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DIVISION S-7—FOREST & RANGE SOILS

Environmental Factors Controlling Soil Respiration in Three Semiarid Ecosystems

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ABSTRACT

Previous research suggests that soil organic C pools may be a feature of semiarid regions that are particularly sensitive to climatic changes. We instituted an 18-mo experiment along an elevation gradient in northern Arizona to evaluate the influence of temperature, moisture, and soil C pool size on soil respiration. Soils, from underneath different tree canopy types and interspaces of three semiarid ecosystems, were moved upslope and/or downslope to modify soil climate. Soils moved downslope experienced increased temperature and decreased precipitation, resulting in decreased soil moisture and soil respiration (as much as 23 and 20%, respectively). Soils moved upslope to more mesic, cooler sites had greater soil water content and increased rates of soil respiration (as much as 40%), despite decreased temperature. Soil respiration rates normalized for total C were not significantly different within any of the three incubation sites, indicating that under identical climatic conditions, soil respiration is directly related to soil C pool size for the incubated soils. Normalized soil respiration rates between sites differed significantly for all soil types and were always greater for soils incubated under more mesic, but cooler, conditions. Total soil C did not change significantly during the experiment, but estimates suggest that significant portions of the rapidly cycling C pool were lost. While long-term decreases in aboveground and belowground detrital inputs may ultimately be greater than decreased soil respiration, the initial response to increased temperature and decreased precipitation in these systems is a decrease in annual soil C efflux.

Soil respiration is the main mechanism of C transfer from the soil to the atmosphere and is a key component of the global C cycle (Schlesinger, 1991; Schimel, 1995). On a global scale, CO_2 release from soil is an order of magnitude larger than CO_2 release from burning fossil fuels and land-use change combined (Houghton et al., 1990; Gates, 1993). Rates of soil respiration are highly sensitive to temperature and may show a large response to small climate changes (Schleser, 1982; Anderson, 1991; Schlesinger, 1991; Jenkinson et al., 1991; Townsend et al., 1992). Research in a variety of ecosystems has demonstrated that increased temperature leads to increased soil respiration and resulting soil CO_2 efflux (Billings et al., 1982; Van Cleve et al., 1990; Peterjohn et al., 1994).

Soil processes in arid and semiarid lands have received considerably less attention, partly because of the relatively small organic C pools and fluxes in these regions (Raich and Potter, 1995; Raich and Schlesinger, 1992; West et al., 1994). Arid and semiarid lands cover as much as one-third of the earth's surface (Whittaker, 1970), and the extent of arid and semiarid lands may increase in response to climate change (Emanuel et al., 1985). While large amounts of inorganic C are typically stored in soils in arid and semiarid ecosystems (Schlesinger, 1982), organic C pools are small (West et al., 1994). Since organic matter C pools are so small, West et al. (1994) concluded that soil organic C pools are a feature of arid and semiarid lands that is very sensitive to climate changes.

Long-term modeling studies indicate that decomposition will increase more than production under a variety of scenarios with increased temperature in a number of ecosystems, including semiarid ecosystems (Jenkinson et al., 1991; West et al., 1994; Schimel, 1995). These studies indicate that the net result will be a decrease in soil organic C. However, annual soil respiration rates in semiarid ecosystems are highly sensitive to soil moisture (Amundson et al., 1989; Kaye and Hart, 1998) and are greater at more mesic locations, even if those locations have lower mean annual temperatures (Quade et al., 1989; Conant et al., 1998). Thus, in semiarid ecosystems, soil respiration increases with both C pool size and mean annual precipitation, but decreases with increases in mean annual temperature.

