg standard trace element mix. After 8 months, the seedlings were harvested, separated into stem and roots, and roots washed to remove any soil. The 160 root and stem samples were oven-dried at 65°C for 24 h and individually weighed. After weighing, each root and stem pair were ground together in a Wiley mill and analyzed for N content by dry combustion on a LECO 1000 CNH analyzer (LECO Corp., St, Joseph, MI).

2.4. *Statistical analysis*

Two-way ANOVA was used to test for harvest and burning effects on soil properties and bioassay results; 0.1 significance level was used to protect against type I errors. Where interactions were significant, *t*-tests were used to determine whether treatment differences existed, and 0.025 significance level was used to further protect against type I errors. As necessary, values were log transformed to meet the assumption of homogeneity of variance.

3. Results

3.1. Stand characteristics

Prior to harvesting and burning, the stand occupying the 15 ha research site was uniform with respect to age of the dominant trees and maximum diameter at 25 cm height (Table 1). Lower stem density and basal area, and slightly higher mean diameter at 25 cm height for the clear-cut portion of the site was due to the disappearance of smaller stems during harvesting and burning. The slightly older dominants and higher basal area in the burnt and unburned forest reflect the years between the 1987 harvest, the 1991 fire, and sampling for tree age in 1998. Timing of the sampling is also reflected in the slightly larger maximum diameter of the dominant tree in the forest treatments.

3.2. Soil analyses

Soil moisture was up to 2.5 times higher in the unburned clear cut than in the other treatments (Table 2). In the ANOVA model for soil moisture, the harvest×burn interaction term was significant, indicating that burning modified the influence of harvesting on moisture (Table 3). The unburned clear cut soils contained more water than unburned forest soil (*t*-test; $p<0.01$), while the burnt clear cut soils contained significantly less water than the unburned clear cut (*t*-test; $p<0.01$; Table 1). The burnt forest soils contained more water than unburned forest soil (*t*-test; $p<0.01$). Soil pH did not differ significantly among the four treatments (Table 2).

Total KCl extractable soil NO_3^- and NH_4^+ ranged from 0.6 μg N g^{-1} soil in the unburned forest to 15.1 μg N g^{-1} soil in the burnt clear cut (Table 2). NH_4^+ represented 88 to 96% of the plant available soil N pool. Harvesting and burning significantly influenced soil NH_4^+ and net N mineralization rates. Harvest×burn interaction terms were significant for these measures, as well as for net nitrification rates, indicating that the effects of burning on soil N supply differed between clear cut and forest. Concentrations of extractable NH_4^+ were significantly higher in soils from the unburned and burnt clear cuts than soils from the unburned and burnt forest (*t*-test; $p<0.01$ for both; Table 2). Net N mineralization rates were also higher in soil from unburned and burnt clear cuts than soils from the unburned and burnt forest (*t*-test; $p=0.02$ and $p<0.01$, respectively). During the 30-day incubation, unburned and burnt clear cut soils mineralized four to six times more N than respective forest soils (2.6 and 6.0 versus 0.7 and 1.0 kg N ha^{-1} per 30 days, respec-

Table 2
Properties for 0–10 cm depth mineral soil[a]

Treatment	Initial extractable (μg N g $soil^{-1}$)		Net N transformations			Soil pH		Moisture (%)
	NH_4^+	NO_3^-	Nitrification (μg N g^{-1} soil per 30 days)	Mineralization (μg N g^{-1} soil per 30 days)	Mineralization (kg N ha^{-1} per 30 days)	Water	($CaCl_2$)	
Unburned forest	0.59	0.04	0.04	0.69	0.74	5.00	4.59	7.7
	(0.10)	(0.01)	(0.02)	(0.10)	(0.11)	(0.07)	(0.08)	(0.4)
Unburned clear-cut	4.40	0.45	0.23	2.54	2.59	5.14	4.55	20.0
	(1.3)	(0.20)	(0.10)	(0.30)	(0.31)	(0.05)	(0.06)	(1.7)
Burnt forest	1.50	0.07	0.19	1.05	0.97	5.43	5.10	12.1
	(0.40)	(0.02)	(0.03)	(0.20)	(0.18)	(0.09)	(0.11)	(1.5)
Burnt clear-cut	13.32	1.79	1.14	5.63	6.02	5.17	4.82	11.6
	(1.8)	(1.1)	(0.70)	(0.90)	(0.96)	(0.04)	(0.07)	(1.2)

