

Carbon and Nitrogen Cycling in Southwestern Ponderosa Pine Forests

Stephen C. Hart, Paul C. Selman, Sarah I. Boyle, and Steven T. Overby

Abstract: Ponderosa pine forests of the southwestern United States were historically characterized by relatively open, parklike stands with a bunchgrass-dominated understory. This forest structure was maintained by frequent, low-intensity surface fires. Heavy livestock grazing, fire suppression, and favorable weather conditions following Euro-American settlement in the late 19th century resulted in a dramatic increase in pine regeneration. Today, many of these forest stands have high stand densities with low understory production, and are susceptible to infrequent, stand-replacing fires. The primary objective of our study was to better characterize the contemporary carbon (C) and nitrogen (N) cycling processes in relatively unmanaged southwestern ponderosa pine stands. We then compared these ecosystem conditions with those of an adjacent stand that had received an ecological restoration treatment that included thinning and prescribed burning. Our results suggest that N availability and aboveground net primary productivity (ANPP) of trees in these forests are low compared to other forests. Restoration treatments decreased ANPP but increased the proportion of ANPP in woody tissues. These treatments also increased soil respiration, water availability, temperature, and net nitrification, but had no effect on net N mineralization and microbial N. We speculate that the understory response to restoration treatments is a key factor affecting the overall ecosystem response in these forests. *FOR. SCI.* 52(6):683–693.

Key Words: Microbial biomass, nitrogen mineralization, nitrification, productivity, soil respiration.

PONDEROSA PINE (*Pinus ponderosa* P. & C. Lawson var. *scopulorum* Engelm.) forests of the southwestern United States were historically characterized by relatively open, parklike stands with a bunchgrass-dominated understory (Covington et al. 1994, 1997). This stand structure was maintained by frequent, low-intensity surface fires (every 2–20 years) that rarely reached the crowns of large trees (Cooper 1960, Dieterich 1980). Heavy livestock grazing, fire suppression, and favorable weather conditions following Euro-American settlement in the latter part of the 19th century resulted in a dramatic increase in pine regeneration in many of these forests (Cooper 1960, White 1985, Savage et al. 1996). Today, southwestern ponderosa pine forests generally have high stand densities with low understory production, and are susceptible to infrequent, stand-replacing fires (Covington and Moore 1994, Swetnam and Baisan 1996, Moore et al. 2006).

Due to factors such as the low productivity and low timber value of these forests, comparatively little is known about their function relative to other coniferous forests of the United States (e.g., Pacific Northwest and Southeast). Indeed, this is true of many of the semi-arid forests of the

Inland West (Johnson et al. 1997, 1998). Recent work attempting to restore the structure and function of southwestern ponderosa pine forests to pre-Euro-American conditions has increased our knowledge of the controls and rates of various ecosystem processes in these forests (e.g., Boyle et al. 2005, Hart et al. 2005b, Kaye et al. 2005). Nevertheless, we still have insufficient information across a variety of different ponderosa pine stands to elucidate the contemporary range in ecosystem functions in southwestern ponderosa pine forests.

The primary objective of our study was to better characterize carbon (C) and nitrogen (N) cycling processes in contemporary, southwestern ponderosa pine stands in a relatively unmanaged condition. We also compared these ecosystem conditions in one of the unmanaged stands with those of an adjacent stand that had received an operational ecological restoration treatment that included thinning and prescribed burning. Finally, we contrasted the ecosystem pools and processes in these southwestern ponderosa pine forests with those of other ponderosa pine-dominated forests in the western United States.

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Methods

Study Sites and Design

The study area is at an elevation of about 2,255 m above sea level, with gentle topography and a cool, subhumid climate. Approximately half of the 57 cm of annual precipitation in this area falls as winter snow and the other half as rain during intense summer convective storms (Schubert 1974). The summer growing season is characterized by an extensive dry period, which generally lasts from May to July, followed by a wetter period after the onset of monsoonal summer rains (Bailey and Covington 2002). Soils are derived from basalt and are classified as a complex of fine, smectitic, frigid Typic Argiborolls and Mollic Eutroboralfs (Miller et al. 1995). Our study sites were a subset of the Grand Canyon Forests Partnership's initial wildland-urban interface (WUI) experimental treatments that were started in 1998 in cooperation with the Coconino National Forest and the Rocky Mountain Research Station, US Forest Service, USDA. One of the major goals of these treatments was to develop operational methods for reducing wildfire hazard in the WUI around Flagstaff (Fulé et al. 2001). These treatments were evaluated on three, noncontiguous experimental blocks (EBs) in or adjacent to the Fort Valley Experimental Forest, approximately 15 km NW of Flagstaff, AZ (35°16'19"N, 111°41'22"W). Each EB contained a 14.2-ha replicate of the three thinning levels (restoration treatments) and a control, with the treatments assigned randomly within each block (i.e., randomized block design). The EBs were based on the proportion of presettlement trees (>120 years old) within the stands, which differed among EBs as a consequence of past management history. More harvest entries within a given stand resulted in fewer presettlement trees, a greater number of total trees per unit area, and a stand with a more even-aged structure (dating to 1919). Within each EB, stand conditions were relatively homogeneous, with basal areas of replicate stands differing by less than 7.8 m²/ha.

Our original study design included the highest thinning level that best approximated pre-Euro-American settlement conditions following the treatment and the control of each of the three EBs. However, differences in the operators, equipment used to thin each of the EBs, the method and amount of slash burned, and length of time required to implement the treatments resulted in stand and soil conditions that varied considerably among the EBs following treatment (Fulé et al. 2001). These differences in application of the treatments among the EBs required us to change our study design; we conducted measurements within the three unmanaged control stands (designated as "U," one in each EB) and the treated stand in EB 3 that was the first EB to be completed (EB 3-R). The stand densities of the three unmanaged stands (EB 1-U, 2-U, and 3-U) were 1,760, 1,094, and 709 trees/ha, respectively. The basal areas of these same stands were 33.9, 39.1, and 40.1 m²/ha, respectively. Stand conditions within these three EBs are representative of those currently found in contemporary southwestern ponderosa pine stands (mean tree density for all ponderosa pine stands

in Arizona is about 620 trees/ha, and about 50% of these stands have basal areas between 23 and 46 m²/ha; O'Brien 2002). Additionally, although the stand densities do vary among the EBs, stands in all three EBs are at a similar developmental stage, with relative density indices ranging from 0.70 to 0.74 (well into the zone of self-thinning for ponderosa pine; Long and Shaw 2005).

