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SOIL RESPONSES TO MANAGEMENT, INCREASED PRECIPITATION, AND ADDED NITROGEN IN PONDEROSA PINE FORESTS

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Abstract. Forest management, climatic change, and atmospheric N deposition can affect soil biogeochemistry, but their combined effects are not well understood. We examined the effects of water and N amendments and forest thinning and burning on soil N pools and fluxes in ponderosa pine forests near Flagstaff, Arizona (USA). Using a ^{15}N-depleted fertilizer, we also documented the distribution of added N into soil N pools. Because thinning and burning can increase soil water content and N availability, we hypothesized that these changes would alleviate water and N limitation of soil processes, causing smaller responses to added N and water in the restored stand. We found little support for this hypothesis. Responses of fine root biomass, potential net N mineralization, and the soil microbial N to water and N amendments were mostly unaffected by stand management. Most of the soil processes we examined were limited by N and water, and the increased N and soil water availability caused by forest restoration was insufficient to alleviate these limitations. For example, N addition caused a larger increase in potential net nitrification in the restored stand, and at a given level of soil N availability, N addition had a larger effect on soil microbial N in the restored stand. Possibly, forest restoration increased the availability of some other limiting resource, amplifying responses to added N and water. Tracer N recoveries in roots and in the forest floor were lower in the restored stand. Natural abundance $\delta^{15}N$ of labile soil N pools were higher in the restored stand, consistent with a more open N cycle. We conclude that thinning and burning open up the N cycle, at least in the short term, and that these changes are amplified by enhanced precipitation and N additions. Our results suggest that thinning and burning in ponderosa pine forests will not increase their resistance to changes in soil N dynamics resulting from increased atmospheric N deposition or increased precipitation due to climatic change. Restoration plans should consider the potential impact on long-term forest productivity of greater N losses from a more open N cycle, especially during the period immediately after thinning and burning.

Key words: *climatic change; $\delta^{15}N$; forest restoration; microbial biomass; N isotope tracer; nitrification; nitrogen fertilization; nitrogen mineralization; precipitation.*

INTRODUCTION

A century of fire suppression has substantially altered stand structure in ponderosa pine (*Pinus ponderosa* P. & C. Lawson var. *scopulorum* Engelm.) forests in the western United States (Covington et al. 1994, 1997). Because these altered stands increase the risk of stand-replacing wildfires (Covington and Moore 1994), there is great interest in reestablishing stands with lower tree densities and a higher frequency of low-intensity surface fires, typical of conditions prior to European settlement (Cooper 1960). How such management activities alter ponderosa pine ecosystems will depend on the simultaneous and potentially interactive effects of other environmental changes, such as changing climate and increasing atmospheric nitrogen (N) deposition. For example, thinning and burning of ponderosa pine forests can alter the availability of both N (Kaye and Hart 1998, MacKenzie et al. 2004, Gundale et al. 2005, Kaye et al. 2005) and water (Hart et al. 2005, 2006, Simonin et al. 2006), affecting the microbial, plant, and ecosystem processes sensitive to availability of these often limiting resources.

Water and N additions to soil can increase soil microbial N (Bissett and Parkinson 1980, Hart and Stark 1997, Joergensen and Scheu 1999, Schimel et al. 1999, Grogan et al. 2000, Illeris et al. 2003, Allen and Schlesinger 2004) and soil N transformations, including N mineralization and nitrification (Tietema et al. 1992, van Miegroet and Johnson 1993, Fenn et al. 2005). If forest thinning and burning increase soil water and N, how will these interact with higher precipitation and N inputs through fertilization or N deposition? These changes could be additive, in which case processes limited by N or water would respond linearly to the combined increase in N or water availability. Or the responses could saturate if the increase in resource availability in the combined treatment exceeds demand.

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In other words, enhanced N and water availability following restoration could relieve limitations by these resources, reducing the sensitivity of soil processes in restored stands to increased precipitation and atmospheric N deposition. Alternatively, if thinning and burning enhance the availability of other soil resources that also limit soil microbial N pools and fluxes, responses to combined treatments may be larger than predicted by a simple additive model. Here, we combined stand management treatment with manipulations of precipitation and N availability to examine responses of the soil microbial biomass, soil N pools, and potential net N transformations to their combined effects.

Materials and Methods

The study area is at an elevation of ~2255 m above sea level, with gentle topography and a cool, subhumid climate. Mean annual precipitation in the area is 577 mm, half of which occurs as winter snow and the other half as summer rain. This experiment occurred as part of the Flagstaff Urban-Wildland Interface project (Fulé et al. 2001, Hart et al. 2006), located ~24 km northwest of Flagstaff, Arizona, USA (35°16′ N, 111°45′ W). We compared two stands (each 14.2 ha in area) that, prior to treatment, had similar tree densities and basal areas (Hart et al. 2006): EB3-1, a control stand with high tree density (709 trees/ha), high basal area (40.1 m^2/ha), and an intact forest floor; and an adjacent "restored" stand, EB3-2, that had been thinned to reduce tree density from 800 to 91 trees/ha, and to reduce basal area by from 39.7 to 8.5 m^2/ha. These stands are typical of ponderosa pine forests in the region: mean tree density in stands in Arizona is 620 trees/ha, and 50% of these stands have a basal area ranging from 23 to 46 m^2/ha (O'Brien 2002). These adjacent stands also have similar slope (7%) and aspect (southeast). The soils in both stands are derived from basalt and are classified as a complex of fine, smectitic, frigid, Typic Argiborolls and Mollic Eutroboralfs according to USDA soil taxonomy (Miller et al. 1995).

The thinning treatment was designed to recreate a clumped distribution of trees based on the location of harvested trees (as evidenced by large-diameter stumps) that were established prior to Euro-American settlement of the area (late 1800s). In the restored stand, thinning was completed in September 1999, and in February 2000, slash from the thinning operation was grouped into piles within the stand and burned. Soon after, the entire stand was broadcast burned (Fulé et al. 2001). More information on stand conditions and treatments can be found in Fulé et al. (2001) and Hart et al. (2006).

Within each stand (i.e., plot), 20 subplots were established on a 60-m interval grid as part of a related experiment to monitor understory plant species. Within each stand, we used 10 of these subplots, alternate grid points among the 20, for experimental treatments of increased precipitation and N amendment. Our use of small plots with simulated resource additions within these two forest stands sacrificed true replication of stand management in favor of their implementation on realistically large scales; factorial, replicated manipulations of water, nitrogen, and stand management on this scale would have been prohibitively expensive. Our use of inferential statistics constitutes pseudoreplication (sensu Hurlbert 1984). However, the main effects of restoration we observed were consistent with those found from similar past work using replicated designs investigating effects of restoration alone (e.g., Kaye et al. 2005), supporting our use of this unreplicated system as a means to test interactive effects of stand management and resource amendments.

At each subplot within each stand, three polyvinyl chloride rings were inserted 1 cm into the mineral soil, forming a triad with 1-m spacing between rings. Each ring within a subplot was then randomly assigned to one of three treatment groups: Water (W), Nitrogen + water (NW), or Unamended (U). Water addition roughly simulated a doubling of mean annual precipitation. Nitrogen addition simulated intensive fertilizer treatments commonly used in forest plantation management. We added N at a rate of 45 g $N \cdot m^{-2} \cdot yr^{-1}$, an amount shown to maximize fertilization benefits to pine trees in plantations (Lamontagne and Schiff 2000). The NW treatment included water addition at the same rate as the W treatment, allowing evaluation of the effects of added N with minimal limitation by water. Ammonium nitrate (NH_4NO_3) was dissolved in the same volume of water as added to the W treatment rings (3.41 L per ring per measurement period). The use of ^{15}N-depleted NH_4NO_3 allowed us to trace the fate of the added N in the soil (Hart and Myrold 1996). Water and N additions began on 10 July 2000 and continued at intervals of two weeks or longer until 6 November 2000, for a total of nine additions, such that each W ring received 30.69 L H_2O (51.9 cm) and each NW ring received the same amount of water plus 2.5 g N (42.35 g N/m^2). No water or N was added over the winter (November 2000 to April 2001) when snow covered the surface soil or when the surface soil was frozen. Water and N additions for the 2001 growing season began on 14 May and continued at intervals of two weeks or longer until 30 July 2001, for a total of six additions. Thus, for the 2001 growing season, each W ring received 20.46 L H_2O (34.6 cm) and each NW ring received the same amount of water plus 1.67 g of N (28.24 g N/m^2).