[a] Mean with standard error in parentheses; $n=10$ for all comparisons.

tively). Soils from the burnt clear cut had significantly higher concentrations of NH_4^+ and higher net N mineralization rates than soils from the unburned clear cut (*t*-test; $p<0.01$; Tables 2 and 3); differences in extractable soil NO_3^- and net nitrification rates were not significant. The effects of burning on bicarbonate extractable and NaOH extractable P were significant ($p<0.01$; $p=0.02$, respectively; Table 4). Neither harvesting, nor the burn×harvest interaction terms were significant for these soil P fractions. Neither burning nor harvesting significantly influenced anion exchange resin P or HCl extractable P.

Table 3
Summary ANOVA results for logged soil moisture, extractable N, and net N transformation data

Variable	Source	df	*F*	*P*
Extractable NH_4	Harvest	1	56.91	0.001
	Burn	1	21.46	0.001
	Harvest×Burn	1	13.48	0.001
Extractable NO_3	Harvest	1	3.32	0.077
	Burn	1	1.28	0.266
	Harvest×Burn	1	1.19	0.283
Net N mineralization	Harvest	1	50.83	0.001
	Burn	1	13.94	0.001
	Harvest×Burn	1	8.50	0.006
Net N nitrification	Harvest	1	2.61	0.115
	Burn	1	1.09	0.303
	Harvest×Burn	1	2.19	0.147
Soil moisture	Harvest	1	21.86	0.001
	Burn	1	2.06	0.160
	Harvest×Burn	1	25.10	0.001

Table 4
Phosphorus fractions for 0–10 cm depth mineral soil[a]

Treatment	Soil phosphorus fractions (μg P g soil^{-1})			
	Resin	Bicarbonate	NaOH	HCl
Unburned forest	9.4	38.3	111.4	50.9
	(0.91)	(3.8)	(13.2)	(4.0)
Unburned clear-cut	9.5	42.4	121.3	57.1
	(1.2)	(2.9)	(12.6)	(5.3)
Burnt forest	9.1	52.3	143.5	67.8
	(0.79)	(5.5)	(13.2)	(8.3)
Burnt clear-cut	10.0	55.7	146.4	56.1
	(1.3)	(5.2)	(6.2)	(4.4)

[a] Mean with standard error in parentheses; $n=10$ for all comparisons.

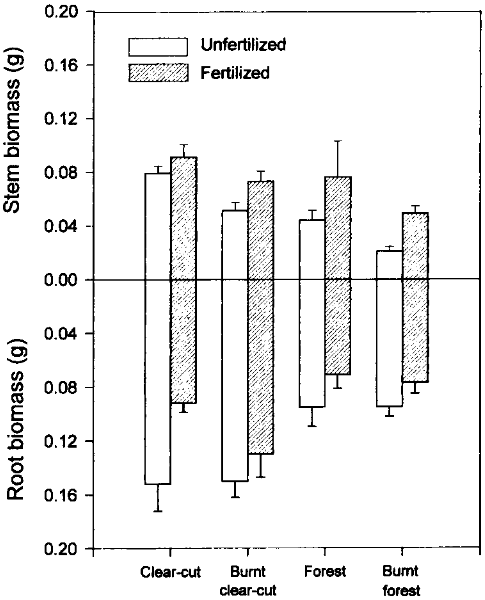

Fig. 2. Mean seedling stem and root biomass with standard errors following harvest at the end of the month bioassay ($n=10$). In all cases fertilization significantly influence shoot to root ratios, shifting C allocation aboveground to stems and away from roots.

