Water and Nutrient Outflow Following the Ecological Restoration of a Ponderosa Pine-Bunchgrass Ecosystem

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Abstract

In the late 1800s, fire suppression, livestock grazing, and a wet and warm climate led to an irruption of pine regeneration in *Pinus ponderosa* Laws. (ponderosa pine) forests of the southwestern United States. Pines invaded bunchgrass openings, causing stand structure changes that increased the number of stand-replacing fires. Ecological restoration, via thinning and prescribed burning, is being used to decrease the risk of stand-replacing fires and ameliorate other effects of pine invasion. The effects of aboveground restoration on belowground processes are poorly understood. We used a hydrologic model and soil water nutrient concentrations, measured monthly below the rooting zone, to estimate restoration effects on nutrient losses by leaching from a mature ponderosa pine forest near Flagstaff, Arizona. Replicated restoration treatments included thinning to pre-1880 stand densities (partial restoration), thinning plus forest floor fuel reduction followed by a prescribed burn (complete restoration), and an untreated control. Water outflow occurred only between January and May and was lowest from the control (47 and 28 mm in 1995 and 1996) and highest from the partial restoration treatment (67 and 59 mm in 1995 and 1996). The concentrations (typically <0.10 mg/ L) and estimated annual losses (<0.02 kg/ha) of NH_4^+-N, PO_4^{3-}-P, and organic P were similar among treatments. Nitrate and organic N concentrations were as high as 0.80 mg N/L; however, these concentrations and estimated annual losses (<0.13 kg N/ha) were similar among treatments. Our results suggest that restoration will not enhance nutrient loss by leaching or alter stream chemistry in ponderosa pine forests.

Introduction

Historically, ponderosa pine forests of the southwestern United States were composed of sparse clusters of trees (~50 trees per ha) surrounded by bunchgrass openings (Cooper 1960; Covington et al. 1994, 1997). Frequent (2–12 years) low-intensity fires, competition with grasses, and drought limited pine regeneration in the bunchgrass openings (Pearson 1950; White 1985; Savage et al. 1996; Swetnam & Baisan 1996). Following Euro-American settlement in the late 1800s, fire suppression, livestock grazing, and a wet and warm climate eliminated constraints on pine regeneration, allowing most bunchgrass openings to be filled with dense thickets of small pines. Consequently, the contemporary forest landscape (Fig. 1) typically has stand densities exceeding 1000 trees per ha, only 10%

Figure 1. The control treatment of the ecological restoration experiment at the Gus Pearson Natural Area near Flagstaff, Arizona. The high density of small ponderosa pines and low herbaceous biomass depicted here are typical of contemporary ponderosa pine forests of the southwestern United States. Most of the small trees established following Euro-American settlement of the area in the late 1800s.

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bunchgrass cover, and an increased frequency of stand-replacing fires (Weaver 1952; Covington & Moore 1994; Covington et al. 1994, 1997; Swetnam & Baisan 1996).

Ecological restoration is being used to decrease the number of stand-replacing fires, increase the production and diversity of herbaceous species, decrease mortality of old trees, and increase water and nutrient availability (Covington et al. 1997). In 1993 and 1994, a replicated restoration experiment was established to test effects of two restoration treatments on a mature ponderosa pine forest near Flagstaff, Arizona (Fig. 2). Restoration treatments included thinning to presettlement stand densities (partial restoration), and thinning in conjunction with forest floor fuel reduction and a prescribed burn (complete restoration). We previously reported that restoration treatments increased net N mineralization rates at this site (Kaye & Hart 1998). Elevated nutrient cycling rates caused by, or in conjunction with, reduced plant uptake have been shown to increase nutrient losses from some ecosystems (Likens et al. 1969; Vitousek & Melillo 1979; Vitousek et al. 1982). However, if nutrient immobilization into plant regrowth or microbial biomass is high, nutrient losses may not occur (Coats et al. 1976; Richter et al. 1982; Vitousek & Matson 1985; Knight et al. 1991).