Soil sampling occurred on 29 June 2001, prior to the onset of summer rains, and on 3 August 2001, after rains had begun. We sampled the surface mineral soil (0–5 cm depth) in both June and August. In August, we also sampled the forest floor and top 15 cm of mineral soil, for a more integrated assessment of treatment effects at the end of the experiment. For the 0–5 cm depth samples, four 2 cm diameter mineral soil cores were taken randomly within each subplot, and combined to give one sample per subplot (Oakfield Apparatus Company, Oakfield, Wisconsin, USA). Prior to sampling mineral soil in August, the entire O horizon (forest

floor) was removed from each ring. Then, two 4.8 cm inner diameter cores were taken from each ring to a depth of 15 cm, one for soil and microbial analyses and a second for root analyses. Bulk densities were determined at this time in each plot and were found to be very similar: 0.878 ± 0.035 g/cm^3 for the control and 0.883 ± 0.027 g/cm^3 for the restored stands (mean ± SE, $n = 10$).

All soils were stored at 4°C before processing. Samples for extractable and microbial N were processed within four days of collection; roots were extracted within two weeks of collection, and potential net N mineralization assays were begun within four weeks of collection. Soils from the 0–5 cm depth were sieved field-moist through a 2-mm sieve to remove roots and coarse fragments before use in analyses. Soils from the 0–15 cm depth were passed through a 4-mm sieve to remove roots and coarse fragments, because of the higher clay content of soil over this depth interval. Subsamples of the material passing through the sieve were analyzed for water content, extractable NO_3^- and NH_4^+ concentrations, microbial N, and potential N mineralization. Soil water content was determined gravimetrically at 105°C for each soil sample, and all soil data are expressed on an oven-dry mass basis. Soil pH was determined in a 1:2 suspension of air-dry soil to 0.01 mol/L $CaCl_2$ solution using an Orion 720A pH meter (Allometrics, Incorporated, Baton Rouge, Louisiana, USA).

Soil microbial N was determined on the sieved, 0–5 cm and 0–15 cm samples using the chloroform fumigation-extraction method described by Davidson et al. (1989). One 10-g field-moist subsample from each sample was immediately extracted with 50 mL of 0.5 mol/L K_2SO_4. A paired subsample was fumigated with hydrocarbon stabilized $CHCl_3$ in a vacuum-sealed desiccator for five days. After five days, the fumigated subsamples were removed from the desiccator and extracted with 50 mL of 0.5 mol/L K_2SO_4. Extracts were shaken for one hour, and then filtered (Whatman No. 1 paper, prerinsed with deionized water [Whatman, Incorporated, Florham Park, New Jersey, USA]). Extracts were digested using a modified micro-Kjeldahl digestion (Davidson et al. 1989, Haubensak et al. 2002) and analyzed for total N using a salicylate method on a Lachat AE Flow Injection Auto-analyzer (Lachat Instruments, Milwaukee, Wisconsin, USA). The N-flush caused by fumigation was calculated by subtracting the total N in the unfumigated extracts from the corresponding total N in fumigated extracts. The N-flush was divided by a k_{en} of 0.20, which accounts for the extraction efficiency of lysed microbial cells, and converts chloroform labile-N values to biomass-N (Davidson et al. 1989, Hart et al. 1994).

Potential net N mineralization was determined in laboratory incubations with samples from the 0–15 cm depth. A 10-g soil subsample was extracted with 50 mL of 2 mol/L KCl to determine initial soil NO_3^- and NH_4^+ concentrations. Field-moist soil subsamples (30 g) were then weighed into plastic specimen cups and adjusted to a gravimetric water content of 30% by adding deionized water. The cups were covered with slowly gas-permeable polyvinylidene chloride plastic (Handi-Wrap, Dow Chemical Midland, Michigan, USA) and incubated at 24°C. After 30 days, 10 g of incubated soil was removed and extracted in 50 mL of 2 mol/L KCl. All KCl extracts were analyzed for NH_4^+ and NO_3^- concentrations using an automated colorimetric system (Lachat QuikChem 8000 Flow Injection Analzyer). Potential net nitrification (net NO_3^- production) and net N mineralization ($NO_3^- + NH_4^+$ production) rates were calculated as the final minus initial concentrations of N (per kilogram of dry soil), divided by 30 days. The potentially mineralizable N pool was estimated as total N mineralized during the incubation expressed on an areal basis (kilograms per hectare). This differs slightly from potential net N mineralization rates (in micrograms per gram per day) because it accounts for plot-specific soil bulk densities.

We used the acid-base diffusion technique to prepare soil extractable and microbial N samples for isotopic analysis (Hart et al. 1993, Holmes et al. 1998). Initial and final extracts from the potential net N mineralization assay were diffused sequentially, initially for NH_4^+, and then for NO_3^- by adding Devarda's alloy. After Kjeldahl digestion, the chloroform-fumigated and non-fumigated extracts from the microbial biomass assay were also diffused for ^{15}N analysis.

Roots were removed by sieving and hand-picking, and separated into three categories based on visual criteria: ponderosa pine live roots, ponderosa pine dead roots, and other roots (almost exclusively from herbaceous species the vast majority of which were live). Following removal from the soil, roots were dried at 60°C and weighed to the nearest 0.001 g. The mass of dead ponderosa pine roots was considerably lower in the restored stand (67.4 ± 23.4 g/m^2; mean ± SE) than in the control stand (108.7 ± 15.6 g/m^2), suggesting that the sum of live and dead roots reflected root growth after the fine roots from cut trees had decayed following stand thinning. Ponderosa pine fine roots were analyzed for carbon (C) and N concentration and isotopic composition as described below. The supply of root material for the other categories was exhausted in other analyses, so we used values for ponderosa pine live roots to estimate total root C, N, and ^{15}N contents.

Forest floor samples were dried at 70°C and weighed to determine forest floor mass. Forest floor material and ponderosa pine live roots were ground using a Wiley mill to 40 mesh (<425 μm). Mineral soil (0–15 cm) was ground to a fine powder using a roller mill. Subsamples of these materials were weighed into tin boats, and analyzed for %C, %N, and $\delta^{15}N$, by coupled Dumas combustion, isotope-ratio mass spectrometry at the Colorado Plateau Stable Isotope Laboratory.[5] Natural

[5] ⟨www.isotope.nau.edu⟩

abundance ^{15}N data are presented as the difference between sample and standard in the ratio of heavy and light isotopes:

$$\delta^{15}N = (R_{sam}/R_{std} - 1) \times 1000‰$$

where R_{sam} is the molar $^{15}N/^{14}N$ ratios of the sample material, and R_{std} is the molar $^{15}N/^{14}N$ ratio of the international standard material, N_2 in air: 0.003676. The $\delta^{15}N$ values of NO_3^- and NH_4^+ produced during the laboratory incubation were calculated using mass balance.

To test for the overall effects of stand management, we used a split-plot ANOVA with stand management as the independent factor and treatment (unamended, water added, or N and water added) as the split-plot effect (because resource addition treatments were arranged in triads, as described above). For response variables sampled over time, we used a repeated-measures, split-plot ANOVA. We used this same design but included only the U and W plots to test for the effects of added water. We compared only the W and NW plots to test for the effects of added N. This comparison isolated the effects of added N because the N added to these plots was delivered with water, equivalent to that received in the water-amended plots, and because the W and NW plots did not differ in soil water content (P. C. Selmants et al., *unpublished manuscript*). In addition to isolating the effects of added water or N, these tests provide a means to assess water by restoration and N by restoration interactions. To test for differences between stands in the distribution of the ^{15}N-depleted tracer, we used one-way ANOVAs with stand management as the independent factor. We used analysis of covariance and simple regression to explore possible mechanisms underlying the responses to water and N addition that we observed. For all tests, we used an alpha value of 0.10, established prior to conducting the statistical analyses.

