Restoration and Canopy-Type Effects on Soil Respiration in a Ponderosa Pine–Bunchgrass Ecosystem

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ABSTRACT

In ponderosa pine (*Pinus ponderosa* Douglas ex P. Lawson & Lawson)–bunchgrass ecosystems of the western USA, fire exclusion by Euro-American settlers facilitated pine invasion of grassy openings, increased forest floor detritus, and shifted the disturbance regime toward stand-replacing fires, motivating ecological restoration through thinning and prescribed burning. We used in situ soil respiration over a 2-yr period to assess belowground responses to pine invasion and restoration in a ponderosa pine–bunchgrass ecosystem near Flagstaff, AZ. Replicated restoration treatments were: (i) partial restoration — thinning to presettlement conditions; (ii) complete restoration — removing trees and forest floor material to presettlement conditions, native grass litter addition, and prescribed burning; and (iii) control. Within treatments, we sampled beneath different canopy types to assess the effects of pine invasion into grassy openings on soil respiration. Growing season soil respiration was greater in the complete restoration (346 ± 24 g CO_2–C m^{-2}) and control (350 ± 8 g CO_2–C m^{-2}) than the partial restoration (301 ± 5 g CO_2–C m^{-2}) in 1995. In 1996, the complete (364 ± 17 g CO_2–C m^{-2}) and partial (328 ± 7 g CO_2–C m^{-2}) restoration treatments had greater growing season respiration rates than the control (302 ± 13 g CO_2–C m^{-2}). Results suggest that restoration effects on soil respiration depend on interannual soil water patterns and may not significantly alter regional C cycles. Soil respiration from grassy openings was 15% greater than from soil beneath presettlement or postsettlement pines in 1995 and 1996. A lack of active management will decrease belowground catabolism if pines continue to expand at the expense of grassy openings.

RECENT ESCALATION of atmospheric CO_2 concentrations has promoted a great deal of research on terrestrial C storage. Soil detritus contains a large portion of terrestrial C and small changes in this large pool may have important impacts on the global C budget (Jenkinson et al., 1991; Raich and Schlesinger, 1992; Schlesinger, 1977; Turner et al., 1995). In ponderosa pine forests of the intermountain western USA, C is accumulating in the forest floor due to fire suppression and other anthropogenic disturbances (Cooper, 1960; Covington et al., 1994; Covington and Moore, 1994; Covington and Sackett, 1986). To ameliorate the effects of these disturbances, ecological restoration treatments including thinning and prescribed fire are currently being implemented (Covington et al., 1997; Covington and Sackett 1984, 1986, 1992; Kaufmann et al., 1994). Large-scale restoration will likely alter regional C cycles by reducing the number of stand-replacing fires, increasing the number of surface fires, removing tree biomass, and increasing herbaceous biomass. However, it is unclear how restoration will affect the catabolism of detritus that has accumulated during 120 yr of fire exclusion.

In addition to potential changes in regional C cycles, restoration will alter the ecology of specific restoration sites. Our research was conducted near Flagstaff, AZ in a ponderosa pine–bunchgrass ecosystem typical of the Intermountain West (Covington et al., 1997). In this relatively dry part of the ponderosa pine range, the pine–bunchgrass community is climax (Moir and Dieterich, 1988; Pyne et al., 1996; Steele, 1987). Before Euro-American settlement (ca. 1870 near Flagstaff), these communities were characterized by frequent (every 2–12 yr), low-intensity fires that rarely reached the crowns of large trees (Cooper, 1960; Dieterich, 1980). Fire eliminated a majority of pine regeneration and maintained grassy openings between groups of large pines. Fire suppression and grazing, followed by a wet and warm climate in the early 1900s, led to an irruption of pine regeneration that reached a maximum in 1919 (Cooper, 1960; Savage et al., 1996; White, 1985). As pine densities increased, pine litter accumulated and the fire regime became infrequent and stand-replacing, making ecosystem restoration imperative (Covington and Moore, 1994; Covington et al., 1994, 1997; Swetnam and Baisan, 1996).

In order to test the effects of potential restoration management strategies on ecosystem function and structure, a replicated ecological restoration experiment was established in a mature ponderosa pine–bunchgrass ecosystem within the Gus Pearson Natural Area in 1993 and 1994 (Covington et al., 1997). We previously reported that ecological restoration increased and pine invasion decreased microbial N transformation rates at this site (Kaye and Hart, 1998). Here we report the systemic belowground response to pine invasion and ecological restoration, using soil respiration as an integrative measure of soil biological activity.

MATERIALS AND METHODS

Study Site and Treatments

The Gus Pearson Natural Area lies within the U.S. Forest Service Fort Valley Experimental Forest, ≈10 km northwest of Flagstaff, AZ. The site is at an elevation between 2195 to 2255 m with a southwest aspect and a slope of 0 to 5%. Mean annual precipitation is 56.7 cm, half of which falls as snow, and half as summer monsoonal rains (Schubert, 1974). Mean annual air temperature is 7.5°C, with a mean of 94 frostfree days. The soil is derived from flow and cinder basalt and is classified as Brolliar stony clay loam, a fine, montmorillonitic

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Abbreviations: ANOVA, analysis of variance; dbh, diameter at breast height; GIS, geographic information system; IRGA, infrared gas analyzer; P_n, net photosynthesis; PAR, photosynthetically active radiation; R_d, dark respiration.

Typic Argiboroll. The surface soil (0–15 cm) texture is a silt-loam (≈23% sand, 56% silt, and 21% clay), and surface soil pH (water) is ≈6.8. The area was never logged, but livestock grazing occurred between 1876 and 1910.

The dominant vegetation is a ponderosa pine forest of uneven age, composed of mature presettlement trees (37 to 104 cm diameter at breast height, dbh) surrounded by postsettlement pines (<36 cm dbh) or relict bunchgrass openings. Before treatment, grass biomass beneath the pines was <9 g m^{-2}, and postsettlement trees covered ≈80% of the area relative to 10% cover by grassy openings and presettlement pines (Covington et al., 1997). Major herbaceous species found in the relict bunchgrass openings include: the grasses — Arizona fescue (*Festuca arizonica* Vasey), mountain muhly [*Muhlenbergia montana* (Nutt.) Hitchc.], mutton bluegrass [*Poa fendleriana* (Steud.) Vasey], pine dropseed [*Blepharoneuron tricholepis* (Torr.) Nash.], black dropseed (*Sporobolus interruptus* Vasey), and bottlebrush squirreltail (*Sitanion hysterix* Nutt.); the forbs — showy aster (*Aster commutatus* Torr. and Gray), spreading fleabane (*Erigeron divergens* Torr. and Gray), showy goldeneye (*Viguiera multiflora* Nutt.), western ragweed (*Ambrosia psilistachya* DC.), and snakeweed (*Guterrezia* spp.); and the shrub, buckbrush (*Ceanothus fendlerii* Steud.).

Fifteen 0.25-ha plots were established and assigned to three treatments: control, partial restoration, and complete restoration. Because a fuel break was needed to protect buildings of the historical Fort Valley Experiment Station, the ten restoration-treatment plots were assigned randomly (five as partial restoration and five as complete restoration) to plots closest to the buildings. The remaining five plots were assigned to the control treatment. All treatment areas had similar forest floor mass and similar mineral soil organic matter (OM) content, total N content, and anaerobically mineralizable N before treatment (P.Z. Fulé and S.C. Hart, Northern Arizona University, 1993, unpublished data). For the partial-restoration treatment, we removed aboveground postsettlement tree biomass from the site. Complete restoration included postsettlement tree removal, forest floor manipulation, and a prescribed burn. Forest floor manipulation entailed raking aside the Oi layer (2–4 yr of litterfall), removing the Oa and Oe layers from the site, and then returning the Oi layer to the soil surface along with ≈672 kg ha^{-1} (≈1 yr of herbaceous production) of native grasses and forbs mowed from nearby Hart Prairie. Forest-floor manipulations emulated the fuel load of presettlement forests. The complete-restoration treatment was designed to test whether ecosystem structure and function could be restored quickly through intense manipulations (Covington et al., 1997). The partial-restoration treatment was designed to test whether thinning alone could restore ecosystem structure and function. Thinning was implemented in the fall of 1993 and prescribed burning in the fall of 1994. Post-treatment soil sampling for soil respiration and other parameters began in the spring of 1995. In both restoration treatments, excess postsettlement trees were retained to ensure sufficient survival for restoring tree density to presettlement levels. Further treatment and fire details are given in Covington et al. (1997).

