

# Restoration of a ponderosa pine forest increases soil CO<sub>2</sub> efflux more than either water or nitrogen additions

Paul C. Selmants<sup>1,2\*</sup>, Stephen C. Hart<sup>1,2</sup>, Sarah I. Boyle<sup>1,2</sup>, Catherine A. Gehring<sup>2,3</sup> and Bruce A. Hungate<sup>2,3</sup>

<sup>1</sup>School of Forestry, Northern Arizona University, Flagstaff, AZ 86011, USA; <sup>2</sup>Merriam-Powell Center for Environmental Research, Northern Arizona University, Flagstaff, AZ 86011, USA; and <sup>3</sup>Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86011, USA

## Summary

1. Ecological restoration often involves returning ecosystem structure to some predisturbance reference state, but ecosystem function must also recover if restoration efforts are to be self-sustaining over the long term. In the south-western United States, ponderosa pine forest structure was altered by disruption of the fire regime following Euro-American settlement. Forest structure is now being restored to presettlement conditions through the application of thinning and burning treatments. However, the effects of these treatments on below-ground ecosystem processes remain unclear.

2. We conducted a water and nitrogen (N) addition experiment in adjacent restored and unrestored ponderosa pine stands and compared soil CO<sub>2</sub> efflux in response to these treatments over a 13-month period. Our goals were to (i) quantify water and N limitation to below-ground carbon (C) cycling in contemporary high-density ponderosa pine forests; and (ii) determine if restoration alleviates water and N limitations.

3. Restoration thinning and burning increased soil CO<sub>2</sub> efflux, along with surface soil water content, temperature and herbaceous fine root biomass, while total fine root biomass decreased as a result of restoration.

4. Water and N additions increased C flux from soils to a similar degree in both restored and unrestored ponderosa pine stands, but the increase was relatively small when compared to that stimulated by restoration.

5. *Synthesis and applications.* An understanding of how ecosystem processes respond to treatments designed to restore ecosystem structure is critical in ensuring the long-term success of restoration efforts. Here we show that, although water and N stimulate C flux from soils in these semi-arid forests, restoration treatments have a much greater effect on soil C balance than increased water and N availability by themselves. This suggests that increased quality of C inputs from a recovering understorey herbaceous community is a key component of restoring ecosystem function (e.g. below-ground C cycling) in south-western ponderosa pine forests.

**Key-words:** carbon cycle, ecological restoration, nitrogen fertilization, ponderosa pine, soil respiration, south-western United States, water limitation

## Introduction

Prior to Euro-American settlement (*c.* 1880), ponderosa pine *Pinus ponderosa* var. *scopularum* Englem. forests of the south-western United States were characterized by frequent (2–20 years), low-intensity surface fires which maintained large, grass-dominated openings between mature trees (Cooper 1960; Dieterich 1980). Tree density in these presettlement

stands ranged from ~30 to 140 trees ha<sup>-1</sup>, with herbaceous plants making up as much as 80% of the total canopy cover (Covington & Sackett 1992; Covington *et al.* 1994). Following settlement by Euro-Americans, fire suppression and livestock grazing combined with an unusually wet and warm climate in the early 1900s led to increased pine regeneration and a subsequent dramatic increase in tree density (White 1985; Savage, Brown & Feddema 1996). Contemporary south-western ponderosa pine forests average 727 trees ha<sup>-1</sup> but can reach maximum densities > 2000 trees ha<sup>-1</sup> (Covington *et al.*

\*Correspondence author. E-mail: paul.selmants@nau.edu

1997; O'Brian 2002). This change in forest structure has led to increased forest floor (O horizon) depth, decreased herbaceous plant production, increased susceptibility to insect outbreaks and a shift in the fire regime to one that is more infrequent and stand-replacing (Covington & Moore 1994; Covington *et al.* 1994, 1997). Anthropogenic alteration of forest structure has also affected ecosystem function by sequestering large amounts of carbon (C) and nitrogen (N) in slowly decomposing pine litter, thereby reducing rates of below-ground C and N cycling (Klemmedson, Meier & Campbell 1985; Kaye & Hart 1998a,b; Hart *et al.* 2006).

Ecological restoration treatments, including thinning and prescribed burning, are currently being implemented to remove tree biomass, reduce the risk of stand-replacing fires and increase understorey herbaceous productivity (Kaufmann *et al.* 1994; Covington *et al.* 1997). The reduction in leaf area that accompanies restoration reduces water loss through evapotranspiration, thus increasing soil water availability (Kaye *et al.* 1999; Simonin *et al.* 2006). In addition, soil N transformation rates and the combined respiration of below-ground autotrophic and heterotrophic components (soil CO<sub>2</sub> efflux) were higher in thinned and burned ponderosa pine stands compared to untreated stands 2 years after treatments were applied (Kaye & Hart 1998a,b). These studies suggest that restoration thinning and burning treatments in south-western ponderosa pine forests increase soil water and N availability, leading to increased below-ground biological activity as indicated by higher soil CO<sub>2</sub> efflux rates. Despite this evidence, the degree to which restoration thinning and burning alleviates water and N limitations to below-ground biological activity remains unclear. There are few studies of below-ground responses to thinning and burning treatments in semi-arid south-western forests, and no experiments that have manipulated water and N availability to test whether these factors indeed limit soil respiration.

We conducted a water and N addition experiment in adjacent restored and unrestored 16-ha ponderosa pine stands in northern Arizona, United States. Our objectives were to quantify water and N limitation to below-ground C cycling in contemporary high-density south-western ponderosa pine forests and the degree to which restoration treatments relieve these water and N limitations. We hypothesized that (i) increased water and N availability, soil surface temperatures and a large pulse of dead fine root material following restoration should lead to higher soil CO<sub>2</sub> efflux rates in the restored stand compared to the unrestored stand; and (ii) water and N additions would lead to increased soil CO<sub>2</sub> efflux rates in the unrestored stand but not in the restored stand, because enhanced water and N availability following restoration would ameliorate the response of soil respiration to added water and N.