Results and Discussion

Extractable nitrogen

Water addition significantly increased concentrations of extractable NO_3^- and NH_4^+ in the top 5 cm of mineral soil (Fig. 1A, B; for statistics, see Table 1). These effects were greater in June than in August (Time $\times$ H_2O interactions; Table 1). In June, soils were relatively dry (7.5% in the U plots), and water addition caused a large (86%) increase in soil water content. Soils were wetter in August (12.6% in the U plots), after the rainy season had begun, and water addition caused a smaller increase in soil water content (22%). Thus, the wetter soils in August likely minimized the effect of water additions. These results are consistent with past studies finding that water addition enhances inorganic N availability (Tietema et al. 1992, van Miegroet and Johnson 1993). Nitrogen addition also significantly increased concentrations of extractable NO_3^- and NH_4^+ in both June and August (Fig. 1A, B), indicating that our treatments were effective in increasing inorganic N availability.

The restored stand had consistently higher concentrations of extractable NO_3^- in the top 0–5 cm compared to the control stand, but stands did not differ in extractable NH_4^+. The absolute increases in extractable NO_3^- caused by added N and water were similar in the two stands (Fig. 1). For extractable NH_4^+, the increase caused by N addition was greatest in the control stand in June (Fig. 1B; Table 1, Time $\times$ Nitrogen $\times$ Stand Management interaction).

Microbial nitrogen

Nitrogen addition increased soil microbial N in the surface 5 cm of soil (Fig. 1C, Table 1), consistent with findings from some forests (Hart and Stark 1997, Joergensen and Scheu 1999, Allen and Schlesinger 2004), but not others (Söderström et al. 1983, Gallardo and Schlesinger 1994, Priha and Smolander 1995, Forge and Simard 2001, Ekblad and Nordgren 2002, Lee and Jose 2003). Water addition also increased microbial N (Fig. 1C), indicating that water availability limited the size of the soil microbial biomass in these forests, a phenomenon that has been demonstrated in other ecosystems as well (Bissett and Parkinson 1980, Schimel et al. 1999, Grogan et al. 2000, Illeris et al. 2003). On average, microbial N increased by 56% from June to August; there were no interactions among time, stand management, and resource amendments for microbial N. At all depths and times, the effects of added water and N were similar among stand management scenarios (no significant interactions).

The response of soil microbial N to added N declined with increasing concentrations of soil inorganic N (Fig. 2A. Here, response is the difference in microbial N between the NW and W plots, averaged across both sampling dates.) In an analysis of covariance, soil inorganic N concentration was a significant covariate for soil microbial N ($P = 0.002$). Thus, N limitation of the microbial N appears to decline over the observed range of variation in soil N availability, consistent with our hypothesis expecting smaller responses to added N in the restored stand because of higher ambient inorganic N availability. Analysis of covariance also suggested an effect of stand management: At a given level of soil inorganic N availability, the response of the soil microbial N to N addition was greater in the restored stand compared to the control stand ($P = 0.086$). The greater response of soil microbial N to N addition in the restored stand could reflect decreased competition for N between microorganisms and plant roots, as fine root biomass was significantly lower in the restored stand. Alternatively, thinning and burning could have increased the availability of some other limiting resource to the microbial biomass (Neary et al. 1999), such as carbon (Hart et al. 1994), allowing a response of soil microbial N to added N despite already higher inorganic N availability. Overall, these results

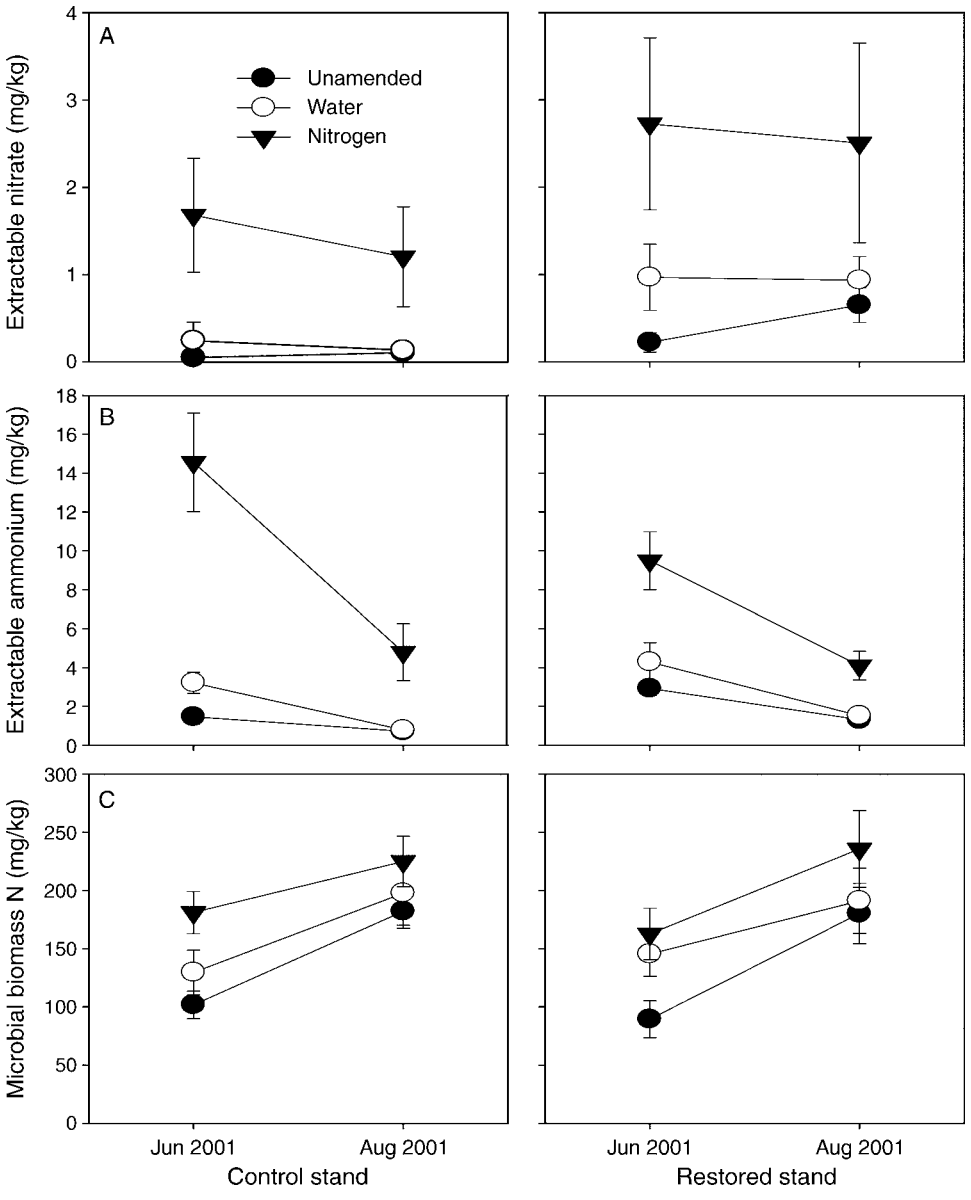

FIG. 1. (A) Extractable soil nitrate, (B) ammonium, and (C) microbial N in the unamended plots (solid circles), water-amended plots (open circles), and nitrogen-amended plots (solid triangles), in forest stands under control (left panels) and restored (right panels) conditions. Values are means ± SE ($n = 10$) for June and August 2001 samples for the 0–5 cm mineral soil depth.

provide only partial support for our expectation that the increase in N availability caused by restoration would be sufficient to alleviate N limitation of soil microbial N.