Nutrient leaching following disturbance (in this case restoration treatment) is problematic when leachates pollute stream water or when a limiting nutrient is lost from the ecosystem. Soil leaching losses are most readily measured using the small watershed approach (Bormann & Likens 1967). However, this method is often not very useful in the semiarid Southwest because the bedrock is typically permeable to deep seepage, and precipitation patterns are so variable that stream water sampling and runoff quantification are difficult. Furthermore, estimates of treatment-induced changes in nutrient leaching using the small watershed approach require that the treatment be applied to an entire watershed, which is impractical for many restoration efforts. We coupled a hydrologic model that estimates water outflow with monthly measurements of nutrient concentrations in soil water below the rooting zone to estimate nitrogen (N) and phosphorus (P) exports from control and restoration treatments from April 1995 to March 1997. Because restoration increases net N mineralization rates (Kaye & Hart 1998), we hypothesized that N concentrations in soil water would be higher in restoration treatments relative to the control. Similarly, we hypothesized that nutrient outflow would be higher following restoration because reductions in leaf area should decrease evapotranspiration.

Figure 2. The partial (thinning only) and complete (thinning, forest floor manipulation, and a prescribed burn) restoration treatments of the ecological restoration experiment at the Gus Pearson Natural Area near Flagstaff, Arizona. Ecological restoration to presettlement conditions required the removal of most of the postsettlement tree biomass. The resulting stands had greater herbaceous biomass than the pretreatment stands and would likely support surface, rather than stand replacing fires.

Methods

Study Site and Treatments

The research was conducted in the Gus Pearson Natural Area within the U.S. Forest Service Fort Valley Experimental Forest, 10 km northwest of Flagstaff, Arizona. Mean annual precipitation is 577 mm, half of which falls as snow, and half as summer monsoonal rains (Schubert 1974; Savage et al. 1996). 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 *Pinus ponderosa* (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 (herbaceous species are listed in Kaye & Hart 1998). Before treatment, postsettlement trees covered approximately 80% of the area relative to 10% cover by grassy openings and presettlement pines (Fig. 1).

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 (five as partial restoration and five as complete restoration) to the plots closest to the buildings. The remaining five plots were assigned to the control, which was left untreated. The partial restoration treatment removed (via whole-tree harvesting) most of the aboveground postsettlement tree biomass from the site to test whether thinning alone could restore ecosystem structure and function. The complete restoration treatment included postsettlement tree removal, forest floor manipulation, and a prescribed burn and was designed to test whether ecosystem structure and function could be restored quickly through intense manipulations (Covington et al. 1997). Forest floor manipulation included raking aside the Oi layer and removing the Oa and Oe layers from the site. The Oi layer (two to four years 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. Thinning was implemented in the fall of 1993 and the prescribed burn in the fall of 1994. Figure 2 includes both partial and complete restoration plots following treatment. More details on the treatments and fire are presented 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 × 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).

Soil Nutrient Concentrations

Porous ceramic cup (~1.1 μm openings) tension lysimeters (Soilmoisture Equipment Corporation, Santa Barbara, California, U.S.A.) were used to collect soil water below the rooting zone. A lysimeter was installed at a fixed distance (4 m) but random direction from the center of each subplot, unless coarse fragments or bedrock prevented augering a hole to a 150 cm depth below the ground surface. If such an obstruction was encountered, adjacent locations were probed with a metal rod along the circumference of the subplot until a 150 cm depth was reached, or until the greatest soil depth for that subplot was determined. Once the sampling location was established, a hole was dug using a bucket auger. Lysimeter porous cups were firmly placed in silica flour (200 mesh) that had been poured into each hole, and each hole was then filled with a slurry made from the original soil. Depths of porous cups ranged from 70 to 150 cm below the ground surface, which is below almost all of the fine roots and most of the coarse roots at this site. All lysimeters were installed by January 1995 and sample collection began immediately. Here we report data beginning in April 1995 to avoid possible effects of installation disturbance on nutrient concentrations (Vitousek et al. 1982).

