ECOLOGICAL RESTORATION ALTERS NITROGEN TRANSFORMATIONS IN A PONDEROSA PINE–BUNCHGRASS ECOSYSTEM

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Abstract. Ponderosa pine–bunchgrass ecosystems of the western United States were altered following Euro-American settlement as grazing and fire suppression facilitated pine invasion of grassy openings. Pine invasion changed stand structure and fire regimes, motivating restoration through forest thinning and prescribed burning. To determine effects of restoration on soil nitrogen (N) transformations, we replicated (0.25-ha plots) the following experimental restoration treatments within a ponderosa pine–bunchgrass community near Flagstaff, Arizona: (1) partial restoration—thinning to presettlement conditions, (2) complete restoration—removal of trees and forest floor to presettlement conditions, native grass litter addition, and a prescribed burn, and (3) control. Within treatments, we stratified sampling to assess effects of canopy cover on N transformations. Forest floor net N mineralization and nitrification were similar among treatments on an areal basis, but higher in restoration treatments on a mass basis. In the mineral soil (0–15 cm), restoration treatments had 2–3 times greater annual net N mineralization and 3–5 times greater annual net nitrification than the control. Gross N transformation measurements indicate that elevated net N mineralization may be due to increased gross N mineralization, while elevated nitrification may be due to decreased microbial immobilization of nitrate. Net N transformation rates beneath relict grassy openings were twice those beneath postsettlement pines. These short-term (1 yr) results suggest that ecological restoration increases N transformation rates and that prescribed burning may not be necessary to restore N cycling processes.

Key words: ^{15}N; N mineralization; nitrification; northern Arizona; Pinus ponderosa *Laws.; ponderosa pine–bunchgrass communities; prescribed burning; restoration ecology; tree thinning.*

INTRODUCTION

Before Euro-American settlement, ponderosa pine–bunchgrass ecosystems were characterized by frequent, low-intensity fires that rarely reached the crowns of large trees. These fires destroyed most pine regeneration and maintained grassy openings between groups of large pines. Ponderosa pine (*Pinus ponderosa* Laws.) forests of the inland western United States changed dramatically following Euro-American settlement in the late 1800s. Fire suppression, timber extraction, exotic species introductions, and livestock grazing greatly altered ecosystem patterns and processes (Cooper 1960, Covington and Moore 1994, Covington et al. 1994).

These anthropogenic factors, in conjunction with a wet and warm climate in the early 1900s, led to an irruption of pine regeneration, which reached its peak in 1919 (White 1985, Savage et al. 1996). Abundant and permanent establishment of pines in grassy openings increased stand densities and forest floor litter accumulation, causing the fire regime to become infrequent and stand-replacing (Covington and Moore 1994,

Covington et al. 1994, Swetnam and Baisan 1996). Stand-replacing fires, which were anomalous in presettlement forests, threaten timber resources, adjacent homes, and species or communities dependent on the presettlement stand structure and fire regime (Covington et al. 1994, Kolb et al. 1994, Covington et al. 1997). In addition, sequestration of nutrients in pine litter that decomposes more slowly than grass litter (Hunt et al. 1988) may have decreased nutrient availability in the contemporary forest relative to the presettlement forest, though this hypothesis is largely untested (Weaver 1951, Cooper 1960, Covington and Sackett 1984). Covington et al. (1994) suggested that ecological restoration, if implemented within a 15–30 yr window, could ameliorate the above problems.

Restoration efforts, including thinning of postsettlement trees and prescribed burning, are becoming common in ponderosa pine–bunchgrass ecosystems (Covington and Sackett 1984, 1986, 1992, Kaufmann et al. 1994). However ecological effects of restoration, including effects on linkages between aboveground restoration and belowground biogeochemical processes, are poorly understood. Nitrogen (N) limits plant growth in many ponderosa pine ecosystems (Wagle and Kitchen 1972), and both thinning (Vitousek and Matson 1985, Fisk and Fahey 1990, Frazer et al. 1990, Van Miegroet et al. 1992) and prescribed burning (Chris-

tensen 1973, Klemmedson 1976, Covington and Sackett 1984, 1986, 1992, White 1986, Binkley et al. 1992, Carriera et al. 1994, Wright and Hart 1997) are known to alter N availability. The effects of prescribed fire and thinning are rarely observed independently at the same site (Pietikäinen and Fritze 1995). In addition, most researchers have used one-time estimates of N pool sizes or laboratory estimates of net N transformation rates to assess changes in soil N; these measures alone may be poor indices of plant-available N in situ (Hart et al. 1994). Given the economic and ecological importance of ponderosa pine forests, the scale of current restoration efforts, and the importance of N to ponderosa pine productivity, greater understanding of restoration effects on the N cycle is a research imperative in the Southwest (Covington et al. 1994, Covington et al. 1997).