In contrast with this pattern indicating a declining response to added N, responses of soil microbial N to added water did not consistently vary with soil water content. (The effect of soil water content as covariate was $P = 0.336$; the effect of restoration was $P = 0.642$; Fig. 2B.) If anything, after omitting a single outlier (marked with an asterisk in Fig. 2B), the response of soil microbial N to added water was enhanced at higher soil water content (effect of soil water content as covariate, $P = 0.041$), opposite to the response we observed to added N. (Differences between stands were still not apparent after omitting the outlier from the analysis, $P = 0.416$.) Even though restoration increased soil water content (Fig. 2B and Hart et al. 2006), responses of soil microbial N to added water were unaltered by restoration. These results are not consistent with our hypothesis that responses to added water would be smaller in the restored stand.

Potential net nitrogen mineralization

Water addition did not affect potential net N mineralization ($P = 0.140$), whereas N addition increased it substantially ($P < 0.001$; Fig. 3A). Potential

TABLE 1. Statistical results from ANOVA tests for differences in extractable and microbial nitrogen in response to stand management and manipulations of soil water and nitrogen availability.

Form of nitrogen	Stand management			Water addition				Nitrogen addition			
	SM	T	T×SM	H_2O	H_2O×SM	T×H_2O	T×H_2O×SM	N	N×SM	T×N	T×N×SM
NO_3^-	0.086	0.689	0.427	0.024	0.129	0.083	0.403	0.027	0.738	0.440	0.800
NH_4^+	0.689	<0.001	0.336	0.011	0.836	0.033	0.669	<0.001	0.072	<0.001	0.043
Microbial	0.918	<0.001	0.777	0.085	0.703	0.229	0.482	0.006	0.709	0.963	0.429

Notes: Results are shown from the 0–5 cm depths for two sampling times. The first three columns show *P* values from repeated-measures ANOVAs examining effects of stand management (SM), time (T), and their interaction. The remaining columns show results from split-plot repeated-measures ANOVAs assessing the effects of water addition (H_2O) and nitrogen addition (N), and their interactions with time and stand management. See *Materials and Methods* for further details on the statistical analyses and experimental design. Means and standard errors are shown in Fig. 1.

net N mineralization nearly doubled in the restored stand compared to the control ($P = 0.001$), and there were no treatment by stand management interactions. Potential net N mineralization showed no tendency to decline in response to added N as background N availability increased; the slope of the regression line was positive (0.35), though not significant ($P = 0.152$, $r^2 = 0.111$; data not shown). Potential net nitrification increased with added N, but decreased with added water ($P = 0.019$, Fig. 3B).

Potential net nitrification was substantially higher in the restored stand (Fig. 3B). In this same experiment, in situ net nitrification (also 0–15 cm mineral soil depth) was also found to be higher in the restored stand compared to the control stand, yet in situ net N mineralization was unaffected, because restoration increased the proportion of mineralized N that was nitrified (Hart et al. 2006). Thus, our finding of higher potential net N mineralization was not reflected in higher rates observed in situ. Together, these results indicate that stand restoration increases nitrification, and can increase potential net N mineralization, though this may not be manifest as increased net N mineralization in situ. Including initial inorganic N pool size as a covariate eliminated the significant effect of stand management on potential net nitrification ($P = 0.509$), suggesting that N made available through restoration can explain the higher rates of potential net N mineralization that we observed in the restored stand compared to the control stand.

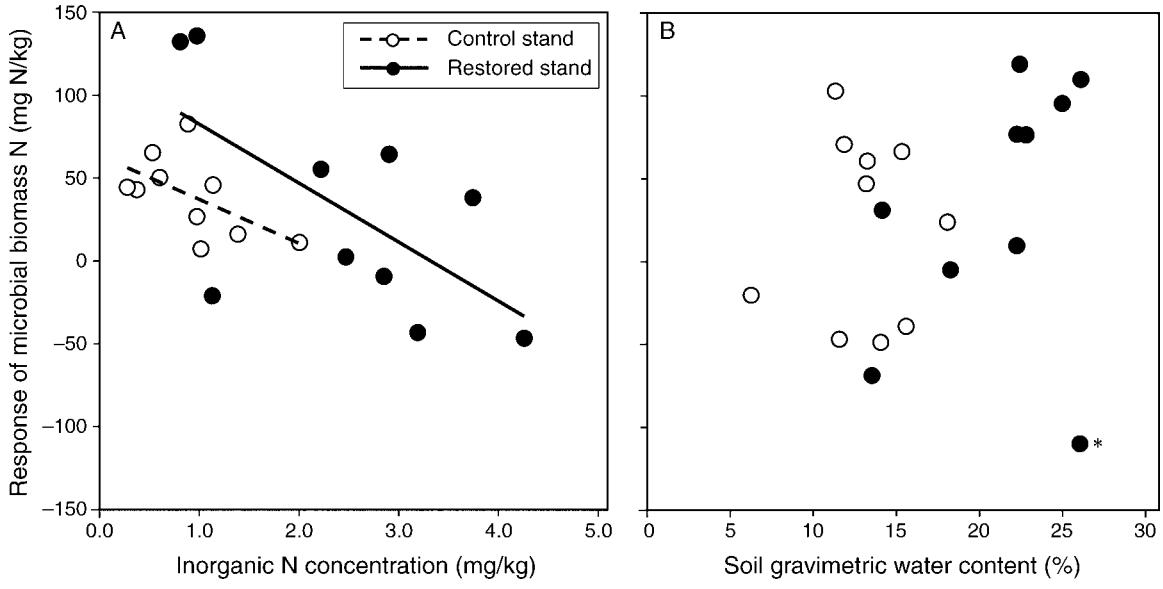

FIG. 2. Responses of soil microbial nitrogen (N) to (A) inorganic N and (B) water additions as functions of (A) ambient inorganic N concentration and (B) soil water content, for the control stand (open circles) and restored stand (solid circles). For panel A, lines show significant least-squares linear regressions: responses to added N declined with increasing inorganic N concentration in both the control stand (dashed line; response = −26[N] + 64, $r^2 = 0.32$) and in the restored stand (solid line; response = −36[N] + 118, $r^2 = 0.40$). The absolute responses of the soil microbial N pool were calculated as the difference between treatment and control pairs for individual plots: for N (panel A), the response is the difference between microbial N in the N-amended and water-amended plots, because the N-amended plots also received water (see *Methods*); for water (panel B), the response is the difference between microbial N in the water-amended and unamended plots. A possible outlier in panel B is marked with an asterisk.

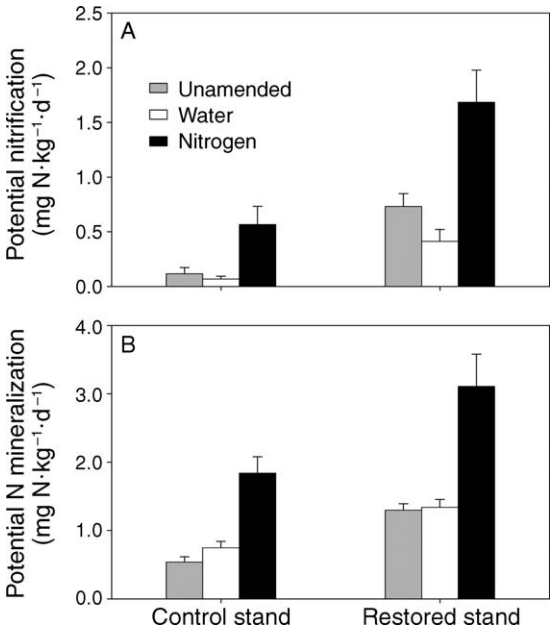

FIG. 3. Potential rates of net mineralization and nitrification in control and restored stands, as influenced by water and inorganic nitrogen amendments, for soils sampled in August (0–15 cm mineral soil depth). Means (bars) + 1 SE (vertical lines) are shown ($n = 10$).