## Materials and methods

### STUDY SITE AND DESIGN

This experiment was conducted within the Fort Valley Experimental Forest 15 km north-west of Flagstaff, Arizona as part of the Grand

Canyon Forest Partnership's Flagstaff Urban–Wildland Interface (FUWI) project. The study area is approximately 2250 m in elevation with a gentle topography and a cool, subhumid climate. Mean annual precipitation is 577 mm, half of which occurs as winter snow and the other half as late summer rain. The basalt-derived soils are classified as a complex of fine, smectitic, frigid, Typic Argiborolls and Mollic Eutroboralfs, according to USDA soil taxonomy (Miller *et al.* 1995).

We compared two adjacent 16 ha stands: an untreated stand with high bole density (709 trees ha<sup>-1</sup>, basal area = 40.1 m<sup>2</sup> ha<sup>-1</sup>) and intact forest floor, and a treated stand that had been thinned in September 1999, reducing bole density from 800 to 91 trees ha<sup>-1</sup> (basal area reduced from 39.7 to 8.5 m<sup>2</sup> ha<sup>-1</sup>). Slash from the harvesting operation within the treated stand was grouped into piles and burned in February of 2000. The entire treated stand was broadcast-burned in April of 2000. Experimental thinning and burning treatments were conducted in cooperation with the Coconino National Forest and USDA Forest Service Rocky Mountain Research Station. The major goals of these treatments were to develop operational methods for reducing wildfire hazard in the wildland–urban interface around Flagstaff and to re-establish ecosystem structure and function to presumed conditions in these forests prior to Euro–American settlement in the late 1880s (Covington *et al.* 1997; Fulé *et al.* 2001).

Within each of the two stands, a 60 × 60-m grid was established with 20 grid points serving as permanent plot centres for long-term understorey and overstorey vegetation monitoring. At the even-numbered plot centres within each stand ( $n = 10$  per stand), we inserted three place-holding rings (27.5-cm diameter polyvinylchloride) 1 cm into the ground to mark subplot locations, forming a triad with 1-m spacing between subplots. Each subplot at each plot centre was assigned randomly to one of three treatments: unamended (U), water amended (W) and water plus nitrogen amended (W + N). Water amendment was intended to alleviate water limitation by simulating a doubling of mean annual precipitation, currently 577 mm year<sup>-1</sup>. Nitrogen was added in the form of ammonium nitrate (NH<sub>4</sub>NO<sub>3</sub>) at a rate of 45 g N m<sup>-2</sup> year<sup>-1</sup>, an amount shown to maximize fertilization benefits in forest plantation management (Lamontagne & Schiff 2000), and was dissolved in the same volume of water added to the W treatment subplots (3.41 L per subplot per measurement period). The W + N amendment was intended to alleviate both water and N limitation at the same time.

Water and N amendments began on 10 July 2000 and continued every 2 weeks until 6 November 2000. A total of nine additions were made over this period, with each W ring receiving 30.69 L of H<sub>2</sub>O (519 mm) and each W + N ring receiving the same volume of H<sub>2</sub>O as well as 2.39 g of N (42.35 g N m<sup>-2</sup>). No water or N was added over the winter measurement period (November 2000–April 2001) because we assumed that both tree growth and microbial activity were limited by low temperatures and not water or N availability. Water and N amendments for the 2001 growing season began on 14 May and continued every 2 weeks until 30 July 2001. A total of six amendments were made over this period, with each W ring receiving 20.46 L of H<sub>2</sub>O (346 mm) and each W + N ring receiving the same volume of H<sub>2</sub>O plus 1.6 g of N (28.24 g N m<sup>-2</sup>). Over the entire 13 month measurement period, each W ring received a total of 1384 mm of added water and each W + N ring received the same amount of water plus 70.59 g m<sup>2</sup> of added N. Precipitation data from a nearby weather station indicate that we added > 2.5 times the amount of water that fell as precipitation during this period (514 mm; <http://www.rmrs.nau.edu/weather/stations/>), and we added ~350 times more N than is typical for this area from atmospheric deposition, ~2 kg N ha<sup>-1</sup> year<sup>-1</sup> (<http://www.epa.gov/castnet/sites/grc474.html>).

## SOIL CO<sub>2</sub> EFFLUX MEASUREMENTS

We measured net soil CO<sub>2</sub> efflux over a 13-month period within each treatment subplot in both the restored and unrestored stands using the soda lime static chamber technique (Edwards 1982; Grogan 1998; Kaye & Hart 1998b), which uses a mixture of NaOH and CaO or Ca(OH)<sub>2</sub> (granular 1.68–3.36 mm, 6–12 mesh) to absorb CO<sub>2</sub> evolved from the soil surface and trapped inside the chamber. This method provides a simple, inexpensive means to obtain multiple, nearly simultaneous 24-h integrated measurements (Hutchinson & Rochette 2003). In an earlier experiment comparing unthinned and restored ponderosa pine stands, measurements of soil respiration using the soda lime static chamber technique were well correlated with those from dynamic chamber infrared gas analyser (IRGA) measurements (Kaye & Hart 1998b). We used chambers with a relatively large surface area (~595 cm<sup>2</sup>) compared to those of the typical IRGA dynamic chamber (~81 cm<sup>2</sup>), thus lowering the coefficient of variation among samples and increasing the precision of plot-level estimates of soil CO<sub>2</sub> efflux (Davidson *et al.* 2002; Ryan & Law 2005).