On the 15th of each month, a 50 kPa vacuum was applied to each lysimeter. Twenty-four hours later, the vacuum was released, water in the lysimeter was collected, the mass of the collection was recorded, and the sample was frozen until analyses began. Ammonium (NH_4^+) and nitrate plus nitrite ($NO_3^- + NO_2^-$) concentrations were determined on a Lachat AE flow Injection Autoanalyser (Lachat Instruments, Inc., Milwaukee, Wisconsin, U.S.A.) using the indophenol-blue (Lachat Instruments, Inc. 1990) and cadmium reduction-diazotiation (Lachat Instruments, Inc. 1992*a*) methods, respectively. Because NO_2^- levels were negligible, ($NO_3^- + NO_2^-$) are reported as NO_3^-. Total N (organic + NH_4^+) and P (organic + PO_4^{3-}) were determined by modified micro-Kjeldahl digestion (Parkinson & Allen 1975; Pace et al. 1982) and flow injection analysis using the salicylate (Lachat Instruments, Inc. 1992*b*) and molybdate-ascorbic acid (Lachat Instruments, Inc. 1992*c*) methods, respectively. Organic N and organic P were determined by subtracting NH_4^+-N and PO_4^{3-}-P concentrations from the total N and P concentrations, respectively. Nutrient concentrations from each subplot were weighted by multiplying the concentration in the subplot by the ratio of the mass of water collected in that subplot to the total mass of water collected in the plot on that sampling date.

Some authors have found that porous ceramic cups adsorb PO_4^{3-}-P (Hansen & Harris 1975; Nagpal 1982; Bottcher et al. 1984) while others have found no adsorption (Levin & Jackson 1977). Despite these mixed results, ecologists frequently use ceramic cup lysimeters to estimate P leaching (Adams & Attiwill 1991; Chorover et al. 1994; Johnson et al. 1997) because alternative materials (Teflon and fritted glass) are fragile, expensive, and perform poorly in unsaturated soils (Bottcher et al. 1984; Litaor 1988). We caution that the PO_4^{3-} leaching values reported here may be underestimated due to PO_4^{3-} adsorption by the lysimeter ceramic cups.

Hydrologic Model

The models MT-CLIM (Running et al. 1987; Glassy & Running 1994) and Forest-BGC (Running & Coughlan 1988) were used to calculate water outflow from the plots. MT-CLIM was used to calculate daily incoming solar radiation from inputs of daily minimum and maximum air temperature, dewpoint, precipitation, latitude (35.26°), aspect (220.0°), slope (1.13°), elevation (2205 m), and east and west horizons (both 0.0°). Daily minimum and maximum air temperatures were measured at one point within each treatment (1 m height) using a CR10 Campbell Scientific datalogger and radiation-shielded thermistors (Campbell Scientific Inc., Logan, Utah, U.S.A.). Precipitation was measured in an open area between plots using the same datalogger and an unheated tipping bucket rain gauge (Texas Electronics, Inc., Dallas, Texas, U.S.A.). When air temperatures were below 0°C, we used snow-water equivalent data from the Bellemont, Arizona National Oceanic and Atmospheric Administration (NOAA) weather station. We used a linear regression of dewpoint versus night minimum air temperature from the Flagstaff, Arizona NOAA weather station (dewpoint = 0.7 * minimum air temp + 2.51; $r^2 = 0.63$; $n = 359$) to estimate dewpoint (Running et al. 1987; Glassy & Running 1994). The Flagstaff and Bellemont weather stations are similar in elevation to, and about equidistant from (~15 km) our site. The daily solar radiation output from MT-CLIM was input into Forest-BGC along with all MT-CLIM input parameters, initial snowpack, initial soil water content, soil water holding capacity (1600 m^3/ha), leaf carbon (C), and specific leaf area. We modelled initial water content and snowpack by simulating hydrologic fluxes beginning in July 1994 when soil water content was at a minimum (450 m^3/ha) and no snowpack was present. The Forest-BGC model was run separately for each plot and year (1995, 1996, and 1997) using field-based estimates of leaf biomass measured in that plot and year. Soil water holding capacity (i.e., plant available water in Forest-BGC) was estimated from the difference between volumetric water content in the upper 30 cm of mineral soil at field capacity and the minimum soil water content observed in this layer during the year (typically late June; Feeney 1997). Leaf C was determined by adding grass and pine foliar C (M.M. Moore, P.Z. Fulé, and W.W. Covington, Northern Arizona University, Flagstaff, Arizona, U.S.A., unpublished data, 1994–1996, and assuming C is 50% of mass) for each plot. The specific leaf area (SLA) for grasses was 42.0 m^2/kg, which is the mean of values reported for the two most common grasses at our site (*Sitanion hysterix* (Nutt.) and *Muhlenbergia montana* (Nutt.) Hitchc.; Naumburg 1996). The SLA for pines was 9.0 m^2/kg (Stone 1997). The SLA for a plot was determined using the biomass-weighted mean of pine and grass SLAs. Forest-BGC multiplied SLA (per unit C) by foliar C to determine the leaf area index for each plot (Table 1). The daily water outflow values from Forest-BGC were summed to produce monthly estimates. Monthly nutrient losses were determined by multiplying mass-weighted concentrations (see above) measured mid-month by modeled water outflow estimates for that month.