A combination of thinning and burning was used in the restoration treatment of EB 3 (hereafter called "restored stand" or "EB 3-R") to re-establish the structure and function of the ecosystem to a condition similar to that found in these forests before Euro-American settlement in the late 1880s (Covington et al. 1997). All living presettlement trees were retained. Within a 30-m radius of each evidence of a dead presettlement tree, one or two large (>40.6 cm dbh [~ 1.4 m; dbh]) or three small (<40.6 cm dbh) trees were selected to replace the loss of that tree. All other trees were removed from the site through a whole-tree harvest operation conducted in the winter of 1998. This thinning approach substantially lowered stand density (from 800 to 91 trees/ha and from 39.7 to 8.5 m²/ha of basal area) and resulted in an aggregated or "clumpy" stand structure. This structure was characteristic of southwestern ponderosa pine forest before Euro-American settlement of the region (Covington et al. 1997). Slash from the harvesting operation was grouped into piles within the stand, and in the spring of 2000 these piles were burned individually. Soon after, the entire treatment area was broadcast-burned (Fulé et al. 2001).

Within each stand, a 60 m $\times$ 60 m grid was established with 20 grid points. All trees over breast height were measured on a 0.04-ha (11.28-m radius) circular plot centered on the grid point. Tree diameters were originally measured in all stands from August through November 1998, and then re-measured during this same period in 2003 for the unmanaged stands in EB 1 and 2, in 2004 for the EB 3 restored stand, and in 2005 for the EB 3 unmanaged stand. Litterfall and soil-based measurements were made between a 12- and 16-m radius from each grid point along an azimuth selected randomly (~ 15 m² area).

Net N Transformations and Microbial Biomass N

We measured rates of net N mineralization and nitrification in situ using the covered core technique (Hart et al. 1994b) at all the odd-numbered grid points (plots; $n = 10$ /stand). We used six sequential incubation periods with the incubation length ranging from 35 to 137 (over winter) days (Oct. 19 to Dec. 4, 2000; Dec. 5, 2000 to Apr. 20, 2001; Apr. 21 to Jun. 6, 2001; Jun. 7 to Jul. 18, 2001; Jul. 19 to Sep. 17, 2001; and Sep. 18 to Oct. 22, 2001). These lengths were chosen to represent relatively constant soil water content conditions. At each sampling location and at the beginning of each sampling date, two intact mineral soil cores (5 cm I.D., 0–15 cm depth) contained in polycarbonate sleeves were extracted (AMS

Core Sampler, American Falls, ID) after carefully removing the forest floor (i.e., O horizon), if present. This soil depth contains, on average, the A horizon in this soil type. One core was returned to the laboratory in a cooler (kept at $\approx 4^{\circ}\text{C}$) for estimation of total inorganic N pool sizes (within 48 h). The other core was covered with a polyethylene cap that had six small holes (0.8 mm diam.) drilled into its top to allow gas exchange but to minimize changes in water content during the incubation period. The bottom of the core was left open. The core was then returned to the hole from which it came and any forest floor that was removed was returned over the core. After the incubation period, cores were removed and returned to the laboratory on blue ice and processed in a similar manner as the initial cores.

Soils from initial and incubated cores were sieved field-moist through a 4-mm sieve, and the <4 mm fraction was weighed. Subsamples were then removed for gravimetric water content determination (105°C , 72 h) and approximately 20 g (field-moist weight) was extracted with 100 ml of 2 M KCl. Soil suspensions were shaken on a reciprocating mechanical shaker (90 cycles per minute) for 1 hour and then filtered through Whatman no. 1 filter paper that had been preleached with deionized water. The filtered extracts were analyzed colorimetrically on a Lachat AE Flow-Injection Analyzer (Lachat Instruments, Milwaukee, WI) for NH_4^+ and NO_3^- (Lachat Instruments, Inc., Milwaukee, WI, 2000. QuickChem method no. 10-107-04-1-C; Lachat Instruments, Inc., Milwaukee, WI, 2001. QuickChem method no. 12-107-06-1-B), respectively. Mass-based estimates of inorganic N pool sizes were converted to area-based estimates using the mean bulk density (oven-dry weight of <4 -mm fraction per unit volume) of the 12 cores taken from each plot.

Microbial biomass N was estimated using the chloroform fumigation-extraction method (Haubensak et al. 2002) in the initial mineral soil cores taken for estimating net N transformations (except for the second incubation period, where microbial N was not determined). One 10-g field-moist, sieved subsample from each soil core was immediately extracted with 50 ml of 0.5 M K_2SO_4 . A paired subsample was fumigated with hydrocarbon stabilized CHCl_3 in a vacuum-sealed desiccator for 5 days. After 5 days, the fumigated subsamples were removed from the desiccator and extracted with 50 ml of 0.5 M K_2SO_4 . Extracts were shaken for 1 hour, and then filtered. Both sets of extracts were digested using a modified micro-Kjeldahl digestion and analyzed for total N using a salicylate method (Lachat Instruments, Inc., Milwaukee, WI, 1994. QuickChem method no. 13-107-06-2-D) on a Lachat AE Flow-Injection Analyzer. 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. A k_{EN} of 0.20 was used to convert chloroform-labile N values to microbial N (Davidson et al. 1989, Hart et al. 1994a).

Carbon Fluxes and Nitrogen Uptake

We measured litterfall to estimate aboveground net primary productivity (ANPP), aboveground N uptake, and total belowground carbon allocation (TBCA), and as a component of the C and N cycles of the stands. One littertrap (0.07 m^2) was placed at each grid point ($n = 20$ per stand). Littertraps were installed in August, 2000, and litter was collected from the traps every few months over a 1-year period. In the laboratory, all woody litter >1 cm in diameter was discarded and the remaining material was oven-dried (70°C) and weighed. Litter was then ground ($<425 \mu\text{m}$) using Wiley Mills (Thomas Scientific, Swedesboro, NJ) and subsamples were analyzed for total C and N concentrations on a Flash EA 1112 NC Analyzer (ThermoElectron Corporation, Waltham, MA).