Within each plot, we stratified sampling beneath three or four canopy types. This sampling stratification was motivated by our desire to detect changes resulting from pine invasion and by previous research that showed that forest floor and soil responses to prescribed fire differed among canopy types (Covington and Sackett, 1986, 1992). Canopy-type sample areas (subplots) were selected randomly from the population of potential subplots for a given canopy type within each plot. In all treatments, we located subplots beneath presettlement pines, postsettlement pines, and in grassy openings (n = 3 treatments × 3 canopy types × 5 replicates = 45 subplots). Postsettlement-removed subplots were established in the partial- and complete-restoration treatments only, in areas where postsettlement pines had been removed (n = 2 treatments × 1 canopy type × 5 replicates = 10 subplots).

Microclimatic Measurements

Volumetric water content (0–15 cm mineral soil depth) was determined in all 55 subplots within 3 d of each soil respiration measurement with a Trace Systems (Soil Moisture Corp., Santa Barbara, CA) time domain reflectometry unit calibrated using the equation of Topp et al. (1980). Daily mean soil temperatures (7.5-cm mineral soil depth) were measured with a CR10 Campbell Scientific (Campbell Scientific Inc., Logan, UT) datalogger and thermistors. Temperature was measured in all canopy types within two plots of each treatment (n = 8 in each restoration treatment and 6 in the control) beginning 1 Jan. 1995 in the presettlement and postsettlement-retained subplots within the control treatment, and 23 June 1995 in all other subplots. Soil water content and temperature from beneath canopy types were scaled to the plot level using a geographic information system (GIS).

Root Biomass Measurements

The biomass of pine and grass fine roots (<2-mm diameter) was measured on the weekday nearest the 15th of every month from April to October in 1995 and 1996. A 5-cm-diameter core was extracted (AMS Core Sampler, American Falls, ID) from the mineral soil (0–15 cm depth) and roots were separated from soil in the lab with a hydropneumatic elutriator (Scienceware Bel-Art products, Pequannock, NJ). Elutriated roots were collected on stack sieves (500 μm and 2 mm); separated into live pine, dead pine, and grass (live and dead grass roots were not differentiated) categories; dried at 70°C for 48 h; and weighed. In this paper, we present total fine-root biomass (i.e., the sum of live pine, dead pine, and grass roots). For each monthly sampling, roots from the same treatment and canopy type were combined, and the mass loss on ignition (550°C for 6 h) of these composites was used to convert the oven-dry mass of the roots to ashfree oven-dry mass. Note that in these semiarid ponderosa pine–bunchgrass ecosystems, the vast majority of fine roots occur within the 0- to 15-cm mineral soil layer, with few fine roots present within the forest floor (Wright, 1996).

Organic Matter, Nitrogen, and Phosphorus

Organic matter and total N and P were determined in the forest floor (entire O horizon) and mineral soils (0–15 cm depth) collected from all 55 subplots in May, 1995. Organic matter was determined by mass loss on ignition and organic C was estimated using the mass ratio of 1.724 g of C per gram of OM (Nelson and Sommers, 1982). Total N (organic + NH_4^+) and P (organic + PO_4^{3-}) were determined by modified micro-Kjeldahl digestion (Parkinson and Allen, 1975) and flow injection analysis using the salicylate (Lachat Instruments, Inc., 1992a) and molybdate-ascorbic acid (Lachat Instruments, Inc., 1992b) methods, respectively.

Soil Respiration Measurements

Soil respiration was measured using the soda lime static chamber technique (Edwards, 1982), which has been used in a number of recent experiments (Bowden et al., 1993; Millikin and Bowden, 1996; Raich et al., 1990; Toland and Zak, 1994; Townsend et al., 1995). This method may underestimate high CO_2 flux rates relative to dynamic chamber methods (Nay et

al., 1994); however, soda lime remains the most feasible method for measuring daily fluxes and obtaining the sample size ($n \approx 15$) needed to detect in situ differences in soil respiration among treatments (Cropper et al., 1985; Raich et al., 1990). In 1995, we sampled twice each month from June to October and once each month in May and November. In 1996, we sampled twice each month from May to October and once each month in April and November. The sampling location at each subplot was determined by taking a random direction and securing a place-holding ring 4 m from the subplot center. The place-holding ring extended 1 cm into the O horizon, fitted snuggly against the sampling chamber, acted as a diffusive barrier for lateral gas flow, and allowed all measurements to be taken at the same location. The soda lime method uses a mixture of NaOH and CaO or $Ca(OH)_2$ (granular 1.68–3.36 mm, 6–12 mesh) to absorb CO_2 that evolves from the soil surface and is trapped beneath an air-tight chamber. We oven dried the soda lime (60 g oven-dry weight) for 24 h at 105°C in small (8-cm diameter) polypropylene containers. Following drying, the containers were sealed with airtight lids, cooled in a desiccator, weighed to one ten thousandth of a gram, transported to the field, opened, and placed under an opaque chamber (27.5 cm in diameter, 20 cm tall). The chamber was pushed ≈1 cm into the forest floor and secured with weights. After 24 h, the chamber was removed and the soda lime container was sealed, returned to the laboratory, dried, cooled, and weighed. To correct for CO_2 absorbed during sample handling, 11 blanks were included on every sample date. Blanks were treated as the samples except they were placed under the chambers for only 30 s. Net sample weight gain minus mean net blank weight gain multiplied by 1.41 yields the CO_2 flux integrated over the incubation period. The factor 1.41, measured by Edwards (1982), corrects for the mass of water released as soda lime reacts with CO_2. These values were divided by the chamber surface area and incubation time. Soda lime was replaced after it gained 5% of its initial weight.

Total growing season respiration was determined by using each measurement as a midpoint between sequential sampling dates. Half of the nonmeasurement days between sequential measurements were assigned to each measurement date. The soil respiration value from each measurement date was then multiplied by the number of nonmeasurement days assigned to that measurement. Winter respiration was determined using a nonlinear regression with soil temperature [CO_2–C = $0.0079 \times (°C)^2$; $r^2 = 0.43$; $n = 244$; $P < 0.001$], based on data pooled from all three treatments but only from subplots where temperature was measured. Only measurement dates with soil water content >0.2 $m^3\ m^{-3}$ were included in the regression because winter soil water content is consistently high, and soil respiration is probably more sensitive to temperature when water is not limiting. Annual soil respiration was calculated as modeled winter respiration plus measured growing season respiration.

While most subplots within our study area had little to no herbaceous ground cover, herbaceous vegetation was abundant in the grassy opening canopy type. We tested the influence of herbaceous net photosynthesis (P_n) on our soil respiration measurements using nine clipped sample sites (three per treatment) adjacent to the primary sample area. Herbaceous vegetation was continuously clipped from clipped sample sites throughout the growing season. Soil respiration was measured simultaneously on these paired clipped and unclipped areas on each sampling date.