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 repeated measures analysis of variance (ANOVA) with canopy type and treatment as factors. 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 Geographic Information System (GIS). This GIS contained 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 repeated measures ANOVA with treatment as the factor. A factorial ANOVA was used for cumulative losses. 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 =

Table 1. All-sided leaf area index (LAI) and export of nutrients and water from the Gus Pearson Natural Area near Flagstaff, Arizona. Data are means (and one standard error, $n = 5$). For a given year, treatments with different superscripted lowercase letters were statistically different ($p < 0.10$). When no lowercase letters are given, values are not statistically different.

	April, 1995–March, 1996			*April, 1996–March, 1997*		
Parameter	*Control*	*Partial Restoration*	*Complete Restoration*	*Control*	*Partial Restoration*	*Complete Restoration*
LAI (m^2/m^2)	8.5 (0.2)^b	5.2 (0.2)^a	5.0 (0.5)^a	8.3 (0.2)^b	5.1 (0.6)^a	4.4 (0.3)^a
Water (mm)	47 (1)^a	67 (3)^b	62 (7)^b	28 (1)^a	59 (8)^b	59 (16)^b
NH_4^+-N (kg/ha)	0.001 (0.000)	0.000 (0.000)	0.002 (0.001)	0.000 (0.000)	0.000 (0.000)	0.001 (0.001)
NO_3^--N (kg/ha)	0.004 (0.003)	0.025 (0.019)	0.123 (0.110)	0.000 (0.000)	0.088 (0.062)	0.001 (0.001)
Organic-N (kg/ha)	0.020 (0.002)	0.054 (0.024)	0.120 (0.114)	0.004 (0.003)	0.037 (0.017)	0.058 (0.035)
Total-N (kg/ha)	0.024 (0.005)	0.080 (0.042)	0.245 (0.224)	0.004 (0.003)	0.125 (0.077)	0.060 (0.034)
PO_4^{3-}-P (kg/ha)	0.007 (0.002)	0.010 (0.003)	0.010 (0.003)	0.015 (0.010)	0.007 (0.001)	0.010 (0.004)
Organic-P (kg/ha)	0.002 (0.001)	0.007 (0.006)	0.072 (0.070)	0.000 (0.000)	0.003 (0.002)	0.016 (0.015)
Total-P (kg/ha)	0.009 (0.003)	0.017 (0.006)	0.082 (0.070)	0.015 (0.010)	0.011 (0.003)	0.026 (0.019)

0.10 significance level (version 4.5, Abacus Concepts, Inc., Berkeley, California, U.S.A.).

Results and Discussion

We are unable to assess quantitatively if the water outflows from our treated and control plots predicted by FOREST-BGC are accurate. However, water outflow predicted by FOREST-BGC for hypothetical forests in Florida, Tennessee, and Wisconsin were similar to actual measurements from gauged watersheds in those forest types (Running & Coughlan 1988). Furthermore, for our site, FOREST-BGC accurately predicted the relative volume of soil water collected in tension lysimeters placed below the rooting zone; very little if any water was collected in lysimeters during periods when the model predicted no outflow, while large volumes of water were collected during the months of predicted high outflow (data not shown). Hence, we feel that the modeled quantities and temporal patterns of water outflow are reasonably accurate and precise.

Estimated monthly water outflow (Fig. 3) and annual water outflow (Table 1) were greater in the complete and partial restoration treatments than the control. Water outflow was limited to the late winter and early spring months. Apparently, summer monsoonal rains were insufficient to saturate the soil profile and result in deep percolation, a result supported by measurements of volumetric soil water content during this period (Feeney 1997). Our estimates of water loss (Table 1) are lower than the 80-year annual mean (193 mm) estimated by Savage et al. (1996) using a modified Thornthwaite-Mather water balance model parameterized for the same site. Total precipitation was 347 mm during the April 1995–March 1996 period and 406 mm during the April 1996–March 1997 period, which are considerably below the 80-year mean annual precipitation measured at this site (577 mm for the period 1912–1993; Savage et al. 1996). Nevertheless, both models provide similar temporal patterns of water outflow, showing little outflow during the summer. Summer monsoons also did not generally increase stream flow in ponderosa pine (Baker 1986) and chaparral watersheds (Hibbert et al. 1974) located near the Mogollon rim (~50 km south of our site). These results suggest that nutrient losses from restored ponderosa pine forests, if they occur, will be restricted to a narrow temporal window from approximately January to May.