3.3. Seedling bioassay

We expect that disturbance of the soil during sampling and establishment of the bioassay experiment altered nutrient availability. However, because all soils were processed identically, we have no reason to suspect that these effects were biased or that relative differences among treatments were artificial. At the end of the 8-month bioassay, soils from the unburned clear cut supported the largest seedlings (Figs. 2 and 3). The effects of harvesting, burning and fertilization on stem biomass were all significant ($p<0.01$); no interaction terms were significant. For root biomass, the effect of harvesting was significant ($p<0.01$). Fertilization significantly decreased root biomass; however, the harvest×fertilization interaction term was also significant ($p=0.07$). For total seedling biomass, only the effect of harvesting was significant ($p<0.01$). Despite greater soil N availability in burnt treatments (Table 2), seedlings grown in soils from the burnt treatments were not significantly larger than those grown in soils from respective unburned treatments. In fact, seedling stems were significantly smal-

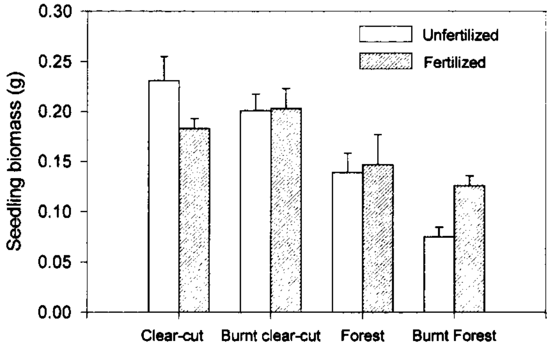

Fig. 3. Mean total seedling biomass (stems plus roots) with standard errors following harvest at the end of the 8-month bioassay (n=10).

ler in the burnt treatments (Fig. 2). Seedlings from unburned treatments had significantly higher shoot to root ratios than respective Burnt treatments (p<0.01). Fertilization also significantly increased shoot to root ratios (p<0.01). Harvesting, and the burn×fertilization and harvest×burn×fertilization interaction terms were not significant. The effects of harvesting and burning on total N uptake were significant (p<0.01 and p=0.03, respectively; Fig. 4); their interaction and the effects of fertilization were not significant. The harvest×fertilization interaction term was significant (p<0.01) for both total N uptake and seedling biomass; fertilization apparently had contrasting influences on N uptake and seedling growth, depending on whether soils were from the clear cut or forest treatments.

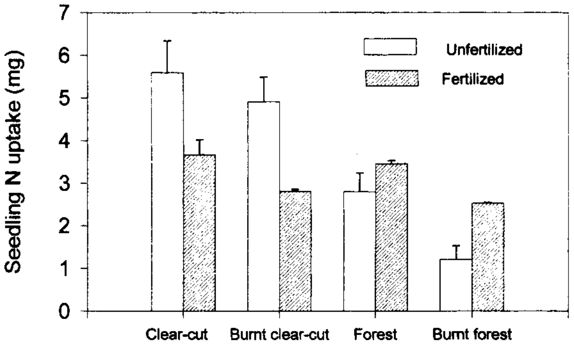

Fig. 4. Mean nitrogen uptake per seedling with standard errors following harvest at the end of the 8-month bioassay (n=10).

4. Discussion

Harvesting in lodgepole pine forests in southern Wyoming increased long-term soil N availability, and also improved growth and reduced fertilization response of bioassay seedlings. This pattern is consistent with previous studies showing that increased temperature, moisture, and disturbance to soil resulting from harvesting can stimulate microbial activity and nutrient mineralization rates in soil (Vitousek and Matson, 1985). At sites where harvest practices do not include burning of residual slash, decomposition of added nutrient-rich fine material, and the export of nutrient-poor boles may also increase soil N supply compared with whole-tree harvest or undisturbed forest (Vitousek and Matson, 1985).

The influence of burning on soil N cycling can also be large, and depends on the extent to which soils are heated, on chemical changes in soil following incorporation of ash, and the interaction of these two influences (Khanna et al., 1994). Fuel loading and spatial distribution of fuel, fuel moisture content, physical and biological properties of the soil, and the meteorological conditions preceding and following a burn are the primary factors influencing soil heating and ash production (Dunn et al., 1979; Raison, 1979; Raison et al., 1985; Binkley et al., 1992; Giardina et al., 2000). These factors will vary within a site (Romanya et al., 1994) and across sites (Walker et al., 1986). One year after fire passed through our site, extractable NH_4^+ and net N mineralization rates were 3- and 2-fold higher in soils from the burnt clear cut and burnt forest than in soils from respective unburned treatments. Previous studies have documented a mixture of responses to burning. In pine forest of North Carolina, USA, Vitousek and Matson (1985) reported that net N mineralization rates were similar between intensive windrow burning and less intensive roller chopping of logging slash, and Binkley et al. (1992) measured little change in soil N availability after 30 years of annual prescribed burns. In conifer forest of Central Oregon, USA, Pilz and Perry (1984) observed slightly higher mineralizable N in unburned clear cut that in burned clear cut soils. In pine forest of Arizona, USA, Kaye and Hart (1998) reported that prescribed burning decreased net N mineralization and nitrification rates in mineral soil, but increased gross N mineralization rates. Some variability across studies could relate to the different methodologies used to estimate N availability or to different sampling depths.