Measurements were made every 2 weeks during the growing season (July–December 2000 and May–August 2001) and once a month over the winter period (January–April 2001). Measurements during the growing season of both 2000 and 2001 were made 2 days after water and N additions to avoid any immediate pulse effects. Water additions of a similar volume to a nearby ponderosa pine forest revealed a nearly 10-fold increase in soil CO<sub>2</sub> efflux within 30 min of water addition and a decline over the next 24 h (J.R. Brown, Northern Arizona University, unpublished data). Soda lime (60-g oven-dried weight) was placed in 8-cm diameter polypropylene containers and oven-dried at 105 °C for 24 h. After cooling in a desiccator, containers were weighed to within 0.001 g, transported to the field, opened, and placed under an opaque white chamber (27.5-cm diameter × 20 cm tall). After 24 h, the containers were removed, sealed and returned to the laboratory for drying, cooling and weighing. Six blanks were included per stand to account for CO<sub>2</sub> gain during handling; blanks were treated the same as the samples except that blanks were placed under chambers for only 30 s. Soil CO<sub>2</sub> efflux from each individual chamber over the 24-h measurement period was calculated as net sample weight gain minus mean net blank weight gain multiplied by a correction factor of 1.69, which accounts for the mass of water released when soda lime reacts with CO<sub>2</sub> (Grogan 1998). All 24-h measurements of soil CO<sub>2</sub> efflux at all subplots in both stands were begun between 10 a.m. and 12 p.m.

Annual estimates of C flux from soils were calculated using each measurement as a midpoint between sequential measurement dates. Half the non-measurement days between sequential measurements were assigned to each measurement date. The soil CO<sub>2</sub> efflux value from each measurement was then multiplied by the number of non-measurement days assigned to that measurement date, and these values were summed to produce an annual estimate of soil CO<sub>2</sub> efflux (Kaye & Hart 1998b; Hart *et al.* 2006).

## FINE ROOT BIOMASS AND OTHER SOIL MEASUREMENTS

At the end of the 13-month experiment, in August 2001, we used a 4.8-cm diameter core to take one mineral soil sample from the middle of each subplot to a depth of 15 cm for root analyses. Fine roots are not found in the forest floor of these semi-arid forests (Hart, Classen & Wright 2005). Roots were removed by sieving (< 4 mm) and hand-picking and separated into three categories based on visual criteria: live ponderosa pine roots, dead ponderosa pine roots and live herbaceous

roots (all herbaceous roots appeared live). Following removal from the soil, roots were dried at 60 °C and weighed to the nearest 0.001 g.

In each stand, soil temperature and soil volumetric water content were measured within each ring at the beginning of the CO<sub>2</sub> measurement period to assess the influence of microenvironmental factors on soil CO<sub>2</sub> efflux, to characterize the abiotic conditions within each stand and to determine the influence of water and N amendments on the soil environment. Soil temperature was measured using digital probe thermometers (VWR, West Chester, PA, USA) at a depth of 7.5 cm below the ground surface (measured from the top of the O horizon), and soil volumetric water content was measured using a Trase Systems Time Domain Reflectometry (TDR) unit (Soilmoisture Corp., Santa Barbara, CA, USA). TDR probes were installed permanently inside each ring at depth of 15 cm measured from the top of the O horizon.

Surface mineral soil samples (0–15 cm) were collected from outside the rings in both stands ( $n = 10$  per stand) once a month throughout the 13-month measurement period as part of a separate experiment to assess restoration effects on soil net N transformations (Hart *et al.* 2006). Soil samples were composited across time-periods and analysed for total C, total N and pH. Surface soil total organic C and N concentrations were measured in each stand using a Flash EA 1112 C and N Analyser (ThermoElectron Corp., Waltham, MA, USA). Surface soil pH was determined for each stand in a 1 : 2 suspension of air-dried mineral soil to 0.01 M CaCl<sub>2</sub> solution using an Orion 720 A pH meter (Allometrics, Inc., Baton Rouge, LA, USA).

## STATISTICAL ANALYSES

We used two-factor, repeated measures multivariate analysis of variance (MANOVA) with restoration treatment (restored vs. unrestored) and amendment (U, W and W + N) as main effects to test for differences in soil CO<sub>2</sub> efflux, soil volumetric water and surface soil temperature. We used a multivariate test because the assumption of independent observations was not met (Kuehl 2000), i.e. pairs of repeated measures on the same subplots tended to be correlated [Mauchly's  $W < 0.001$ ,  $\chi^2 = 458.15$ ,  $P(\chi^2 > 458.15) < 0.001$ ]. Where there were no treatment by amendment interactions, we used *post-hoc* contrasts to differentiate the effects of W vs. W + N amendments. Two-factor ANOVA was used to test for differences in estimated annual soil CO<sub>2</sub> efflux and fine root biomass among treatment and amendment types. Where main effects were significant ( $P < 0.05$ ) and interactions were not, we used Tukey's honestly significant difference (HSD) as a mean separation test. Statistical analyses were performed using the SAS JMP IN version 5.1 software package (SAS Institute Inc., Cary, NC, USA);  $\alpha = 0.05$  for all tests.

Because we sacrificed true replication of restoration treatments in favour of implementing those treatments on realistically large scales, our study design is not replicated at the stand level. Thus, our use of inferential statistics to assess the main effects of restoration thinning and burning on soil CO<sub>2</sub> efflux, soil moisture, soil temperature and fine root biomass constitutes pseudoreplication. However, the two stands compared here are directly adjacent to each other with the same soil type, slope (~7%) and aspect (south-east). Both stands had nearly identical tree density and basal area before thinning and burning treatments were applied, and both have similar soil characteristics, even after treatments were applied (Table 1). In addition, our results are consistent with previous research using replicated designs to investigate the effects of restoration alone (e.g. Kaye & Hart 1998b). We suggest these factors provide strong support for our use of this unreplicated system as a means to test the potentially interactive effects of restoration treatments and water and N amendments.