In the restored stand, potential net nitrification exhibited larger changes in response to water (management × water interaction, $P = 0.075$) and N addition (management × N interaction, $P = 0.035$) compared to the control stand (Fig. 3B). The enhancement of potential net nitrification was actually greater at higher background levels of inorganic N availability ($P = 0.010$, $r^2 = 0.317$; Fig. 4). This positive interaction between added N and restoration is similar to findings for a loblolly pine plantation (Gurlevik et al. 2004). Increased N availability caused by restoration was insufficient to alleviate N limitation of nitrification. The effect of N addition on nitrification in ponderosa pine forests can saturate with increasing N inputs, as shown for a ponderosa pine forest in California receiving high rates of atmospheric N deposition (Fenn et al. 2005). Other pine forests exhibit little evidence for such saturating responses: in *Pinus sylvestris*, NO_3^- accumulation increased with urea additions from 0 to 150 kg N/ha, with no evidence of saturation (Aarnio and Martikainen 1995). At our site, saturation of the response of nitrifiers to high NH_4^+ availability may occur only at NH_4^+ concentrations higher than we observed. Furthermore, restoration through thinning and burning may liberate other soil resources, favoring nitrifiers and allowing a sustained increase with NH_4^+ availability. Because nitrification is a key process regulating ecosystem N mobility (Robertson 1982), the positive interaction we found suggests that the combination of thinning, burning, and N additions could alter the distribution of N within ecosystem components, potentially increasing N losses.

Across both stands, potential net N mineralization increased with average soil water content measured in the field, and this relationship held from under 10% to well over 30% gravimetric soil water content (Fig. 5A). This relationship indicates water limitation of the mineralizable soil N pool over a wide range of ambient soil water contents in these forests, including the ranges spanned by the stand management activities we examined here. Restoration caused a greater enhancement of soil water content (23.7 ± 1.1% [mean ± SE] for the restored stand vs. 15.1 ± 0.8% for the control stand, means across all U, W, and WN plots) than did experimental water addition (17.2 ± 1.3% for the U treatment vs. 21.7 ± 1.3% for the W treatment). There are several possible explanations for this difference: (1) reduced evapotranspiration with restoration (Simonin et al. 2006) may have exceeded the experimental water addition; (2) water amendment may have stimulated transpiration, reducing the impact on observed soil water content; or (3) movement of the added water outside the relatively small plots receiving the amendment treatment could have diluted the effect of water addition on observed soil water content. Whatever the mechanism, it appears that the amount of water added experimentally was insufficient to elicit a detectable increase in potential net N mineralization (Fig. 3A), despite apparent water limitation of the process (Fig. 5A). Alternatively, stand restoration may have increased availability of other resources limiting to potential net N

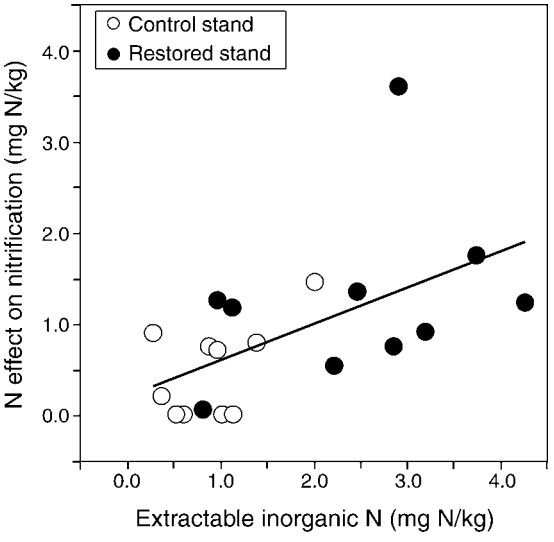

FIG. 4. Relationship between inorganic nitrogen (N) concentrations (average from both sampling dates for the water-amended plots) and the effect of added N on net nitrification during the laboratory incubation (calculated as the difference between potential net nitrification in the N + water-amended and the water-amended plots). Open circles show results from the control stand, and solid circles show results from the restored stand.

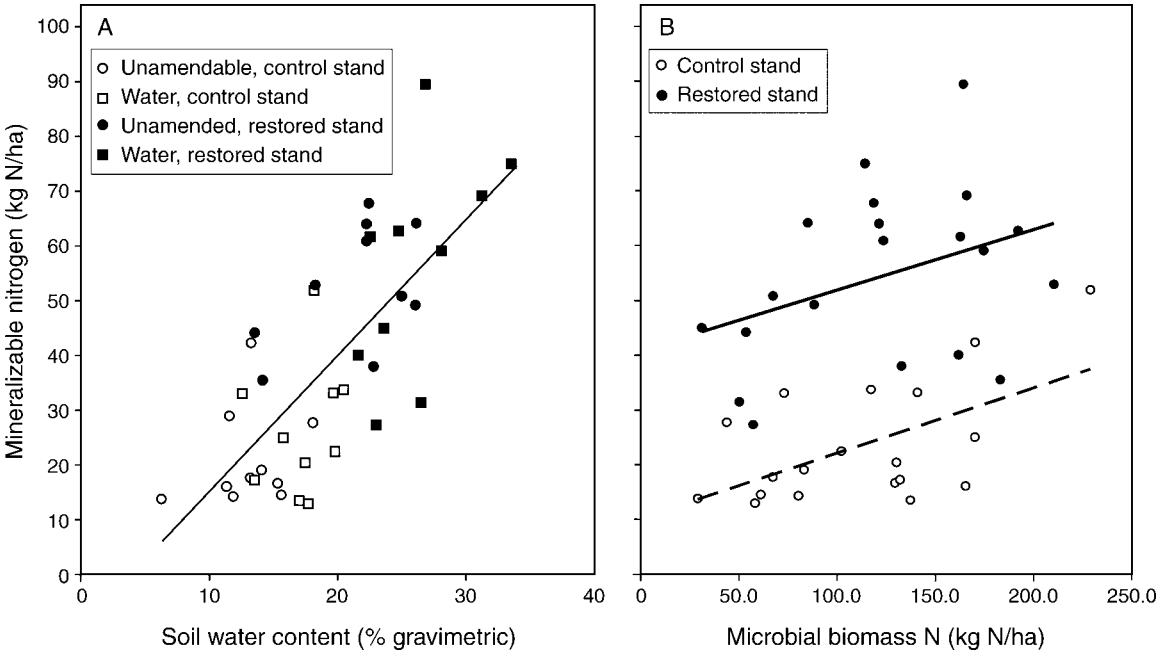

FIG. 5. Relationships between mineralizable nitrogen (N) pools and (A) soil gravimetric water content and (B) microbial N for the control and water-amended plots (N-amended plots were excluded; see *Methods*). In panel A, the least-squares linear regression for mineralizable N as a function of soil water content shown is: mineralizable N = 2.52 × soil water content − 9.83 ($r^2 = 0.548$, $P < 0.001$, $n = 40$). In panel B, the relationships shown between mineralizable N and microbial N are: for the control stand, mineralizable N = 0.12 × microbial N + 10.09 ($r^2 = 0.32$, $P = 0.012$, $n = 19$); and, for the restored stand, mineralizable N = 0.11 × microbial N + 40.76 ($r^2 = 0.14$, $P = 0.105$, $n = 20$).

mineralization. Potential net N mineralization was also positively correlated with soil microbial N, though the relationship was independent of the effect of stand management (Fig. 5B). Net rates of N transformations were also unrelated to soil temperature (data not shown), indicating that the slightly warmer soil temperatures in the restored compared to the control stand (average of 0.8°C for U plots [P. C. Selmants et al., *unpublished manuscript*]) did not influence potential net N mineralization.

