

INITIAL CARBON, NITROGEN, AND PHOSPHORUS FLUXES FOLLOWING PONDEROSA PINE RESTORATION TREATMENTS

JASON P. KAYE,^{1,6} STEPHEN C. HART,^{2,3} PETER Z. FULÉ,^{2,4} W. WALLACE COVINGTON^{2,4}
MARGARET M. MOORE,² AND MARGOT W. KAYE⁵

¹Department of Crop and Soil Sciences, The Pennsylvania State University, University Park, Pennsylvania 16802 USA

²School of Forestry, Northern Arizona University, Flagstaff, Arizona 86011 USA

³Merriam-Powell Center for Environmental Research, Northern Arizona University, Flagstaff, Arizona 86011 USA

⁴Ecological Restoration Institute, Northern Arizona University, Flagstaff, Arizona 86011 USA

⁵School of Forest Resources, The Pennsylvania State University, University Park, Pennsylvania 16802 USA

Abstract. Southwestern ponderosa pine forests were dramatically altered by fire regime disruption that accompanied Euro-American settlement in the 1800s. Major changes include increased tree density, diminished herbaceous cover, and a shift from a frequent low-intensity fire regime to a stand-replacing fire regime. Ecological restoration via thinning and prescribed burning is being widely applied to return forests to the pre-settlement condition, but the effects of restoration on ecosystem function are unknown. We measured carbon (C), nitrogen (N), and phosphorus (P) fluxes during the first two years after the implementation of a replicated field experiment comparing thinning and composite (thinning, forest floor fuel reduction, and prescribed burning) restoration treatments to untreated controls in a ponderosa pine forest in northern Arizona, USA. Total net primary productivity ($260 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) was similar among treatments because a 30–50% decrease in pine foliage and fine-root production in restored ecosystems was balanced by greater wood, coarse root, and herbaceous production. Herbaceous plants accounted for <20% of total plant C, N, and P uptake in the controls but from 25% to 70% in restored plots. Total plant N uptake was $\sim 3 \text{ g N}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ in all treatments, but net N mineralization was just one-half and two-thirds of this value in the control and composite restoration, respectively. Element flux rates in controls generally declined more in a drought year than rates in restoration treatments. In this ponderosa pine forest, ecological restoration that emulated pre-settlement stand structure and fire characteristics had a small effect on plant C, N, and P fluxes at the whole ecosystem level because lower pine foliage and fine-root fluxes in treated plots (compared to controls) were approximately balanced by higher fluxes in wood and herbaceous plants.

Key words: ecological restoration; fire suppression; net primary productivity; nutrient cycling; *Pinus ponderosa*; prescribed fire; thinning.

INTRODUCTION

Humans affect all terrestrial ecosystems (Vitousek et al. 1997), but some ecosystems are not resilient to human-induced disturbances, and large changes in structure and function follow perturbation (Holling 1973, Perry et al. 1989). In some cases, post-disturbance changes represent a shift from a “natural” stable ecological state to an alternative stable state that may persist indefinitely (Scheffer et al. 2001). One goal of restoration ecology is to return the structure and function of these ecosystems to the pre-disturbance stable state, exemplified by the “natural” range of ecological variability (Jackson et al. 1995, Covington et al. 1997, Moore et al. 1999). This paper focuses on ecological restoration of ponderosa pine forests of the southwestern United States that were not resilient to the

disruption of natural fire regimes by Euro-Americans in the mid-1800s.

Prior to Euro-American settlement, frequent fires (every 2–20 yr), herbaceous competition, and drought limited southwestern ponderosa pine regeneration but rarely killed large trees (Pearson 1950, Cooper 1960, White 1985, Swetnam and Baisan 1996). Some pre-settlement ponderosa pine forests contained $\sim 80\%$ herbaceous cover and 20% tree canopy cover (Covington and Sackett 1992) with ~ 30 –140 trees/ha (Covington et al. 1994). Following Euro-American settlement, fire exclusion, livestock grazing, and a wet and warm climate reduced constraints on pine regeneration, allowing herbaceous open spaces to fill with dense thickets of small pines (Savage et al. 1996, Mast et al. 1999). Consequently, contemporary ponderosa pine forests in Arizona average 727 trees/ha (O’Brian 2002), and some stands have >2000 trees/ha and 10% herbaceous cover (Covington et al. 1997). This new forest structure supports a stand-replacing fire regime and expansive herbivorous insect outbreaks (Covington et al. 1994, Kolb

Manuscript received 22 May 2004; revised 9 December 2004; accepted 1 February 2005. Corresponding Editor: M. L. Goulden.

⁶ E-mail: jpk12@psu.edu

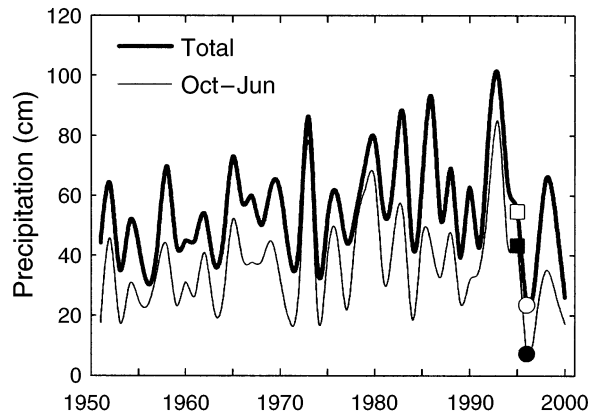


FIG. 1. Precipitation 15 km from our site (in Flagstaff, Arizona, USA), 1950–2000. Total annual precipitation (thick line; open symbols) is the sum of monthly precipitation from October of the preceding year to September of the sample year. Precipitation outside of the monsoon season (July–September) is the sum of precipitation from October of the preceding year to June of the sample year (thin line; solid symbols). Our study period included one near-average year (1995; squares) and one drought year (1996; circles).

et al. 1998). Thus, southwestern ponderosa pine forests have shifted from a stable mixture of herbaceous plants and pines maintained by frequent surface fires to an alternative state with dense pine monocultures susceptible to large stand-replacing fires.

Ecological restoration is being used throughout the Southwest to return ponderosa pine forests to pre-settlement conditions by thinning post-settlement trees and introducing prescribed fires (Covington et al. 1997, Lynch et al. 2000, Allen et al. 2002). These treatments clearly restore the tree density, fuel, and fire characteristics of the pre-settlement forest (Covington et al. 1997, Fulé et al. 2001), but they may also affect fluxes of water, carbon (C), and nutrients, characteristics we refer to collectively as ecosystem function. Predicting ecosystem functional responses to restoration is limited by a lack of both restoration experiments and basic biogeochemical research in dry western forests (Johnson et al. 1997, 1998).

Here we ask, “How do restoration treatments that are designed to emulate pre-settlement aboveground stand structure and fire regimes impact C and nutrient fluxes in ponderosa pine forests?” To answer this question, we measured initial biogeochemical responses to restoration using a replicated field experiment that compared two restoration treatments to untreated controls in an unharvested ponderosa pine forest in Arizona. The thinning restoration treatment removed (via whole tree harvesting) most of the aboveground post-settlement tree biomass from the site. The composite restoration included post-settlement tree removal, manual forest floor fuel reduction, and a prescribed burn (Covington et al. 1997). For the first two years following the application of these treatments, we measured

aboveground and belowground net primary productivity (NPP), plant nitrogen (N) and phosphorus (P) uptake, and soil net N mineralization.

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, USA. Elevation is 2195–2255 m with a southwest aspect and a slope of 0–5%. Mean annual precipitation was 577 mm from 1913 to 1993 (Savage et al. 1996), half of which falls as snow and half as summer monsoonal rains (Schubert 1974). Our research was conducted during one near-average year (1995) and one drought year (1996) with low winter precipitation (Fig. 1). Mean annual air temperature is 7.5°C, with a mean of 94 frost-free days. The soil is derived from flow and cinder basalt and is classified as a Brolliar stony clay loam, a fine, smectitic, Typic Argiboroll. Surface mineral soil (0–15 cm) is approximately 23% sand, 56% silt, and 21% clay with a pH of 6.9 in a 1:1 (mass : volume) solution of soil and 0.01 mol/L CaCl₂. The area was never logged, but livestock grazing occurred between 1876 and 1910. In this paper, “pre-settlement” refers to years prior to 1876, the year of the last surface fire at the site (Dieterich 1980), while “post-settlement” refers to years after 1876. Dominant vegetation is ponderosa pine forest composed of large (37–104 cm diameter at breast height [dbh, measured at 1.37 m above the ground surface]) uneven-aged pre-settlement pines surrounded by small (<37 cm dbh) uneven-aged post-settlement pines or relict herbaceous open spaces dominated by bunchgrasses (herbaceous species are listed in Kaye and Hart [1998a]).