Uncertainties in the factors controlling soil respiration in semiarid ecosystems prompted an experiment to examine the relationship of soil respiration to temperature, precipitation, and soil organic C, hereafter referred to as *soil C*. Specifically, the objective of this research was to examine the effects of modified climate on soil processes in some dominant ecosystem types of the western USA. We wanted to determine (i) whether soil respiration increases with soil moisture and/or temperature increases, (ii) how soil respiration is related to soil C pool size, (iii) whether total soil C pools and concentrations change in response to rapid changes in climate, and (iv) the relative importance of soil C, temperature, and moisture in controlling soil respiration rates in semiarid ecosystems. These issues were addressed by evaluating the effects of a reciprocal transplant experiment of large reconstructed soil columns (mesocosms) and laboratory incubations.

STUDY SITES

The research area is located in the Coconino National forest, north of Flagstaff, AZ, on the leeward side of the San

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Abbreviations: DS, Desert Scrub Site; PJ, Pinyon–Juniper Site; PP, Ponderosa Pine Site; i, interspace cover type; j, juniper cover type; p, pinyon cover type; pp, ponderosa pine cover type.

Table 1. Site descriptions and physical conditions for three sites along an environmental gradient.

Site	Description	Elevation	Mean annual precipitation	Mean annual temperature
		m	mm	°C
DS	Great Basin desert scrub	1987	320	8.5
PJ	Pinyon–juniper woodland	2126	410	7.1
PP	Ponderosa pine forest	2295	530	5.5

Francisco Mountains between 35°25′ N, 111°34′ W and 35°26′ N, 111°40′ W. The area covers a 7-km transition zone with Great Basin Desert scrub (DS) at the lower elevation, pinyon–juniper woodlands (PJ) in the middle, and ponderosa pine forest (PP) at the upper elevation (Table 1). This research area, located on a single grazing allotment supervised by the USDA Forest Service, has a long history (>100 yr) of light-to-moderate grazing. Domestic livestock have not grazed in the area since summer 1993.

The DS Site is dominated by winterfat [*Ceratoides lanata* (Pursh) Moq.], snakeweed [*Gutierrezia sarothrea* (Pursh) Britt. and Rusby], rubber rabbit brush [*Chrysothamnus nauseosus* (Pall.) Britton.], and blue grama grass [*Bouteloua gracilis* (H.B.K.) Lag.]. The PJ Site contains one-seed juniper [*Juniperus monosperma* (Engelm.) Sarg.] and pinyon pine (*Pinus edulis* Engelm.), with blue grama dominant in interspaces. The maximum tree age on this site is 150 to 180 yr old, indicating a history of disturbance in the area. The PP Site is an open, park-like stand of ponderosa pine (*Pinus ponderosa* Doug. ex Laws.), represented by several age classes, with mutton grass [*Poa fendleriana* (Steud.) Vasey], mountain muhly [*Muhlenbergia montana* (Nutt.) Hitchc.], and buck brush (*Ceanothus fendleri* Gray.) in the understory. The PP Site contains several trees >250 yr old with a number of fire scars. Soils at all sites were derived from volcanic material and are classified as Typic Argiborolls at the PP Site grading into Aridic Argiustolls at the PJ Site and Typic Haplustolls at the DS Site. Soils are all sandy loams and are basic (pH = 7.5) to slightly acidic (pH = 6.6). Soil carbonate, detected by reaction with 1 *M* HCl, was present in only one sample collected at the PJ Site under juniper canopy at a 100-cm depth.

We revised the mountain microclimate model of Hungerford et al. (1989) to estimate daily maximum and minimum temperatures at each site. The model uses extant climate data to predict remote site microclimate across mountainous terrain. Climate data were obtained from a nearby weather station, ≈15 km away. Verification data for model predictions came from maximum–minimum thermometers and temperature dataloggers at each location at different periods during the year. Actual data showed the model predictions to be accurate, except for periods when cold air drained into the DS and PJ Sites, resulting in overestimates of minimum daily temperatures; this phenomenon is typical of western mountainous regions (Baker, 1944). Predicted monthly mean temperatures used in this study were within 1.0°C of the actual site data for those periods measured. Mean annual temperatures based on 30 yr of climatic data range from 8.5°C at the DS Site to 5.5°C at the PP Site (Table 1).