Fine roots

Water addition enhanced total fine root biomass and fine root C content (Tables 2 and 3), consistent with past findings that water limits net primary productivity in these forests (Klemmedson et al. 1990, Hart et al. 2006). Water addition did not significantly affect total fine root N content. Fine root biomass and the amounts of N and C contained in fine roots were also insensitive to added N in both the control and restored stands. Thus, fine root growth appears to be more strongly limited by water than by N, at least on the scale of our experimental investigation and comparing a 100% increase in precipitation with a 45 g N/m^2 increase in inorganic N availability. Past measurements indicate N limitation of aboveground primary productivity in these forests (Wagle and Beasley 1968, Heidmann 1985); belowground responses may be disproportionately smaller (Vogt et al. 1986, Gower et al. 1992). Fine root biomass was substantially lower in the restored compared to the control stand, likely reflecting mortality caused by stand thinning. Nitrogen concentrations in fine roots were higher in the restored stand, especially in the unamended plots, such that N stocks in roots were similar among stands in this treatment despite the large reduction in fine root biomass. By reducing root biomass directly, it is likely that restoration reduced competition among roots for water, and possibly for other limiting resources as well. In addition, restoration may have reduced competition for N between roots and soil microorganisms (Kaye and Hart 1997).

Nitrogen concentrations in ponderosa pine fine roots were unaffected by water or N amendments. Carbon concentrations in ponderosa pine fine roots were higher in the restored stand and were lower with added N. Effects on carbon to nitrogen (C:N) ratios in fine roots of ponderosa pine were dominated by changes in N concentration; C:N ratios were consistently lower in the restored stand compared to the control stand, but were unaffected by water or N amendments. Therefore, restoration increased root N concentration more than did the N fertilization treatment, suggesting that reduced competition for N is at least as important in determining root N concentration as is the direct increase of N availability with large inorganic N additions.

TABLE 2. Mean (±SE) biomass, carbon (C), and nitrogen (N) stocks, C and N concentrations, and C:N ratios for ponderosa pine fine root biomass, forest floor, and mineral soil in response to stand management and water and N additions.

Parameters	Control			Restored		
	Unamended	+Water	+Nitrogen	Unamended	+Water	+Nitrogen
Roots						
Biomass (kg/ha)	2479 ± 527	4380 ± 1040	4837 ± 815	1710 ± 558	2711 ± 936	1733 ± 414
N stock (kg/ha)	8.65 ± 1.74	14.99 ± 3.82	18.09 ± 3.02	14.73 ± 5.29	16.54 ± 6.08	9.91 ± 1.80
C stock (kg/ha)	733 ± 143	1423 ± 341	1269 ± 194	677 ± 225	1022 ± 355	545 ± 129
[N] (mg/kg)	3.5 ± 0.4	3.5 ± 0.8	04.4 ± 0.9	8.3 ± 1.5	6.5 ± 2.0	6.3 ± 0.8
[C] (mg/kg)	311 ± 19	328 ± 18	279 ± 23	387 ± 20	380 ± 27	320 ± 27
C:N (kg/kg)	95.2 ± 10.9	123.3 ± 27.3	76.6 ± 10.1	53.9 ± 14.1	67.4 ± 14.5	53.4 ± 5.8
Forest floor						
Mass (Mg/ha)	93.9 ± 26.5	61.1 ± 9.6	56.0 ± 6.8	34.8 ± 14.7	44.8 ± 9.9	35.6 ± 10.5
N stock (kg/ha)	630 ± 110	476 ± 79	504 ± 75	190 ± 83	232 ± 57	217 ± 88
C stock (Mg/ha)	34.4 ± 12.9	20.8 ± 4.5	20.0 ± 3.9	6.6 ± 2.4	8.6 ± 2.5	6.3 ± 2.3
[N] (mg/kg)	7.7 ± 0.5	7.9 ± 0.5	7.9 ± 0.6	5.1 ± 0.3	5.0 ± 0.5	6.0 ± 0.8
[C] (mg/kg)	334 ± 36	338 ± 38	344 ± 35	210 ± 21	189 ± 21	213 ± 38
C:N (kg/kg)	46.2 ± 7.6	42.6 ± 4.2	38.6 ± 3.3	41.2 ± 3.2	39.1 ± 3.2	35.0 ± 3.0
Mineral soil						
N stock (kg/ha)	1450 ± 144	1462 ± 152	1792 ± 158	1773 ± 173	1660 ± 161	1768 ± 123
C stock (Mg/ha)	30.2 ± 2.6	33.7 ± 3.5	35.4 ± 3.0	37.1 ± 3.9	35.7 ± 4.1	38.0 ± 3.3
[N] (mg/kg)	1.1 ± 0.1	1.2 ± 0.1	1.3 ± 0.1	1.3 ± 0.1	1.2 ± 0.1	1.5 ± 0.1
[C] (mg/kg)	23.1 ± 1.9	25.9 ± 2.2	25.9 ± 2.5	27.3 ± 2.8	26.4 ± 3.6	32.0 ± 3.1
C:N (kg/kg)	21.16 ± 0.55	22.41 ± 0.79	19.97 ± 0.62	20.96 ± 0.85	21.43 ± 0.82	21.23 ± 0.63

Forest floor and mineral soil

Forest floor mass, C stock, and N stock were significantly reduced by restoration (Tables 2 and 3). This is likely a consequence of burning, which frequently reduces forest floor mass and causes N losses (MacKenzie et al. 2004, Certini 2005). Probably because of mineral soil adhering to or mixing with the forest floor to a greater degree in the restored compared to the control stand, the restoration treatment also reduced C and N concentrations in the forest floor. For this reason, the reductions in forest floor C (71%) and N (60%) stocks caused by restoration were more pronounced than the reduction in total forest floor mass (45%; Tables 2 and 4). Nitrogen addition had no effect on forest floor mass, C stock, and N stock. The main effects of water addition were also not significant, although water tended to reduce forest floor mass and N stock in the control stand and increase these in the restored stand (interaction term, Table 3).

Stocks and concentrations of C and N in mineral soil were insensitive to added water and to stand management (Tables 2 and 3). Nitrogen addition increased both concentrations and stocks of N in mineral soil. Nitrogen addition reduced the C:N ratio of mineral soil in the control stand. However, in the restored stand, the (nonsignificant) increase in soil %C compensated for the significant increase in %N, resulting in no change in soil C:N.

The total mass of N sampled in the plots (forest floor, root, microbial, extractable, mineralizable plus other soil N) increased with N addition ($P = 0.041$), but was unchanged by water addition ($P = 0.230$). Total N mass in the restored stand did not significantly differ from the control stand ($P = 0.506$); the significant reduction in forest floor N content was partially compensated by the nonsignificantly higher stocks of mineral soil N in the restored stand. The lower N mass in the forest floor could reflect the N losses that occurred with restoration, yet the nonsignificant increase in mineral soil N indicates the potential for such losses to be buffered in deeper soil layers.

TABLE 3. Statistical results from ANOVA tests for differences in the mass and carbon (C) and nitrogen (N) stocks (kg/ha) and concentrations (kg/kg × 100%) in ponderosa pine fine roots, forest floor, and mineral soil.

Parameters	SM	H_2O	$H_2O \times SM$	N	N × SM
Roots					
Biomass	0.002	0.057	0.534	0.725	0.338
N stock	0.960	0.291	0.552	0.605	0.163
C stock	0.106	0.037	0.463	0.150	0.450
% N	<0.001	0.377	0.389	0.105	0.592
% C	0.009	0.820	0.604	0.053	0.840
C:N	0.006	0.325	0.726	0.414	0.443
Forest floor					
Mass	0.061	0.358	0.093	0.266	0.749
N stock	0.006	0.270	0.061	0.902	0.658
C stock	0.012	0.273	0.150	0.516	0.751
% N	<0.001	0.799	0.694	0.083	0.942
% C	0.002	0.625	0.469	0.544	0.723
C:N	0.430	0.306	0.775	0.100	0.977
Soil					
N stock	0.371	0.568	0.488	0.036	0.266
C stock	0.306	0.808	0.361	0.289	0.942
% N	0.346	0.940	0.203	0.007	0.410
% C	0.287	0.503	0.228	0.137	0.142
C:N	0.973	0.276	0.479	0.090	0.049

Notes: The table gives P values for split-plot ANOVAs testing for effects of stand management (SM), additions of water (H_2O) and nitrogen (N), and their interactions with restoration.