Fifteen 0.25-ha plots were established and assigned to three treatments: control, thinning restoration, and composite restoration. A fuel break was needed to protect buildings of the historic Fort Valley Experiment Station, so the 10 restoration treatment plots were assigned randomly (five as thinning and five as composite) to plots closest to the buildings. The remaining five plots were assigned to the control treatment. All areas had statistically similar aboveground wood NPP (stem, bark, and branches) and tree biomass (Table 1), mineral soil organic matter and N concentrations (Stone et al. 1999), and mineral soil anaerobically mineralizable N (S. C. Hart, *unpublished data*) prior to treatment. On-site dendrochronological reconstructions (Mast et al. 1999) determined the stand structure in 1876. For the thinning restoration, most trees that established after 1876 were removed from the site via whole tree harvesting in the fall of 1993 (Table 1). However, some post-1876 trees were left intact to account for regeneration that would have naturally occurred between 1876 and 1993 and to replace pre-1876 trees that had died (Covington et al. 1997). Composite restoration

TABLE 1. Basic ecosystem characteristics of the ponderosa pine forest study area in northern Arizona, USA.

| Characteristic | Treatment† | | |
|---------------------------------------------------------------------|-------------------------|-------------------------|-------------------------|
| | Control | Thinning | Composite |
| 1992 aboveground wood NPP (g C·m ⁻² ·yr ⁻¹)‡ | 28 ^a (3) | 34 ^a (3) | 34 ^a (3) |
| 1992 aboveground tree C (g/m ²) | 6085 ^a (466) | 6274 ^a (233) | 6307 ^a (562) |
| 1995 aboveground tree C (g/m ²) | 6092 ^b (477) | 4099 ^a (321) | 4697 ^a (741) |
| 1995 aboveground tree N (g/m ²) | 23 ^b (1) | 13 ^a (1) | 15 ^a (2) |
| 1995 aboveground tree P (g/m ²) | 2.2 ^b (0.1) | 1.2 ^a (0.1) | 1.4 ^a (0.2) |
| Leaf area index (m ² /m ²)§ | 8.4 ^b (0.2) | 4.8 ^a (0.2) | 5.0 ^a (0.5) |
| Pine basal area (m ² /ha) | 36 ^b (1) | 16 ^a (1) | 18 ^a (2) |
| Live pine density (no. trees/ha) | 4132 ^b (402) | 152 ^a (17) | 166 ^a (10) |
| Pre-settlement pine crown area (%) | 22 ^a (5) | 15 ^a (1) | 26 ^a (7) |
| Herbaceous opening area (%) | 4 ^a (1) | 9 ^a (3) | 8 ^a (2) |
| Post-settlement pine crown area (%) | 74 ^b (5) | 25 ^a (4) | 22 ^a (2) |
| Post-settlement pines removed area (%) | NA¶ | 50 ^a (3) | 44 ^a (6) |
| Forest floor C (g/m ²) | 1814 ^b (696) | 2711 ^b (776) | 487 ^a (182) |
| Mineral soil C (g/m ²) | 2221 ^a (337) | 3127 ^a (407) | 2926 ^a (179) |
| Forest floor N (g/m ²) | 49 ^b (21) | 73 ^b (23) | 12 ^a (5) |
| Mineral soil N (g/m ²) | 133 ^a (11) | 156 ^a (18) | 150 ^a (9) |
| Forest floor P (g/m ²)# | 5.9 ^b (1.1) | 8.8 ^b (1.7) | 1.8 ^a (0.5) |
| Mineral soil P (g/m ²)# | 146 ^a (8) | 174 ^a (13) | 163 ^a (5) |

Notes: Values are means ($n = 5$ plots) with SE in parentheses. Rows with different lowercase letters differed significantly ($\alpha = 0.10$) in a one-way ANOVA. Data from 1992 were collected prior to the application of treatments. All other data are post-treatment. Forest floor soil pools represent the entire O horizon. Mineral soil pools represent the 0–15 cm depth.

† Treatments include (1) control, untreated ponderosa pine forest; (2) thinning restoration, whole-tree harvesting of most of the aboveground post-settlement tree biomass; and (3) composite restoration, thinning followed by manual forest floor fuel reduction and a prescribed burn.

‡ From changes in dbh and allometric equations; comparable to the “pine wood” row in Table 3.

§ Mean of 1995 and 1996 values for all-sided leaf area (Kaye et al. 1999).

|| The percentage of the total plot area covered by the particular vegetation type.

¶ The control does not have areas where post-settlement pines have been removed.

From Kaye and Hart (1998b).

included post-1876 tree removal in the fall of 1993, followed by forest floor manipulation and a prescribed burn in the fall of 1994. Forest floor manipulation prior to the prescribed burn included raking aside the Oi layer and removing the Oa and Oe layers from the site. The Oi layer (2–4 yr of litterfall) was then returned to the soil surface, with ~670 kg/ha of native grasses and forbs mowed from nearby Hart Prairie. These forest floor manipulations were intended to emulate the fuel load of forests prior to fire exclusion and were based on previous local experience suggesting that old-growth tree mortality is high when prescribed burns are not preceded by the reduction of forest floor fuels that accumulated over 120 yr of fire exclusion (Covington et al. 1997).

Within each plot, we stratified sampling beneath three or four canopy types because previous local research showed that soil processes and their responses to fire vary among canopy types (Covington and Sackett 1992). Canopy-type sample areas (circular subplots of 5 m radius) were selected randomly from the population of potential subplots within each plot. All treatments contained subplots beneath pre-settlement pines, post-settlement pines, and in herbaceous openings ($n = 3$ treatments \times 3 canopy types per plot \times 5 plots = 45 subplots). The thinning and composite restoration treatments also contained subplots beneath areas with post-settlement pines removed ($n = 2$ treatments \times 1 canopy type per plot \times 5 plots = 10 subplots). Canopy-

type (subplot) data were scaled to the plot level using a geographic information system (GIS) that contained the area within each plot occupied by a given canopy type (Table 1). To generate the GIS, a stem map of all trees was used to generate a map of post- and pre-settlement tree canopy cover from published relationships between stem and crown diameter (McTague 1988). Based on the crown area map and extensive field checking, we manually digitized areas covered by relict herbaceous openings, post-settlement pine tree crowns, and pre-settlement pine tree crowns.

Once scaled to the plot level ($n = 5$ for all treatments), we used repeated measures ANOVA ($\alpha = 0.10$ for all tests) to assess the overall two-year treatment effect and year by treatment interactions and one-way ANOVA to assess treatment differences within a given year (SYSTAT 7.0; SPSS, Chicago, Illinois, USA). We \log_{10} transformed data prior to statistical analyses when variance was unequal among treatments, but values presented here are means and standard errors of raw (i.e., untransformed) data.

Plant C, N, and P cycling

Aboveground tree measurements.—In 1992, all trees in the study area were mapped to the nearest 0.1 m and dbh was measured. Radial growth since 1992 was measured on increment cores from sample trees in October 1996. All pre-settlement trees were sampled with three short cores taken 120° apart at breast height. In res-

toration treatment plots, a random 50% sample of the retained post-settlement trees was taken with two cores 90° apart. In the control, with 6900 post-settlement trees, 90 trees were sampled in each of two groups: dbh < 10 cm and dbh ≥ 10 cm. The groups were selected based on age–diameter relationships from the 1992 census and subsampled increment cores showing that growth could differ between these size classes. Mortality of the sample since 1992 was monitored, and sample trees that died were replaced with randomly chosen live trees to maintain equal sample sizes.

Increment cores collected in the fall of 1996 were mounted, surfaced, crossdated, and annual radial growth from 1992 to 1996 was recorded to the nearest 0.001 mm on an incremental measuring stage. Annual radial growth increments were averaged per tree, doubled, and added to the measured 1992 dbh to calculate dbh in 1994, 1995, and 1996. We assumed that bark thickness did not change significantly from 1992 to 1996. Predictive relationships were developed to estimate annual growth and dbh of unsampled trees. Linear regression between 1992 dbh and measured annual radial increments in 1995 and 1996 proved to have reasonable explanatory power ($r^2 \sim 0.5$ – 0.8 for natural logarithm and square-root-transformed equations). Separate predictive equations were developed for post-settlement trees from each treatment.