We estimated tree ANPP in each stand by adding annual litterfall estimates measured over 1 year to the annual increase in aboveground biomass (AB) averaged over the 5- to 7-year measurement period. Aboveground biomass at the two measurement periods (1998 (all stands) and 2003 (EB 1-U and EB 2-U), 2004 (EB 3-R), or 2005 (EB 3-U)) was determined using locally derived allometric equations that relate tree diameter to AB. Aboveground uptake of N associated with this ANPP was calculated by summing the measured N content returned in litterfall and the increase in N contained in aboveground tissues; this latter component was estimated from the change in AB and measures of tissue N concentrations (Kaye et al. 2005).

We measured soil respiration (net soil CO_2 efflux) over a 13-month period in each stand using the soda lime closed chamber technique (Edwards 1982) as applied by Kaye and Hart (1998b). Soil respiration includes both microbial and root respiration, and thus provides an index of the biological activity belowground (Kaye and Hart 1998b). Furthermore, soil respiration measurements coupled with litterfall rates can be used to estimate total plant C allocation belowground.

Soil respiration measurements were made at all 20 grid points in each stand every 2 to 3 weeks during the growing season (from July 2000 to December 2000 and May 2001 to August 2001) and approximately monthly over the winter period (from January 2001 to April 2001). Chamber design and sampling protocol were identical to Kaye and Hart (1998b) except a different factor was used to correct for the mass of water released when soda lime reacts with CO_2 . Kaye and Hart (1999b) used the factor of 1.41 that was originally proposed by Edwards (1982). However, we used the value of 1.69 in the current study as Grogan (1998) has shown that the empirically derived value of 1.41 is incorrect; a value of 1.69 reflects the stoichiometry of the reaction of soda lime with water (Grogan 1998). Annual soil respiration rates were estimated using each measurement as a midpoint between sequential sample dates. Half of the nonmeasurement days were assigned to each measurement date. The soil respiration value from each measurement was then multiplied by the number of nonmeasurement days assigned to that measurement, and then these values were

summed to produce an annual estimate (Kaye and Hart 1998b).

The soda lime closed chamber technique as applied here was compared to infrared gas analyzer measurements by Kaye and Hart (1998b) in a ponderosa pine forest stand close to our study site. Although the two methods were found to be highly correlated, the soda lime method tended to underestimate soil respiration even after adjusting for the lower correction factor used by Kaye and Hart (1998b). Hence, the soda lime method may have underestimated soil respiration in the current study.

Total belowground C allocation (TFCA) by plants was estimated in the three unmanaged stands based on mass balance. Assuming that the annual changes in soil C stocks are small relative to soil respiration and litterfall fluxes: TBCA = soil respired C – litterfall C. We did not calculate TBCA for the restored stand because the recent disturbance from the restoration treatments likely violated this quasi steady-state assumption (Raich and Nadelhoffer 1989, Giardina and Ryan 2002).

Microenvironmental Measurements

Soil temperature and volumetric soil water content were measured at the beginning of each 24-h soda lime incubation period to determine the influence of microenvironmental factors on soil respiration and to characterize the abiotic conditions within each stand. Soil temperature was measured at all 20 grid points within each stand using digital probe thermometers (VWR Digital Dial Thermometer, Chester, PA) placed at a 7.5 cm mineral soil depth. Volumetric water content of soil was measured in each stand using a Trace Systems Time Domain Reflectometry unit (Soil Moisture Corporation, Santa Barbara, CA) at the even-number grid points only ($n = 10$). Time domain reflectometry probes were permanently installed to a depth of 15 cm measured from the top of the litter layer.

Statistical Analyses

This study included an observation component (characterizing the ecosystem pools and processes within unmanaged southwestern ponderosa pine stands) and an experimental component (comparing these components between an unmanaged and a restored stand within the same experimental block, EB 3). We did not have any replication of the

restoration treatment at the stand level for the reasons outlined above; hence, we only qualitatively evaluated the effects of the restoration treatment on soil pools and processes. In these qualitative comparisons, the restoration treatment was only compared with the single control stand (EB 3-U), rather than the mean of all three control stands, because of the blocked nature of the original experimental design.

We evaluated temporal changes in soil pool and processes of the replicated unmanaged stands using one-way analyses of variance with sampling date as the factor (ANOVAs; Glantz 2002). The values measured at the various grid points within a stand were averaged before these analyses (i.e., $n = 3$). We compared different sampling dates using the Holm-Sidak method when sampling date was a significant factor (Glantz 2002). Linear regression analysis was used to explore the abiotic controls (soil temperature and water content) on soil respiration. Pearson product-moment correlation analysis was also used to elucidate the potential covariance in net N transformation rates. All statistical tests were performed using SigmaStat software at the $P = 0.050$ significance level (version 3.11, Systat Software, Inc., San Jose, CA).

Results

Net N Transformations, Microbial N, and Extractable N Pools

Mean annual rates of net N mineralization in the surface mineral soil (0–15 cm) ranged from 1.18 to 1.67 $\text{g N m}^{-2} \text{yr}^{-1}$ in the three unmanaged stands (Table 1). The annual rate of net N mineralization in the restored stand was similar to the unmanaged stand in that EB (Table 1). Mean annual net ammonification rates ranged from 0.97 to 1.28 $\text{g N m}^{-2} \text{yr}^{-1}$ in the three unmanaged stands. In EB 3, the annual net ammonification rate was substantially lower in the restored stand compared to its paired unmanaged stand (mean $\pm$ SE: 0.24 ± 0.28 and $1.28 \pm 0.38 \text{ g N m}^{-2} \text{yr}^{-1}$, respectively). Mean annual net nitrification rates were generally low in the unmanaged stands, ranging from 0.06 to 0.47 $\text{g N m}^{-2} \text{yr}^{-1}$ (Table 1). However, the restored stand had a substantially higher net nitrification rate than the unmanaged stand in EB 3 (1.09 and 0.39 $\text{g N m}^{-2} \text{yr}^{-1}$, respectively; Table 1). There was relatively little seasonal variation in net N transformation rates, although sampling