**Table 1.** Surface mineral soil (0–15 cm) characteristics and forest floor mass in adjacent restored and unrestored ponderosa pine stands, northern Arizona, USA. Data are means  $\pm$  1 standard deviation. Data were collected after restoration thinning and burning treatments were applied

Stand	Soil organic C (g m <sup>-2</sup> )	Soil total N (g m <sup>-2</sup> )	Forest floor C (g m <sup>-2</sup> )*	pH
Restored	2960 (250)	145 (15)	662 (241)	5.35 (0.08)
Unrestored	2538 (147)	128 (9)	3440 (1290)	5.26 (0.10)

\*Data from Hart *et al.* (2006).

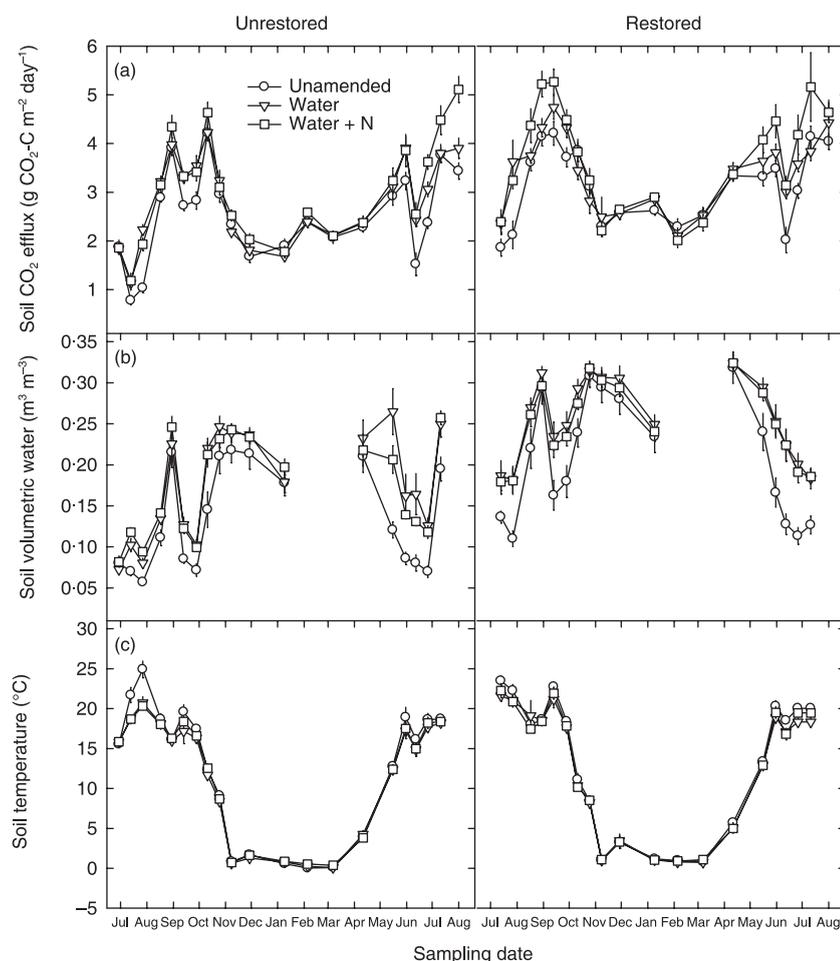
## Results

Both restoration treatment (thinning and burning) and amendment (W and W + N) had significant effects on soil CO<sub>2</sub> efflux (Table 2). CO<sub>2</sub> efflux also varied strongly over time (Table 2). The significant interactions between time and restoration treatment as well as between time and amendment indicate seasonal fluctuations in the magnitude of CO<sub>2</sub> efflux responses to both restoration and water and N amendments (Fig. 1a; Table 2). In both restored and unrestored stands,

watered subplots had significantly higher CO<sub>2</sub> efflux than unamended subplots ( $F = 3.56$ ,  $P = 0.0003$ ; Fig. 1a), and W + N amended subplots had higher CO<sub>2</sub> efflux than W subplots ( $F = 2.55$ ,  $P = 0.008$ ; Fig. 1a).

Surface soil in the restored stand was significantly warmer and wetter than in the unrestored stand over the 13-month measurement period (Fig. 1b,c; Table 2). W and W + N amended subplots were significantly wetter than unamended subplots in both restored and unrestored stands, although the magnitude of this effect varied with time (Fig. 1; Table 2). There was no difference in soil moisture between W and W + N amended subplots ( $F = 1.01$ ,  $P = 0.426$ ), and amendments with W and W + N had no effect on soil temperature (Table 2). Significant time  $\times$  restoration treatment interactions for both soil volumetric water and soil temperature indicate seasonal fluctuations in the magnitude of soil moisture and temperature responses to restoration thinning and burning (Fig. 1; Table 2).

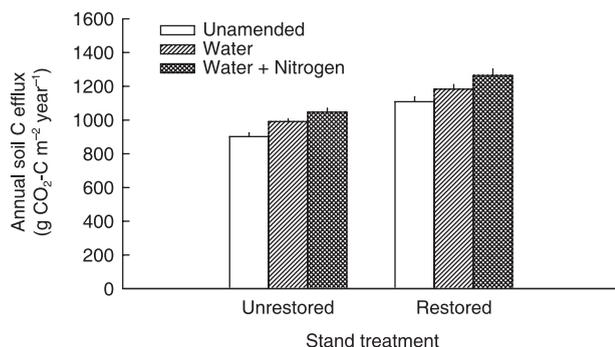
Restoration thinning and burning increased annual C flux from soils by an average of 206 g m<sup>2</sup> year<sup>-1</sup> ( $F = 86.74$ ,  $P < 0.001$ ; Fig. 2). W and W + N amendments increased annual C flux significantly from soils in both the restored and unrestored stands ( $F = 15.49$ ,  $P < 0.001$ ; Fig. 2), but the lack of a significant interaction between restoration treatment and amendment ( $F = 0.113$ ,  $P = 0.89$ ) indicates that W and