This research evaluates how ecological restoration of a ponderosa pine–bunchgrass ecosystem to presettlement structure and function alters gross and net soil N transformations. We established replicated experimental restoration plots in a mature ponderosa pine stand within the Gus Pearson Natural Area near Flagstaff, Arizona (Covington et al. 1997). Within restoration treatments, we stratified sampling under major canopy cover types to assess changes in net N transformations due to postsettlement pine invasion into grassy openings.

METHODS

Study site and treatments

The research was conducted in the Gus Pearson Natural Area within the United States Forest Service Fort Valley Experimental Forest, 10 km northwest of Flagstaff, Arizona. The site elevation is 2195–2255 m, with a southwest aspect and a slope of 0–5%. Mean annual precipitation is 56.7 cm, half of which falls as snow and half as summer monsoonal rains (Schubert 1974). Mean annual air temperature is 7.5°C, with an average of 94 frost-free days. The soil is derived from flow and cinder basalt and is classified as Brolliar stony clay loam, a fine, smectitic, Typic Argiboroll. The area was never logged, but livestock grazing occurred between 1876 and 1910. The dominant vegetation is ponderosa pine forest composed of large (37–104 cm dbh) uneven-aged presettlement pines surrounded by small (<37 cm dbh) uneven-aged postsettlement pines or relict bunchgrass openings. Before treatment, postsettlement trees covered ~80% of the area relative to ~10% cover by grassy openings and presettlement pines. Major herbaceous species found in the relict bunchgrass openings include: the grasses, Arizona fescue (*Festuca arizonica* Vasey), mountain muhly (*Muhlenbergia montana* (Nutt.) Hitchc.), mutton bluegrass (*Poa fendleriana* (Steud.) Vasey), pine dropseed (*Blepharoneuron tricholepis* (Torr.) Nash.), black dropseed (*Sporobolus interruptus* Vasey), and bottlebrush squirreltail (*Sitan-*

ion hysterix Nutt.); the forbs, showy aster (*Aster commutatus* Torr. and Gray) spreading fleabane (*Erigeron divergens* Torr. and Gray), showy goldeneye (*Viguiera multiflora* Nutt.), western ragweed (*Ambrosia psilistachya* DC.), and snakeweed (*Guterrezia* spp.); and the shrub, buckbrush (*Ceanothus fendlerii* Steud.).

Fifteen 0.25-ha plots were established and assigned to three treatments: control, partial restoration, and complete restoration. Because a fuel break was needed to protect buildings of the historical Fort Valley Experiment Station, the 10 restoration treatment plots were assigned randomly (5 as partial restoration and 5 as complete restoration) to the plots closest to the buildings. The remaining 5 plots were assigned to the control treatment. All areas had similar forest floor and mineral soil total C and N contents, and mineral soil anaerobically mineralizable N before treatment (P. Z. Fulé and S. C. Hart, 1993, Northern Arizona University *unpublished data*). Partial restoration included removing most of the aboveground postsettlement tree biomass from the site. Complete restoration included postsettlement tree removal, forest floor manipulation, and a prescribed burn. Forest floor manipulation included raking aside the Oi layer and removing the Oa and Oe layers from the site. The Oi layer (2–4 yr of litterfall) was then returned to the soil surface, along with ~672 kg/ha of native grasses and forbs mowed from nearby Hart Prairie. These forest floor manipulations were intended to emulate the fuel load of presettlement forests. The complete restoration treatment was designed to test whether ecosystem structure and function could be restored quickly through intense manipulations (Covington et al. 1997). The partial restoration treatment was designed to test whether thinning without prescribed burning could restore ecosystem structure and function. Thinning was implemented in the fall of 1993 and the prescribed burn in the fall of 1994. More details on the treatments and fire are given in Covington et al. (1997).

Within each plot, we stratified sampling beneath three or four canopy types. Canopy type sample areas (subplots) were selected randomly from the population of potential subplots for a given canopy type within each plot. In all treatments, we located subplots beneath presettlement pines, postsettlement pines, and in grassy openings (n = 3 treatments × 3 canopy types × 5 replicates = 45 subplots). In the partial and complete restoration treatments, subplots were also established in areas where postsettlement pines had been removed (called "postsettlement removed" subplots; n = 2 treatments × 1 canopy type × 5 replicates = 10 subplots).