Table 1. Mean (and standard error) total C and N, annual microbial N, annual extractable N pools, and annual rates of net N transformations determined in situ in three unmanaged (U) southwestern ponderosa pine stands and one restored (R) southwestern ponderosa pine stand

Stand	Total		Microbial ¹ N	Extractable ¹			Net N transformations	
	C	N		Organic N	NH ₄ ⁺ -N	NO ₃ ⁻ -N	Mineralization	Nitrification
	(g m^{-2}).....						($\text{g N m}^{-2} \text{yr}^{-1}$).....	
EB 1-U	2750 (200)	126 (6)	14.1 (1.3)	1.23 (0.09)	0.16 (0.03)	0.02 (<0.01)	1.18 (0.33)	0.06 (0.05)
EB 2-U	3000 (340)	130 (16)	14.9 (1.0)	1.12 (0.12)	0.23 (0.07)	0.02 (0.01)	1.44 (0.31)	0.47 (0.32)
EB 3-U	2540 (150)	128 (9)	13.2 (0.8)	0.83 (0.12)	0.16 (0.09)	0.01 (0.01)	1.67 (0.40)	0.39 (0.18)
EB 3-R	2960 (250)	145 (15)	13.9 (0.8)	0.86 (0.07)	0.28 (0.05)	0.05 (0.01)	1.33 (0.22)	1.09 (0.20)

All values are for the 0–15 cm mineral soil depth.

¹ Values are means of five (microbial N) or six (extractable N pools) sampling dates over a 1-year period.

date was a significant factor for all three rates (Figure 1). Across all soil samples assessed, net nitrification was weakly correlated with net N mineralization ($r = 0.339$, $P < 0.001$, $n = 240$).

The mean amount of N contained in microbial biomass across the study period was similar among the unmanaged stands, ranging from 13.2 to 14.9 g N m⁻² (Table 1). Furthermore, microbial N in the restored stand was similar to that of the unmanaged stand in EB 3 (Table 1). However, there was considerable temporal variation in microbial N among the unmanaged stands ($P < 0.001$). Microbial N tended to be lowest among all four of the stands during the October and June sampling dates when soil water content was also relatively low (Figures 2 and 3a). Indeed, across all plots, stands, and sampling dates, microbial N was correlated with gravimetric water content ($r = 0.560$, $P < 0.001$, $n = 200$).

Averaged over the study period, extractable organic N pools in the upper 15 cm of mineral soil ranged from 0.83 to 1.23 g N m⁻² among the unmanaged stands. This soil N pool was similar in magnitude in the restored stand compared to the unmanaged stand in EB 3 (Table 1). Ammo-

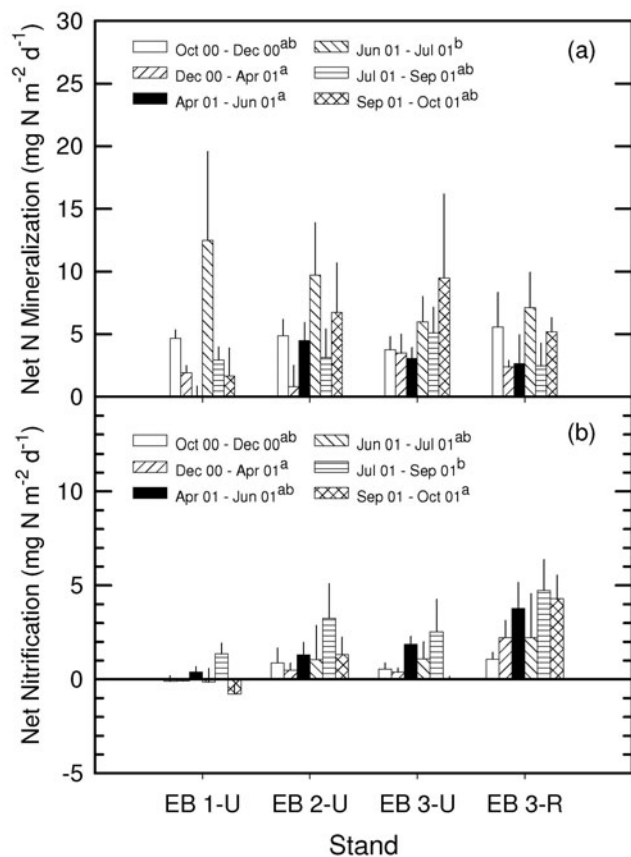


Figure 1. In situ net nitrogen mineralization (a) and nitrification (b) rates in three unmanaged (U) southwestern ponderosa pine stands and one restored (R) southwestern ponderosa pine stand over a 1-year period. Superscripted lowercase letters following the incubation period in the figure legend denote significantly different ($P \leq 0.05$, $n = 3$) net N transformation rates among dates using the Holm-Sidak multiple comparison test. The restored stand (EB 3-R) was not included in this analysis because it was unreplicated. Vertical bars denote one standard error of the mean (within-stand variability; $n = 10$).

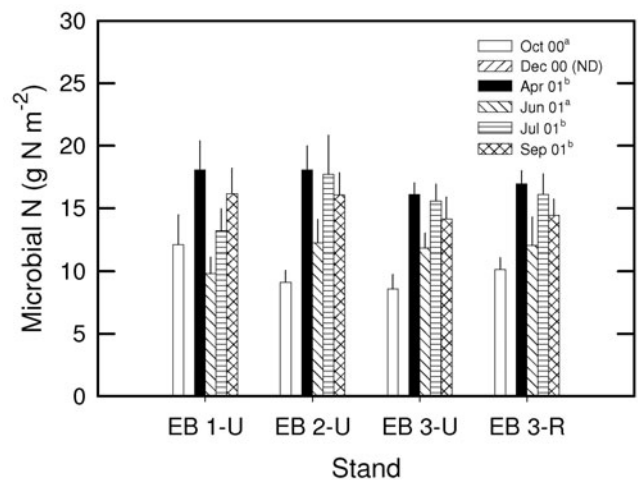


Figure 2. Changes in mean microbial biomass N in three unmanaged (U) southwestern ponderosa pine stands and one restored (R) southwestern ponderosa pine stand over a 1-year period. Superscripted lowercase letters following the sample date in the figure legend denote significantly different ($P \leq 0.05$, $n = 3$) microbial biomass N values among dates using the Holm-Sidak multiple comparison test. The restored stand (EB 3-R) was not included in this analysis because it was unreplicated. ND, not determined. Vertical bars denote one standard error of the mean (within-stand variability; $n = 10$).