The dbh values were combined with allometric equations to calculate tree biomass in 1994, 1995, and 1996. The equations used combined data from 26 felled trees from two separate studies (both conducted within the Fort Valley Experimental Forest; Gholz et al. 1979; W. W. Covington, unpublished data) to fit linear regressions between $\ln(\text{dbh, in centimeters})$ and $\ln(\text{biomass, in kilograms})$ of specific tree components. The final equations were of the following form: dry biomass = $a \times e^{[b + \ln(\text{dbh}) \times c]}$, where a corrects for logarithmic bias (Sprugel 1983), b is the intercept of the linear regression, and c is the slope of the linear regression. The resulting equations were

$$\text{stem wood} = 1.0469e^{[-4.1279 + \ln(\text{dbh}) \times 2.7039]} \quad (1)$$

($P < 0.0001$, $r^2 = 0.96$);

$$\text{stem bark} = 1.0304e^{[-4.2291 + \ln(\text{dbh}) \times 2.2691]} \quad (2)$$

($P < 0.0001$, $r^2 = 0.96$);

$$\begin{aligned} \text{live branch wood and bark} \\ = 1.0425e^{[-6.0278 + \ln(\text{dbh}) \times 2.8655]} \end{aligned} \quad (3)$$

($P < 0.0001$, $r^2 = 0.97$);

$$\begin{aligned} \text{dead branch wood and bark} \\ = 1.1322e^{[-5.3589 + \ln(\text{dbh}) \times 2.250]} \end{aligned} \quad (4)$$

($P < 0.0001$, $r^2 = 0.85$); and

$$\text{foliage} = 1.0672e^{[-4.1317 + \ln(\text{dbh}) \times 2.0159]} \quad (5)$$

($P < 0.0001$, $r^2 = 0.90$).

The minimum diameter of trees used to develop the allometric equations was 16 cm (maximum = 81 cm), but our study site had many smaller trees. We compared predicted biomass to measured biomass of trees from 7.6 to 15.2 cm dbh in the Fort Valley area (J. O. Klemmedson, unpublished data). The predicted and actual values were similar (~5%) for trees ≥ 10 cm. In dbh classes < 10 cm, predicted biomass underestimated measured biomass by as much as 50% for stem wood. Although there were numerous trees smaller than 10 cm dbh in the study area, they comprised only ~7% of the total biomass in 1992 (prior to thinning). Therefore, even relatively large errors in estimating small-tree biomass would have a limited effect on stand biomass estimates and a smaller effect on production values, which are determined by difference.

Aboveground NPP of pine stem wood, bark, and branches in 1995 was calculated as 1995 biomass minus 1994 biomass (similarly, 1996 productivity = 1996 biomass – 1995 biomass). Trees that died during a measurement period were assigned zero NPP for the entire period. Foliar NPP was calculated as the sum of the live foliar mass increment (from changes in dbh and Eq. 5) plus nonwoody tree litterfall. Tree litterfall was collected every other month when the site was free of snow using three collection buckets 120° apart at 3 m from each subplot center. Litter was separated into (1) needles, (2) wood, and (3) bark, cones, and miscellaneous; dried to constant mass (24 h at 70°C); and weighed. Wood litterfall was excluded from NPP estimates because including it would imply that trees (1) produced all of the falling wood during the measurement season or (2) that new wood was produced to replace the falling wood. In reality, most or all of the wood litterfall was produced in the past. New wood production was accounted for in the allometric Eqs. 1, 3, and 4.

Fluxes of aboveground tree biomass were converted to C, N, and P fluxes using the element concentrations in biomass. The C concentration of all live biomass was assumed to be 48% (kilograms of C per kilogram oven dry mass × 100%). The N and P concentrations (also as a dry-mass-based percentage) in pine biomass were measured in 17 trees within the Fort Valley Experimental Forest (W. W. Covington, unpublished data; mean ± SE): live branches, 0.25 ± 0.01% N, 0.030 ± 0.001% P; dead branches, 0.24 ± 0.01% N, 0.012 ± 0.001% P; stem wood, 0.045 ± 0.001% N, 0.0017 ± 0.0002% P; stem bark, 0.124 ± 0.004% N, 0.009 ± 0.001% P; and foliage, 1.12 ± 0.02% N, 0.127 ± 0.003% P. The element concentrations in tree litterfall were determined by combining samples from the three litter traps at each subplot for all collections during the growing season (March or April to September or October) or winter months. These samples were finely ground (<425 μm) and subsampled for digestion (modified micro-Kjeldahl; Parkinson and Allen 1975) and combustion (550°C for 6 h). Digested samples were

analyzed for N and P by flow-injection colorimetry using the salicylate (Lachat Instruments 1992a) and molybdate-ascorbic acid (Lachat Instruments 1992b) methods, respectively. Litterfall C concentration was calculated as the ash-free dry mass (from combustion) divided by 1.724 kg organic matter per kilogram organic C (Nelson and Sommers 1982).

Aboveground herbaceous measurements.—Aboveground herbaceous and shrub production were measured on 1-m² quadrats at each subplot (two quadrats per subplot located 180° apart at 50 cm from the subplot centers) in mid-September when the majority of herbaceous species have peak standing biomass. Quadrat orientation changed annually to avoid clipping the same place twice. Herbaceous aboveground vegetation was clipped; separated into grasses, upland sedges, non-legume forbs, and legumes; dried to constant mass; and weighed. Herbaceous productivity was converted to C, N, and P fluxes using the nutrient concentrations of the collected samples. The C concentration was assumed to be 48% of dry biomass, while N and P concentrations were determined via micro-Kjeldahl digestion as described for litterfall.

The only shrub encountered was buckbrush (*Ceanothus fendleri* Gray). Net productivity was measured in 2.5 m radius circles centered on every subplot using current year twig lengths. Buckbrush plants ($n = 54$) sampled off the subplots established the allometric relationship between current year twig length and mass. Using these data, shrub productivity was $<0.13 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$, so we excluded shrubs from further analyses.

Root measurements.—Coarse tree root NPP was calculated from annual changes in coarse root biomass estimated from annual changes in dbh and an allometric equation relating Douglas-fir (*Pseudotsuga menziesii*) dbh to the biomass of roots $>10 \text{ mm}$ in diameter (Santantonio et al. 1977). A synthesis of 25 studies suggested that the relationship between root biomass and dbh is robust across species and sites (Santantonio et al. 1977). This equation underestimates coarse root NPP by excluding roots from 2 to 10 mm in diameter. Element concentrations in live branches $\geq 7.62 \text{ cm}$ in diameter (0.12% N, 0.009% P; W. W. Covington, unpublished data) converted coarse root biomass production to element uptake, and we assumed that coarse root dry biomass was 48% C.

Fine-root NPP was calculated from the biomass of pine and herbaceous roots $<2 \text{ mm}$ in diameter collected monthly from April to October each year (Kaye and Hart 1998b). One mineral soil core (0–15 cm depth, 5.1 cm inner diameter; AMS Core Sampler, American Falls, Idaho, USA) was taken from a random location within each of the 55 subplots (4 m from the plot center), and roots were separated from soil in the laboratory using a hydropneumatic elutriator (Scienceware Bel-Art Products, Pequannock, New Jersey, USA). Elutriated roots were collected on stacked sieves

(2 mm and 500 μm); separated by hand into live pine, dead pine, and herbaceous categories; dried (70°C) to a constant mass; and weighed. Changes in root mass over time were used to calculate root NPP in several ways (see Appendix), and we concluded that the best estimate of both herbaceous and pine fine-root NPP was the difference between maximum and minimum ash-free, oven-dry mass of live roots during the growing season. To determine C, N, and P concentrations, roots from the same treatment and canopy type were composited and subsamples were digested or combusted as described for litterfall. Fine-root element fluxes were estimated separately for pine and herbaceous roots as the maximum root mass times root element concentration minus minimum root mass times root element concentration. Element concentrations were from the composited live root samples on dates when root mass was maximum or minimum. Nutrient use efficiency was calculated as total NPP (in grams of C per square meter per year) divided by total plant nutrient uptake.

Soil C and N measurements

We measured field net N mineralization using modified resin-core incubations (DiStefano and Gholz 1986, Binkley and Hart 1989) described in detail for our site in Kaye and Hart (1998a). Briefly, the entire O horizon (depth varied from 0 to 18 cm) and underlying mineral soil (0–15 cm) were sampled from each of the 55 subplots. Net N mineralization was calculated from the difference between extractable ($\text{NH}_4^+ + \text{NO}_3^-$)-N pool sizes in field-incubated and initial soil, plus ($\text{NH}_4^+ + \text{NO}_3^-$)-N adsorbed mixed-bed ion exchange resin bags incubated beneath both (O horizon and mineral soil) soil layers. Incubations began in May 1995, and new incubations were initiated every 6 mo until May 1997. Mass-based rates within each subplot were converted to an aerial basis using the mean bulk density of initial and final mineral soil cores or O horizon mass per unit area measured with a 929-cm² sampling template (rather than our 17.7-cm² surface area core) at each subplot. Subsamples from all initial soil cores collected in May of each year (1995, 1996, 1997) were used to determine total soil C and N (Carlo Erba NC2100, Thermo Electron, Milan, Italy), and we report the mean of all three years.