Nitrogen transformation measurements

We used a modified resin–core method (DiStefano and Gholz 1986, Binkley and Hart 1989) to measure net N transformation rates. This method uses ion exchange resin bags to capture soil solution ions leaching below the incubating soil. Initial soil inorganic N pool

sizes are determined from adjacent separate subsamples. Net N mineralization is calculated as the difference in soil ($NH_4^+ + NO_3^-$)-N pool size between incubated and initial soil plus ($NH_4^+ + NO_3^-$)-N adsorbed on the underlying resin bag. Net nitrification is calculated as the difference in soil NO_3^--N pool size between incubated and initial soil plus NO_3^--N adsorbed on the underlying resin bag. We incubated forest floor and underlying mineral soil in 5.1 cm I.D. polyvinyl chloride (PVC) pipe by placing resin bags below the mineral soil and between the mineral soil and forest floor. Resin bags were constructed by placing mixed bed ion exchange resin (30 mL wet, Baker catalog number 4631-01) in a nylon stocking along with a ring of latex tubing and tying the stocking closed. The latex tubing ring pressed the bag against the PVC pipe to ensure that the soil solution passed through the bag. The forest floor was sampled with a polycarbonate tube (4.75 cm I.D.) and then transferred to the PVC incubation pipe. The depth of the forest floor core varied because O horizon depths ranged from 0 to 18 cm. The mineral soil was sampled with the same polycarbonate tube (0–15 cm), using a soil sampling corer (AMS Core Sampler, American Falls, Idaho, USA). The PVC pipe was inverted, a resin bag was placed below the forest floor, the intact mineral soil core was placed below the resin bag, and a second resin bag was placed below the mineral soil. This entire unit was returned to the hole from which the soil was sampled and incubated for 6 mo.

Soils were stored at 4°C (<5 d) until they were weighed and subsampled for gravimetric water content and potassium chloride (KCl) extraction. Rock and organic fragments >5 mm were removed by hand before subsampling. Gravimetric water content was determined by drying mineral soil for 48 h at 105°C and forest floor for 24 h at 70°C. We extracted ~20 mL of field moist soil with 100 (mineral soil) or 25 (forest floor) mL of 2 mol/L KCl. Soil suspensions were mechanically shaken for 0.5 h, filtered (Whatman No. 1 filters, preleached with deionized water), and frozen until immediately prior to analysis. Pool sizes of ammonium (NH_4^+) and nitrate plus nitrite ($NO_3^- + NO_2^-$) were determined on a Lachat AE Flow Injection Autoanalyser (Lachat Instruments, Inc., Milwaukee, Wisconsin, USA), using the indophenol-blue (Lachat Instruments, Inc., 1990) and cadmium reduction-diazotiation (Lachat Instruments, Inc., 1992a) methods, respectively. Because NO_2^- levels were negligible, ($NO_3^- + NO_2^-$) are reported as NO_3^-.

Rocks (2–5 mm) were accounted for by sieving KCl extracts and gravimetric water content subsamples through a 2-mm mesh following analysis. The first (summer) incubation took place from 2 May 1995 through 31 October 1995, while the second (winter) incubation spanned 1 November 1995 through 16 May 1996. The two 6-mo incubation periods were selected based on Arizona's bimodal precipitation pattern de-

scribed above. Cores were incubated in each of the 55 subplots, at a fixed distance (4 m) and random direction from the center of the subplot. Mass-based rates within each subplot were converted to an areal basis using the mean bulk density of initial and final mineral soil cores. Forest floor mass per unit area was measured with a 929-cm² sampling template (rather than our 17.7-cm² surface area core) at each subplot.

The ^{15}N isotope dilution method (Hart et al. 1994) was used to measure gross N transformation rates on intact mineral soil cores (0–15 cm) using the same soil coring device as above, and a 1-d incubation period. We conducted measurements beneath all canopy types within two randomly selected plots from each treatment (22 subplots total), during 30 and 31 August 1995. These dates were chosen because the soil was moist and warm, and we expected gross N transformation rates to be highest at this time. At each subplot, we labeled adjacent t_0 and t_{24} cores with $^{15}NH_4^+$ (25 mg N/L and 99% atom percentage enrichment), labeled adjacent t_0 and t_{24} cores with $^{15}NO_3^-$ (58 mg N/L and 26% atom percentage enrichment), and left one centrally located core unamended to determine initial NH_4^+ and NO_3^- pool sizes. All five cores were taken within a 0.25-m² area. We injected 16 mL (~2 and 4 mg N/kg dry soil for NH_4^+ and NO_3^- cores, respectively) of ^{15}N solution uniformly into the intact soil cores and returned the cores to their original space in the soil, where they incubated for 24 h (Hart et. al. 1994).

Gross rates of N mineralization, nitrification, NH_4^+ immobilization, and NO_3^- immobilization were calculated using $^{14+15}N$ and ^{15}N in t_0 and t_{24} cores, pool sizes of labeled pools, and the equations in Kirkham and Bartholomew (1954). Gross N immobilization was calculated as ($NH_4^+ + NO_3^-$)-N immobilization minus gross nitrification. We determined the extraction efficiency for both NH_4^+ and NO_3^- by labeling and then immediately extracting (100 mL of 2 mol/L KCl to 20 mL field moist soil) the t_0 core and comparing recovery to the unamended soil core. Our ^{15}N diffusion procedure followed Stark and Hart (1996). Gravimetric water content was determined on all samples, and pool sizes of NH_4^+-N and ($NO_3^- + NO_2^-$)-N were determined for every core as described above. Mass-based rates within each subplot were converted to an areal basis using the mean bulk density of all five cores from the subplot. Total N and ^{15}N were determined by continuous-flow direct combustion and mass spectrometry with an ANCA 2020 (Europa Scientific, Cincinnati, Ohio, USA).