nium pools averaged over the study period ranged from 0.16 to 0.23 g N m⁻² among the unmanaged stands, and the restored stand had a greater NH₄⁺ pool size than the unmanaged stand in EB 3 (0.28 ± 0.05 and 0.16 ± 0.09 g N m⁻², respectively; Table 1). Nitrate pools averaged over the study period were small in the unmanaged stands (0.01 to 0.02 g N m⁻²), but this pool was greater in the restored stand than the unmanaged stand in EB 3 (0.05 ± 0.01 and 0.01 ± 0.01 g N m⁻², respectively; Table 1).

Total C and N Pools and Fluxes

Forest floor C and N pools among the unmanaged stands ranged from 1,720 to 3,440 g C m⁻² and 52.4 to 63.0 g N m⁻² (Table 2). The restored stand in EB 3 had forest floor C and N pools that were 19 and 30% lower, respectively, than the unmanaged stand in EB 3 (Table 2). Annual litterfall C and N fluxes ranged from 68.2 to 76.9 g C m⁻² yr⁻¹ and 0.85 to 0.90 g N m⁻² yr⁻¹, respectively (Table 2). In EB 3, the restored stand had litterfall C and N inputs that were 45 and 41%, respectively, of the values in the paired unmanaged stand (Table 2). The reduction in N inputs was due to a reduction in litterfall mass because the litter N concentration was similar between the unmanaged and restored stands (6.39 ± 0.23 and 5.83 ± 0.33 g N kg⁻¹, respectively).

Assuming that the forest floor C and N content are near steady-state within the unmanaged stands, we estimated the mean residence time (MRT = forest floor elemental content/litterfall elemental input; Waring and Schlesinger 1985, Barnes et al. 1998) to be 26.5 to 50.3 years for C and 60.7 to 117 years for N (Table 2). We could not calculate the MRT for C and N in the forest floor of the restored stand because the forest floor had recently been disturbed, and

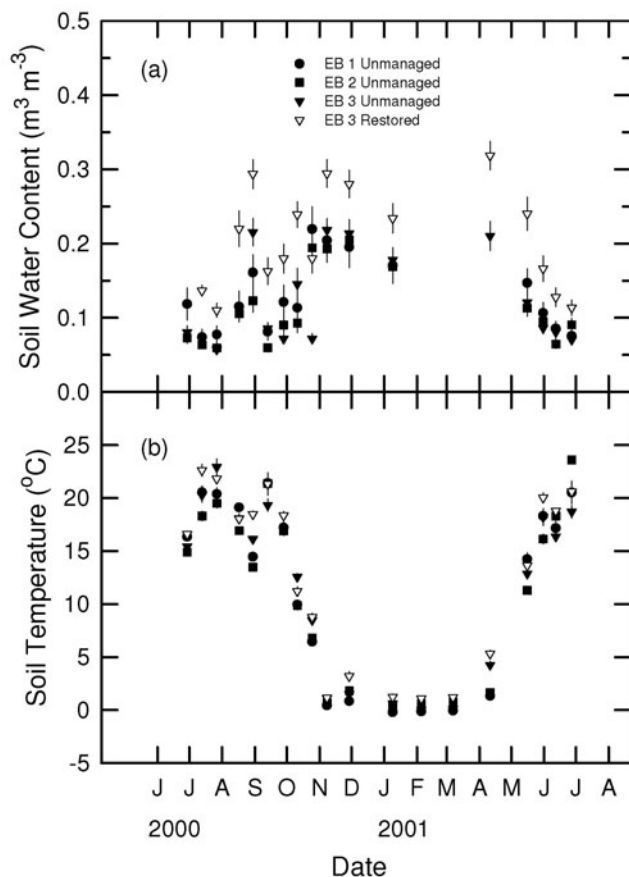


Figure 3. Changes in mean volumetric soil water content (a; upper 15 cm of the soil profile) and mean soil temperature (b; 7.5 cm mineral soil depth) in three unmanaged southwestern ponderosa pine stands and one restored southwestern ponderosa pine stand over the 13-month study period. Vertical bars denote $\pm$ one standard error of the mean (within-stand variability; $n = 10$ for volumetric soil water content and $n = 20$ for soil temperature).

hence we could not assume steady-state conditions. In the unmanaged stands, total C in the surface mineral soil ranged from 2,540 to 3,000 g m⁻² and soil total N ranged from 126 to 130 g m⁻². Both the restored and unmanaged stands in EB 3 had similar mineral soil total C and N stocks (Table 1). Concentrations on a mass basis ranged from 19.1 to 25.5 g C kg⁻¹ and 0.96 to 1.10 g N kg⁻¹ and were similar for the restored and unmanaged stands in EB 3 (data not shown).

Tree AB in the unmanaged stands ranged from 6.6 to 7.7 kg C m⁻² (Table 3). Following restoration in EB 3, tree AB was about 24% of the unmanaged stand value (EB 3 restored = 1.9 ± 0.3 kg C m⁻² and EB 3 unmanaged = 7.7 ± 0.4 kg C m⁻²). The amount of N contained within the tree AB ranged from 21.5 to 25.0 g N m⁻² in the unmanaged stands. In EB 3, the lower amount of N contained in the tree AB of the restored stand than the unmanaged stand was proportional to the lower tree AB in the restored stand (EB 3 restored = 5.9 ± 1.1 g N m⁻² and EB 3 unmanaged = 25.0 ± 1.4 g N m⁻²). Tree ANPP ranged 115 to 122 g C m⁻² yr⁻¹ in the unmanaged stands (Table 3), and tree ANPP in the restored stand was about half that of the unmanaged stand within EB 3 (EB 3 restored = 59.3 ± 8.7

g C m⁻² yr⁻¹ and EB 3 unmanaged = 122 ± 9 g C m⁻² yr⁻¹). Between 31 and 38% of the tree ANPP in the unmanaged stands was as branch and stem wood; however, the amount of ANPP in wood was higher in the restored stand ($42 \pm 3\%$) than in the unmanaged stand within EB 3 ($31 \pm 3\%$).