For nutrients to be leached from the soil, water loss must occur in concert with high concentrations of nutrients in the soil solution. Prescribed fire and thinning typically increase nutrient cycling rates and concentrations in the surface soil of ponderosa pine forests (Wagle & Kitchen 1972; Klemmedson 1976; White 1986; Covington & Sackett 1986, 1992) as the restoration treatments did at our site (Kaye & Hart 1998). When increases in soil nutrient concentrations are not balanced by plant uptake or microbial immobilization, there is potential for nutrient loss (Likens et al. 1969; Coats et al. 1976; Vitousek & Melillo 1979; Vitousek et al. 1982).

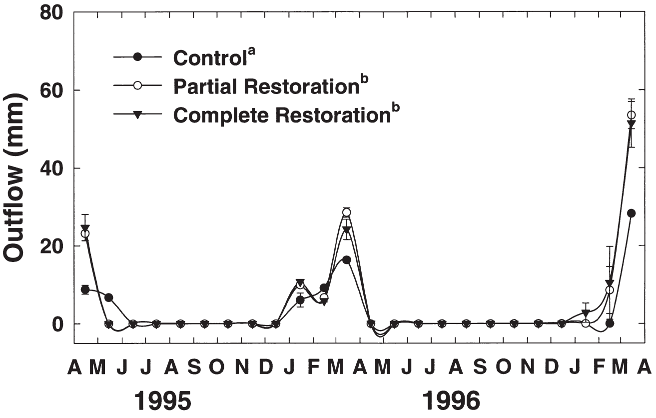

Figure 3. Modeled water outflow from control, partial restoration, and complete restoration treatment plots in the Gus Pearson Natural Area. Vertical bars denote one standard error of the mean ($n = 5$). Treatments with different lowercase letters are statistically different ($p < 0.10$).

We found no differences in nutrient concentrations of soil water collected below the rooting zone of our restoration treatments (Fig. 4) or canopy types (Fig. 5). Similarly, there were no differences in nutrient losses among our restoration treatments by month (Fig. 6) or year (Table 1). Temporal patterns in nutrient loss (Fig. 6) from the site reflected the marked temporal pattern in water loss (Fig. 3) and the consistently low nutrient concentrations in soil water below the rooting zone (Fig. 4). Ammonium and PO_4^{3-} concentrations and outflow were low throughout the collection period. This result was expected because NH_4^+ binds to soil cation exchange sites, and the solubility of PO_4^{3-} is generally low in soil. Organic P is more mobile in soil than PO_4^{3-}-P (Spencer & Stewart 1934; Hilbert et al. 1938; Rolston et al. 1975); however, we found very low organic-P concentrations in deep soil solution and minimal organic-P leaching, despite the abundance of P at this site (the total N: total P ratio for the soil is ~1; Kaye & Hart 1998). Other studies measuring organic-P leaching report similarly small values (Likens et al. 1977; Schindler et al. 1980; Knight et al. 1985; Lowrance et al. 1985). Rolston et al. (1975) showed that organic P penetrated a clay loam soil about 10 cm deeper than inorganic P. It is likely that organic P deposited in the most biologically active portions of the soil (i.e., upper 15 cm of mineral soil; Kaye & Hart 1998) was mineralized to PO_4^{3-} and subsequently adsorbed onto clay minerals, or precipitated out of solution, before the organic P was transported to the deep soil.