Precipitation in this region is bimodal, with intense convectional precipitation during mid-summer and highly variable, low-intensity precipitation during the winter months. We followed the examples of Hanson (1984) and Rowlands (1993), who estimated southwestern regional patterns of precipitation by using a seasonally adjusted regression model with altitude as the independent variable. Site precipitation was based on precipitation at nearby recording stations (15 and 20 km away). Tested against a number of independent regional recording stations at various elevations, our regressions explained 89 and 72% of the variability of measured monthly summer and winter precipitation, respectively. Mean annual precipitation ranges from ≈320 mm yr^{-1} at the DS Site to 530 mm yr^{-1} at the PP Site.

METHODS

Soil Mesocosms

To examine the sensitivity of soil C pools and fluxes to climate, mesocosms consisting of reconstructed soil columns in large plastic pots were incubated at the three sites located at different elevations along the gradient described above. There were six mesocosm types, based on location of soil collection. Bulk mineral soil samples were collected in July 1995 from a 0- to 50-cm depth from four randomly located interspace (i) locations at each of the three sites and from underneath four randomly selected canopies of each tree type (pinyon [p] and juniper [j] at the PJ Site; ponderosa pine [pp] at the PP Site). Soils were passed through a large-mesh (1.5-cm) screen to remove rocks and large roots, and four samples from each mesocosm type were thoroughly mixed on a plastic tarp. At this time, three 5-kg soil samples were taken from each mesocosm type for initial analysis of soil physical and chemical characteristics.

Screened homogenized soils (≈100–120 kg) were placed in large plastic pots (radius = 30 cm, depth = 52 cm). Six drainage holes were punched in the base of each pot to ensure adequate drainage during the course of the experiment. Both litter (O_i horizon, organic horizon in which the original form of vegetative matter is recognizable) and duff (O_a horizon, unrecognizable organic horizon), collected from the site of origin, were placed on top of each respective mesocosm type; amounts corresponded to in situ levels determined by previous sampling (see Table 2). All live vegetation was removed from the soil surface before mesocosm construction, and emerging vegetation was clipped at the soil surface during the incubation period.

Experimental Design

Mesocosm types denote the site of origin (DS, PJ, PP) and the cover type from which the soil originated (i, j, p, pp; Fig. 1). Soils from the PJ Site (PJ-i, PJ-j, and PJ-p) were incubated at the warmer and drier DS Site, the cooler and more mesic PP Site, and the original PJ Site. Soils from the DS Site (DS-i) were incubated at both the DS and PJ Sites. Soils from the PP Site (PP-i and PP-pp) were incubated at the PP and PJ Sites. There were four replicate mesocosms for each combination of mesocosm type and incubation site.

Mesocosms were positioned so that the level of the soil surface inside the mesocosms was equivalent to that of the surrounding soil and were left to equilibrate 30 d before sampling began. All mesocosms were incubated in interspace locations to limit microclimatic variability between replicates. Within each incubation site, the four replicates of each mesocosm type were placed in separate groups; one replicate of each mesocosm type was in each of four groups. This experiment was an unbalanced split-plot design with repeated-measures (Zar, 1996). Incubation site was the among-subjects factor and mesocosm type within each of the incubation sites was the within-subjects factor.

Statistical Analyses

All measurements were taken from each of four replicate mesocosms. Repeated-measures ANOVAs were used to com-

Table 2. Characteristics of soil used to construct soil mesocosms.