The amount of N taken up by the AB ranged from 0.98 to 1.06 g N m⁻² yr⁻¹ in the unmanaged stands. In EB 3, aboveground N uptake was about 42% lower than in the paired unmanaged stand (EB 3 restored = 0.42 ± 0.06 g N m⁻² yr⁻¹ and EB 3 unmanaged = 1.00 ± 0.07 g N m⁻² yr⁻¹). In all four stands, over 80% of the N taken up annually in tree AB went into foliar tissues replacing loss in litterfall (Table 2).

Annual rates of soil respiration from the unmanaged stands ranged from 843 to 891 g C m⁻² yr⁻¹ (Table 3). In EB 3, the restored stand had annual rates of soil respiration about 27% higher than the unmanaged stand (EB 3 restored = $1,070 \pm 20$ g C m⁻² and EB 3 unmanaged = 844 ± 20 g C m⁻²). Soil respiration varied greatly across seasons, and differences in soil respiration rates between the restored and unmanaged stands in EB 3 appeared to vary by sampling date (Figure 4). For the unmanaged stands, soil respiration was poorly correlated to soil temperature when soil water content was <0.18 m³ m⁻³ (r^2 adj. = 0.009, $P < 0.001$, $n = 378$), but the correlation improved considerably when soil water content was >0.18 m³ m⁻³ (r^2 adj. = 0.631, $P < 0.001$, $n = 160$). Similar relationships were found in the restored stand (data not shown). Estimated TBCA ranged from 767 to 823 g C m⁻² yr⁻¹ for the unmanaged stands (Table 3).

Soil Microenvironment

Soil water content (upper 15 cm of soil profile) varied considerably over time among stands (ranging from about 0.05 to 0.30 m³ m⁻³; Figure 3a), and soil water content was generally higher in the restored stand than the unmanaged stand in EB 3. Soil temperature (7.5 cm mineral soil depth) also varied substantially over the year within each stand (ranging from 0 to 25°C), and the overall temporal pattern was similar among the unmanaged stands (Figure 3b). The restored stand in EB 3 generally had soil temperatures 1–3°C higher than those of the paired unmanaged stand (Figure 3b).

Discussion

Carbon and Nitrogen Fluxes in Southwestern Ponderosa Pine Stands

Relatively low annual precipitation, prolonged dry periods during the growing season, and the input of relatively low quality litter (high lignin to N ratio) to the forest floor are defining characteristics of contemporary southwestern ponderosa pine forests (Kaye et al. 2005). The combination of these factors results in relatively low rates of C and N cycling compared to forests from more humid regions. For instance, the MRTs of C and N in the forest floor found in

Table 2. Mean (and standard error) forest floor (O horizon), carbon (C), and nitrogen (N) content, litterfall C and N inputs, and calculated mean residence times (MRT) for C and N in three unmanaged (U) southwestern ponderosa pine stands and one restored (R) southwestern ponderosa pine stand

Stand	Forest floor		Litterfall		MRT	
	C	N	C	N	C	N
	(g m^{-2})		($\text{g m}^{-2} \text{ yr}^{-1}$)		(yr)	
EB 1-U	2080 (430)	60.2 (12.1)	74.5 (18.4)	0.85 (0.14)	50.3 (20.3)	117 (49)
EB 2-U	1720 (300)	52.4 (7.9)	68.2 (8.1)	0.90 (0.12)	26.5 (4.5)	60.7 (8.6)
EB 3-U	3440 (1290)	63.0 (11.0)	76.9 (5.6)	0.86 (0.07)	44.4 (16.5)	70.5 (11.0)
EB 3-R	662 (241)	19.0 (8.3)	34.6 (6.4)	0.35 (0.05)	— ¹	— ¹

¹ MRT cannot be calculated for the restored stand because the forest floor C and N pools are not in steady state.

Table 3. Selected characteristics of carbon (C) and nitrogen (N) cycles in mature ponderosa pine-dominated forests

Site	MAP ¹	MAT ²	Tree AB ³	Tree ANPP ⁴	L _C ⁵	R _S ⁶	TBCA ⁷	L _N ⁸	Net N Min. ⁹	Net Nit. ¹⁰
	(cm)	(°C)	(kg C m^{-2})		($\text{g C m}^{-2} \text{ yr}^{-1}$)				($\text{g N m}^{-2} \text{ yr}^{-1}$)	
AZ, This study ¹¹	57	7.5	6.6–7.7	115–122	68.2–76.9	843–891	767–823	0.85–0.90	1.2–1.7	0.06–0.47
Santa Catalina Mts., AZ ¹²	70–80	6–11	7.7–12.0	236–294						
GPNA, AZ ¹³	57	7.5	6.1	157, 141	96.1, 102	565, 414	469, 312	0.78, 0.99	0.74, 1.3	0.34, 0.73
Blodgett, CA ¹⁴	170	13			198			2.4	1.6	0.5
Tesuque, NM ¹⁵	55	6.5			111			0.64		
Metolius, OR ¹⁶	43–65	8–9	9.8, 10.8	136, 157	129, 132	683, 780	554, 648	1.25–1.55	0.58–0.64	<0.08

¹ MAP, mean annual precipitation; ² MAT, mean annual air temperature; ³ AB, aboveground biomass; ⁴ ANPP, aboveground net primary productivity; ⁵ L_C, needle litterfall carbon; ⁶ R_S, soil respiration; ⁷ TBCA, total belowground carbon allocation (Giardina and Ryan 2002); ⁸ L_N, needle litterfall nitrogen; ⁹ Net N Min., net N mineralization; ¹⁰ Net Nit., net nitrification; ¹¹ Net N min. and net nit. for 0–15 cm mineral soil depth; range in values reflects data from three unmanaged stands (see text); ¹² Whittaker and Niering (1975), range in values reflect data from three stands along an altitudinal gradient; ¹³ Kaye et al. (1998a,b, 2005); net N min. and net nit. for 0–15 cm mineral soil depth; data are for the same stand in two consecutive years; ¹⁴ Hart and Firestone (1989, 1991); net N min. and net nit. for 0–7.5 cm mineral soil depth; ¹⁵ Gosz and White (1986); ¹⁶ Law et al. (1999) and Law et al. (2001); range in C values reflect data from the same stand over two different years. Litterfall N concentration, net N min., and net nit. data (0–7.5 cm mineral soil depth) taken from nearby sites (Monleon and Cromack 1996, Monleon et al. 1997); range in these values reflect data from three different stands with contrasting precipitation.