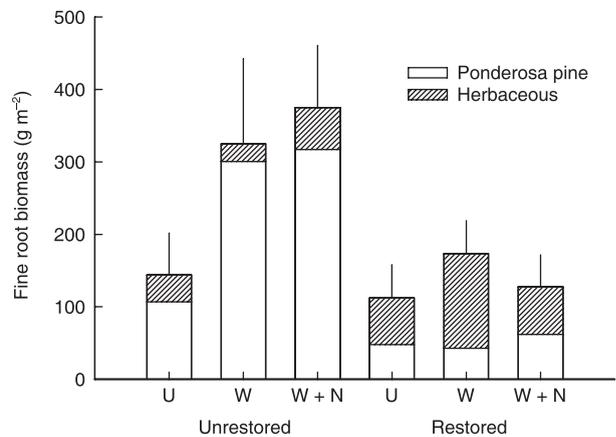
**Fig. 1.** Soil CO<sub>2</sub> efflux (a), volumetric soil water (0–15 cm; b) and soil temperature (7.5 cm; c) over a 13-month period in unamended, water amended, and water + nitrogen (N) amended subplots of adjacent unrestored and restored ponderosa pine stands, northern Arizona, USA. Data are means  $\pm$  1 standard deviation,  $n = 10$ .

**Table 2.** Repeated measures multivariate analysis of variance (MANOVA) of water and nitrogen addition effects on soil CO<sub>2</sub> efflux, volumetric soil water and soil temperature over a 13-month period in restored vs. unrestored ponderosa pine stands, northern Arizona, USA

Source		<i>F</i>	<i>P</i> > <i>F</i>
Soil CO <sub>2</sub> efflux	Between subjects		
	Overall	19.60	< 0.001
	Amendment	19.73	< 0.001
	Treatment	58.14	< 0.001
	Amendment × treatment	0.08	0.922
	Within subjects		
	Time	96.55	< 0.001
	Time × amendment	2.43	< 0.001
	Time × treatment	21.32	0.001
	Time × amendment × treatment	0.93	0.596
Volumetric soil water	Between subjects		
	Overall	24.31	< 0.001
	Amendment	12.34	< 0.001
	Treatment	96.79	< 0.001
	Amendment × treatment	0.03	0.975
	Within subjects		
	Time	107.56	< 0.001
	Time × amendment	1.99	0.007
	Time × treatment	6.54	< 0.001
	Time × amendment × treatment	1.53	0.066
Soil temperature	Between subjects		
	Overall	3.76	0.005
	Amendment	3.04	0.056
	Treatment	12.60	0.001
	Amendment × treatment	0.06	0.937
	Within subjects		
	Time	1398.01	< 0.001
	Time × amendment	1.29	0.177
	Time × treatment	12.30	< 0.001
	Time × amendment × treatment	0.83	0.727



**Fig. 2.** Estimated annual carbon (C) flux from soils in unamended, water amended, and water + nitrogen amended subplots of adjacent unrestored and restored ponderosa pine stands, northern Arizona, USA. Data are means (bars) ± 1 standard deviation (vertical lines), *n* = 10. Both restoration and amendment increased significantly annual C flux from soils (*P* < 0.001 for both factors), but there was no significant restoration by amendment interaction (*P* = 0.89).



**Fig. 3.** Ponderosa pine, herbaceous, and total live fine root (< 2 mm diameter) biomass in unamended (U), water amended (W) and water + nitrogen (W + N) amended subplots of adjacent unrestored and restored ponderosa pine stands, northern Arizona, USA. Data are means (bars) ± 1 standard deviation (vertical lines), *n* = 10. Restoration reduced significantly total live fine root biomass (*P* = 0.014), but amendment had no effect (*P* = 0.134) and there was no significant restoration by amendment interaction (*P* = 0.303).

W + N amendments had similar effects on annual C flux from soils in both the restored and unrestored stands. Water addition increased annual C flux from soils by 89 g m<sup>2</sup> year<sup>-1</sup> in the unrestored stand and 75 g m<sup>2</sup> year<sup>-1</sup> in the restored stand, while W + N amendments increased annual C flux from soils by 144 g m<sup>2</sup> year<sup>-1</sup> in the unrestored stand, and 156 g m<sup>2</sup> year<sup>-1</sup> in the restored stand (Fig. 2).

Restoration thinning and burning significantly reduced total live fine root biomass (ponderosa pine + herbaceous) by an average of 31 g m<sup>2</sup> (*F* = 6.49, *P* = 0.014; Fig. 3), but there were no effects of W or W + N amendments on total live fine root biomass (*F* = 2.09, *P* = 0.134; Fig. 3), nor was there a significant restoration by amendment interaction (*F* = 1.22, *P* = 0.303). There was no difference in dead ponderosa pine fine root biomass between the restored and unrestored stands (*F* = 1.96, *P* = 0.167). Restoration shifted the proportion of live fine root biomass, from predominantly ponderosa pine (~75% of total fine root biomass) in the unrestored stand to a majority of herbaceous fine root biomass (58% of total) in the restored stand (Fig. 3). Despite the overall reduction in fine root biomass, the restored stand had a nearly twofold increase in herbaceous fine root biomass (*F* = 5.27, *P* = 0.026) when compared to the unrestored stand (Fig. 3).

## Discussion

Soil CO<sub>2</sub> efflux represents the major pathway of C loss from terrestrial ecosystems to the atmosphere (Ryan & Law 2005), accounting for ~70% of total ecosystem respiration in temperate forests (Law, Ryan & Anthoni 1999; Janssens *et al.* 2001). As such, CO<sub>2</sub> flux from soils plays a critical role in determining the C balance of forest ecosystems, and is an important indicator of ecosystem response to both natural

and anthropogenic disturbances (Litton *et al.* 2003). Soil CO<sub>2</sub> efflux has been shown to increase in response to thinning and burning treatments across a broad range of forest ecosystems (Gordon *et al.* 1987; Kaye & Hart 1998a; Concilio *et al.* 2005), but the precise mechanisms driving this increase remain unclear. Although soil CO<sub>2</sub> efflux is the combined respiration of autotrophic and heterotrophic below-ground components, we suggest that increased CO<sub>2</sub> flux from soil in the restored stand is largely a heterotrophic response, because restoration thinning and burning treatments reduced both tree above-ground productivity (Hart *et al.* 2006) and standing live fine root biomass.