To account for potential underestimation of high soil respiration rates by the soda lime technique (Nay et al., 1994), we compared soda lime measurements with measurements from an infrared gas analyzer (IRGA) on a subset of plots in September, 1996 and April, 1997. These dates were chosen in order to acquire rates that span the range of values observed at the site. Soda lime measurements were made 24 h prior to IRGA-based measurements at the same subplot ($n = 12$ subplots per date). Because the IRGA and soda lime sampling chambers were identical in volume and diameter, we were able to control for spatial variability in soil respiration by conducting paired IRGA and soda lime measurements within the same place-holding ring on consecutive days. In order to minimize temporal variability in soil respiration, we attempted to sample soda lime and IRGA soil respiration on consecutive days under similar climatic conditions. The IRGA soil respiration unit included a sampling chamber, identical to the soda lime sampling chambers described above, attached to a LI-COR 6200 Portable Photosynthesis Unit (LI-COR, Lincoln, NE). Air was pumped from the sample chamber to the IRGA detector and then back into the chamber in a closed loop. The change in CO_2 concentration over time yields an estimate of soil respiration. At each subplot, the system was allowed to equilibrate with ambient air before measurement. The chamber was then inserted into the place-holding ring, pushed ≈1 cm into the forest floor, and secured with weights. After a 1-min stabilization period, the concentration of CO_2 was recorded for 3 min. At each subplot, IRGA-based measurements were taken at 1200, 1800, 0000, and 0600 h. The linear relationship between soda lime and IRGA estimates (Soda lime = $0.698 + 0.377 \times$ IRGA; $r^2 = 0.47$; $n = 23$; $P < 0.001$) was used to revise our soda lime estimates of daily soil respiration, which were then scaled as described above to calculate total growing season respiration. The IRGA-corrected annual soil respiration was calculated using corrected growing season soil respiration measurements and our temperature-based modeled estimates of winter respiration. We did not correct modeled winter respiration rates using our IRGA data because winter soil respiration was only a small fraction of total growing season respiration, and we did not have actual winter soda-lime measurements on which to apply an IRGA-based correction.

During the April, 1997 comparison, we sampled CO_2 concentrations of ambient air and soda lime chamber headspace. Rubber septa were installed in four chambers and at the end of the 24-h measurements, a syringe was used to sample ambient and chamber headspace air. Samples were stored in evacuated vials that had been flushed with He, and CO_2 concentration was determined in the laboratory by gas chromatography (Shimadzu GC-8A equipped with a thermal conductivity detector, Shimadzu Scientific Instruments, Columbia, MD).

Statistical Analyses

Because the postsettlement-removed canopy type was absent from control plots, we determined canopy-type differences by deleting postsettlement removed data and analyzing presettlement, postsettlement retained, and grass as a two-way analysis of variance (ANOVA) with canopy type and treatment as main effects. Repeated-measures ANOVA was used for daily soil respiration, soil water content, and soil temperature analyses. Standard ANOVA was used for total growing season respiration, total N, total P, OM, bulk density, forest floor density, and fine-root biomass (one ANOVA for each date roots were sampled) analyses. When main effects were significant ($P < 0.10$) and interactions were not, Fisher's LSD was used as a mean separation test. To determine plot-scale treatment effects that included the postsettlement-removed canopy type, we scaled all canopy-type data to the plot level using a GIS. The GIS contained the area within each plot occupied by a given canopy type, allowing us to

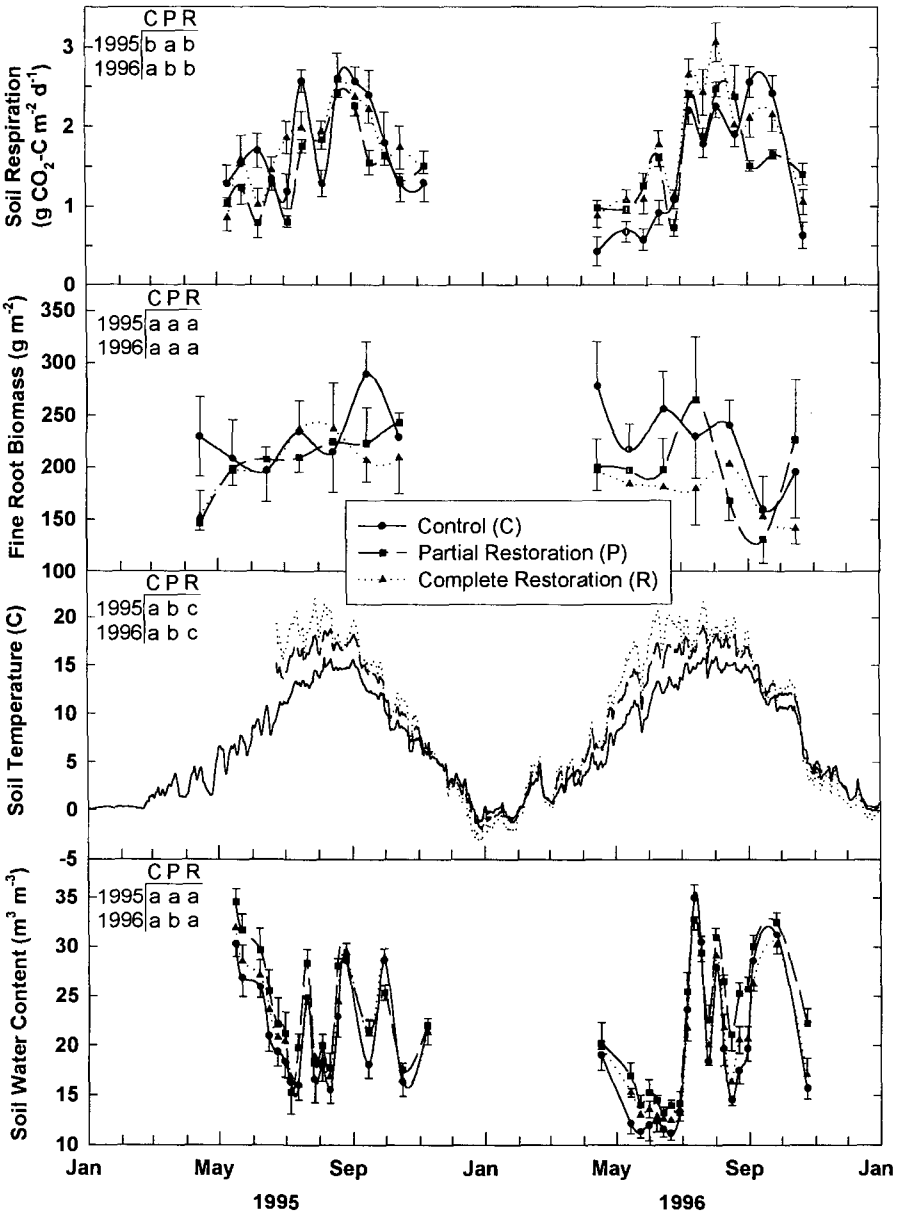

Fig. 1. Soil respiration, fine-root biomass (0–15 cm mineral soil depth), soil temperature (7.5-cm mineral soil depth), and soil water content (0–15 cm mineral soil depth) in the control and two restoration treatments within the Gus Pearson Natural Area near Flagstaff, AZ. Symbols denote means and bars denote ± one standard error. For soil temperature, $n = 2$ and for all other variables, $n = 5$. Where error bars overlapped they were deleted in one or both directions. Temperature measurements did not begin in the restoration treatments until June, 1995. Statistical differences are tabulated in the upper left-hand corner of each graph. Within years, different lowercase letters reflect statistical differences ($P < 0.10$) among the control, partial-restoration, and complete-restoration treatments. Repeated-measures ANOVA was used for all analyses except fine-root biomass, for which standard ANOVA was used for each month separately.

calculate the proportional area of each canopy type within a plot. Once scaled to the plot level, the data were analyzed using a one-way ANOVA (repeated measures or standard as described above) with treatment as the factor. All ANOVA analyses used $\log_{10}$ transformed data due to unequal variance among treatments. We used simple and multiple linear regressions to assess the importance of factors controlling soil respiration. Differences between clipped and unclipped plots were determined using a paired Student's t-test. All regression analyses were performed using the statistical package SigmaStat (version 2.0, Jandel Scientific, San Rafael, CA), and all ANOVA analyses were performed using the statistical package StatView (version 4.5, Abacus Concepts, Inc., Berkeley, CA). The $P < 0.10$ level was used to denote statistical significance; this level was chosen prior to the onset of the experiments.