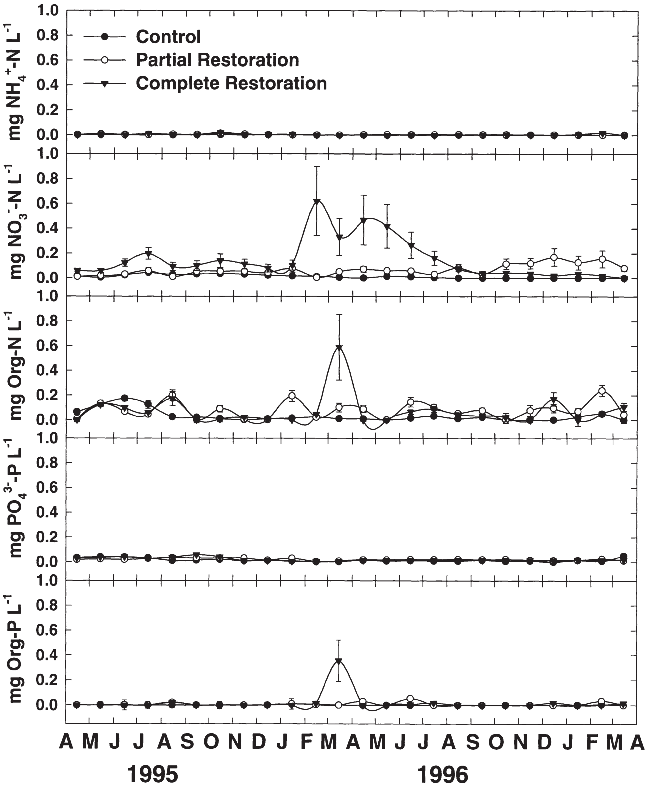

Figure 4. Mass-weighted mean nutrient concentrations in soil water collected monthly below the rooting zone of control, partial restoration, and complete restoration treatment plots in the Gus Pearson Natural Area. Soil water was collected using porous cup tension lysimeters. Vertical bars denote one standard error of the mean ($n = 5$). There were no statistical differences among treatments.

Nitrate is more mobile in soils than NH_4^+, PO_4^{3-}, or organic P, and losses of NO_3^- from disturbed ecosystems are frequently reported (Vitousek & Melillo 1979). At our site during the study period, concentrations of NO_3^- ranged from 0 to 0.8 mg NO_3^--N/L below the rooting zone, but generally were less than 0.2 mg NO_3^--N/L (Fig. 4). Vitousek & Melillo (1979) synthesized data from 18 forested sites with recently disturbed and undisturbed control treatments. They reported mean NO_3^--leaching losses ranging from 0.03 to 125.5 kg N/ha/yr, and stream water and deep soil NO_3^- concentrations ranging from 0.001 to 25 mg N/L. While some of these sites showed increased losses following disturbance (which included various treatments that eliminated or reduced plant nutrient uptake), others did not. In the Southwest, Hibbert et al. (1974) found that converting chaparral to grasslands in Arizona increased stream NO_3^- concentrations from 0.05 to 12.6 mg N/L. However, their converted watershed was considered "deadened" because herbicide applications were part of the conversion treatment. Gosz (1980) found low NO_3^--leaching rates (0.0–0.4 kg N/ha/yr) from forested watersheds in New Mexico that included ponderosa pine forests.

In recent studies assessing the role of thinning on leaching loss of N outside the Southwest, Knight et al. (1991) found deep soil NO_3^- concentrations similar to ours in a thinned *Pinus contorta* (lodgepole pine) forest, but much higher concentrations in a clearcut forest (up to 4 mg N/L). Parsons et al. (1994) created different sized gaps in lodgepole pine forests and found that deep soil NO_3^- concentrations did not increase in small gaps (<5 trees), but did increase as high as 1.6 mg N/L in large gaps (>15 trees). Frazer et al. (1990) found that control and regenerating mixed-conifer forests had deep soil NO_3^- concentrations less than 0.5 mg N/L, while a nearby clear-cut site had concentrations as high as 2 mg N/L. In contrast, Hendrickson et al. (1989) found that removing all biomass greater than 1.3 m in height in a northern mixed forest resulted in lower deep soil NO_3^- concentrations than cutting only trees greater than 9 cm dbh and leaving slash on the site. With the exception of this last study, previous research on the effects of thinning are in agreement with results from our partial restoration treatment, suggesting that forest thinning does not necessarily increase NO_3^- concentrations below the rooting zone.