Consistent with our first hypothesis, we found that restoration thinning and burning led to higher soil CO<sub>2</sub> efflux rates as well as increased surface soil water content (Fig. 1b), temperature (Fig. 1c) and N availability (Hungate *et al.* 2007). These results suggest that enhanced water and N availability following restoration may be largely responsible for higher rates of soil CO<sub>2</sub> efflux. If so, we would expect a strong, positive response of soil CO<sub>2</sub> efflux to added water and N in the unrestored stand, but little to no response in the restored stand, because water and N limitations have already been alleviated by thinning and burning treatments. Contrary to this second hypothesis, water and N amendments increased soil CO<sub>2</sub> efflux to a similar degree in both stands, and their combined effect on C flux from soils was much smaller than that stimulated by restoration thinning and burning. This response suggests that restoration alleviated limitations of other soil resources in addition to water and N. We postulate that increased soil temperature and C availability may be significant factors driving higher C flux from soils in response to restoration thinning and burning.

Soil temperature accounts for much of the seasonal and diel variation in soil CO<sub>2</sub> efflux (Lloyd & Taylor 1994; Hibbard *et al.* 2005). Soil temperature was higher by 1–4 °C in the restored stand, probably because the dramatic reduction in leaf area and forest floor depth led to increased insolation of the mineral soil surface. However, soil respiration in both stands was correlated poorly with temperature when soil water content was below 0.18 m<sup>3</sup> m<sup>-3</sup> (Hart *et al.* 2006), suggesting that temperature exerts a strong control over soil C flux in these semi-arid forest stands only during brief periods of relatively high soil moisture.

Soil CO<sub>2</sub> efflux is also related to substrate availability, and is thus coupled tightly to plant metabolism (Ekblad & Högberg 2001; Högberg *et al.* 2001; Bowling *et al.* 2002) and the decomposition of recently produced organic matter (Trumbore 2000; Giardina & Ryan 2002; Giardina *et al.* 2004). Thus, it is somewhat surprising that restoration thinning and burning, which reduced tree above-ground net primary productivity by ~50% (Hart *et al.* 2006), resulted in increased soil CO<sub>2</sub> efflux. We suggest that a post-restoration pulse of newly dead ponderosa pine fine roots served as an important C source driving higher soil CO<sub>2</sub> efflux in the restored stand. At the end of the 13-month measurement period there was no difference in dead ponderosa pine fine root biomass between the restored and unrestored stands, suggesting that most of

the fine roots killed during tree removal in the restored stand had already decomposed.

In addition to an increase in quantity, our results indicate a post-restoration increase in C substrate quality as well. Recovery of understorey plant species in the restored stand led to a nearly twofold increase in herbaceous fine root biomass. These herbaceous roots have higher N and lower lignin concentrations than ponderosa pine roots (Hart, Classen & Wright 2005; Hungate *et al.* 2007), and thus decompose more rapidly. We suggest that the combination of increased substrate quantity and increased substrate quality following restoration may combine to elicit higher rates of below-ground C cycling (Hart, Classen & Wright 2005).

Restoration of south-western ponderosa pine forests is an attempt to reverse the impact human activities have had on the structure and function of these forests over the past 125 years. However, land managers should also consider whether restored ecosystems are sustainable in future environments altered by human activity through climate change from rising CO<sub>2</sub> concentrations and increased N deposition (Choi 2007). Over a 13-month period, we added > 2.5 times the amount of water that fell as precipitation, and > 350 times the mean yearly amount of atmospheric N deposition (~2 kg ha<sup>-1</sup> year<sup>-1</sup>). Although these additions increased soil CO<sub>2</sub> efflux in both restored and unrestored stands, the degree of increase was relatively small when compared to that stimulated by restoration treatments. This suggests that well above average precipitation or N deposition years are unlikely to elicit threshold shifts in forest C balance when combined with stand thinning and burning treatments.

Our study examined the short-term influence of restoration and increased water and N availability on C flux from soils, which may not reflect the long-term trajectory of restored south-western ponderosa pine forests. Evidence from longer-term studies of thinning and burning treatments indicates that the rapid recovery of understorey herbaceous cover is critical in determining the long-term C balance of restored ponderosa pine forests. Kaye *et al.* (2005) found that, 2 years after treatment, reduced C fluxes in pine foliage and fine roots in restored ponderosa pine stands were balanced by higher fluxes in wood and herbaceous plants, resulting in similar rates of ecosystem-level productivity between restored and unrestored stands. However, in thinned ponderosa pine stands with minimal understorey recovery 6–15 years after treatment, soil C fluxes were lower than in adjacent high-density control stands because of reduced C inputs (Grady & Hart 2006). Our results also suggest that the quantity and quality of C inputs from understorey herbaceous plant production could be an important factor affecting the long-term C balance of restored ponderosa pine forests.

Given the potential increase in net CO<sub>2</sub> flux to the atmosphere, the transition from 'slow' to more 'rapid' below-ground C cycling in restored ponderosa pine stands warrants some concern in the design of restoration strategies. High-density ponderosa pine forests of northern Arizona are currently a net C sink (Potter & Klooster 1999) and our results indicate that, if implemented on a landscape scale, restoration

thinning and burning may reduce the strength of this C sink in the short term. However, without restoration, high-density ponderosa pine forests are highly susceptible to stand-replacing wildfires (Covington *et al.* 1997; Fulé *et al.* 2001), which can rapidly release stored C to the atmosphere as CO<sub>2</sub>. Rapid, disturbance-induced losses of CO<sub>2</sub> are not considered adequately in strength estimates of terrestrial C sinks (Breshears & Allen 2002). Recent evidence from a nearby ponderosa pine forest indicates that a single stand-replacing wildfire can convert large areas of the landscape to a net source of CO<sub>2</sub> for at least a decade (Dore *et al.* in press). When the risk of wildfire induced C losses to the atmosphere is taken into account, regional scale implementation of restoration thinning and burning treatments may be the most reliable option for preserving south-western ponderosa pine forests as a net C sink over the coming decades.