Mesocosm type	O_i horizon	O_a horizon	Mineral soil				
			Soil C	C:N ratio	N	Clay	pH
	g C kg^{-1}				mg N g $soil^{-1}$	%	
DS-i	310 (41)a	–	10.5 (0.5)†a‡	10.5	1.0 (0.4)	13.7 (5.2)	6.7 (0.3)
PJ-i	330 (27)a	–	11.9 (0.4)a	9.2	1.3 (0.3)	13.9 (3.9)	7.0 (0.2)
PJ-j	410 (33)b	280 (54)	17.9 (0.8)b	12.8	1.5 (0.5)	22.7 (4.0)	7.5 (0.2)
PJ-p	450 (30)b	330 (39)	15.8 (1.2)b	11.3	1.4 (0.3)	21.3 (5.3)	7.5 (0.2)
PP-i	470 (33)b	–	12.3 (1.5)a	17.6	0.7 (0.2)	17.9 (6.7)	6.9 (0.3)
PP-pp	470 (25)b	210 (42)	16.2 (0.7)b	20.3	0.8 (0.2)	17.6 (5.5)	6.6 (0.4)

† 95% confidence intervals in parentheses (n = 4).
‡ Different letters indicate significant differences between mesocosm types determined by Scheffé's method.

pare both the influence of the incubation site and the original soil characteristics on soil moisture, soil respiration, and total soil C (Sokal and Rohlf, 1981). Repeated-measures analysis was used to test the significance of effects through the entire course of the experiment (Von Ende, 1993). Two-way ANOVAs were used to test the significance of effects within each sampling period and to compare initial measurements of soil and organic horizon C with measurements made following 22 mo of incubation (Sokal and Rohlf, 1981). Multiple linear regression analyses were used to examine relationships between soil moisture, temperature, soil respiration, and soil respiration normalized per unit C (SAS, 1985). Observations were assigned to four equal-size classes based on soil moisture, and linear regression was used to evaluate the effects of temperature on soil respiration normalized per unit C within each of the four soil moisture classes (SAS, 1985). Differences are reported as significant at the $P < 0.05$ level.

Soil Respiration

Soil respiration was measured each month using the static absorption technique (Van Cleve et al., 1990; Freijer and Bouten, 1991; Raich and Schlesinger, 1992). This method has been criticized because it tends to underestimate soil respiration when rates are high (Nay et al., 1994). However, soil respiration rates at our sites are sufficiently low that alkali absorption methods may be used (see Nay et al., 1994, and results below). Respiration chambers (height = 17 cm, diam. = 15.5 cm) enclosing a container (diam. = 5.9 cm) with 20 mL of 1 *M* KOH were placed on the surface and left in place for 24 h. Absorbed CO_2 was then precipitated with 3 *M* $BaCl_2$ and titrated with 1 *M* HCl using phenolphthalein indicator to determine the change in pH and, therefore, the amount of CO_2 absorbed. Blanks consisted of a sealed chamber of the same volume also enclosing a container of 1 *M* KOH. Alkali absorption methods are inaccurate if the surface area of the absorbent solution covers <6% of the soil surface area (Raich and Schlesinger, 1992; Nay et al., 1994); however, the absorptive surface covered 14% of the soil surface area inside the chamber for our measurements. Soil respiration measurements are reported both as *soil respiration per day* in each mesocosm and as *soil respiration normalized per unit C* (including soil, litter, and duff C) in each mesocosm. Gravimetric soil moisture was measured concurrently with soil respiration measurements.

Physical and Chemical Analyses

Total C concentrations of mineral soil, litter, and duff were measured on the three subsamples of each substrate for each mesocosm type collected during mesocosm construction. Mineral soil samples were oven-dried, passed through a 2-mm mesh sieve, and ground to fine powder. Litter and duff samples were oven-dried and ground to <0.4 mm using a Wiley mill