RESULTS AND DISCUSSION

Soil respiration measurements include the combined net efflux of CO_2 from the soil surface resulting primarily from the activities of plant roots and soil heterotrophic microorganisms. Variability in our soil respiration measurements probably resulted from multifarious mechanisms, including variability in root (Fig. 1 and 2) and microorganism density and activity, microclimate

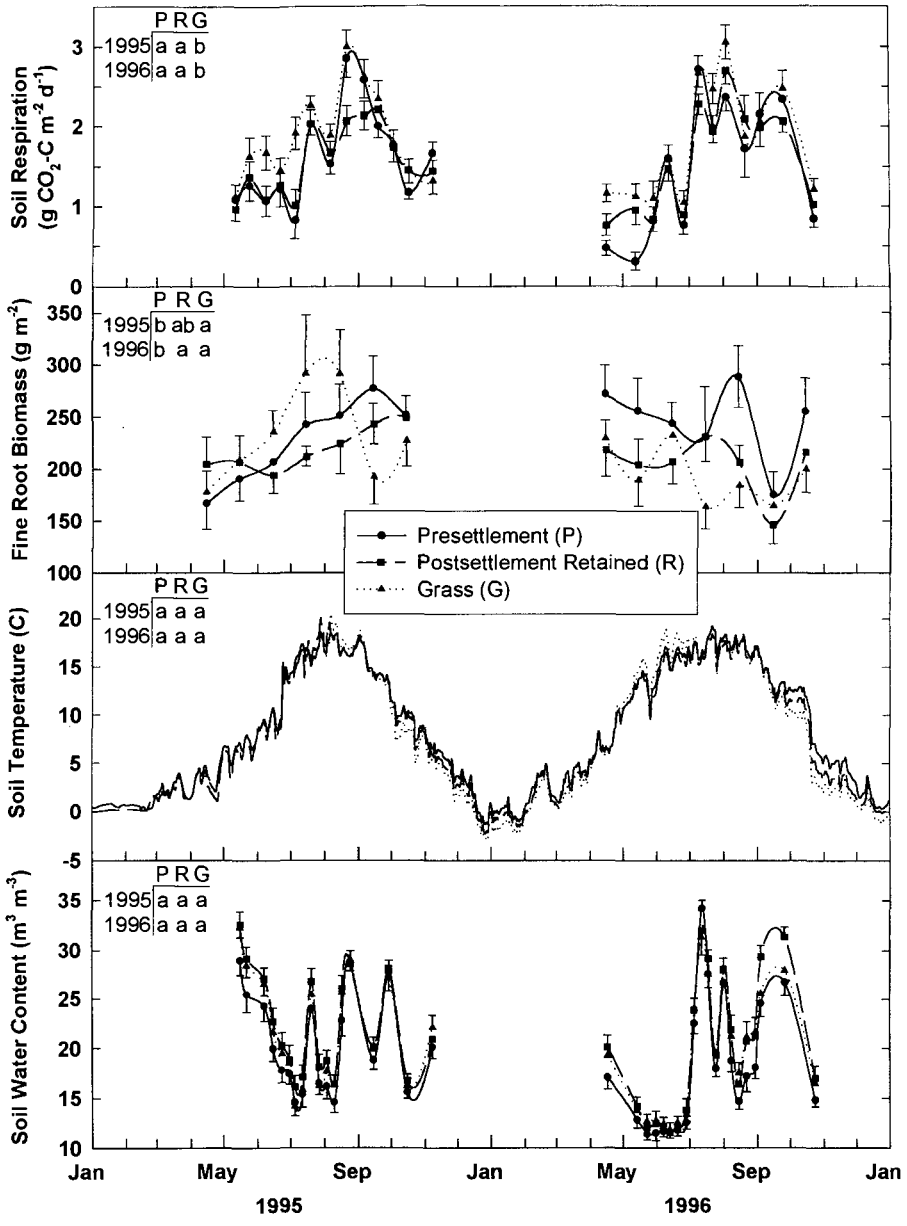

Fig. 2. Soil respiration, fine-root biomass (0–15 cm mineral soil depth), soil temperature (7.5-cm mineral soil depth), and soil water content (0–15 cm mineral soil depth) from soils beneath three canopy types within the Gus Pearson Natural Area near Flagstaff, AZ. Symbols denote means and bars denote ± one standard error. For soil temperature, $n = 6$ and for all other variables, $n = 15$. Where error bars overlapped they were deleted in one or both directions. Temperature measurements did not begin in the grass canopy type until June, 1995. Statistical differences are tabulated in the upper left-hand corner of each graph. Within years, different lowercase letters reflect statistical differences ($P < 0.10$) among presettlement, postsettlement-retained, and grass canopy types. Differences in fine-root biomass occurred in September, 1995 and August, 1996 only. Differences in all other variables are from repeated-measures ANOVA on all dates.

(Fig. 1 and 2), and substrate availability (Table 1). In our discussion, we attempt to isolate which of the above mechanisms caused differences in soil respiration among restoration treatments and canopy types.

Effects of Ecological Restoration on Soil Respiration

There were no differences in mineral soil N, P, OM, C/N ratio, or fine-root biomass among treatments (Table 1, Fig. 1). However, forest floor N, P, and OM were lower in the complete-restoration treatment than partial restoration or control (Table 1). If forest floor N, P, or OM were major factors influencing soil respiration rates, we would expect the complete-restoration treatment to have the lowest soil respiration rates. Daily (Fig. 1) and total growing season (Table 2) soil respiration rates were greatest in the complete-restoration and control treatments in 1995, and greatest in the partial- and complete-restoration treatments in 1996. These results suggest that forest floor and mineral soil N, P, and OM availability do not account for the treatment differences in soil respiration observed at this site.

All treatments showed significant relationships be-

Table 1. Selected mean (and one standard error) soil characteristics for the Gus Pearson Natural Area restoration site.