Nitrogen limits the growth of lodgepole pine in southern Wyoming (Binkley et al., 1995). However, patterns of seedling growth and N uptake only partly corresponded to patterns of net N mineralization. Harvesting increased seedling growth, as would be predicted from our lab-based index of N supply, while burning had the opposite effect on seedling growth, in contrast to our lab-based estimates. There are several potential explanations for this discrepancy. Net N mineralization is the balance of gross rates of N mineralization and immobilization by soil microbes (Hart et al., 1994). Higher immobilization at equal gross mineralization rates, lower gross mineralization at equal immobilization rates, or a combination of these could generate our results. For example, if seedlings grown in soil from unburned treatments competed more effectively with microbes for mineral N than seedlings grown in soils from burnt treatments, then higher seedling growth and N uptake may have co-occurred with lower net N mineralization rates, particularly if lower net N mineralization rates in unburned soils corresponded to higher gross mineralization rates. Finally, pine seedling growth and capacity for nutrient acquisition depend on ectomycorrhizal infection (Read, 1994). We did not examine mycorrhizal infection rate in the field or in the bioassay seedlings. However, reduced plant growth and N uptake in the burnt soils could reflect decreased ectomycorrhizal infection rates due to negative effect of fire on these fungal populations (Dunn et al., 1979). In a comparison of *Pseudotsuga menziesii* seedlings growing in central Oregon, USA (non-mycorrhizal when out-planted into burnt and unburned clear cuts), slash burning reduced the percentage of seedling root tips that were infected (Pilz and Perry, 1984). Similarly, artificial burning of conifer soils in Arizona, USA resulted in large decreases in mycorrhizal infection rates (Klopatek et al., 1988). In Ontario, Canada, burn intensity correlated positively with mycorrhizal infection rates and seedling survivorship in 2-year old pine seedlings (non-mycorrhizal when out-planted into burnt and unburned clear cuts; Herr et al., 1994).

Losses of N in biomass parallel those of carbon (C), and slash burning and stand-replacing wild fire can cause substantial losses of N from consumed fine fuels and forest floor material (Raison et al., 1985). Following stand-replacing wild-fire, nutrient-poor bole wood (C:N of 1000 or more) will remain on site where it will be partly consumed during future fires or become slowly incorporated into soil. At our site, tree boles from the previous forest covered ~9% of the soil surface (Fig. 1). Decaying boles act as strong sinks for mineral N (Fahey, 1983), even into late stages of decomposition (Busse, 1994). Hence, the combination of immediate volatilization losses of N and longer-term immobilization of N by low quality wood following stand replacing wild-fire should reduce N availability to colonizing vegetation.

Large diameter woody material is suggested to play an important role in the retention of N in lodgepole pine forests (Fahey, 1983; Fahey et al., 1985); in contrast to wild fire disturbance, harvest operations greatly reduce the return of large wood to forest soils. It is unlikely, however, that harvest without slash burning will adversely affect the long-term N capital of a site compared with the loss of N incurred over minutes during stand replacing wild fire. In considering the C budget of a lodgepole pine forest, bole wood is not the only significant C source to soils. Leaf litter fall can return over 50 Mg C ha^{-1} to soil during 100 years of lodgepole pine stand development (Fahey, 1983), with twigs, cones, root litter, and stem and root mortality substantially augmenting this return. Following harvest, the return of C in slash debris to soil could also buffer the effects of bole removal on soil N retention. For example, in pine forest in southeastern USA, at sites where slash was roller chopped, soil microbes immobilized significantly more ^{15}N (added to track mineralized N) than treatments where slash was piled and burned (85 and 60%, respectively; Vitousek and Matson, 1985). In these roller chopped plots, residual forest floor material accounting for 25% of the recovered label.