Organic matter, nitrogen, and phosphorus

Organic matter and total N and phosphorus (P) were determined in forest floor and mineral soil collected in May, 1995. Organic matter was determined by mass loss on ignition (550°C for 6 hr), and total C was estimated using the ratio of 1.724 g organic matter/g C (Nelson and Sommers 1982). Total N (organic + NH_4^+) and P (organic + PO_4^{3-}) were determined by mod-

TABLE 1.   Selected soil characteristics for the Gus Pearson Natural Area restoration site. Table entries are means with 1 SE in parentheses.

Soil characteristic	Control		Partial restoration		Complete restoration	
Forest floor (O horizon)						
Areal density (Mg/ha)	63.74	$(9.59)^b$	92.83	$(15.96)^b$	20.53	$(3.11)^a$
Total N (kg/ha)	473.3	$(109.8)^b$	702.0	$(104.9)^b$	83.4	$(26.5)^a$
Total P (kg/ha)	59.1	$(10.6)^b$	87.7	$(16.7)^b$	18.1	$(5.4)^a$
Organic matter (Mg/ha)	33.40	$(6.94)^b$	56.32	$(9.00)^b$	7.01	$(2.40)^a$
C:N‡	43.2	(3.2)	46.6	(2.2)	47.4	(3.0)
Mineral soil (0–15 cm)						
Summer soil temperature (C)§	12.2	$(0.2)^a$	14.4	$(0.1)^b$	15.9	$(0.1)^c$
Winter soil temperature (C)§	3.2	(0.1)	3.7	(0.1)	4.0	(0.1)
Summer water content (m³/m³)‖	0.21	(0.06)	0.24	(0.07)	0.23	(0.06)
Bulk density (Mg/m³)¶	0.91	(0.03)	0.95	(0.04)	0.94	(0.02)
Total N (kg/ha)	1431.2	(115.3)	1726.1	(168.3)	1662.3	(89.4)
Total P (kg/ha)	1455.4	(87.7)	1742.6	(134.9)	1629.5	(51.0)
Organic matter (Mg/ha)	92.51	(5.55)	112.60	(9.27)	101.65	(3.18)
C:N‡	37.7	(1.0)	38.0	(0.7)	35.8	(1.6)

† Treatments with different lowercase letters (a, b, c) within a row are statistically different ($P < 0.10$); when no lowercase letters are given, values are not statistically different.

‡ C calculated assuming 1.724 g organic matter/g organic C (Nelson and Sommers 1982).

§ Summer soil temperature spans from 23 June through 31 October 1995, and winter soil temperature from 1 November 1995 through 16 May 1996.

‖ Summer soil water content from 16 May through 8 November 1995.

¶ Calculated from the mass of soil (< 2 mm) contained in a core of known volume which included rock volume.

ified micro-Kjeldahl digestion (Parkinson and Allen 1975) and flow injection analysis using the salicylate (Lachat Instruments, 1992*b*) and molybdate-ascorbic acid (Lachat Instruments, Inc. 1992*c*) methods, respectively.

Microclimatic measurements

Volumetric water content was determined twice per month from 16 May 1995 through 8 November 1995 using a Trace Systems (Soil Moisture Corp., Santa Barbara, California, USA) time domain reflectometry (TDR) unit (Topp et al. 1980). Soil water content was determined at every subplot in the mineral soil (0–15 cm). Daily mean, minimum, and maximum soil temperatures were measured at a depth of 7.5 cm into the mineral soil using a CR10 Campbell Scientific (Campbell Scientific Inc., Logan, Utah, USA) datalogger and thermistors. Temperature measurements began 1 January 1995 in the control and 23 June 1995 in restoration treatments and were conducted on all subplots within two plots of each treatment.

Statistical analyses

Because the postsettlement removed canopy type did not exist in the control treatment, we determined canopy type differences by deleting postsettlement removed data and analyzing presettlement, postsettlement retained, and grass data as a two-way analysis of variance (ANOVA), with canopy type and treatment as factors. When main effects were significant ($P < 0.10$) and interactions were not, Fisher's LSD was used as a mean separation test. To determine plot-scale treatment effects that included the postsettlement removed canopy type, we scaled all canopy-type data to the plot level using a geographical information system (GIS). This GIS con-

tained the area within each plot occupied by a given canopy type, allowing us to calculate the proportional area of each canopy type within a plot. Once scaled to the plot level, the data were analyzed using a one-way ANOVA, with treatment as the factor. Due to the reduced sample size in the ^{15}N isotope dilution experiment, we only used this scaling method when the effect of canopy type was significant (gross nitrification). When canopy type was not significant, we pooled data from all canopy types and used a one-way ANOVA on treatment (gross N mineralization, gross N immobilization, and gross NO_3^- immobilization). Soil temperature and water content data were scaled using the GIS and then analyzed using a repeated-measures ANOVA on treatment. We log 10 transformed data for ANOVA analyses when variance was unequal among treatments and canopy types. All statistical analyses were performed using the statistical package StatView at the $P = 0.10$ significance level (version 4.5, Abacus Concepts, Inc., Berkeley, California, USA).