Soil horizon/Characteristic	Treatment†			Canopy type†		
	Control	Partial restoration	Complete restoration	Presettlement	Postsettlement retained	Grass
Forest floor (O horizon)						
Areal density (g m−2)	6374.7 (958.7)b	9 282.6 (1595.9)b	2 053.0 (311.0)a	11 835.9 (2180.5)c	4747.8 (949.1)b	2100.1 (382.0)a
Total N (g m−2)	47.3 (11.0)b	70.2 (10.5)b	8.3 (2.7)a	104.8 (24.2)b	32.0 (8.2)a	9.6 (2.5)a
Total P (g m−2)	5.9 (1.1)b	8.8 (1.7)b	1.8 (0.5)a	9.1 (1.7)c	4.2 (1.7)b	1.7 (0.4)a
Organic matter (g m−2)	3340.2 (693.6)b	5 631.9 (900.4)b	700.9 (239.8)a	8 023.3 (1856.2)c	2164.4 (535.9)b	814.6 (245.7)a
C/N‡	43.2 (3.2)	46.6 (2.2)	47.4 (3.0)	41.2 (2.6)	45.9 (2.9)	46.6 (3.6)
Mineral soil (0–15 cm)						
Bulk density (Mg m−3)§	0.91 (0.03)	0.95 (0.04)	0.94 (0.02)	0.87 (0.03)	0.91 (0.03)	0.90 (0.04)
Total N (g m−2)	143.1 (11.5)	172.6 (16.8)	166.2 (8.9)	169.2 (13.8)	150.2 (7.2)	163.5 (10.1)
Total P (g m−2)	145.4 (8.8)	174.3 (13.5)	163.0 (5.1)	148.4 (6.9)	158.5 (7.3)	153.20 (8.1)
Organic matter (g m−2)	9251.1 (554.8)	11 260.1 (926.9)	10 164.5 (318.5)	10 604.4 (670.0)	9664.6 (403.1)	9730.5 (501.6)
C/N‡	37.7 (1.0)	38.0 (0.7)	35.8 (1.6)	37.6 (1.6)	37.6 (0.9)	34.9 (1.0)

† Values from the same row with different lowercase letters are statistically different ($P < 0.10$); when no lowercase letters are given, values are not statistically different. Canopy-type differences in forest floor areal density were dependent on treatment, as the presettlement plots had the highest forest floor density in the control and partial restoration treatments, while forest floor density was similar among canopy types in the complete-restoration treatment.
‡ C calculated assuming 1.724 g organic matter per gram organic C (Nelson and Sommers, 1982).
§ Calculated from the mass of soil (<2 mm) contained in a core of known volume, which included rock volume.

tween respiration and soil temperature [Table 3; CO_2 = constant × (°C)^2; n ranged from 46–100 for individual years and from 105–183 for both years combined; $P < 0.001$; $r^2 = 0.34$–0.47]; however, growing season soil temperature (Fig. 1) was highest in the complete-restoration treatment. The consistently high soil respiration rates in the complete-restoration treatment (346 ± 24 and 364 ± 17 g CO_2–C m^{-2} in 1995 and 1996) probably resulted from elevated soil temperatures relative to other treatments. Logarithmic and simple linear regression models were also used to assess the temperature–respiration relationship, but the temperature-squared model produced the highest correlation coefficients. Multiple regression models including total N, OM, soil water content, soil temperature, and fine-root biomass did not explain more variance in complete restoration soil respiration than temperature alone (data not shown).

The control treatment had the lowest soil temperatures in both years, yet soil respiration in the control was high in 1995 (350 ± 8 g CO_2–C m^{-2}) and low in 1996 (302 ± 13 g CO_2–C m^{-2}). Differences in soil water between the 2 yr provide the best explanation for this decrease. In 1995, the study site experienced typical precipitation (reflected in soil water content; Fig. 1) and respiration was not correlated with soil water content (Table 3; simple linear regression; $r^2 < 0.06$; P ranged from < 0.001 to > 0.10; n ranged from 194–260). In 1996, a drought year, the control had the lowest soil water content (Fig. 1). Soil water content explained 40% of the variation in control respiration in 1996, but only about 20% of the variation in respiration from the treatments (Table 3; $P < 0.001$; n ranged from 179–240). In wet years, the control plots probably maintain high soil respiration, while in dry years soil respiration is reduced by water limitation. The lack of soil water in 1996 probably had negative effects on soil respiration in the restora-

Table 2. Soil respiration at the Gus Pearson Natural Area near Flagstaff, AZ in 1995 and 1996. Data are means (and one standard error) in g CO_2–C m^{-2} time period^{-1}.

Time period/Method	Restoration treatment			Canopy type		
	Control	Partial restoration	Complete restoration	Presettlement	Postsettlement retained	Grass
			1995			
Growing season						
Soda lime†	350 (8)b	301 (5)a	346 (24)b	326 (17)a	314 (14)a	373 (15)b
IRGA-corrected‡	559	431	558	496	466	620
Winter§	6	9	11	15	10	16
Annual¶						
Soda lime	356	310	357	341	324	389
IRGA-corrected‡	565	440	569	511	476	636
			1996			
Growing season						
Soda lime†	302 (13)a	328 (7)b	364 (17)b	307 (15)a	325 (13)a	377 (18)b
Modeled§	241	344	406	339	324	357
IRGA-corrected‡	407	475	572	420	467	607
Winter§	7	12	10	16	9	6
Annual¶						
Soda lime	309	340	374	323	334	383
IRGA-corrected	414	487	582	436	476	613

† Values from the same row with different lowercase letters are statistically different ($P < 0.10$). Canopy-type differences in 1996 growing season respiration were dependent on restoration treatment.
‡ Calculated using regression relating infrared gas analyzer (IRGA) and soda lime estimates. Data were not compared statistically.
§ Calculated using regression relating soda lime soil respiration and soil temperature at the 7.5-cm mineral soil depth. Data were not compared statistically.
¶ Calculated as growing season respiration for soda lime or IRGA methods plus modeled winter soil respiration.

Table 3. Relationships (r^2) between soil microclimate and soil respiration at the Gus Pearson Natural Area near Flagstaff, AZ.

	Restoration treatment			Canopy type		
Variable/Year	Control	Partial restoration	Complete restoration	Presettlement	Postsettlement retained	Grass
Soil water content‡						
1995	0.06	0.01ns	0.03†	0.02†	0.00ns	0.00ns
1996	0.40	0.23	0.19	0.30	0.24	0.25
Both years	0.22	0.08	0.03	0.14	0.08	0.06
Soil temperature§						
1995	0.47	0.41	0.38	0.40	0.39	0.47
1996	0.40	0.39	0.34	0.32	0.46	0.39
Both years	0.42	0.40	0.35	0.35	0.41	0.42

† Denotes significance at $P < 0.10$, other values were significant at $P < 0.001$, and correlations were positive. ns =not significant ($P > 0.10$).
‡ Simple linear regression; volumetric soil water content, 0–15 cm mineral soil depth; n = 179 to 260 for individual years and 373 to 500 for both years combined.
§ Nonlinear regression [respiration = constant × (temperature)^2]; soil temperature is at the 7.5-cm mineral soil depth; n = 46 to 100 for individual years and 105 to 183 for both years combined.

tion treatments as well. However, soil water explained only 20% of the variability in restoration treatment soil respiration, and soil respiration increased in the drought year in both restoration treatments (Table 2). These results suggest that factors other than soil water content control soil respiration rates in the restoration treatments.

Soil temperature most likely drives soil respiration rates in the complete-restoration treatment; however, soil temperature does not explain why growing season soil respiration in the partial-restoration treatment increased from 1995 (301 ± 5 g CO_2–C m^{-2}) to 1996 (328 ± 7 g CO_2–C m^{-2}). Fine-root biomass did not increase between years (Fig. 1). Soil OM, and N were not significantly ($P > 0.10$) correlated with soil respiration (data not shown). High spatial variability in soil respiration and C and N availability may be partially responsible for the poor correlations among these soil characteristics because soil C and N were assayed up to 1 m away from the soil respiration measurements.

We know of no other field measurements of soil respiration in ponderosa pine forests. Vose et al. (1995) measured soil respiration beneath outdoor-irrigated 3-yr-old ponderosa pine seedlings and their rates were similar to our lower rates (0.46–0.56 g CO_2–C m^{-2} d^{-1}). The daily flux rates we measured (0.3–3.5 g CO_2–C m^{-2} d^{-1}) are similar to soda lime estimates for other ecosystems (Table 4). However, annual flux rates from our semiarid site, using either soda lime (309–374 g CO_2–C m^{-2} yr^{-1}) or IRGA-corrected (414–582 g CO_2–C m^{-2} yr^{-1}) data, were generally lower than measurements in other temperate forests by the same method (Table 4).