RESULTS

Carbon fluxes

We did not detect (Fig. 2) treatment effects on total aboveground ($140 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$), total belowground ($120 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$), or total ecosystem NPP ($260 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$), but we did observe large treatment effects on C fluxes in several ecosystem components (Table 2). The largest single component of aboveground NPP (expressed as C fluxes throughout) was pine foliage, which was 30–40% lower in restored plots (79–99 g

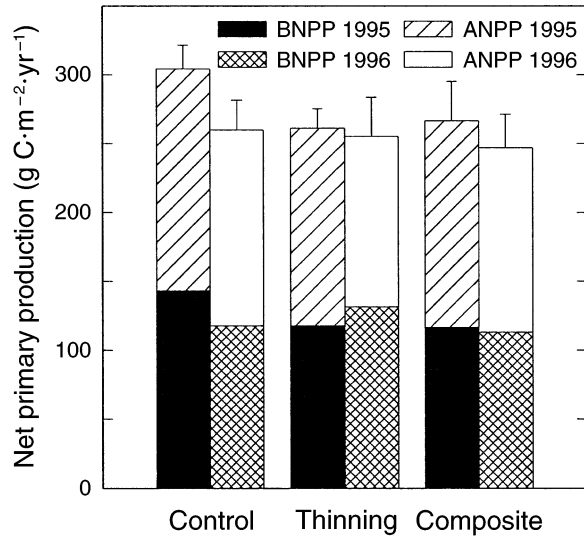


FIG. 2. Total net primary production (NPP) in untreated control, thinning restoration, and composite restoration treatments. Bars depict means + SE ($n = 5$ plots). There were no significant differences among treatments in aboveground NPP (ANPP), belowground NPP (BNPP), or total NPP for individual years or repeated-measures ANOVA ($P > 0.10$).

$\text{C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) than control plots ($128 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$). Wood production was greater in restoration treatments than the control (Table 2), and in 1996 the 152 trees/ha (Table 1) remaining after thinning produced three times more wood than the 4132 trees/ha in control plots. Aboveground herbaceous production was more than two times greater in restored plots (8.0 to $17.5 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) than controls ($<4.0 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$).

The largest belowground NPP fluxes were herbaceous and pine fine-root production (Table 2). Herbaceous fine-root NPP was similar among treatments and ranged from 20 to $70 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$. Pine fine-root NPP was generally higher in the control ($\sim 100 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) than the restoration treatments (43 – $70 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$). Less than 20% of fine-root NPP was herbaceous in control plots, while 25–70% of fine-root NPP was her-

baceous in restoration treatment plots. Pine coarse-root NPP was higher in restoration treatments than the control in both years (Table 2), but coarse roots constitute only about 10% of belowground NPP. Roots accounted for $\sim 46\%$ of total NPP in all treatments (Fig. 2).

Nitrogen cycling

Total plant N uptake was $3 \text{ g N}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ in all treatments and 50–60% of that N remained in fine roots (Fig. 3). Pine N uptake was lower in restoration treatments (1.4 – $2.1 \text{ g N}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) than the control ($\sim 2.5 \text{ g N}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$), mainly because of differences in foliar N uptake in 1996 (Table 3). Pine fine-root N uptake (0.6 – $1.4 \text{ g N}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) was lower in restoration treatments than controls by repeated measures ANOVA, but not for individual years (Table 3). Other pine tissues took up very little N (coarse roots and wood $<0.01 \text{ g N}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$).

Herbaceous N uptake showed little treatment variation in 1995, but by 1996 herbaceous N uptake in restoration treatments (1.0 – $1.4 \text{ g N}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) was 3–4 times higher than the control (Table 3). Increased N uptake was driven by changes in herbaceous biomass, as foliar and root tissue N concentrations were similar among treatments (data not shown). Overall, herbaceous plants accounted for $<12\%$ of total plant N uptake in the control and from 25 to 50% in restoration treatments. Pines were about twice as efficient as herbaceous plants in using N to synthesize C, but whole ecosystem N use efficiency ($\sim 92 \text{ kg C/kg N}$) did not vary greatly among treatments (Table 3).

Net N mineralization (Fig. 3) was greatest in the partial restoration treatment ($\sim 3 \text{ g N}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) in both years. In the composite restoration, net N mineralization was $\sim 2 \text{ g N}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ in both years and control values were 1.0 and $1.6 \text{ g N}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ in 1995 and 1996, respectively. Treatment effects on net N mineralization (and interannual variability in the control) were driven by changes in net nitrification as net ammonification did not vary greatly among treatments (Fig. 3).

TABLE 2. Pine and herbaceous components of the ecosystem carbon (C) budget; values are mean $\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ (with SE in parentheses; $n = 5$ plots).

| Component | Treatment, 1995 | | | Treatment, 1996 | | | Repeated-measures <i>P</i> |
|--------------------|---------------------------|--------------------------|---------------------------|---------------------------|---------------------------|---------------------------|-------------------------------|
| | Control | Thinning | Composite | Control | Thinning | Composite | |
| Pine wood† | 29.2 ^a (2.7) | 41.7 ^b (3.5) | 38.6 ^b (1.8) | 12.2 ^a (1.4) | 36.4 ^b (3.7) | 28.4 ^b (1.1) | <0.01 |
| Pine foliage‡ | 127.9 ^a (12.4) | 83.7 ^a (3.6) | 99.1 ^a (20.7) | 128.8 ^b (12.9) | 78.9 ^a (5.3) | 92.2 ^a (16.3) | 0.08 |
| Pine coarse roots | 14.1 ^a (1.4) | 18.7 ^b (1.5) | 18.0 ^b (1.2) | 5.9 ^a (0.7) | 16.2 ^b (1.7) | 13.0 ^b (0.2) | <0.01 |
| Pine fine roots | 102.8 ^a (11.7) | 69.6 ^a (9.5) | 67.9 ^a (17.5) | 92.3 ^b (11.5) | 43.3 ^a (11.9) | 64.3 ^{ab} (12.2) | 0.02 |
| Herbaceous foliage | 3.6 ^a (1.7) | 17.6 ^b (3.2) | 12.0 ^b (3.2) | 1.1 ^a (0.3) | 8.4 ^b (2.4) | 13.2 ^b (5.8) | <0.01 |
| Herbaceous roots | 26.7 ^a (8.6) | 30.0 ^a (9.3) | 31.1 ^a (9.1) | 19.5 ^a (4.4) | 72.0 ^a (31.5) | 35.9 ^a (18.6) | 0.27 |
| Pine total | 274.0 ^a (9.8) | 213.6 ^a (6.4) | 223.5 ^a (34.5) | 239.2 ^a (20.9) | 174.8 ^a (19.4) | 197.8 ^a (27.1) | 0.11 |
| Herbaceous total | 30.3 ^a (8.0) | 47.5 ^a (11.8) | 43.0 ^a (11.7) | 20.6 ^a (4.3) | 80.5 ^b (31.2) | 49.1 ^{ab} (19.9) | 0.08 |

Notes: Within a given year, rows with different lowercase letters differed significantly ($P < 0.10$) in a one-way ANOVA on that year alone. The repeated-measures *P* value is for the effect of treatment considering each year as a repeated measure.

† Aboveground wood and bark growth increment of stems and branches.

‡ Needle, cone, and bark litterfall plus new foliage growth increment.

Phosphorus cycling

Total plant P uptake (Fig. 3) was similar among treatments (0.36–0.53 g P·m⁻²·yr⁻¹). Belowground P uptake was lower in restoration treatments (0.23 g P·m⁻²·yr⁻¹) than controls (0.36 g P·m⁻²·yr⁻¹) in 1995, mainly due to relatively high pine fine-root P uptake in control plots (Table 4). Root P uptake accounted for 53–67% of total plant P uptake in all treatments (Fig. 3). Pine foliar P uptake was 30% lower in restored plots than in control plots (0.15 g P·m⁻²·yr⁻¹). This decline was approximately balanced by increases in herbaceous foliar P uptake following restoration (Table 4). Herbaceous roots took up substantial amounts of P (0.09–0.18 g P·m⁻²·yr⁻¹) but rates did not vary among treatments. Herbaceous plants accounted for <20% of plant P uptake in the control and from 25 to 50% in the restoration treatments. Woody tissues took up more P in restoration treatments than controls, but P uptake in these tissues was small (0.001–0.008 g P·m⁻²·yr⁻¹). For tissues with large P fluxes (foliage and fine roots), thinning and composite restoration treatments had statistically similar P uptake (Table 4). Unlike N, P use efficiency was not necessarily lower in herbaceous plants (6.4–7.8 kg C/kg P) than pines (5.9–8.0 kg C/kg P) and restored plots had higher P use efficiency than the controls (Table 4).

DISCUSSION

Despite the removal of >2000 post-settlement trees/ha, forest floor manipulations, and prescribed burning, we did not detect restoration effects on plant C, N, and P cycling at the whole ecosystem level (Figs. 2 and 3). In contrast, we observed large differences in element cycling between controls and restoration treatments for certain ecosystem components (Tables 2, 3, and 4). Restored plots generally had significantly greater element cycling in wood and herbaceous plants than controls, but these differences were approximately balanced by a shift toward less element cycling in pine litterfall and fine roots in the restored plots. Thus, rapid adjustments in vegetative growth within two years of restoration appear to enable stability in plant element cycling at the whole ecosystem level.