TABLE 4. Mass (g/m^2) of the ^{15}N-depleted tracer recovered in soil pools and during laboratory incubations, and the percentage of each pool derived from the ^{15}N tracer in the nitrogen-amended plots (NDFF) in the control and restored stands.

Source	Mass (g/m^2)			NDFF (%)		
	Control	Restored	*P*	Control	Restored	*P*
Soil N pools						
NO_3^-	0.04 ± 0.02	0.05 ± 0.01	0.777	34.2 ± 5.5	37.8 ± 3.4	0.646
NH_4^+	0.12 ± 0.02	0.16 ± 0.03	0.437	43.3 ± 2.9	37.3 ± 4.5	0.319
Extractable	0.55 ± 0.08	0.59 ± 0.12	0.782	30.7 ± 3.2	35.6 ± 4.8	0.414
Microbial	4.30 ± 0.61	3.50 ± 0.61	0.379	28.0 ± 2.2	22.1 ± 2.8	0.124
Fine roots	0.68 ± 0.12	0.38 ± 0.06	0.039	37.3 ± 3.0	42.8 ± 3.6	0.345
Forest floor	3.32 ± 0.31	1.96 ± 0.59	0.059	7.6 ± 0.9	11.0 ± 1.3	0.053
Mineral soil	12.10 ± 1.80	10.40 ± 1.80	0.527	6.9 ± 1.0	5.8 ± 0.8	0.409
Laboratory incubations						
Ammonia	1.93 ± 0.25	1.59 ± 0.39	0.470	35.7 ± 2.2	27.6 ± 5.0	0.155
Nitrogen	0.75 ± 0.23	2.05 ± 0.53	0.038	28.8 ± 4.2	32.8 ± 5.2	0.555
Mineral soil	2.68 ± 0.35	3.64 ± 0.85	0.310	35.3 ± 2.5	31.7 ± 4.5	0.495

Notes: Values are means ± SE ($n = 10$). *P* values from one-way ANOVAs comparing the two stands are also shown.

^{15}N tracer distribution and recovery in control and restored stands

Where they occurred, differences between control and restored stands in the distribution of the depleted-^{15}N tracer reflected patterns observed for total N. Restoration increased the amount of depleted-^{15}N recovered as NO_3^- in the potential net N mineralization assay (Table 4), reflecting the effect of restoration on net nitrification. Restoration increased the percentage of forest floor N that was derived from the ^{15}N-depleted fertilizer, but at the same time decreased the mass of depleted ^{15}N recovered in the forest floor (Table 4). Thus, while forest floor material in the restored stand was a stronger sink for N on a relative basis (e.g., per mass of forest floor material), the absolute recovery of depleted ^{15}N in the restored stand was lower due to the reduction in total forest floor mass. Restoration also reduced recovery of depleted ^{15}N in fine roots, reflecting the strong reduction in fine root biomass and N content. Recovery of depleted ^{15}N in other pools examined (extractable NO_3^-, extractable NH_4^+, extractable total inorganic N, extractable N, microbial N, and total N in the mineral soil) were statistically indistinguishable between the two stands (Table 4). Mean total recovery of the depleted ^{15}N tracer was lower in the restored stand (125 ± 18 kg N/ha) compared to the control stand (156 ± 18 kg N/ha), but this difference was not significant ($P = 0.233$).

Of the labeled N added, we recovered 18% in the restored stand and 23% in the control stand, lower recovery than that observed for some other forest soils (Binkley and Hart 1989, Hart et al. 1993, Perakis and Hedin 2001). The high rate of N additions and added water likely increased leaching and gaseous losses of N. Distribution of the ^{15}N-depleted tracer also suggested relatively rapid rates of N cycling; except for forest floor and mineral soil, the percentage of total N derived from the ^{15}N-depleted tracer was relatively similar among ecosystem compartments (22–43%, Table 4), indicating that sufficient N exchange had occurred among these pools to approach steady-state distribution of the ^{15}N-depleted tracer. Another mechanism contributing to the low tracer recovery could have been that the added N was taken up by fine roots and distributed out of the small plots.

Natural abundance of $\delta^{15}N$

The restored stand had lower $\delta^{15}N$ values in extractable NO_3^-, but exhibited higher $\delta^{15}N$ values in most other soil N pools assessed: extractable NH_4^+, total inorganic extractable N, total extractable N, soil microbial N, and the NH_4^+ produced in the laboratory incubation (Table 5). The restored and control stands did not differ in the $\delta^{15}N$ signatures of ponderosa pine fine roots, the forest floor, and total mineral soil, suggesting that the differences observed in the more rapidly cycling soil N pools did not merely reflect spatial variation. Rather, these patterns could indicate a more open N cycle in the restored stand; nitrification, a strongly fractionating process (Delwiche and Steyn 1970, Feigin et al. 1974, Yoshida 1988), produces NO_3^- with a ^{15}N-depleted signature, while leaving the remaining NH_4^+ pool enriched in ^{15}N. The overall enrichment in the total extractable and microbial N pools is consistent with greater N efflux out of these pools, indicating the potential for restoration to enhance N mobility (Robinson 2001, Dijkstra et al. 2006*a*, *b*). Leaching losses did not increase during the first two years after stand restoration in a similar experiment (Kaye et al. 1999). It is not known whether restoration increases N gas fluxes from soil. Furthermore, internal sinks for mobilized N, such as uptake by understory grasses and remaining ponderosa pine trees, the soil microbial biomass, and the mineral soil, may create an effective buffer against N losses. Water addition had no effect on natural abundance $\delta^{15}N$ of any ecosystem compartment examined (Table 5). Short-term manipulations of water availability may be insufficient to create experimentally the patterns observed along precipitation gradients, where plant and soil $\delta^{15}N$ decrease with increasing precipitation (Mariotti et al. 1980, Austin and Vitousek 1998, Handley et al. 1999, Schuur and Matson 2001, Amundson et al. 2003).

TABLE 5. Natural abundance $\delta^{15}N$ values (‰ vs. N_2 in air) from the unamended and water-amended plots in the control and restored stands.

Source	Control		Restored		*P*		
	Unamended	Water	Unamended	Water	Water	Management	Water × management
NO_3^-	1.58 ± 1.79	3.41 ± 0.64	−0.10 ± 0.85	−1.44 ± 0.98	0.825	0.006	0.159
NH_4^+	0.78 ± 0.71	−0.71 ± 0.94	5.05 ± 1.14	6.26 ± 2.17	0.919	<0.001	0.309
Inorganic	0.70 ± 1.06	0.56 ± 0.95	3.40 ± 0.80	3.48 ± 1.41	0.980	0.011	0.916
Extractable	3.00 ± 0.28	2.53 ± 0.49	3.38 ± 0.36	3.73 ± 0.52	0.891	0.071	0.335
Microbial	4.57 ± 1.55	4.91 ± 0.45	6.72 ± 0.53	7.94 ± 0.90	0.402	0.008	0.634
Ammonified	2.09 ± 0.36	0.36 ± 0.63	4.55 ± 0.90	3.94 ± 0.76	0.106	<0.001	0.430
Nitrified	1.39 ± 0.40	0.90 ± 2.36	−0.19 ± 0.39	1.61 ± 1.29	0.636	0.753	0.409
Mineralized	1.95 ± 0.32	0.22 ± 0.47	2.27 ± 0.58	2.97 ± 0.56	0.307	0.004	0.020
Forest floor	−0.48 ± 0.48	−0.49 ± 0.16	−0.43 ± 0.330	−0.30 ± 0.32	0.868	0.731	0.854
Roots	1.54 ± 1.28	−0.12 ± 2.56	1.19 ± 2.64	−0.21 ± 1.66	0.485	0.918	0.954
Mineral soil	5.57 ± 0.13	5.06 ± 0.31	4.84 ± 0.36	5.45 ± 0.33	0.860	0.565	0.069

Notes: Values for ammonified, nitrified, and mineralized N were calculated by mass balance using beginning and final $\delta^{15}N$ and inorganic N concentrations from the laboratory incubations. Because of the added ^{15}N tracer in the N plots, natural abundance data are not available for that treatment.