Tree removal, which occurred in both of our restoration treatments, may increase, decrease, or not change soil respiration rates (Edwards and Ross-Todd, 1983; Ewel et al., 1987; Gordon et al., 1987; Hendrickson et al., 1989; Mattson and Smith, 1993; Toland and Zak, 1994; Weber, 1990); no clear mechanistic pattern has emerged in the literature. However, it is probable that increased soil respiration is due to increasing soil water content and temperature. If regrowth into harvested areas is rapid, soils may not incur changes in microclimate and soil respiration may not be altered. If regrowth is slow, low root respiration, and low microbial respiration resulting from reduced plant C inputs, probably result in low soil respiration rates. In our experiment, we observed differences in microclimate but not differences in root biomass among treatments. Weber (1985) measured soil respiration in five burned Jack pine (*Pinus banksiana* Lambert) sites, and concluded that recurring stand-replacing fires reduced soil respiration relative to a single stand-replacing fire, and that surface fire effects depended on burn depth. Weber (1990) and O'Connell (1987) compared burned sites with controls and found that burning may decrease or not change soil respiration. Weber (1990) hypothesized that reductions in soil respiration following fire may be due to reduced soil water content resulting from higher surface soil

Table 4. Selected in situ estimates of daily and annual soil respiration (g CO_2–C m^{-2} time period^{-1}). Values are the range of estimates reported for a given site.

Ecosystem type	Daily	Annual	Method†	Reference
Mixed deciduous	0.5–2.8	371–402	S	Bowden et al., 1993
Mixed deciduous	1.5–2.8	No data	S	Mattson and Smith, 1993
Mixed deciduous	0.0–6.8	1065	IRGA	Edwards and Harris, 1977
Conifers and hardwoods	2.0–5.8	No data	S	Hendrickson et al., 1989
Northern hardwoods	0.1–6.5	707–794	IRGA	Reiners, 1968
Northern hardwoods	1.5–3.0	469–487	S	Toland and Zak, 1994
Aspen	1.0–3.9	371–400	S	Schletner and Van Cleve, 1984
Black spruce	1.4–3.6	367–370	S	Schletner and Van Cleve, 1984
White spruce	1.3–3.9	394–428	S	Schletner and Van Cleve, 1984
Birch	1.0–3.9	359–451	S	Schletner and Van Cleve, 1984
Grassland	3.6–7.3	No data	IRGA	Norman et al., 1992
Tropical forest	5.7–8.5	2400–2630	S	Townsend et al., 1995
Tropical pasture	5.3–11.0	2260–3180	S	Townsend et al., 1995
Slash pine	0.3–5.9	850–1300	IRGA	Ewel et al., 1987

† S denotes measurements using an alkali absorption technique such as the soda lime method. IRGA denotes measurements using an infrared gas analyzer.

temperatures in the burned treatments. Our results suggest that increased soil temperatures following fire do not always cause decreased soil respiration rates relative to controls.

The intra- and interannual patterns discussed above suggest potentially important relationships between soil respiration, temperature, and water content. In both years and in all treatments, soil respiration was low (0.3–1.6 g CO_2–C m^{-2} d^{-1}) at the beginning and end of the growing season and peaked (2.7–3.5 g CO_2–C m^{-2} d^{-1}) in either August or September (Fig. 1). This seasonal variation in soil respiration is controlled primarily by the relationship between temperature and soil respiration (Fig. 1, Table 3). However, this temperature response can be modified by extremes in water availability, as was observed in 1996, when a delayed monsoon season repressed control soil respiration rates well into the summer (Fig. 1). Thus, while temperature may control general seasonal patterns in CO_2 flux, soil water content probably controls interannual variation in this pattern.

While our data suggest that soil temperature and water content control soil respiration at the Gus Pearson Natural Area, several factors limit the strength of this conclusion. We measured the response to thinning during the second and third growing seasons following treatment. Thinning effects on important labile C pools during the first growing season following treatment, though potentially large, were not measured. Similarly, soil C pools and microclimate will change in the future as grass biomass increases. Our study does not include these long-term changes in soil C or microclimate. Finally, no variable or combination of variables explained more than 50% of the variation in soil respiration. Other factors not measured in this study (e.g., microbial biomass), probably account for some of the unexplained variability. However, the heterogeneity of the soil environment seems to preclude isolation of one or a few variables that explain the majority of variability in field soil respiration.

Winter soil respiration, modeled from soil temperature, was small (<20 g CO_2–C m^{-2}) relative to growing season soil respiration. Annual soil respiration followed the same patterns among treatments and canopy types as growing season respiration. The model used to predict winter soil respiration (based on soda lime measurements) predicted total 1996 growing season respiration for both treatments and canopy types within 12% of the actual measurements for five out of six simulations (Table 2). Growing season respiration could not be simulated in 1995 because temperature data were not available for the entire season.

Effects of Pine Invasion on Soil Respiration

Soil respiration beneath the grass canopy type was greater than presettlement and postsettlement-retained canopy types in 1995 and 1996 by repeated-measures (Fig. 2) analysis. Similarly, total growing season respiration was 14 to 23% greater in the grass canopy type than in pine canopy types (Table 2). In 1996, differences among canopy types depended on treatment (significant treatment × canopy type interaction); respiration in the presettlement canopy type was greater than the postsettlement-retained canopy type in the control, but less than the postsettlement-retained canopy type in the restoration treatments. These results suggest that the presettlement forest, having a greater grass cover (Cooper, 1960; Covington et al., 1997), probably had relatively greater soil respiration rates than the contemporary forest. However, because the relict grassy openings at our site were briefly grazed (1876–1910) and are smaller than presettlement grassy openings, they are not perfect analogues for the presettlement bunchgrass community. To our knowledge, there are no previous measurements of soil respiration in sites where forest and grass canopy types are adjacent. Raich and Schlesinger (1992) analyzed data from nine grasslands and 23 temperate coniferous forests and found them to have statistically similar respiration rates.

Because our grass, postsettlement-retained, and presettlement canopy types were in close proximity, they experienced the same macroclimate. Consequently, soil respiration differences among canopy types are probably due to plant-induced changes in microclimate, soil substrate, or soil microbial communities. Soil temperature and water content were similar across canopy types (Fig. 2) and similarly correlated with all canopy types for a given year (Table 3). Mineral soil fine-root biomass, OM, N, P, and C/N ratio were similar among canopy types (Fig. 2, Table 1). Forest floor OM, N, and P were lowest in the grass canopy type (Table 1), suggesting that these parameters do not drive soil respiration differences among canopy types. We reported elsewhere that net N transformation rates were higher in the grass canopy type than in presettlement or postsettlement-retained canopy types (Kaye and Hart, 1998), suggesting higher microbial activity. Greater microbial biomass in the grassy openings may also result in higher soil respiration relative to pine canopy types (Smith and Paul, 1990). Finally, a greater bacteria/fungi ratio in the grassy openings may result in higher CO_2 evolution because bacteria typically have lower C-use efficiencies than fungi (Holland and Coleman, 1987).