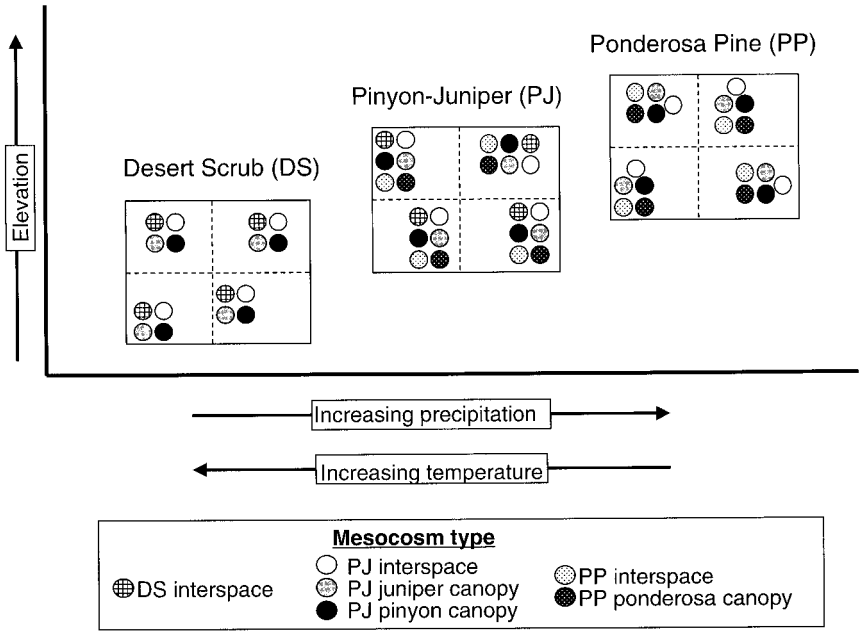

Fig. 1. Summary of experimental design showing all mesocosms incubated at each site. Mesocosm types indicate the site of origin and cover type. Four replicates of each mesocosm type are shown.

(Arthur H. Thomas, Philadelphia, PA). Carbon and N concentrations for finely ground soil and surface materials were determined using a Perkin-Elmer 2400 CHN analyzer (Perkin-Elmer, Norwalk, CT). Organic C concentrations were assumed to be equal to total C concentrations since carbonates were not present. Soil bulk density was determined by collecting and weighing an intact sample of known volume. Corrections were made for the portion of material captured during sieving. Mineral soil, litter, and duff samples collected from each mesocosm following 22 mo of incubation were analyzed in the same manner. Total C in each mesocosm was determined by multiplying soil C concentration, bulk density, and the volume of the container filled with soil plus the C contents of litter and duff material at the beginning and end of the experiment.

Conceptually, soil organic C is assigned to three fractions based on the turnover rates (active, intermediate, and passive) (Parton et al., 1988; Townsend et al., 1995). Long-term laboratory incubations were used to estimate the sizes of different C pool fractions and the relative contributions of each to total soil respiration using the method described by Townsend et al. (1995) and Paul et al. (1999). Mineral soil samples from a 0- to 25-cm depth were collected in February 1996 and composited by mesocosm type. Soil samples were returned to the lab and passed through a 2-mm mesh sieve. Four replicate samples (1.5 kg per mesocosm type) in PVC tubes (diam. = 10 cm) sealed on one end were incubated in the dark at 25°C and 50% of field moisture capacity for 12 mo. Soil respiration was measured biweekly by capturing evolved CO_2 in 10 mL of 1 *M* KOH in a beaker (diam. = 5 cm) placed on the soil surface and titrating with 1 *M* HCl (Freijer and Bouten, 1991). The soil respiration rate decreased substantially within the first 8 wk to a relatively constant rate. Once the soil respiration rate reaches a steady rate, all soil respiration is derived from the intermediate pool (Townsend et al., 1995). All previous soil respiration exceeding this amount was derived from the active soil C pool (Townsend et al., 1995).

Soil texture was determined using a hydrometer method similar to that of Gee and Bauder (1986). Soil pH was determined for 5-g soil samples in a 1:1 soil/0.01 *M* $CaCl_2$ solution using a glass electrode pH meter (McLean, 1982).