RESULTS AND DISCUSSION

Ecological restoration and nitrogen transformations

Our results show that ecological restoration greatly altered soil characteristics and N transformation rates in this ponderosa pine–bunchgrass ecosystem. Posttreatment soil characteristics are summarized in Table 1. Important differences include increased summer soil temperature in the restoration treatments relative to the control, and decreased forest-floor density, total N, and organic-matter content in the complete restoration treatment relative to the partial restoration or control treatments. Mineral soil NH_4^+-N pool sizes were gen-

TABLE 2. Soil ammonium (NH_4^+) and nitrate (NO_3^-) pool sizes at the Gus Pearson Natural Area near Flagstaff, Arizona. Data are means (and 1 SE) in kg N/ha.

Treatment‡	Mineral soil†		Forest floor†	
	NH_4^+-N	NO_3^--N	NH_4^+-N	NO_3^--N
2 May 1995				
Control	1.19 (0.11)[a]	0.33 (0.22)	0.54 (0.22)	0.03 (0.01)
Partial restoration	4.15 (0.57)[c]	0.91 (0.24)	1.29 (0.39)	0.10 (0.05)
Complete restoration	2.33 (0.52)[b]	0.90 (0.59)	1.40 (0.58)	0.09 (0.05)
1 November 1995				
Control	1.17 (0.18)[a]	0.07 (0.11)	2.35 (1.20)	0.05 (0.03)
Partial restoration	1.43 (0.14)[ab]	0.02 (0.07)	3.84 (1.12)	0.60 (0.43)
Complete restoration	2.08 (0.38)[b]	0.07 (0.07)	1.77 (0.64)	0.03 (0.01)

† Mineral soil is 0–15 cm, and forest floor is the entire O horizon.

‡ For a given N form and sampling date, treatments with different lowercase letters (a, b, c) are statistically different ($P < 0.10$); when no lowercase letters are given, values are not statistically different.

erally greater in the restoration treatments than in the control (Table 2). Nitrate-N pool sizes in the mineral soil and NH_4^+-N and NO_3^--N pool sizes in the forest floor were similar among treatments for both dates. Several previous investigators have reported similar changes in inorganic N pool sizes in southwestern pon-

derosa pine forests following prescribed fire and thinning (Klemmedson et al. 1962, Wagle and Kitchen 1972, Klemmedson 1976, Kovacic et al. 1986, Ryan and Covington 1986, White 1986, Covington and Sackett 1992).

Net N transformations were analyzed on an annual basis because there was a significant interaction between treatment, canopy type, and incubation season. Rates were greatest in the partial restoration treatment in the summer and greatest in the complete restoration treatment in the winter (data not shown). In the forest floor, annual net N transformation rates were generally similar among treatments on an areal basis (Fig. 1), but greater in the two restoration treatments on a mass basis (Fig. 2). Mass-based forest floor annual net nitrification was 2.2, 0.9, and 0.2% of total forest floor N in the complete restoration, partial restoration, and control treatments, respectively. Annual net N mineralization on a mass basis was 2.8, 1.2, and 0.5% of total forest floor N in the complete restoration, partial
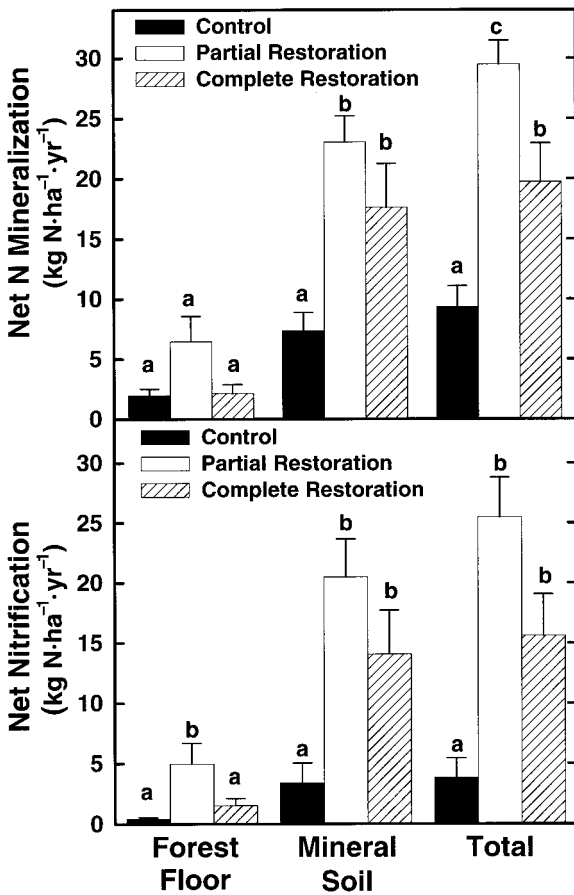