Several studies have reported increases in plant-available pools of soil P following fire. DeBano and Klopatek (1988) found that burning resulted in a short-term increase in bicarbonate extractable P (45 days), and ascribed this increase to the release of P in litter ash. Romanya et al. (1994) reported large increases in bicarbonate extractable P and in NaOH extractable inorganic P seven months after slash burning, during which substantial rain had fallen. At our site, burn-related increases in the bicarbonate extractable P pool may have been caused by an input of P from consumed forest floor, logging debris, and organic matter in the surface cm of mineral soil (Walker et al., 1986). In the year between burning and sampling, a portion of this input would equilibrate with the lesser available P fractions in soil, explaining the increase in the NaOH P fraction. For the burnt forest, higher soil moisture and a large input of needles and roots also may have influenced these P fractions. Soil pH regulates soil P dynamics; however, burning and harvesting had no significant longer-term influence on soil pH, and variations in soil pH did not correspond to changes in soil P fractions.

Would regenerating seedlings in the field respond similarly to harvesting and fire? The laboratory analyses and glass-house bioassay were consistent with regards to the effects of harvesting on N supply, however both were conducted under conditions of controlled moisture and temperature. We suggest that our methods underestimate the treatment differences that would be encountered in the field. For example, soil moisture was maintained at near field capacity for the incubations and the bioassay seedlings were regularly watered. In the field, burning and harvesting resulted in important differences in soil moisture among the four treatments. At the time of sampling, soil moisture was much higher in the unburned clear cut than in burnt clear-cut soil (Table 2), probably due to the mulching effect of a thick forest floor in the unburned clear cut. Conversely, significantly higher soil moisture in burnt forest than in the unburned forest soil were likely related to larger interception and transpiration losses in the forest. Because soil moisture influences seedling survivorship and growth during drought prone summers in the Rocky Mountains, and is a primary control on nutrient mineralization rates, differences in soil moisture would accentuate differences in the growth of regenerating seedlings in the field.

We also limited our comparisons to the surface 10 cm of mineral soil. Because substantial quantities of N can be mineralized from the forest floor of lodgepole pine forests (up to 60% of total N mineralized; Stump and Binkley, 1993), burn-related losses of forest floor material, an important source of relatively labile C to heterotrophic micro-organisms, would accentuate observed differences in N supply and seedling growth (Table 1). The comparatively large size of bioassay seedlings grown in the burnt clear cut soils may indicate that the delay in slash burning (~4 years) resulted in a large enough release of nutrients from decomposing slash material to soil to partially offset the detrimental effects of forest floor loss.

Roller chopping without burning is increasingly being used to manage slash in lodgepole pine harvests in Wyoming, and our results would support this less intensive management approach. However, other factors influencing seedling establishment, seedling growth, and residue management decisions need to be kept in mind. These include the effects of residue management on microclimate; seedling predation and herbivory; fire and disease hazard reduction; air quality and stream chemistry; wildlife habitat; and, forage production (Berntsen, 1980; DeByle, 1980; Vitousek and Matson 1985; Lopushinsky et al., 1992). For example, at a wetter, lower elevation site in Washington, USA, residual logging slash reduced air movement and resulted in an unfavorably warm microclimate for seedlings compared with burn treatments (Lopushinsky et al., 1992). In contrast, Vitousek and Matson (1985) measured lower maximum but higher minimum soil temperatures in roller chopped versus pile and burned treatments.

At a high elevation site in Colorado, USA, chipping and redistributing lodgepole pine slash reduced seedling biomass and survivorship compared with either broadcast burn or pile and burn treatments (DeByle, 1980). At our high elevation site, seedling establishment in the unburned clear cut was abundant (~1 seedling per m^2) and seedlings appeared healthy (pers. obs. of the authors). These observations suggest either that slash did not adversely affect seedling performance, the effects of the slash were short-lived, or the effects of higher nutrient and water availability on seedling growth more than offset any adverse effects of slash.

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