RESULTS

Initial Soil Characteristics

Soil C concentration was greater for soils from underneath canopies than for interspace soils (Table 2). Litter C concentration was significantly less for the DS-i and PJ-i mesocosms and C concentration of duff material did not vary between the different mesocosm types (Table 2). Clay concentration of the soil was least for DS-i and PJ-i soils, while soil N tended to be least for the PP-i and PP-pp soils, though differences were not significant (Table 2). Soil pH was not significantly different between mesocosm types.

Soil Moisture

Soil mesocosms incubated at the DS Site were significantly drier than identical mesocosms incubated at the PJ Site, by an average of 32 g H_2O kg soil^{-1} (Table 3). Likewise, soil moisture was significantly greater at the PP Site for three of the mesocosm types by an average of 37 g H_2O kg soil^{-1} (Table 3). Soil moisture varied between mesocosms within each of the three incubation sites as well, with interspace soils tending to be drier than canopy soils, which were covered with litter and duff (Table 3).

The effect of the incubation site on soil moisture varied with time and the incubation site (Fig. 2). Within any particular mesocosm type, mesocosms incubated at the DS Site had significantly lower soil moisture than those incubated at the PJ Site during most sample periods (Fig. 2). Except for the PP-i mesocosm type, differences between mesocosms incubated at the PJ and PP Sites were significant less than half the time, and differences for the PP-pp mesocosms were significant least often throughout the course of the experiment. Soil moisture reached nadir during June 1996 for all mesocosms at all sites (Fig. 2).

Soil Respiration

Soil respiration rates were greatest at the highest (coolest, most mesic) site at which a mesocosm type was incubated, though differences in average soil respiration throughout the course of the experiment between mesocosms incubated at neighboring sites were not significant (Table 3). When identical mesocosms were incubated at both the DS and PP Sites, however, soil respiration was always significantly greater at the PP Site (Table 3). Patterns of soil respiration rates followed those of soil water content for all mesocosm types at all sites (Table 3).

Within each incubation site, soil respiration tended to be greatest for mesocosms with soil collected under canopies (Table 3). Soil respiration was generally highest in the wettest soils, the PJ-j, PJ-p, and PP-pp soils, which also tend to have higher concentrations of soil C (Table 2).

Differences between identical mesocosms incubated at neighboring sites were significant less than half the time, but differences between the DS and PP Sites were often significant (Fig. 3). Significant differences between identical mesocosms at different incubation sites were less frequent than those for soil moisture (Fig. 2 and 3). Soil respiration rates between different mesocosm types within each site also varied seasonally, especially during wetter periods of high soil respiration (Fig. 3). Soil respiration was greatest during summer months and less during winter months for all mesocosm types at all sites (Fig. 3).

When soil respiration rates were normalized per unit C in each mesocosm, rates were significantly different between incubation sites for all mesocosms except the PP-pp soil (Fig. 4). The PP Site yielded the greatest rates of normalized soil respiration, while mesocosms incubated at the DS Site had the lowest normalized soil respiration rates. Additionally, differences in soil respiration rates within incubation sites disappeared when soil respiration rates were normalized for the total amount of C in each mesocosm (Fig. 4).

Soil respiration was positively correlated with soil moisture both within and between incubation sites for most sampling periods. Overall, temperature was negatively correlated with soil respiration, with exceptions occurring at the coolest times. Soil moisture was posi-

Table 3. Average annualized soil moisture at 5–15 cm depth and soil respiration for all six mesocosm types at each site.

Mesocosm type	Soil moisture			Soil respiration		
	DS	PJ	PP	DS	PJ	PP
	g H_2O kg $soil^{-1}$			mg CO_2 C m^{-2} d^{-1}		
DS-i	80† (6)a ‡	96 (9)b		780 (86)a	880 (91)a	
PJ-i	120 (11)a	150 (11)b	190 (12)c	810 (71)a	950 (67)ab	1400 (210)b
PJ-j	140 (11)a	170 (10)b	200 (14)c	1270 (140)a	1450 (140)ab	1650 (160)b
PJ-p	140 (19)a	190 (10)b	200 (11)b	1220 (100)a	1400 (110)ab	1570 (180)b
PP-i		150 (10)a	140 (10)a		1040 (100)a	1200 (100)a
PP-pp		160 (13)a	200 (8)b		1500 (180)a	1550 (180)a