FIG. 1. Annual net N mineralization and nitrification rates expressed on an areal basis for the forest floor (O horizon) and mineral soil (0–15 cm) at the Gus Pearson Natural Area restoration site. Vertical bars denote 1 SE. For a given soil horizon, bars with different lowercase letters are statistically different ($P < 0.10$).
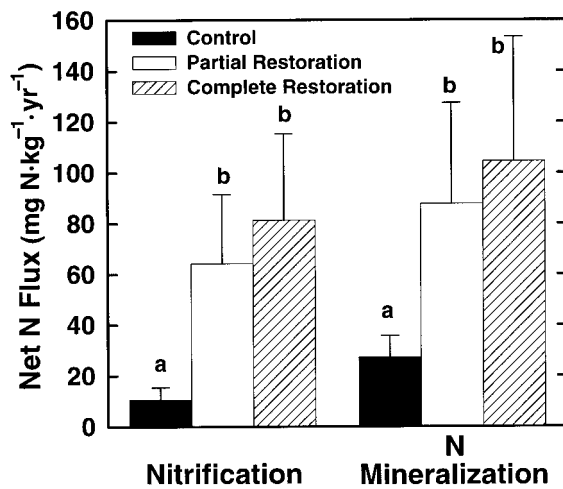

FIG. 2. Annual net N mineralization and nitrification rates expressed on a per unit mass basis for the forest floor (O horizon) at the Gus Pearson Natural Area restoration site. Vertical bars denote 1 SE. For a given N transformation, bars with different lowercase letters are statistically different ($P < 0.10$).
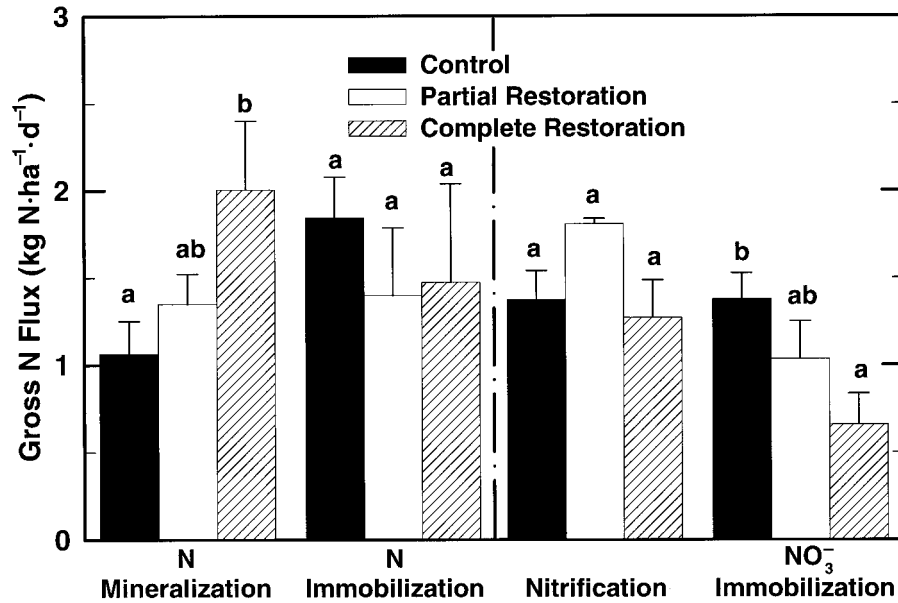
Fig. 3. Mean gross N transformation rates in the mineral soil (0–15 cm) at the Gus Pearson Natural Area restoration site. Vertical bars denote 1 SE. For a given N transformation, bars with different lowercase letters are statistically different ($P < 0.10$).

restoration, and control, respectively. Thus, while forest floor N and C reserves were greatly reduced in the complete restoration treatment (Table 1), a greater percentage of the total N was transformed, and net N transformation rates remained high. These results suggest that substrate availability or the microclimate was more favorable in the complete restoration forest floor than in other treatments. We did not find differences in forest floor substrate quality (i.e., C:N) among treatments (Table 1); however, mineral soil temperatures (Table 1) suggest that forest floor temperatures (not measured) were likely higher in the complete restoration treatment than other treatments.