Carbon fluxes

Fire exclusion has allowed a substantial accumulation of C in the forest floor (O horizon) and biomass of western forests, making these ecosystems a nationally important C sink over the last century (Houghton et al. 2000, Pacala et al. 2001, Schimel et al. 2002). Ecological restoration may alter inputs (total NPP) or outputs (decomposition, fuel and tree removal, fire) of C, with implications for C storage in fire-prone forests and thus, the U.S. C budget. We did not detect short-term restoration effects on total ecosystem NPP (Fig. 2). In addition, treatment effects on biological C fluxes (Fig. 2, Table 2) were small compared to C exports

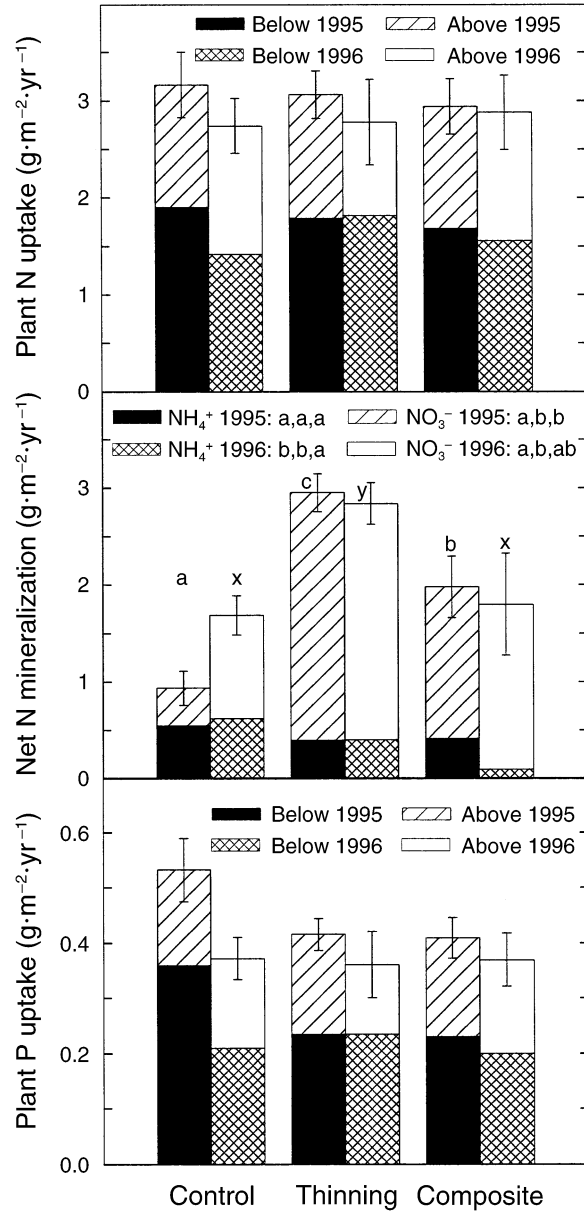


FIG. 3. Total plant nitrogen (N) uptake, soil (entire O horizon plus 0–15 cm mineral soil) net N mineralization, and total plant phosphorus (P) uptake in untreated control, thinning restoration, and composite restoration treatments. Values are means ($n = 5$ plots) \pm SE. For plant N uptake, there were no significant differences ($P < 0.10$) among treatments for individual years or by repeated-measures ANOVA. For net N mineralization, repeated-measures ANOVA on both years resulted in no significant differences in net NH₄⁺ production (net ammonification), but net N mineralization and net NO₃⁻ production (net nitrification) had significant treatment ($P < 0.01$) and year-by-treatment ($P < 0.05$) effects. For individual years, lowercase letters (abc for 1995; xyz for 1996) above bars denote treatment differences in net N mineralization, and lowercase letters in the key denote treatment differences in either NH₄⁺ or NO₃⁻ fluxes. Net N mineralization data from 1995 are from Kaye and Hart (1998a). For plant P uptake, the only significant difference among treatments was higher belowground P uptake in 1995 in controls than in either restoration treatment.

TABLE 3. Pine and herbaceous components of the ecosystem nitrogen (N) budget.

| Component | Treatment, 1995 | | |
|---------------------------------------------------------------------------|--------------------------|--------------------------|--------------------------|
| | Control | Thinning | Composite |
| Plant nitrogen uptake ($\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) | | | |
| Pine wood† | 0.06 ^a (0.01) | 0.09 ^b (0.01) | 0.08 ^b (0.00) |
| Pine foliage‡ | 1.10 ^a (0.15) | 0.74 ^a (0.04) | 0.84 ^a (0.18) |
| Pine coarse roots | 0.02 ^a (0.00) | 0.03 ^b (0.00) | 0.03 ^b (0.00) |
| Pine fine roots | 1.40 ^a (0.10) | 1.20 ^a (0.17) | 1.19 ^a (0.30) |
| Herbaceous foliage | 0.10 ^b (0.05) | 0.44 ^b (0.10) | 0.33 ^b (0.09) |
| Herbaceous roots | 0.48 ^a (0.16) | 0.56 ^a (0.18) | 0.47 ^a (0.13) |
| Pine total | 2.59 ^a (0.21) | 2.06 ^a (0.16) | 2.14 ^a (0.42) |
| Herbaceous total | 0.58 ^a (0.14) | 1.00 ^a (0.26) | 0.80 ^a (0.21) |
| Nitrogen use efficiency (kg C/kg N) | | | |
| Pine | 107.4 ^a (5.0) | 105.2 ^a (5.2) | 107.5 ^a (4.3) |
| Herbaceous | 51.9 ^a (3.0) | 48.2 ^a (2.2) | 53.8 ^a (3.0) |
| Ecosystem | 98.1 ^b (4.8) | 86.1 ^a (3.0) | 90.4 ^{ab} (1.7) |

Notes: Values are means ($n = 5$ plots) with SE in parentheses. Within a given year, rows with different lowercase letters differed significantly ($P < 0.10$) in a one-way ANOVA on that year alone. The repeated-measures P value is for the effect of treatment considering each year as a repeated measure.

† Uptake in aboveground wood and bark of stems and branches.

‡ Uptake in needle, cone, and bark litterfall plus new foliage growth increments.

that occurred when the restoration treatments were implemented. Thinning removed ~ 1770 g C/m² from each restoration treatment. In the composite restoration, forest floor manipulations and prescribed fire removed another 1426 and 175 g C/m², respectively, for a total of 3370 g C/m² (Kaye and Hart 1998b). It would take a decade or more for post-treatment differences (treatment value minus control value) in NPP (statistically zero, but certainly < 50 g C·m⁻²·yr⁻¹; Fig. 2) or soil respiration (< 90 g C·m⁻²·yr⁻¹; Kaye and Hart 1998b) to cumulatively equal the one-time C fluxes that occurred from mechanical thinning and prescribed burning. The fate of thinned tree biomass and the intensity of prescribed fires remain the most important factors controlling the initial impact of restoration on regional C budgets. On longer time scales, C fluxes in the res-

toration treatments may diverge from one another, or from the control, for a number of reasons, including: (1) future pine establishment in thinned stands, (2) future prescribed-fire C losses, and (3) changes in the relative production of slow (e.g., wood) vs. fast (e.g., herbaceous foliage) turnover plant tissues. The long-term C storage potential of untreated forests must be viewed in light of the likelihood of a stand-replacing fire that would rapidly transfer C stored in aboveground biomass and the forest floor to the atmosphere (~ 8000 g C/m²; Table 1).

Our estimates of pine aboveground NPP (Table 2) are lower than three ponderosa-pine-dominated stands in southeastern Arizona (240–300 g C·m⁻²·yr⁻¹; Whitaker and Niering 1975) but they are comparable to 20 young and old ponderosa pine stands across Oregon

TABLE 4. Pine and herbaceous components of the ecosystem phosphorus (P) budget.

| Component | Treatment, 1995 | | |
|-----------------------------------------------------------------------------|----------------------------|----------------------------|----------------------------|
| | Control | Thinning | Composite |
| Plant phosphorus uptake ($\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) | | | |
| Pine wood† | 0.005 ^a (0.000) | 0.008 ^b (0.001) | 0.007 ^b (0.000) |
| Pine foliage‡ | 0.151 ^a (0.021) | 0.106 ^a (0.008) | 0.115 ^a (0.024) |
| Pine coarse roots | 0.003 ^a (0.000) | 0.003 ^b (0.000) | 0.003 ^b (0.000) |
| Pine fine roots | 0.283 ^b (0.029) | 0.155 ^a (0.031) | 0.164 ^a (0.044) |
| Herbaceous foliage | 0.016 ^a (0.008) | 0.068 ^b (0.012) | 0.056 ^b (0.014) |
| Herbaceous roots | 0.075 ^a (0.025) | 0.077 ^a (0.020) | 0.064 ^a (0.018) |
| Pine total | 0.441 ^b (0.038) | 0.272 ^a (0.029) | 0.289 ^a (0.058) |
| Herbaceous total | 0.091 ^a (0.022) | 0.145 ^a (0.030) | 0.121 ^a (0.031) |
| Phosphorus use efficiency (kg C/kg P) | | | |
| Pine | 5.91 ^a (0.28) | 7.68 ^b (0.28) | 7.45 ^b (0.23) |
| Herbaceous | 6.36 ^a (0.23) | 6.69 ^a (0.41) | 6.65 ^a (0.04) |
| Ecosystem | 5.98 ^a (0.26) | 7.34 ^b (0.91) | 7.17 ^b (0.12) |

Notes: Values are means ($n = 5$ plots) with SE in parentheses. Within a given year, rows with different lowercase letters differed significantly ($P < 0.10$) in a one-way ANOVA on that year alone. The repeated-measures P value is for the effect of treatment considering each year as a repeated measure.