Fire has variable effects on NO_3^- leaching depending mostly on fire intensity. Weston and Attiwill (1990) found that crown and slash fires caused prolonged elevations in deep soil NO_3^- concentrations in *Eucalyptus regnans* forests while a surface fire did not. Richter et al. (1982) reported no increase in stream water or deep soil NO_3^- concentrations following several prescribed surface fires in *Pinus taeda* (loblolly pine) forests. Schindler et al. (1980) compared two burned watersheds to a control and found that fire increased NO_3^- leaching in one burned watershed but not the other. The authors concluded that fire-accelerated nutrient losses would not affect site fertility or stream ecology. Adams and Attiwill (1991) found no increase in NO_3^- leaching losses following a logging plus burning treatment in Tasmania. Chorover et al. (1994) observed increases in streamwater NO_3^- following surface fire in a mixed-conifer forest; however, N losses were much smaller than inputs from wet deposition. Our results corroborate those above suggesting that light intensity fires do not necessarily increase NO_3^- leaching from forests.

Deep soil concentrations (Figs. 4–6) and annual leaching losses (Table 1) of organic N were similar to that of NO_3^-. Organic N can be released in large quantities from decomposing litter (Fahey et al. 1985; Qualls et al. 1991; Northup et al. 1995) and concentrations in deep soil lysimeters or stream water are frequently as high or higher than inorganic N concentrations (Gosz 1980; Sollins & McCorison 1981; Parsons et al. 1994; Hedin et al.

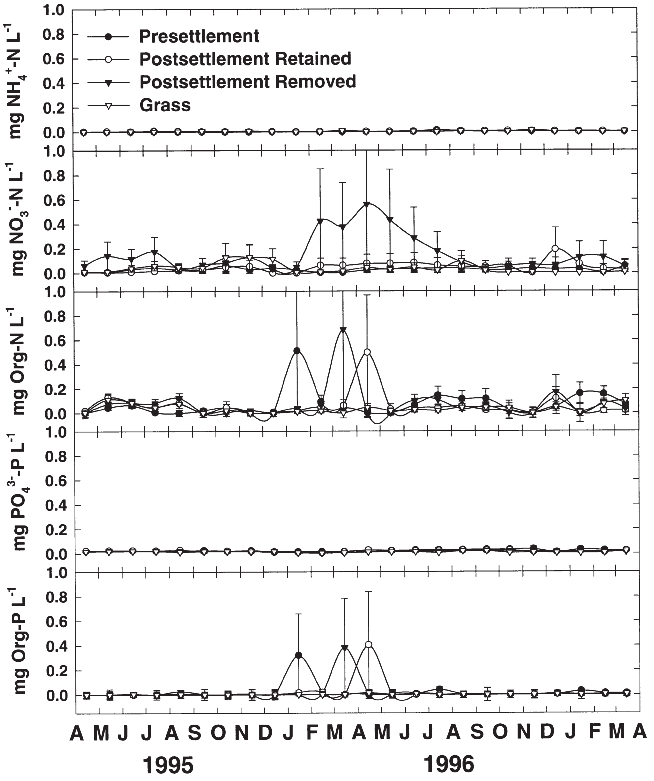

Figure 5. Mean nutrient concentrations in soil water collected monthly below the rooting zone of four different canopy types in the Gus Pearson Natural Area. Soil water was collected using porous cup tension lysimeters. Vertical bars denote one standard error of the mean ($n = 15$ for all canopy types except for postsettlement removed where $n = 10$). There were no statistical differences among canopy types.