In the mineral soil and total surface soil (forest floor + mineral soil), the restoration treatments had three to five times greater annual net nitrification rates and two to three times greater annual net N mineralization than the control (Fig. 2; $P < 0.10$). Net nitrification accounted for 41, 86, and 78% of total surface soil net N mineralization in the control, partial restoration, and complete restoration treatments, respectively. Other investigators have reported elevated net N transformation rates following a single prescribed fire (Schoch and Binkley 1986, White 1986, Knoepp and Swank 1995). However, in soil beneath Oregon ponderosa pine, Monleon et al. (1997) found no increase in field net N transformations following prescribed fire. In addition, the net N mineralization rates of Monleon et al. (1997) were lower than our rates, and only a small fraction of the N mineralized was nitrified. The authors attributed the low rates to low site fertility. Accelerated net N transformation rates, and increases in the proportion of net N mineralization from net nitrification following

temperate forest harvesting, are also frequently reported (Vitousek and Matson 1985, Hart and Firestone 1989, Frazer et al. 1990), and comparable to those observed in our partial restoration treatment.

Differences in net N transformations are caused by differences in the relative rates of gross microbial mineralization and immobilization of NH_4^+ and NO_3^-. Because we observed treatment differences in mineral soil gross N mineralization but not gross N immobilization (Fig. 3), we suggest the increased annual net N mineralization rate (Fig. 1) following our restoration treatments was likely due to increased microbial production of NH_4^+ rather than decreased N immobilization. Conversely, because gross nitrification rates were similar across treatments, while gross NO_3^- immobilization varied, we suggest that increased annual net nitrification rates in restoration treatments (Fig. 1) were likely due to decreased microbial immobilization of NO_3^- (Fig. 3), rather than increased gross nitrification. Previously, elevated NO_3^- pool sizes and net nitrification rates following fire were assumed to result from increased gross nitrification (Christensen et al. 1973, Covington and Sackett 1986, White 1986). Our results are based on 1-d measurements; further testing of fire and harvesting effects on gross N transformations must include several measurements within and among years. Our gross N transformation rates are similar to those found in several other temperate coniferous forests (Hart et al. 1994, Stark and Hart 1997). However, gross nitrification rates at our site were higher than those reported for infertile, granitic New Mexico ponderosa pine soils (Stark and Hart 1997). This discrepancy is likely due

to the optimal climate under which we conducted our experiment or inherent differences in site fertility.

Gross microbial N transformations, which determine net N cycling rates and plant-available N, are driven in part by microclimate and substrate quantity and quality. Mineral soil substrate quality (i.e., C:N) and soil moisture were similar among treatments at our site, while soil temperature was elevated in the restoration treatments relative to the control (Table 1). Thus, temperature is likely the primary mechanism controlling the increased gross and net N transformation rates following our restoration treatments.

Because we rarely observed statistical differences between N transformations in the partial and complete restoration treatments (Figs. 1, 2, and 3), removal of postsettlement trees, rather than forest floor manipulation and burning, was likely the main factor influencing N transformation rates at this site. While short-term alteration of N transformations is probably due to thinning alone, future restoration management will use chronic prescribed fire to maintain stand densities achieved by the initial thinning. Consequently, our treatments may diverge with time, as successive interval burns act on the complete restoration treatment. Chronic fire may not alter soil N (Richter et al. 1982) or may decrease N availability (Bell and Binkley 1989, Binkley et al. 1992, Carriera et al. 1994). In a ponderosa pine–bunchgrass ecosystem near our study site, prescribed fire (without preburn thinning or forest floor manipulation) produced short-term increases in N availability (Covington and Sackett 1986, 1992), but after 20 yr of burning (2-yr intervals), controls had higher N availability than burned plots (Wright and Hart 1997). Long-term research is needed to determine whether N transformation rates at the Gus Pearson Natural Area remain elevated through several fire intervals fueled by grass rather than pine litter.

Canopy type and nitrogen transformations

Before Euro-American settlement, fires burned through southwestern ponderosa pine forests every 2–12 yr (Swetnam and Baisan 1996), and pines rarely regenerated in grassy openings (White 1985, Savage et al. 1996). Consequently, presettlement canopy cover at our site was ~81% grassy openings and ~19% pines (Covington et al. 1997). Fire has been excluded in northern Arizona for ~120 yr, and most grassy openings have been replaced by dense thickets of small, postsettlement pines (Moir and Dieterich 1988, Covington and Moore 1994, Covington et al. 1994). It has long been hypothesized that postsettlement pine invasion slowed decomposition and nutrient cycling rates (Weaver 1951, Cooper 1960, Covington and Sackett 1984). We assessed effects of pine invasion on soil N transformations by comparing rates beneath grass and pine canopy types. Because the relict grassy openings at our site were briefly grazed (1876–1910) and are smaller than presettlement grassy openings, they are
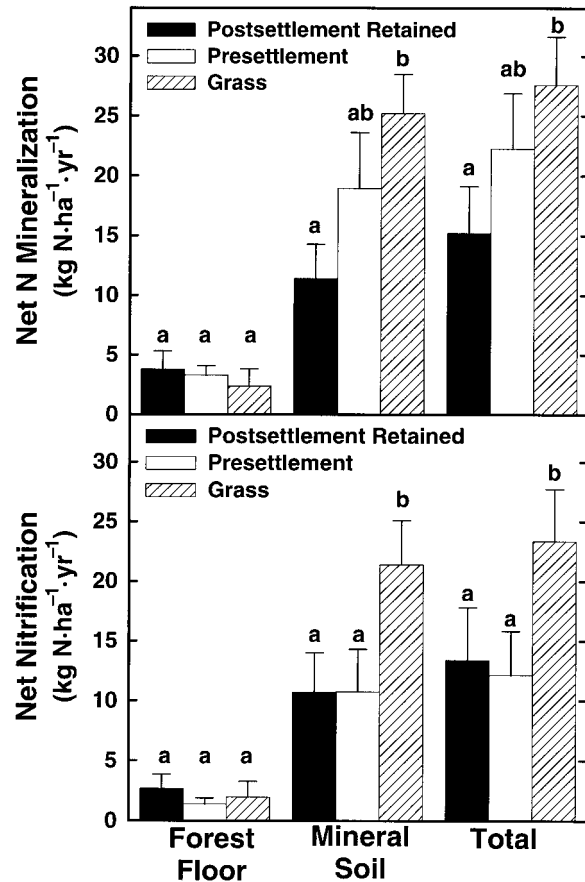