† Uptake in aboveground wood and bark of stems and branches.

‡ Uptake in needle, cone, and bark litterfall plus new foliage growth increment.

TABLE 3. Extended.

| Control | Treatment, 1996 | | Repeated-measures <i>P</i> |
|--------------------------|---------------------------|--------------------------|----------------------------|
| | Thinning | Composite | |
| 0.03 ^a (0.00) | 0.08 ^c (0.01) | 0.06 ^b (0.00) | <0.01 |
| 1.26 ^b (0.14) | 0.68 ^a (0.05) | 0.87 ^a (0.15) | 0.07 |
| 0.01 ^a (0.00) | 0.03 ^c (0.00) | 0.02 ^b (0.00) | <0.01 |
| 1.13 ^a (0.18) | 0.59 ^a (0.20) | 0.89 ^a (0.19) | 0.10 |
| 0.04 ^a (0.01) | 0.20 ^b (0.05) | 0.39 ^b (0.16) | <0.01 |
| 0.28 ^a (0.05) | 1.20 ^b (0.50) | 0.65 ^a (0.36) | 0.17 |
| 2.43 ^b (0.29) | 1.37 ^a (0.25) | 1.84 ^b (0.34) | 0.09 |
| 0.32 ^a (0.04) | 1.41 ^b (0.49) | 1.04 ^b (0.41) | 0.04 |
| 100.6 ^a (5.4) | 134.6 ^b (11.6) | 110.3 ^a (4.5) | 0.08 |
| 63.4 ^b (6.5) | 55.1 ^{ab} (1.7) | 47.4 ^a (2.0) | 0.20 |
| 95.7 ^a (3.8) | 94.2 ^a (4.0) | 88.3 ^a (6.2) | 0.21 |

(76–236 g C·m⁻²·yr⁻¹; Law et al. 2001). Whitaker and Niering's (1975) stands had higher wood and foliage production than our stands, while Law et al. (2001) generally found higher wood production and lower foliage production than our stands. We hypothesize that low wood production in our control plots (compared to other studies) results from the abundance of slow-growing, small-diameter trees (Covington et al. 1997, Mast et al. 1999). Increased wood production following thinning (Table 2) has been observed over decades at other southwestern (Pearson 1950, Ronco et al. 1985) and western (Cochran and Barrett 1998) ponderosa pine forests and likely relates to increases in water and N availability for the retained trees. Increased understory productivity following forest thinning has also been observed across the Southwest (M. M. Moore, *personal observations*) and Northwest (McConnell and Smith 1970, Riegel et al. 1992) and has persisted for 10 yr at our site (C. Casey and M. M. Moore, *unpublished data*). Increased light availability was likely the main

factor stimulating increased herbaceous production (Naumberg et al. 2001), in addition to higher N and water availability.

Following thinning with fuel reduction and prescribed burning treatments (our composite treatment) did not alter aboveground C fluxes compared to thinning alone. Previous studies have shown that prescribed burning can cause declines in wood growth (Busse et al. 2000), especially when forest floor fuel loads are not reduced prior to burning (Peterson et al. 1994). Our results suggest that thinning and forest floor fuel reduction can prevent post-burn declines in tree growth.

Our estimates of fine-root turnover (annual productivity/maximum root mass = 0.65 yr⁻¹ for pine and 0.92 yr⁻¹ for herbaceous roots in both years) fall in the range of other ecosystems with similar precipitation (Gill and Jackson 2000). Hart et al. (*in press a*) used sequential soil cores to estimate ponderosa pine fine-root NPP within 10 km of our site in untreated controls and plots burned for 20 yr at 2-yr intervals. Their con-

TABLE 4. Extended.

| Control | Treatment, 1996 | | Repeated-measures <i>P</i> |
|----------------------------|----------------------------|-----------------------------|----------------------------|
| | Thinning | Composite | |
| 0.002 ^a (0.000) | 0.007 ^c (0.001) | 0.005 ^b (0.000) | <0.01 |
| 0.154 ^b (0.019) | 0.083 ^a (0.006) | 0.103 ^a (0.016) | 0.07 |
| 0.001 ^a (0.000) | 0.003 ^c (0.000) | 0.002 ^b (0.000) | <0.01 |
| 0.168 ^a (0.031) | 0.084 ^a (0.024) | 0.121 ^a (0.029) | 0.02 |
| 0.006 ^a (0.002) | 0.036 ^b (0.010) | 0.061 ^b (0.026) | 0.02 |
| 0.040 ^a (0.008) | 0.149 ^a (0.063) | 0.076 ^a (0.043) | 0.25 |
| 0.325 ^b (0.042) | 0.177 ^a (0.030) | 0.232 ^{ab} (0.045) | 0.02 |
| 0.046 ^a (0.008) | 0.184 ^b (0.062) | 0.138 ^{ab} (0.055) | 0.08 |
| 7.51 ^a (0.23) | 7.73 ^a (0.22) | 7.99 ^a (0.11) | <0.01 |
| 6.94 ^b (0.50) | 7.49 ^a (0.15) | 7.80 ^a (0.39) | 0.22 |
| 7.38 ^a (0.21) | 7.73 ^a (0.15) | 7.80 ^a (0.16) | <0.01 |

trol ($96 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) and burned plot ($74 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) values were comparable to our control and restored plots (Table 2), respectively. Law et al. (2001), using a C budget approach in young and old ponderosa pine stands in Oregon, USA, estimated fine-root production values twice as large those reported here (Fig. 2). The Oregon site has lower litterfall and greater soil respiration than our site (Kaye and Hart 1998b), so soil C mass balance predicts greater belowground C allocation in Oregon (Raich and Nadelhoffer 1989).

N and P cycling

Nitrogen and phosphorus fertilizers increase ponderosa pine growth in the Southwest (Wagle and Beasley 1968, Heidmann 1985), and we expected that plant N uptake would be correlated with plant-available N in soil. However, the control and composite restoration treatments had net N mineralization rates one-half and two-thirds as large as plant uptake, respectively (Fig. 3). The discrepancy between plant N uptake and resin core net N mineralization rates could have been caused by treatment effects on plant-microbe competition, plant N uptake from soil deeper than our incubations, plant uptake of organic N, or differences between our resin core estimate and actual net N mineralization in the field.

In other forests, thinning and prescribed burning typically increase inorganic N availability for <5 yr following disturbance (Attiwill and Adams 1993), so it is possible that net N mineralization in control and restoration treatments will become similar over time (Monleon et al. 1997, DeLuca and Zouhar 2000). Alternatively, lower N use efficiency by herbaceous plants (Table 3) could induce a feedback in which high-N litter increases net N mineralization rates in the restoration treatments over the long term (Hobbie 1992). Net N mineralization rates in relict herbaceous openings at our site are higher than in soils beneath post-settlement pines (Kaye and Hart 1998a), supporting this positive feedback hypothesis.

Mechanical thinning and fire produced N fluxes comparable to the annual biological flux rates described above (Fig. 3). We calculated (using the mass of tree C removed and whole-tree C:N mass ratios) that thinning removed from 2.7 to 3.2 g N/m^2 from both treatments, and in the composite restoration, forest floor manipulation and the prescribed fire removed an additional $\sim 2.5 \text{ g N/m}^2$ (based on pre- and post-treatment differences in standing stock; Hart et al., *in press b*). Fire-related N losses were more than an order of magnitude larger than annual soil leaching losses from the site (Kaye et al. 1999), supporting the hypothesis that the N cycles of semi-arid forests are distinct from well-studied humid forests due to the importance of frequent fire (Johnson et al. 1997, 1998).