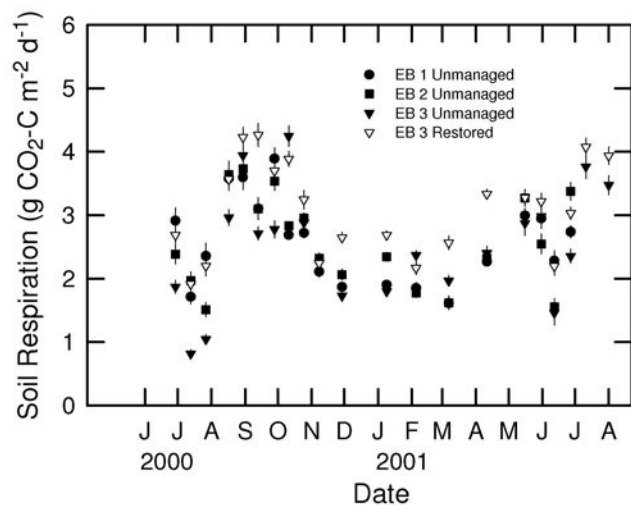


Figure 4. Changes in mean soil respiration (net CO₂ efflux) rate in three unmanaged southwestern ponderosa pine stands and one restored southwestern ponderosa pine stand over the 13-month study period. Vertical bars denote $\pm$ one standard error of the mean (within-stand variability; $n = 20$).

our study are among the lowest reported for forests worldwide (Vogt et al. 1986, Hart and Firestone 1991). These exceedingly slow rates of decomposition and net N release have been substantiated using litterbag studies in similar

southwestern ponderosa pine forests (Klemmedson et al. 1985, Hart et al. 2005b).

Net rates of N transformations in the surface mineral soil, where the majority of fine roots are found in southwestern ponderosa pine ecosystems (Hart et al. 2005a), are low compared to other forests (Binkley and Hart 1989), as are the rates of N uptake into AB (Perry 1994, Barnes et al. 1998, Fisher and Binkley 2000). Low rates of net N mineralization and net nitrification are also characteristic of contemporary ponderosa pine forests throughout the western United States (Table 3). Low net N transformation rates compared to N uptake coupled with low annual precipitation and high evapotranspiration lead to very low losses of N from leaching, even following disturbances (i.e., thinning and burning) that occur during restoration (Johnson et al. 1997, 1998, Kaye et al. 1999).

Our measurements of ANPP within the unmanaged ponderosa pine stands are some of the lowest reported for other ponderosa pine stands in the southwestern United States and elsewhere (Table 3), as well as in other forests (Perry 1994). Part of the explanation for the low ANPP values reported in our study is that the stands that we evaluated had lower standing AB compared to these other forests (Table 3). Nevertheless, based on the relationship between peak standing foliar biomass (FSB) and ANPP found by Webb et al. (1983) across terrestrial biomes of the United States, our stands should have ANPP between 450 and 500

$\text{g C m}^{-2} \text{ yr}^{-1}$ (FSB calculated from litterfall data; Hart and DiSalvo 2005). Furthermore, using Lieth's (1973) equations relating mean annual precipitation (MAP) or mean annual air temperature (MAAT) to ANPP across terrestrial ecosystems worldwide, our stands should have ANPP values of about 400 (MAP) or 650 (MAAT) $\text{g C m}^{-2} \text{ yr}^{-1}$. In contrast, using a more recent analysis of MAP-ANPP relationships across biomes of North America (Knapp and Smith 2001), we estimate that our stands should have ANPP about 140 $\text{g C m}^{-2} \text{ yr}^{-1}$. This latter value is much closer to the actual values we measured in these stands (Table 3), but still is about 20% high. We speculate that the low ANPP of southwestern ponderosa pine ecosystems are due, in part, to the seasonality of the precipitation and low relative humidities leading to high vapor pressure deficits and reduced net photosynthetic rates (Kolb and Stone 2000). There have been few assessments of N limitations to ANPP in southwestern ponderosa pine forests, but those that have occurred have showed modest increases in diameter growth following N addition (Wagle and Beasley 1968, Heidmann 1985). Nevertheless, low N supply to trees could also contribute to the low rates of ANPP compared to predicted values based on structural (foliar biomass) and abiotic (MAAT and MAP) variables.

Our estimates of TBCA using mass balance are high relative to other ponderosa pine forests (Table 3), as well as other forests in general (Litton et al., submitted for publication). Indeed, the ratio of ANPP to TBCA in the unmanaged stands assessed in our study was about 0.15, near the lowest value reported for forests (range of 0.12 to 1.75; Litton et al., submitted for publication). Other forests that had low ANPP-to-TBCA ratios included an 11-year-old *Acacia mearnsii* forest in Australia (0.13) and two pine forests (0.12 in a 23-year-old ponderosa pine stand in Oregon, and 0.26 in a 7- to 9-year-old *Pinus elliotii* stand in Florida). Our estimates of soil respiration were higher than previous values reported in a nearby ponderosa pine forest at the Gus Pearson Natural Area (GPNA), but similar to soil respiration rates from ponderosa pine forests in the Pacific Northwest (Table 3). Part of the reason for the lower values from GPNA is that respiration was not measured during the winter months but modeled using soil temperature-respiration relationships from the growing season (Kaye and Hart 1998b). Based on our measured soil respiration rates during the winter in this study and at the GPNA (S.C. Hart, Northern Arizona University, unpublished data 2005), these modeled values substantially underestimate actual soil respiration during the winter. Apparently, significant soil respiration occurs from these forests even when the mineral soil temperature is near 0°C. Previous research in ponderosa pine forests (e.g., Law et al. 1999) and other ecosystems have found substantial soil respiration occurring under snowpack during the winter (e.g., Grogan and Chapin 1999).