FIG. 4. Annual net N transformation rates in the forest floor (O horizon) and mineral soil (0–15 cm) at the Gus Pearson Natural Area restoration site in different canopy types. Because there were no treatment × canopy type interactions, means are for all treatments pooled together. The "postsettlement removed" canopy type was removed from this analysis because it was not present in control plots. Vertical bars denote 1 SE. For a given soil horizon, bars with different lowercase letters are statistically different ($P < 0.10$).

not perfect analogues for the presettlement bunchgrass community. In addition, changes in climate, atmospheric chemistry, and fire regimes could cause contemporary grassy openings to differ from presettlement grassy openings. In order to infer effects of pine invasion on N transformation rates, we assume that differences between the contemporary and presettlement grassy openings are small relative to differences between the pine and grassy opening canopy types.

Annual net N mineralization and net nitrification rates in the forest floor did not differ among canopy types (Fig. 4). However, in the mineral soil and total surface soil, the grass canopy type had ~2 × the annual net N mineralization rates as the postsettlement retained canopy type. These results suggest that: (1) presettlement forests, having a greater grass component than contemporary forests, likely had higher ecosystem-level N cycling rates, and (2) if pines continue to invade relict grassy openings, ecosystem-level N cy-

cling may decrease. It is unclear whether the postsettlement pine thickets will ever self-thin to resemble the presettlement pine clusters at our site (Moir and Dieterich 1988). If this does occur, our results suggest that net nitrification rates will remain depressed, while net N mineralization rates will increase to levels similar to the grass canopy type (Fig. 4). A shift from NO_3^- to NH_4^+ as the predominant inorganic N form may still reduce plant-available N relative to grassy openings. Soil NO_3^- is more mobile, and thus more accessible to plants than NH_4^+, and plants likely compete more successfully with soil microorganisms for NO_3^- than NH_4^+ (Kaye and Hart 1997).

The mechanisms causing decreased net N transformation rates below the postsettlement retained canopy type are unclear. We did not detect differences in mineral soil water content, temperature, or substrate quality among canopy types (data not shown). However, our measures of substrate quality were crude. Grass litter typically has lower lignin and higher N content than coniferous litter (Hart et al. 1993). Hunt et al. (1988) showed that grass litter decomposed more rapidly than lodgepole pine litter and that soil net N mineralization rates were faster in shortgrass prairie than in lodgepole pine forest. It is possible that a measure of lignin:N ratio (Van Cleve et al. 1993) would indicate differences in substrate quality that we did not detect using our estimates of OM and total N content.

CONCLUSIONS

Our results suggest that partial or complete ecological restoration increases net N transformation rates in this southwestern ponderosa pine-bunchgrass ecosystem. If the grassy openings at our site have N transformation rates similar to presettlement grassy openings, then restoration brought the Gus Pearson Natural Area closer to presettlement conditions. Increased net N transformation rates were probably due to increased gross N mineralization and decreased gross NO_3^- immobilization. Because our complete and partial restoration treatments yielded similar N transformation rates, it may not be necessary to implement complete restoration to increase N availability. However, other factors, such as fuel loading, maintenance of stand structure, and herbaceous biodiversity should be considered before prescribed fire is discounted as a management tool. If fire suppression persists without restoration efforts, the anticipated replacement of grassy openings by pine thickets will greatly reduce N transformation rates in ponderosa pine-bunchgrass ecosystems. This experiment was not replicated at the site level. Future research should assess whether the patterns found at the Gus Pearson Natural Area apply to other southwestern ponderosa pine–bunchgrass ecosystems. In addition, this research documents short-term (1 yr) results that may not reflect long-term responses to the treatments. We continue to monitor changes in N transformations at this site to assess these longer-term trends.

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