Total plant P uptake was about an order of magnitude lower than N uptake (Fig. 3), but differences in P cycling among restoration treatments were similar to

those described above for N. We estimate (see N calculations above) that thinning removed $0.26\text{--}0.32 \text{ g P/m}^2$ from both restoration treatments and forest floor manipulations and that the prescribed burn removed an additional 0.09 g P/m^2 from the composite restoration plots. Thus, the quantity of P lost from the site when the treatments were applied is comparable to one year of plant P uptake (Fig. 3).

Drought, restoration, and ecosystem function

During our experiment, 1995 had typical precipitation while 1996 was among the driest years of the previous five decades (Fig. 1). Soil water content from April to June was 30% lower in 1996 than 1995 (Kaye and Hart 1998b, Feeney et al. 1998). We hypothesized that element fluxes in restored plots would be less affected by drought than controls because reduced leaf area following restoration (Table 1) decreases evaporative water loss (Kaye et al. 1999), allowing longer storage of winter precipitation in soils (Feeney et al. 1998, Kaye and Hart 1998b).

To test this hypothesis, we used the interaction term (year by treatment) in repeated measures ANOVA to determine whether the effect of drought (the year effect in the ANOVA) depended on restoration treatment. Soil net N mineralization and nitrification, wood NPP and nutrient uptake, herbaceous aboveground NPP and nutrient uptake, coarse-root NPP and nutrient uptake, pine fine-root P uptake, and previously published soil respiration data (Kaye and Hart 1998b) all had significant year by treatment interactions ($P < 0.05$). In all cases, this interaction occurred because process rates in the control were more greatly altered by drought than rates in restored ecosystems. In all but one case (net N mineralization), drought decreased element fluxes in the control.

Our analysis assumes that drought was the dominant cause of interannual variability in ecosystem function. However, interannual changes (or lack of changes) in ecosystem function in the restored plots may reflect a large biogeochemical response to recent restoration treatments, rather than an ecosystem with increased drought resistance. Long-term measurements of ecosystem function will provide a stronger test of the idea that restored ecosystems display less variability in ecosystem function in response to drought (Knapp and Smith 2001).

CONCLUSION

In general, we found that restored ecosystems had similar plant C, N, and P cycling rates as untreated controls. However, this stability in whole ecosystem element cycles resulted from important trade-offs among ecosystem components. We detected very few differences between the thinning and composite restoration treatments, but we expect that reestablishment of dense tree cover in the thinning treatment will cause these treatments to diverge in the future (Covington et

al. 2001). Nutrients did not appear to be major drivers of post-treatment C fluxes, as stands with variable soil net N mineralization had similar NPP and plant N uptake. In contrast, statistical treatment by year interactions suggest that element fluxes in untreated forests may respond more to drought than element fluxes in restored ecosystems. On decadal time scales, the biological C fluxes that we measured will have a small influence on ecosystem C storage compared to potential abiotic fluxes in prescribed fires, wildfires, and thinning.

The restoration treatments applied here may not be appropriate for other forests. The key to successful restoration is not to apply a single prescription to apparently similar forests, but rather to use ecological principles (e.g., adaptive ecosystem management in light of historical variability and reference conditions; Kaufmann et al. 1994, Moore et al. 1999, Swetnam et al. 1999) to guide site- or region-specific restoration. Under these guidelines, ecological restoration enables a much broader range of management approaches than fire suppression alone (Allen et al. 2002). Ultimately, southwestern forests will be managed for numerous resources simultaneously. The success of restoration may depend on the ability of restored ecosystems to sustain C sequestration, nutrient retention, water yield, water quality, forage production, and wood production, while at the same time reducing fire danger and increasing biodiversity, wildlife habitat, and recreational opportunities. Managing for all of these resources simultaneously may be impossible. However, our research suggests that management based on ecological restoration of pre-settlement stand structure and fire characteristics does not negatively impact resources derived from plant C, N, and P cycling in the short term.

ACKNOWLEDGMENTS

This research was supported by McIntire-Stennis appropriations to the School of Forestry at Northern Arizona University, the National Science Foundation (DEB-9322706), and the Southwest Fire Initiative, Ecological Restoration Institute at Northern Arizona University. The United States Department of Agriculture Forest Service, Rocky Mountain Research Station and Coconino National Forest provided the research site. David Schimel, Michael Goulden, and three anonymous reviewers provided exceptional reviews that greatly improved the manuscript.

LITERATURE CITED

- Allen, C. D., M. Savage, D. A. Falk, K. F. Suckling, T. W. Swetnam, T. Schulke, P. B. Stacey, P. Morgan, M. Hoffman, and J. T. Klingel. 2002. Ecological restoration of southwestern ponderosa pine ecosystems: a broad perspective. *Ecological Applications* **12**:1418–1433.
- Attiwill, P. M., and M. A. Adams. 1993. Tansley review no. 50, nutrient cycling in forests. *New Phytologist* **124**:561–582.
- Binkley, D., and S. C. Hart. 1989. The components of nitrogen availability assessments in forest soils. *Advances in Soil Science* **10**:57–112.
- Busse, M. D., S. A. Simon, and G. M. Riegel. 2000. Tree-growth and understory responses to low-severity prescribed burning in thinned *Pinus ponderosa* forests of central Oregon. *Forest Science* **46**:258–268.
- Cochran, P. H., and J. W. Barrett. 1998. Thirty-five-year growth of thinned and unthinned ponderosa pine in the Methow Valley of northern Washington. United States Department of Agriculture Forest Service, Pacific Northwest Research Station Research Paper PNR-RP-502.
- Cooper, C. F. 1960. Changes in vegetation, structure, and growth of southwestern pine forests since white settlement. *Ecological Monographs* **30**:129–164.
- Covington, W. W., R. L. Everett, R. Steele, L. L. Irwin, and A. N. D. Auclair. 1994. Historical and anticipated changes in forest ecosystems of the inland west of the United States. *Journal of Sustainable Forestry* **2**:13–63.
- Covington, W. W., P. Z. Fulé, S. C. Hart, and R. P. Weaver. 2001. Modeling ecological restoration effects on ponderosa pine forest structure. *Restoration Ecology* **9**:421–431.
- Covington, W. W., P. Z. Fulé, M. M. Moore, S. C. Hart, T. E. Kolb, J. N. Mast, S. S. Sackett, and M. R. Wagner. 1997. Restoration of ecosystem health in southwestern ponderosa pine forests. *Journal of Forestry* **95**:23–29.
- Covington, W. W., and S. S. Sackett. 1992. Spatial variation in soil mineral nitrogen following prescribed burning in ponderosa pine. *Forest Ecology and Management* **54**:175–191.
- DeLuca, T. H., and K. L. Zouhar. 2000. Effects of selection harvest and prescribed fire on the soil nitrogen status of ponderosa pine forests. *Forest Ecology and Management* **138**:263–271.
- Dieterich, J. H. 1980. Chimney Spring forest fire history. United States Department of Agriculture Forest Service, Rocky Mountain Forest and Range Experiment Station Research Paper RM-RP-220.
- DiStefano, J. F., and H. L. Gholz. 1986. A proposed use of ion exchange resins to measure nitrogen mineralization and nitrification in intact soil cores. *Communications in Soil Science and Plant Analysis* **17**:989–998.
- Feehey, S. R., T. E. Kolb, M. R. Wagner, and W. W. Covington. 1998. Influence of thinning and burning restoration treatments on presettlement ponderosa pines at the Gus Pearson Natural Area. *Canadian Journal of Forest Research* **28**:1295–1306.
- Fulé, P. Z., A. E. M. Waltz, W. W. Covington, and T. A. Heinlein. 2001. Measuring forest restoration effectiveness in reducing hazardous fuels. *Journal of Forestry* **99**:24–29.
- Gholz, H. L., C. C. Grier, A. C. Campbell, and A. T. Brown. 1979. Equations for estimating biomass and leaf area of plants in the Pacific Northwest. Research Paper 41. Oregon State University, Forest Research Laboratory, Corvallis, Oregon, USA.
- Gill, R. A., and R. B. Jackson. 2000. Global patterns of root turnover for terrestrial ecosystems. *New Phytologist* **147**:13–31.
- Hart, S. C., A. T. Classen, and R. J. Wright. *In press a*. Long-term interval burning alters fine root and mycorrhizal dynamics in a ponderosa pine forest. *Journal of Applied Ecology*.
- Hart, S. C., T. H. DeLuca, G. S. Newman, D. M. MacKenzie, and S. I. Boyle. *In press b*. Post-fire vegetative dynamics as drivers of microbial community structure and function in forest soils. *Forest Ecology and Management*.
- Heidmann, L. J. 1985. Heavy fertilization increases diameter growth slightly in a 55-year-old ponderosa pine stand in central Arizona. United States Department of Agriculture Forest Service, Rocky Mountain Forest and Range Experiment Station Research Note RM-452.
- Hobbie, S. E. 1992. Effects of plant species on nutrient cycling. *Trends in Ecology and Evolution* **7**:336–339.
- Holling, C. S. 1973. Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics* **4**:1–23.