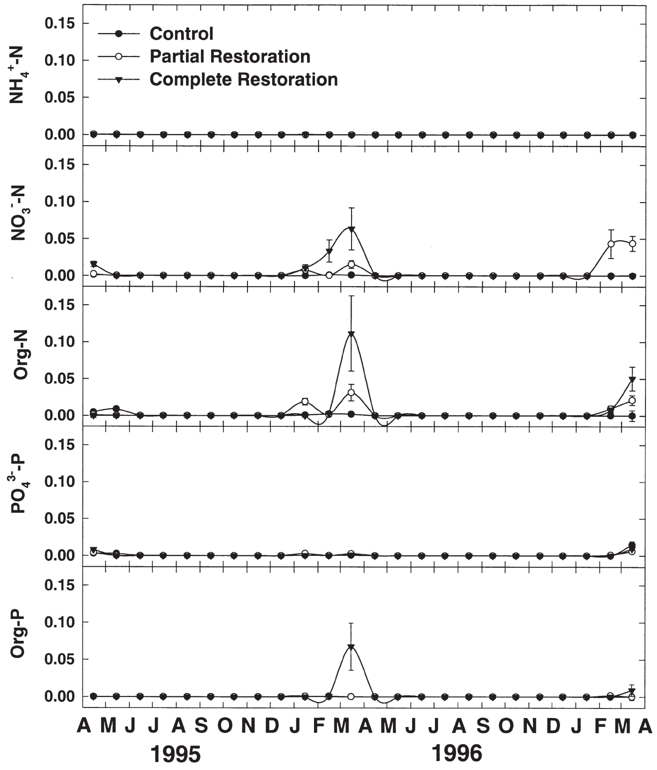

Figure 6. Monthly estimates of nutrient export by leaching from control, partial restoration, and complete restoration treatment plots in the Gus Pearson Natural Area. Units are in kg/ha/mo. Vertical bars denote one standard error of the mean ($n = 5$). There were no statistical differences among treatments.

1995; Lowrance et al. 1985). While organic N is typically an important fraction of N leached from forest ecosystems, organic N losses from our site and many of the sites discussed above were not large enough to greatly impact the total N stock within the ecosystem

Total nutrient losses from our site showed patterns similar to those of the inorganic and organic constituents described above (Table 1). There were no statistical differences among treatments and we do not consider the 0.1–0.2 kg N/ha/yr increase in total N losses from the restoration treatments to be biologically significant. Net N mineralization rates at this site are 25–35 kg N/ha/yr in the restoration treatments and soil total N stocks (forest floor + 0 to 15 cm mineral soil) are ~1500 kg N/ha (Kaye & Hart 1998).

Several mechanisms may have contributed to the low nutrient losses from our restoration and control treatments. Previous research suggests that when plant regrowth is slow or experimentally prevented following disturbance, nutrient losses can be large (Likens et al. 1969; Hibbert et al. 1974; Knight et al. 1991). More productive ecosystems tend to lose more N than less productive ecosystems following disturbance (Vitousek et al. 1982). Microbial immobilization and plant uptake of N are important factors controlling N loss (Coats et al. 1976; Vitousek & Matson 1985), but abiotic retention of N in soils may also mitigate N loss (Magill et al. 1997). We found decreased gross microbial immobilization of NO_3^- in our restoration treatments, but restoration did not alter gross microbial immobilization of NH_4^+ (Kaye & Hart 1998). Because these gross microbial immobilization rates were measured only once in August (when no water was exported from the site), we cannot rule out microbial immobilization of N as a mechanism reducing nutrient losses from the restoration treatments. Increased production by grasses (Fig. 2; Covington et al. 1997) and by trees remaining after thinning may be the major factors decreasing nutrient losses following ponderosa pine restoration.

There are several caveats that should temper extrapolations from our data. First, future research should replicate this work at the site level by measuring nutrient losses from operational restoration treatments in other ponderosa pine forests. Second, our data document the short-term, but not the immediate, disturbance effects of the restoration treatments. Implementation of the restoration treatments after the installation of the lysimeters would have destroyed many, if not most, of the lysimeters, so we were unable to collect soil solutions for immediate post-treatment estimates of nutrient loss. Consequently, nutrient losses that occurred in the spring of 1994, following the thinning treatment in the fall of 1993, were not measured. The prescribed burn occurred in the fall of 1994, but the hydrologic model estimated that no water left the site between the fall of 1994 and January 1995. Nutrient concentrations in soil solution below the rooting zone from January through March 1995 (data not shown) were similar to those shown in Figure 3, suggesting that we did not miss a pulse of nutrient loss resulting from the prescribed burn.

Conclusions

Nutrient losses following ecological restoration of this ponderosa pine forest appear to be small because: (1) nutrient concentrations in the soil below the rooting zone are low; and (2) water outflow from the ecosystem by deep percolation is low and temporally limited. Consequently, ecological restoration will likely not cause significant changes in stream water chemistry or terrestrial nutrient stocks because of increased nutrient losses by leaching. Increased production by grasses and residual trees following restoration are the most likely mechanisms for nutrient retention. Coupling measurements of nutrient concentrations in the deep soil solution using tension lysimetry with a hydrologic model appears to be a viable method for determining nutrient losses from restoration experiments that do not meet the criteria for the small watershed nutrient budget approach.

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