## Acknowledgements

We thank A. Foley, D. Guido, B. Housley and R. Mueller for field and laboratory assistance. Thanks also to W. van der Putten, P. Hulme and two anonymous reviewers for helpful comments on the manuscript. Funding for this research was provided by McIntire-Stennis appropriations to the School of Forestry at NAU, the state of Arizona, and USDA Forest Service Joint Venture Agreement RMRS-99161-RJVA.

## References

- Bowling, D.R., McDowell, N.G., Bond, B.J., Law, B.E. & Ehleringer, J.R. (2002) <sup>13</sup>C content of ecosystem respiration is linked to precipitation and vapor pressure deficit. *Oecologia*, **131**, 113–124.
- Breshears, D.B. & Allen, C.D. (2002) The importance of rapid, disturbance-induced losses in carbon management and sequestration. *Global Ecology and Biogeography*, **11**, 1–5.
- Choi, Y.D. (2007) Restoration ecology to the future: a call for new paradigm. *Restoration Ecology*, **15**, 351–353.
- Concilio, A., Ma, S., Li, Q., LeMoine, J., Chen, J., North, M., Moorehead, D. & Jensen, R. (2005) Soil respiration response to prescribed burning and thinning in mixed-conifer and hardwood forests. *Canadian Journal of Forest Research*, **35**, 1581–1591.
- Cooper, C.F. (1960) Changes in vegetation, structure, and growth of south-western pine forests since white settlement. *Ecological Monographs*, **30**, 129–164.
- Covington, W.W., Everett, R.L., Steele, R., Irwin, L.L. & Auclair, A.N.D. (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., Fulé, P.Z., Moore, M.M., Hart, S.C., Kolb, T.E., Mast, J.N., Sackett, S.S. & Wagner, M.R. (1997) Restoration of ecosystem health in southwestern ponderosa pine forests. *Journal of Forestry*, **95**, 23–29.
- Covington, W.W. & Moore, M.M. (1994) Southwestern ponderosa forest structure: changes since Euro-American settlement. *Journal of Forestry*, **92**, 39–47.
- Covington, W.W. & Sackett, S.S. (1992) Spatial variation in soil mineral nitrogen following prescribed burning in ponderosa pine. *Forest Ecology and Management*, **54**, 175–191.
- Davidson, E.A., Savage, K., Verchot, L.V. & Navarro, R. (2002) Minimizing artifacts and biases in chamber-based measurements of soil respiration. *Agricultural and Forest Meteorology*, **113**, 21–37.
- 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. Rocky Mountain Research Station, Ogden, UT.
- Dore, S., Kolb, T.E., Montes-Helu, M., Sullivan, B.W., Winslow, W.D., Hart, S.C., Kaye, J.P., Koch, G.W. & Hungate, B.A. (in press) Long-term impact of a stand-replacing fire on ecosystem CO<sub>2</sub> exchange of a ponderosa pine forest. *Global Change Biology*.
- Edwards, N.T. (1982) The use of soda-lime for measuring respiration rates in terrestrial ecosystems. *Pedobiologia*, **23**, 321–330.
- Ekblad, A. & Höglberg, P. (2001) Natural abundance of <sup>13</sup>C in CO<sub>2</sub> respired from forest soils reveals speed of link between tree photosynthesis and root respiration. *Oecologia*, **127**, 305–308.
- Fulé, P.Z., McHugh, C., Heinlein, T.A. & Covington, W.W. (2001) Potential fire behavior is reduced following forest restoration treatments. *Proceedings of Conference on Ponderosa Pine Ecosystems Restoration and Conservation: Steps Toward Stewardship* (ed. G.K. Vance, *et al.*), pp. 28–35. USDA Forest Service RMRS-P-22. Rocky Mountain Research Station, Ogden, UT.
- Giardina, C.P., Binkley, D., Ryan, M.G., Fownes, J.H. & Senock, R.S. (2004) Belowground carbon cycling in a humid tropical forest decreases with fertilization. *Oecologia*, **139**, 545–550.
- Giardina, C.P. & Ryan, M.G. (2002) Total belowground carbon allocation in a fast growing Eucalyptus plantation estimated using a carbon balance approach. *Ecosystems*, **5**, 487–499.
- Gordon, A.M., Schletter, R.E. & Van Cleave, K. (1987) Seasonal patterns of soil respiration and CO<sub>2</sub> evolution following harvesting in the white spruce forests of interior Alaska. *Canadian Journal of Forest Research*, **17**, 304–310.
- Grady, K.C. & Hart, S.C. (2006) Influences of thinning, prescribed burning, and wildfire on soil processes and properties in southwestern ponderosa pine forests: a retrospective study. *Forest Ecology and Management*, **234**, 123–135.
- Grogan, P. (1998) CO<sub>2</sub> flux measurement using soda-lime: correction for water formed during CO<sub>2</sub> adsorption. *Ecology*, **79**, 1467–1468.
- Hart, S.C., Classen, A.T. & Wright, R.J. (2005) Long-term interval burning alters fine root and mycorrhizal dynamics in a ponderosa pine forest. *Journal of Applied Ecology*, **42**, 752–761.
- Hart, S.C., DeLuca, T.H., Newman, G.S., MacKenzie, M.D. & Boyle, S.I. (2005) Post-fire vegetative dynamics as drivers of microbial community structure and function in forest soils. *Forest Ecology and Management*, **220**, 166–184.
- Hart, S.C., Selmants, P.C., Boyle, S.I. & Overby, S.T. (2006) Carbon and nitrogen cycling in southwestern ponderosa pine forests. *Forest Science*, **52**, 683–693.
- Hibbard, K.A., Law, B.E., Reichstein, M. & Sulzman, J. (2005) An analysis of soil respiration across northern hemisphere temperate ecosystems. *Biogeochemistry*, **73**, 29–70.
- Höglberg, P., Nordgren, A., Buchmann, N., Taylor, A.F., Ekblad, A., Höglberg, M.N., Nyberg, G., Ottoson-Lofvenius, M. & Read, D.J. (2001) Large-scale forest girdling shows that current photosynthesis drives soil respiration. *Nature*, **411**, 789–792.
- Hungate, B.A., Hart, S.C., Selmants, P.C., Boyle, S.I. & Gehring, C.A. (2007) Soil nitrogen responses to management, increased precipitation, and added nitrogen in ponderosa pine forests. *Ecological Applications*, **17**, 1352–1365.
- Hutchinson, G.L. & Rochette, P. (2003) Non-flower-through steady-state chambers for measuring soil respiration: numerical evaluation of their performance. *Soil Science Society of America Journal*, **67**, 166–180.
- Janssens, I.A., Lankreijer, H., Matteucci, G., Kowalski, A.S., Buchmann, N., Epron, D., Pilegaard, K., Kutsch, W., Longdoz, B., Grunwald, T., Montagnani, L., Dore, S., Rebmann, C., Moors, E.J., Grelle, A., Rannik, U., Morgenstern, K., Oltchev, S., Clement, R., Gudmundsson, J., Minerbi, S., Berbigier, P., Ibrom, A., Moncrieff, J., Aubinet, M., Bernhofer, C., Jensen, O., Vesala, T., Granier, A., Schulze, E.D., Lindroth, A., Dolman, A.J., Jarvis, P.G., Ceulemans, R. & Valentini, R. (2001) Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. *Global Change Biology*, **7**, 269–278.
- Kaufmann, M.R., Graham, R.T., Boyce, D.A. Jr, Moir, W.H., Perry, L., Reynolds, R.T., Bassett, R.L., Mehlhop, P., Edminster, C.B., Block, W.M. & Corn, P.S. (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. Rocky Mountain Research Station, Ogden, UT.
- Kaye, J.P. & Hart, S.C. (1998a) Ecological restoration alters nitrogen transformations in a ponderosa pine–bunchgrass ecosystem. *Ecological Applications*, **8**, 1052–1060.
- Kaye, J.P. & Hart, S.C. (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., Hart, S.C., Cobb, R.C. & Stone, J.E. (1999) Water and nutrient outflow following the ecological restoration of a ponderosa pine–bunchgrass ecosystem. *Restoration Ecology*, **7**, 252–261.
- Kaye, J.P., Hart, S.C., Fulé, P.Z., Covington, W.W., Moore, M.M. & Kaye, M.W. (2005) Initial carbon, nitrogen, and phosphorus fluxes following ponderosa pine restoration treatments. *Ecological Applications*, **15**, 1581–1593.
- Klemmedson, J.O., Meier, C.E. & Campbell, R.E. (1985) Needle decomposition and nutrient release in ponderosa pine ecosystems. *Forest Science*, **31**, 647–660.
- Kuehl, R.O. (2000) *Design of Experiments: Statistical Principles of Research Design and Analysis*, 2nd edn. Duxbury Press, Pacific Grove, CA.