- Houghton, R. A., J. L. Hackler, and K. T. Lawrence. 2000. Changes in terrestrial carbon storage in the United States. 2. The role of fire and fire management. *Global Ecology and Biogeography* **9**:145–170.
- Jackson, L. L., N. Lopoukhine, and D. Hillyard. 1995. Ecological restoration: a definition and comments. *Restoration Ecology* **3**:71–75.
- Johnson, D. W., R. B. Susfalk, and R. A. Dahlgren. 1997. Nutrient fluxes in forests of the eastern Sierra Nevada Mountains, United States of America. *Global Biogeochemical Cycles* **11**:673–681.
- Johnson, D. W., R. B. Susfalk, R. A. Dahlgren, and J. M. Klopatek. 1998. Fire is more important than water for nitrogen fluxes in semi-arid forests. *Environmental Science and Policy* **1**:79–86.
- Kaufmann, M. R., R. T. Graham, D. A. Boyce, Jr., W. H. Moir, L. Perry, R. T. Reynolds, R. L. Bassett, P. Mehlhop, C. B. Edminster, W. M. Block, and P. S. Corn. 1994. An ecological basis for ecosystem management. United States Department of Agriculture Forest Service, Rocky Mountain Forest and Range Experiment Station General Technical Report GTR-RM-246.
- Kaye, J. P., and S. C. Hart. 1998a. Ecological restoration alters nitrogen transformations in a ponderosa pine-bunchgrass ecosystem. *Ecological Applications* **8**:1052–1060.
- Kaye, J. P., and S. C. Hart. 1998b. Restoration and canopy-type effects on soil respiration in a ponderosa pine-bunchgrass ecosystem. *Soil Science Society of America Journal* **62**:1062–1072.
- Kaye, J. P., S. C. Hart, R. C. Cobb, and J. E. Stone. 1999. Water and nutrient outflow following the ecological restoration of a ponderosa pine-bunchgrass ecosystem. *Restoration Ecology* **7**:252–261.
- Knapp, A. K., and M. D. Smith. 2001. Variation among biomes in temporal dynamics of aboveground primary production. *Science* **291**:481–484.
- Kolb, T. E., K. M. Holmberg, M. R. Wagner, and J. E. Stone. 1998. Regulation of ponderosa pine foliar physiology and insect resistance mechanisms by basal area treatments. *Tree Physiology* **18**:375–381.
- Lachat Instruments. 1992a. QuikChem method number 13-107-06-2-D. Lachat Instruments, Milwaukee, Wisconsin, USA.
- Lachat Instruments. 1992b. QuikChem method number 10-115-01-1-C. Lachat Instruments, Milwaukee, Wisconsin, USA.
- Law, B. E., P. E. Thornton, J. Irvine, P. M. Anthony, and S. Vantuyt. 2001. Carbon storage and fluxes in ponderosa pine forests at different developmental stages. *Global Change Biology* **7**:755–777.
- Lynch, D. L., W. H. Romme, and M. L. Floyd. 2000. Forest restoration in southwestern ponderosa pine. *Journal of Forestry* **98**:17–24.
- Mast, J. N., P. Z. Fulé, M. M. Moore, W. W. Covington, and A. E. M. Waltz. 1999. Restoration of presettlement age structure of an Arizona ponderosa pine forest. *Ecological Applications* **9**:228–239.
- McConnell, B. R., and J. G. Smith. 1970. Response of understory vegetation to ponderosa pine thinning in eastern Washington. *Journal of Range Management* **23**:208–212.
- McTague, J. P. 1988. Estimation of stand density with probability proportional to size from aerial photography. *Western Journal of Applied Forestry* **3**:89–92.
- Monleon, V. J., K. Cromack, Jr., and J. D. Landsberg. 1997. Short and long-term effects of prescribed underburning on nitrogen availability in ponderosa pine stands in central Oregon. *Canadian Journal of Forest Research* **27**:369–378.
- Moore, M. M., W. W. Covington, and P. Z. Fulé. 1999. Reference conditions and ecological restoration: a southwestern ponderosa pine perspective. *Ecological Applications* **9**:166–177.
- Naumburg, E., L. E. DeWald, and T. E. Kolb. 2001. Shade responses of five grasses native to southwestern U.S. *Pinus ponderosa* forests. *Canadian Journal of Botany* **79**:1001–1009.
- Nelson, D. W., and L. E. Sommers. 1982. Total carbon, organic carbon, and organic matter. Pages 539–579 in A. L. Page, R. H. Miller, and D. R. Keeney, editors. *Methods of soil analysis. Part 2. Chemical and microbiological properties*. Agronomy Monograph 9. Agronomy Society of America, Madison, Wisconsin, USA.
- O'Brian, R. A. 2002. Arizona's forest resources, 1999. United States Department of Agriculture Forest Service, Rocky Mountain Forest and Range Experiment Station Resource Bulletin RMRS-RB-2.
- Pacala, S. W., et al. 2001. Consistent land- and atmosphere-based U.S. carbon sink estimates. *Science* **292**:2316–2320.
- Parkinson, J. A., and S. E. Allen. 1975. A wet oxidation procedure suitable for the determination of nitrogen and mineral nutrients in biological material. *Communications in Soil Science and Plant Analysis* **6**:1–11.
- Pearson, G. A. 1950. Management of ponderosa pine in the Southwest. Agricultural Monograph 6. United States Department of Agriculture Forest Service, Washington, D.C., USA.
- Perry, D. A., M. P. Amaranthus, J. G. Borchers, S. L. Borchers, and R. E. Brainerd. 1989. Bootstrapping in ecosystems. *Bioscience* **39**:231–237.
- Peterson, D. L., S. S. Sackett, L. J. Robinson, and S. M. Haase. 1994. The effects of repeated prescribed burning on *Pinus ponderosa* growth. *International Journal of Wildland Fire* **4**:239–247.
- Raich, J. W., and K. J. Nadelhoffer. 1989. Belowground carbon allocation in forest ecosystems: global trends. *Ecology* **70**:1346–1354.
- Riegel, G. M., R. F. Miller, and W. C. Krueger. 1992. Competition for resources between understory vegetation and overstory *Pinus ponderosa* in northeastern Oregon. *Ecological Applications* **2**:71–85.
- Ronco, F., Jr., C. Edminster, and D. Trujillo. 1985. Growth of ponderosa pine thinned to different stocking levels in northern Arizona. United States Department of Agriculture Forest Service, Rocky Mountain Forest and Range Experiment Station Research Paper RM-RP-262.
- Santantonio, D., R. K. Hermann, and W. S. Overton. 1977. Root biomass studies in forest ecosystems. *Pedobiologia* **17**:1–31.
- Savage, M., P. M. Brown, and J. Feddema. 1996. The role of climate in a pine forest regeneration pulse in the southwestern United States. *Écoscience* **3**:310–318.
- Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. *Nature* **413**:591–596.
- Schimmel, D., T. Kittel, S. Running, R. Monson, A. Turnipseed, and D. Anderson. 2002. Carbon sequestration studied in western U.S. mountains. *Eos, Transactions of the American Geophysical Union* **83**:445–449.
- Schubert, G. H. 1974. Silviculture of southwestern ponderosa pine: the status-of-our-knowledge. United States Department of Agriculture Forest Service, Rocky Mountain Forest and Range Experiment Station Report RM-RP-123.
- Sprugel, D. G. 1983. Correcting for bias in log-transformed allometric equations. *Ecology* **64**:209–210.
- Stone, J. E., T. E. Kolb, and W. W. Covington. 1999. Effects of restoration thinning on presettlement *Pinus ponderosa* in northern Arizona. *Restoration Ecology* **7**:172–182.
- Swetnam, T. W., C. D. Allen, and J. L. Betancourt. 1999. Applied historical ecology: using the past to manage for the future. *Ecological Applications* **9**:1189–1206.

- Swetnam, T. W., and C. H. Baisan. 1996. Historical fire regime patterns in the southwestern United States since AD 1700. Pages 11–32 in C. D. Allen, editor. Fire effects in southwestern forests. United States Department of Agriculture Forest Service, Rocky Mountain Forest and Range Experiment Station General Technical Report RM-GTR-246.
- Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of Earth's ecosystems. *Science* **277**:494–499.
- Wagle, R. F., and R. S. Beasley. 1968. Two year effects of thinning and nutrient treatments on the growth of ponderosa pine. *Journal of the Arizona Academy of Sciences* **5**:45–55.
- Whitaker, R. H., and W. A. Niering. 1975. Vegetation of the Santa Catalina Mountains, Arizona. V. Biomass, production, and diversity along the elevation gradient. *Ecology* **56**:771–790.
- White, A. S. 1985. Presettlement regeneration patterns in a southwestern ponderosa pine stand. *Ecology* **66**:589–594.

APPENDIX

A description of the methods for calculating fine-root production is available in ESA's Electronic Data Archive: *Ecological Archives* A015-046-A1.