Methodological Considerations

In this experiment, we assessed two important methodological concerns for soil respiration measurements: (i) how does the presence of herbaceous vegetation affect soil respiration measurements, and (ii) does soda lime underestimate soil respiration relative to IRGA measurements? If P_n of the herbaceous vegetation within our unclipped soil respiration chambers was greater than dark respiration (R_d) of aboveground tissue, soil respiration would be underestimated because plants would assimilate some CO_2 from the sampling chamber. On the other hand, if P_n was less than aboveground R_d, aboveground herbaceous respiration would cause an overestimate of soil respiration. Aboveground herbaceous vegetation will not bias soil respiration measurements if P_n = aboveground R_d during the

measurements. On sunny days [photosynthetically active radiation (PAR) ≈ 1800 μmol m^2 s^{-1}] about 250 μmol m^2 s^{-1} of PAR passes through the respiration chambers. Naumberg (1996) found that P_n rates of mountain muhly and bottlebrush squirreltail, the two most common grasses at our site, were ≈0.15 μmol CO_2 g^{-1} s^{-1} at 250 μmol m^{-2} s^{-1} of PAR. While it is clear that some P_n was occurring in the soil respiration chambers, it is difficult to determine whether this photosynthesis was balanced by aboveground R_d. The mean difference between soil respiration in unclipped and clipped areas was greater than zero (unclipped − clipped = 0.18 g CO_2–C m^{-2} d^{-1}, combining 1995 and 1996 data; $P < 0.005$; $n = 196$ pairs), suggesting that P_n was less than aboveground R_d during measurements, and that including grasses causes an overestimation of soil respiration. However, we cannot rule out the possibility that clipping decreases root density and microbial activity, causing an underestimation of soil respiration. Because the difference between clipped and unclipped plots is <10% of the mean soil respiration from unclipped grassy plots (1.91 g CO_2–C m^{-2} d^{-1}), experiments including clipped herbaceous plots may be comparable to experiments using unclipped plots.

Nay et al. (1995) provided strong evidence that soda lime overestimates low CO_2 fluxes and underestimates high CO_2 fluxes in the laboratory. Our field comparison, and field comparisons by other researchers (Cropper et al., 1985; Ewel et al., 1987), show the same result. Underestimates arise at high flux rates because soda lime cannot absorb CO_2 at rates similar to the soil evolution rate. This causes chamber CO_2 concentrations to rise above ambient concentrations, decreasing the diffusion gradient between the soil and atmosphere. Overestimates arise at low flux rates because soda lime reduces CO_2 concentrations within the chamber below ambient concentrations, increasing the diffusion gradient between the soil and atmosphere. Of the 4 chambers tested, we found that the CO_2 concentration in the chamber headspace was lower than ambient air in one chamber, and higher than ambient air in three chambers. The mean difference between ambient and headspace CO_2 was 31.1 μmol CO_2 mol^{-1} of air (headspace – ambient; $P = 0.2$; paired t-test). Our growing season soda lime soil respiration measurements were 24 to 40% lower than our IRGA-corrected estimates, which ranged from 407 to 620 g CO_2–C m^{-2} (Table 2). While soda lime may underestimate large fluxes, it appears adequate for assessing overall treatment effects on belowground catabolism (Bowden et al., 1993; Gordon et al., 1987; Millikin and Bowden, 1996; Townsend et al., 1995; Weber, 1985, 1990). When a C budget is needed, soda lime measurements should be calibrated with a subsample of IRGA-based measurements, or IRGA-based measurements alone should be used.

Management Implications

The grassy openings in this study are remnants of bunchgrass communities that used to flourish between sparse pines. In the contemporary forest, most grassy openings have been invaded by pines that completely alter ecosystem structure and function (Covington et al., 1994, 1997; Covington and Moore, 1994; Kaye and Hart, 1998). If fire suppression continues, further invasion of grassy openings by small pines will probably reduce belowground CO_2 production and productivity. If the dense postsettlement pine plots mature into forests resembling the presettlement plots, belowground catabolism will not increase (Fig. 2; Table 2). However, forest management that includes wildfire suppression without thinning or prescribed burning is not likely to continue. The small pine thickets have caused large-scale changes in ecosystem health (Kolb et al., 1994) and in regional fire regimes (Swetnam and Baisan, 1996). Active restoration management, or a stand-replacing fire, will probably precede further substantial pine invasion.

The total C evolved from stand-replacing fires is much greater than that of surface fires. Prior to treatment, our complete-restoration forest floor contained 1937 g C m^{-2}. An intense stand-replacing fire at our site would have released most of this forest floor C (plus C in combusted living-plant biomass) to the atmosphere as CO_2. Our forest floor manipulations removed 1450 g C m^{-2} and added 34 g C m^{-2} of native grass litter, for a net preburn total of 557 g C m^{-2} as forest floor detritus (Covington et al., 1997). The prescribed burn released only 175 g C m^{-2} of this forest floor detritus as atmospheric CO_2–C. Clearly, the net effect of restoration on regional C cycles will depend greatly on the fate of C removed manually as tree biomass (1760 g C m^{-2}) from the partial- and complete-restoration treatments, and as forest floor detritus from the complete-restoration treatment.

Averaging 1995 and 1996 data, annual soil respiration CO_2–C effluxes from our treatments were about 490, 464, and 576 g C m^{-2} yr^{-1} in the control, partial restoration and complete restoration, respectively. Thus, while annual soil respiration is similar in magnitude to CO_2–C loss from the prescribed fire, it is a small flux relative to a stand-replacing fire or the manual removal of C conducted as part of the restoration treatments. Furthermore, the mean difference between the control and treatments (−26 or 86 g C m^{-2} yr^{-1}) suggests that altered catabolism 1 to 2 yr following restoration will have a minor influence on regional C cycles.

Our experiment was not replicated at the site level and did not include multiple burn intervals. Wright (1996) found that 20 yr of prescribed fire at 2-yr intervals reduced fine-root production and biomass relative to controls in a nearby ponderosa pine forest (the Chimney Springs site). Because roots contribute to soil respiration directly through root respiration, and indirectly by supplying C to soil microorganisms, lower root productivity may result in lower soil respiration. However, there was no preburn fuel reduction (neither thinning nor forest floor manipulation) at the Chimney Springs site, and grass biomass was much lower than at our site (J.P. Kaye, 1996, personal communication). Long-term soil respiration may not decrease following future prescribed fires at our site because, unlike trees, be-

lowground grass biomass tends to increase following prescribed fires (Ojima et al., 1994).

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REFERENCES

Bowden, R.D., K.J. Nadelhoffer, R.D. Boone, J.M. Melillo, J.B. Garrison. 1993. Contributions of aboveground litter, belowground litter, and root respiration to total soil respiration in a temperate mixed hardwood forest. Can. J. For. Res. 23:1402–1407.

Cooper, C.F. 1960. Changes in vegetation, structure, and growth of southwestern pine forests since white settlement. Ecol. Monogr. 30:129–164.

Covington, W.W., and M.M. Moore. 1994. Post-settlement changes in natural fire regimes and forest structure: Ecological restoration of old-growth ponderosa pine forests. J. Sustainable For. 2:153–181.

Covington, W.W., and S.S. Sackett. 1984. The effect of a prescribed burn in southwestern ponderosa pine on organic matter and nutrients in woody debris and forest floor. For. Sci. 30:183–192.

Covington, W.W., and S.S. Sackett. 1986. Effect of periodic burning on soil nitrogen concentrations in ponderosa pine. Soil Sci. Soc. Am. J. 50:452–457.

Covington, W.W., and S.S. Sackett. 1992. Soil mineral nitrogen changes following prescribed burning in ponderosa pine. For. Ecol. Manage. 54:175–191.

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. J. Sustainable For. 2:13–63.

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. J. For. 95:23–29.

Cropper, W.P., Jr., K.C. Ewel, and J.W. Raich. 1985. The measurement of soil CO_2 in situ. Pedobiologia 28:35–40.

Dieterich, J.M. 1980. Chimney Spring forest fire history. USDA For. Serv. Rocky Mountain For. Range Exp. Stn. Res. Paper RM-222.

Edwards, N.T. 1982. The use of soda-lime for measuring respiration rates in terrestrial systems. Pedobiologia 23:321–330.

Edwards, N.T., and B.M. Ross-Todd. 1983. Soil carbon dynamics in a mixed deciduous forest following clear-cutting with and without residue removal. Soil. Sci. Soc. Am. J. 47:1014–1021.