- Lamontagne, S. & Schiff, S. (2000) Response of soil microorganisms to an elevated nitrate input in an open *Pinus banksiana* Cladina forest. *Forest Ecology and Management*, **137**, 13–22.
- Law, B.E., Ryan, M.G. & Anthoni, P.M. (1999) Seasonal and annual respiration of a ponderosa pine ecosystem. *Global Change Biology*, **5**, 169–182.
- Litton, C.M., Ryan, M.G., Knight, D.H. & Stahl, P.D. (2003) Soil-surface carbon dioxide efflux and microbial biomass in relation to tree density 13 years after a stand replacing fire in a lodgepole pine ecosystem. *Global Change Biology*, **9**, 680–696.
- Lloyd, J. & Taylor, J.A. (1994) On the temperature dependence of soil respiration. *Functional Ecology*, **8**, 315–323.
- Miller, G., Ambos, N., Boness, P., Reyher, D., Robertson, G., Scalzone, K., Steinke, R. & Subirge, T. (1995) *Terrestrial Ecosystem Survey of the Coconino National Forest*. USDA Forest Service Southwestern Region, Albuquerque, NM, 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. Rocky Mountain Research Station, Ogden, UT.
- Potter, C.S. & Klooster, S.A. (1999) Detecting a terrestrial biosphere sink for carbon dioxide: interannual ecosystem modeling for the mid-1980s. *Climatic Change*, **42**, 489–503.
- Ryan, M.G. & Law, B.E. (2005) Interpreting, measuring, and modeling soil respiration. *Biogeochemistry*, **73**, 3–27.
- Savage, M., Brown, P.M. & Feddema, J. (1996) The role of climate in a pine forest regeneration pulse in the southwestern United States. *Ecoscience*, **3**, 310–318.
- Simonin, K., Kolb, T.E., Montes-Helu, M. & Koch, G.W. (2006) Restoration thinning and influence of tree size and leaf area to sapwood area ratio on water relations of *Pinus ponderosa*. *Tree Physiology*, **26**, 493–503.
- Trumbore, S. (2000) Age of soil organic matter and soil respiration: radiocarbon constraints on belowground C dynamics. *Ecological Applications*, **10**, 399–411.
- White, A.S. (1985) Presettlement regeneration patterns in a southwestern ponderosa pine stand. *Ecology*, **66**, 589–594.

Received 2 July 2007; accepted 10 January 2008

Handling Editor: Wim van der Putten