Summary of mechanisms

Restoration increased extractable NO_3^- and potential net N mineralization and nitrification, building on past work showing that thinning and burning in ponderosa pine forests often increase rates of N cycling and soil N availability (Kaye and Hart 1998, DeLuca and Zouhar 2000, Choromanska and DeLuca 2002, Gundale et al. 2005). A suite of mechanisms likely contributes to these responses to restoration and to interactions between restoration and water and N additions (Fig. 6). The direct effects of thinning on plant mortality above- and belowground cause a pulse of carbon input to soil (P. C. Selmants et al., *unpublished manuscript*), reduce leaf area and thus transpiring surface, causing increased soil water content (Hart et al. 2006, Simonin et al. 2006), and reducing plant nutrient uptake. Burning of slash and forest floor material increases soil nutrient availability directly, and may contribute to interactions between restoration and resource amendments that we observed: the stronger response of microbial N to increasing soil inorganic N concentrations, and the increasing response of nitrification to added N in the restored stand, for example. These mechanisms are consistent with the notion that ponderosa pine forests prior to Euro-American settlement exhibited more rapid rates of nutrient cycling, promoted by frequent burning and an active herbaceous understory community (Mutch et al. 1993, Moore et al. 1999).

We found only partial support for the hypothesis that thinning and burning, by increasing N and water availability, would alleviate water and N limitation of soil processes in the restored stand. Fine root growth exhibited water limitation in both restored and control stands. While responses of the soil microbial N pool to added inorganic N declined with increasing N availability (consistent with our hypothesis), restoration altered this relationship such that responses were greater at any given level of N availability (inconsistent with our hypothesis). This response suggests that restoration increased the availability of some other resource (Fig. 6). Furthermore, responses of the soil microbial N pool to added water, and responses of potential net N mineralization to added water and inorganic N, were just as great in the restored stand as in the control, and in some cases were even greater (e.g., net nitrification). Overall, our results show that stand thinning and burning does not reduce the sensitivity of belowground processes to N and water amendments, despite increasing the availability of these resources. If these results are general, combined increases in resource availability, via well above average precipitation years, atmospheric N deposition, or N fertilization, appear unlikely to elicit threshold shifts in belowground processes when combined with stand thinning and burning treatments.

Based on these responses, we postulate that restoration alleviated limitations of other soil resources in addition to N and water. Soil respiration increased with restoration (Hart et al. 2006) and with water addition (P. C. Selmants et al., *unpublished manuscript*), suggesting increased C availability to soil heterotrophic soil microorganisms. Other resources, such as soil phosphorus, could increase as well, as observed after burning (Neary et al. 1999, Hungate et al. 2003). In this way, multiple resource limitations may drive positive interactions between stand management and changes in resource availability caused by climatic and atmospheric change. These results point to the challenge of considering multiple resource interactions when examining biogeochemical consequences of forest management, atmospheric, and climatic change.

Management implications and future directions

The transition from "slow" to "more rapid" nutrient cycles warrants some consideration in the design of forest restoration strategies, especially regarding the potential for nutrient losses during the transition phase from the removal of "postsettlement" tree biomass to full understory recovery. We found symptoms of higher N losses in the thinned and burned stand, when

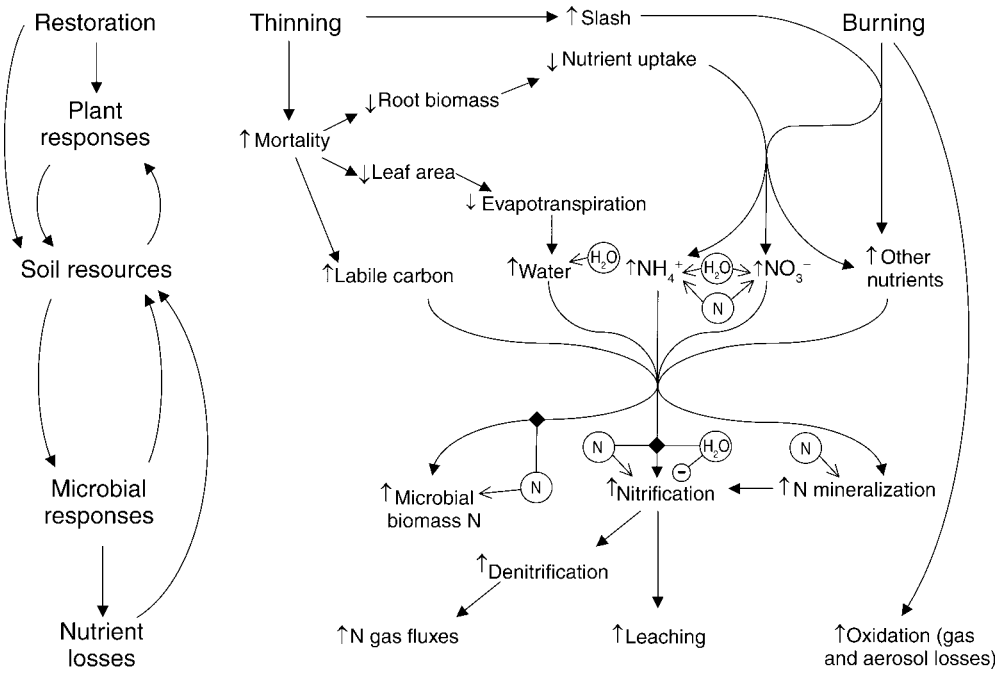

FIG. 6. Postulated and experimentally supported mechanisms through which forest restoration treatments (i.e., thinning and burning) affect soil nitrogen (N) cycling, and interactions with water and N amendments. The left flow chart shows a generic framework for scales of responses and feedbacks within the plant–soil system. Specific mechanisms are shown in the right flow chart, with the horizontal alignment indicating the scale at which mechanisms operate. Mechanisms for the effects of thinning and burning are indicated by arrows with solid heads and outlined heads, respectively, whereas effects of N and water supplementation are indicated by circled N and circled H_2O, respectively. Cases where N or H_2O were found to modify the responses to restoration are indicated by arrows with a diamond-shaped head.

combined with N and water additions. Higher natural abundance $\delta^{15}N$ signatures in most ecosystem N compartments, lower tracer recover in forest floor and fine roots, and higher rates of nitrification, both potential (this study) and in situ (Hart et al. 2006), all indicate a system with enhanced N mobility, and possibly higher N losses. On the other hand, the low net N transformation rates and semiarid climate typical of ponderosa pine forests can minimize N leaching (Kaye et al. 1999, Hart et al. 2006) and probably gaseous N losses as well. Future research testing whether thinning and burning enhances N losses would be valuable, possibly including a large-scale ^{15}N tracer study documenting ^{15}N recovery over a longer time period (e.g., Nadelhoffer et al. 2004). Such an experiment could be combined with seeding native herbaceous vegetation after thinning and burning, to test whether more rapid recovery of the understory vegetation would establish a sink for mobilized N and thereby minimize N losses. Forest managers contemplating the conversion of contemporary, closed-canopy ponderosa pine forests, containing large stocks of slowly cycling nutrients, to an open savanna with more rapid nutrient cycling should consider the potential for increased nutrient mobility and losses, especially when the understory vegetation biomass fails to increase dramatically as a result of the treatments, or when repeated interval burning is to be implemented as part of the management strategy (Wright and Hart 1997, Hart et al. 2006).

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