Ewel, K.C., W.P. Cropper, and H.L. Gholz. 1987. Soil CO_2 evolution in Florida slash pine plantations. I. Changes through time. Can. J. For. Res. 17:325–329.

Gordon, A.M., R.E. Schletner, and K. Van Cleve. 1987. Seasonal patterns of soil respiration and CO_2 evolution following harvesting in the white spruce forests of interior Alaska. Can. J. For. Res. 17:304–310.

Hendrickson, O.Q., L. Chatarpaul, and D. Burgess. 1989. Nutrient cycling following whole-tree and conventional harvest in northern mixed forest. Can. J. For. Res. 19:725–735.

Holland, E.A., and D.C. Coleman. 1987. Litter placement effects on microbial and organic matter dynamics in an agroecosystem. Ecology 68:425–433.

Jenkinson, D.S., D.E. Adams, and A. Wild. 1991. Model estimates of CO_2 emissions from soil in response to global warming. Nature 351:304–306.

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. USDA For. Serv., Rocky Mountain For. Range Exp. Stn. Gen. Tech. Rep. RM-246.

Kaye, J.P., and S.C. Hart. 1998. Ecological restoration alters nitrogen transformations in a ponderosa pine–bunchgrass ecosystem. Ecol. Appl. (In press.)

Kolb, T.E., M.R. Wagner, and W.W. Covington. 1994. Concepts in ecosystem health. J. For. 92:10–15.

Lachat Instruments, Inc. 1992a. QuikChem method no. 13-107-06-2-D. Milwaukee, WI.

Lachat Instruments, Inc. 1992b. QuikChem method no. 10-115-01-1-C. Milwaukee, WI.

Mattson, K.G., and H.C. Smith. 1993. Detrital organic matter and soil CO_2 efflux in forests regenerating from cutting in West Virginia. Soil Biol. Biochem. 25:1241–1248.

Millikin, C.S., and R.D. Bowden. 1996. Soil respiration in pits and mounds following an experimental forest blowdown. Soil Sci. Soc. Am. J. 60:1951–1953.

Moir, W.H., and J.H. Dieterich. 1988. Old-growth ponderosa pine from succession in pine–bunchgrass forests in Arizona and New Mexico. Natural Areas J. 8:17–24.

Nay, S.M., K.G. Mattson, and B.T. Bormann. 1994. Biases of chamber methods for measuring soil CO_2 efflux demonstrated with a laboratory apparatus. Ecology 75:2460–2463.

Naumburg, E. 1996. Shade response of five grass species of southwestern ponderosa pine forests. M.S. thesis, Cline Library, Northern Arizona Univ., Flagstaff.

Nelson, D.W., and L.E. Sommers. 1982. Total carbon, organic carbon, and organic matter. p. 539–579. *In* A.L. Page et al. (ed.) Methods of soil analysis. Part 2. 2nd ed. Agron. Monogr. 9, ASA and SSSA, Madison, WI.

Norman, J.M., R. Garcia, and S.B. Verma. 1992. Soil surface CO_2 fluxes and the carbon budget of a grassland. J. Geophys. Res. 97:18845–18853.

O'Connell, A.M. 1987. Litter decomposition, soil respiration and soil chemical and biochemical properties at three contrasting sites in *karri* (*Eucalyptus diversicolor* F. Muell.) forests of southwestern Australia. Aust. J. Ecol. 12:31–40.

Ojima, D.S., D.S. Schimel, W.J. Parton, and C.E. Owensby. 1994. Long- and short-term effects of fire on nitrogen cycling in tallgrass prairie. Biogeochemistry 24:67–84.

Parkinson, J.A., and S.E. Allen. 1975. A wet oxidation procedure suitable for the determination of nitrogen and mineral nutrients in biological material. Commun. Soil Sci. Plant Anal. 6:1–11.

Pyne, S.J., P.L. Andrews, and R.D. Laven. 1996. Fire ecology. p. 207–208. *In* Introduction to wildland fire. John Wiley & Sons, New York.

Raich, J.W., R.D. Bowden, and P.A. Steudler. 1990. Comparison of two static chamber techniques for determining carbon dioxide efflux from forest soils. Soil Sci. Soc. Am. J. 54:1754–1757.

Raich, J.W., and W.H. Schlesinger. 1992. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. Tellus 44B:81–99.

Reiners, W.A. 1968. Carbon dioxide evolution from the floor of three Minnesota forests. Ecology 49:471–483.

Savage, M., P.M. Brown, and J. Feddema. 1996. The role of climate in a pine forest regeneration pulse in the southwestern United States. Ècoscience 3:310–318.

Schlesinger, W.H. 1977. Carbon balance in terrestrial detritus. Ann. Rev. Ecol. Syst. 8:51–81.

Schletner, R.E., and K. Van Cleve. 1985. Relationships between CO_2 evolution from soil, substrate temperature, and substrate moisture in four mature forest types in interior Alaska. Can. J. For. Res. 15:97–106.

Schubert, G.H. 1974. Silviculture of southwestern ponderosa pine: the status-of-our-knowledge. USDA For. Serv. Rocky Mountain For. Range Exp. Stn. Res. Paper RM-123.

Smith, J.L., and E.A. Paul. 1990. The significance of soil microbial biomass estimations p. 357–395. *In* J-M. Bollag and G. Stotzky (ed.) Soil biochemistry. Vol. 6. Marcel Dekker, New York.

Steele, R. 1987. Ecological relationships of ponderosa pine. p. 71–76. *In* D.M. Baumgartner and J.E. Lotan (ed.) Ponderosa pine: The species and its management. Symposium proceedings. Spokane, WA. 29 Sept.–1 Oct. 1987, Washington State Univ. Coop. Ext., Pullman, WA.

Swetnam, T.W., and C.H. Baisan. 1996. Historical fire regime patterns in the southwestern United States since AD 1700. p. 11–32. *In* C.D. Allen (ed.) Fire effects in southwestern forests. USDA For. Serv.

Rocky Mountain For. Range Exp. Stn. Gen. Tech. Rep. RM-GTR-246.

Toland, D.E., and D.R. Zak. 1994. Seasonal patterns of soil respiration in intact and clear-cut northern hardwood forests. Can. J. For. Res. 24:1711–1716.

Topp, C.G., J. Davis, and A.P. Annan. 1980. Electromagnetic determination of soil water content measurements in coaxial transmission lines. Water Resour. Res. 16:574–582.

Townsend, A.R., P.M. Vitousek, and S.E. Trumbore. 1995. Soil organic matter dynamics along gradients in temperature and land use on the island of Hawaii. Ecology 76:721–733.

Turner, D.P., G.J. Koerper, M.E. Harmon, and J.J. Lee. 1995. A carbon budget for forests of the conterminous United States. Ecol. Appl. 5:421–436.

Vose, J.M., K.J. Elliott, D.W. Johnson, R.F. Walker, M.G. Johnson, and D.T. Tingey. 1995. Effects of elevated CO_2 and N fertilization on soil respiration from ponderosa pine (*Pinus ponderosa*) in open-top chambers. Can. J. For. Res. 25:1243–1251.

Weber, M.G. 1985. Forest soil respiration in eastern Ontario jack pine ecosystems. Can. J. For. Res. 15:1069–1073.

Weber, M.G. 1990. Forest soil respiration after cutting and burning in immature aspen ecosystems. For. Ecol. Manage. 31:1–14.

White, A.S. 1985. Presettlement regeneration patterns in a southwestern ponderosa pine stand. Ecology 66:589–594.

Wright, R.J. 1996. Fire effects on fine roots, mycorrhizal fungi, and nutrient dynamics in southwestern ponderosa pine forests. M.S. thesis, Cline Library, Northern Arizona Univ., Flagstaff.