Soil water availability limits the rates of many ecosystem processes in southwestern ponderosa pine forests. In our study, the overriding control of water was clearly shown by the poor correlation found between temperature and soil

respiration under water-limiting conditions, but not when water was relatively available. Additionally, experimental additions of water to both the restored and unmanaged stands within EB 3 resulted in a substantial increase in soil respiration and ponderosa pine live fine-root biomass (fine-root biomass increase statistically significant in unmanaged stand only; Selmants et al., submitted for publication). At GPNA, Boyle et al. (2005) found that changes in water availability following the summer monsoonal rains increased soil enzyme activities and changed the ability of the culturable soil microflora to use a variety of substrates in the soil. We also found that microbial N pools covaried significantly with soil water availability in our study. However, not all soil processes appear to be as sensitive to changes in soil water content. For instance, net N transformation rates showed relatively few statistically significant changes across incubation periods in our study. Nevertheless, the low ANPP-to-TBCA values in southwestern ponderosa pine stands may be a response to the relatively low soil water availabilities in the forests (Litton et al., submitted for publication).

Potential Effect of Ecological Restoration on Ponderosa Pine Ecosystem Function

The operational restoration treatment assessed in our study was unreplicated, hence we are unable to predict how other southwestern ponderosa pine forests would respond to similar restoration treatments. Nevertheless, the effects of restoration on C and N cycling processes in this operational treatment were largely consistent with a replicated restoration experiment at the nearby GPNA that was conducted using more intensive treatments on a much smaller scale (Covington et al. 1997). For instance, in our study, despite an ~90% reduction in tree density and ~80% reduction in basal area, tree ANPP was only reduced by ~50% following the application of the restoration treatment. The drastic reduction in stand density in the restored stand was partially offset by increased wood production in the remaining trees. Similar results were reported by Kaye et al. (2005) at GPNA for the initial 2 years following treatment. Also similar to some previous research at GPNA, soil respiration was enhanced following restoration treatments in our study. Kaye and Hart (1998b) found that soil respiration rates were enhanced during a dry year (1996) and not during a more average precipitation year (1995) following restoration treatments at GPNA. The 2 years during which we measured soil respiration were also dry years (~34 and ~38 cm yr^{-1} for 2000 and 2001, respectively; data averaged from three nearby weather stations; USDA Forest Service RMRS, www.rmrs.nau.edu/weather/stations/, July 23, 2005). Both in our study and at GPNA, soil temperature increased during the growing season following restoration treatments. These increases in soil temperature are likely responsible, in part, for the higher respiration rates in the restored stands observed in these studies (Kaye and Hart 1998b, Hart et al. 2005b). Finally, the soil microbial biomass as a whole seems relatively unresponsive to these

restoration treatments both in our study and at GPNA, but in both studies certain microbial groups appear to be enhanced. For instance, at both GPNA and in our study, net nitrification rates were higher following the restoration treatments, and these increases in nitrification rates appear to be due to increased nitrifier population sizes (Hart et al. 2005b).

There were important differences in ecosystem response to the operationally applied restoration treatments in our study compared to the highly controlled, experimental treatments applied at a much smaller scale at GPNA. For instance, we found that net N mineralization did not increase significantly immediately following the restoration treatments, unlike the result at GPNA (Kaye and Hart 1998a, Kaye et al. 2005). Furthermore, we found that thinning and burning associated with the restoration treatments in our study increased soil water availability relative to the unmanaged stand, but the control treatment at GPNA actually had higher soil water availability (Hart et al. 2005b).

What accounts for the differences in ecosystem responses to the restoration treatments conducted in our case study with those previously conducted at the replicated restoration study at GPNA? We speculate that differences in understory growth (primarily bunchgrasses in both study locations; see Korb et al. 2003 and Moore et al. 2006 for species list) after the thinning and burning treatments largely explain the contrasting ecological responses in these studies (Hart et al. 2005b). At GPNA, herbaceous cover responded immediately and dramatically to the restoration treatments (Covington et al. 1997, Moore et al. 2006). However, herbaceous cover did not increase significantly during the first couple of years following restoration treatment in our study (Korb et al. 2003). Large increases in herbaceous biomass could account for the decrease in surface soil water availability at GPNA following restoration, because bunchgrasses have higher leaf-specific transpiration rates than ponderosa pine (Kaye et al. 1999, Naumburg et al. 2001). Furthermore, increases in understory biomass could also explain the increases in net N mineralization following restoration because their higher litter quality (lower C:N ratio) than pine litter leads to greater N release during decomposition (Hart et al. 2005b). It is unclear why there was such a positive herbaceous response at GPNA compared to these operational restoration study sites. Nevertheless, the influence of previous management and the much greater ground disturbance that occurred in the operational restoration treatments than in the small-scale, experimental restoration treatments at GPNA may be important (Korb et al. 2003, Moore et al. 2006).

Contemporary southwestern ponderosa pine stands are relatively low-productivity coniferous forests with very conservative N cycles. Apparently, low soil water availability is a major driver controlling ecosystem processes in these forests. Restoration of southwestern ponderosa pine forests to their pre-Euro-American structure appears to decrease tree ANPP but increase the proportion of production in woody tissues. Future research needs to elucidate the factors that lead to poor understory response following restoration treatments and ways to enhance herbaceous pro-

ductivity. Current research using operational-scale restoration treatments, with replicated designs and applying the same harvesting methods across treatments, should help elucidate if the ecosystem changes following restoration treatments observed in this case study are generalizable across the southwestern ponderosa pine forest type (see Fire and Fire Surrogate Study, Jim McIver, www.fs.fed.us/ffs/, May 23, 2006).

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