† Values are followed by 95% confidence intervals in parentheses (n = 4).
‡ Different letters indicate significant differences between columns determined by Scheffé's method.

tively related to soil respiration and explained between 10 and 45% of the variation in soil respiration within a sampling period, with the largest correlations occurring during the summer months of both years ($P < 0.001$). Total mesocosm C explained a maximum of 22% of the variation in soil respiration within a sampling period, but soil respiration and total mesocosm C were not always positively correlated. Together, soil moisture, temperature, and soil C explained a maximum of 53% of the measured variation in soil respiration for any sampling period ($P < 0.001$).

Normalized soil respiration rates were weakly correlated with temperature ($r^2 = 0.08$; $P < 0.001$) and soil moisture ($r^2 = 0.11$; $P < 0.001$). When normalized soil respiration data were divided into four soil-moisture classes (each with 25% of the total observations), temperature explained only 21, 20, and 22% ($P < 0.05$) of the variability in soil respiration rates for the three driest moisture classifications (all <200 g H_2O kg $soil^{-1}$). However, for the wettest soils (>200 g H_2O kg $soil^{-1}$), temperature explained 63% of the variability in soil respiration ($P < 0.001$).

Organic Carbon Pools

No changes were detected in C or N contents of the mineral soil, litter, or duff, following 22 mo of incubation, though mineral soil C content tended to decrease with time for all mesocosms. Results from laboratory incubations indicate that the active C pool was between 1.7 and 4.7% of mineral soil C (Table 4), generally agreeing with the results of others (Paul and Clark, 1989; Townsend et al., 1995). The active C pool was a larger portion of the mineral soil C pool for the DS-i and PJ-i soils than for the other soils. The amount of C respired was larger than the estimated size of the mineral–soil active pool for all mesocosms (Table 4).

DISCUSSION

An earlier soil respiration study of unmanipulated soils conducted at these semiarid sites concluded that both temperature and precipitation influence soil respiration rates (Conant et al., 1998). Results from this study support that conclusion. These results also indicate that increases in soil respiration rates in response to increased temperature are constrained by soil moisture.

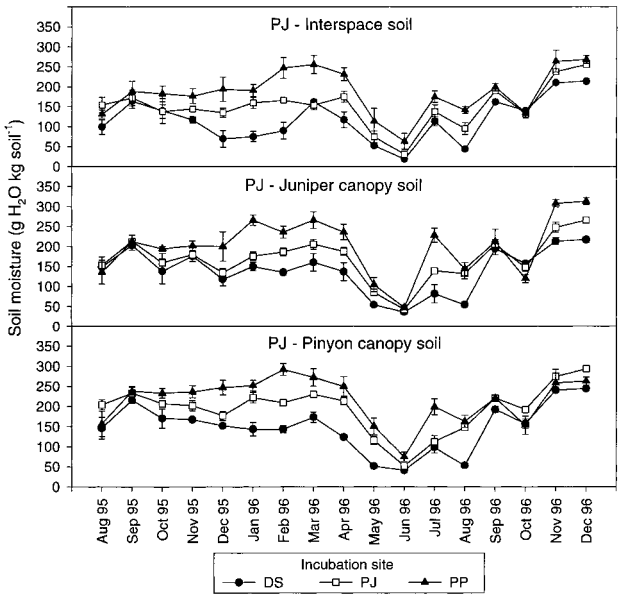

Fig. 2. Seasonal pattern of soil moisture for the three PJ mesocosm types incubated at each of the three incubation sites (DS, desert scrub; PJ, pinyon–juniper; PP, ponderosa pine). Values are the average of four replicate measurements (±95% confidence intervals).

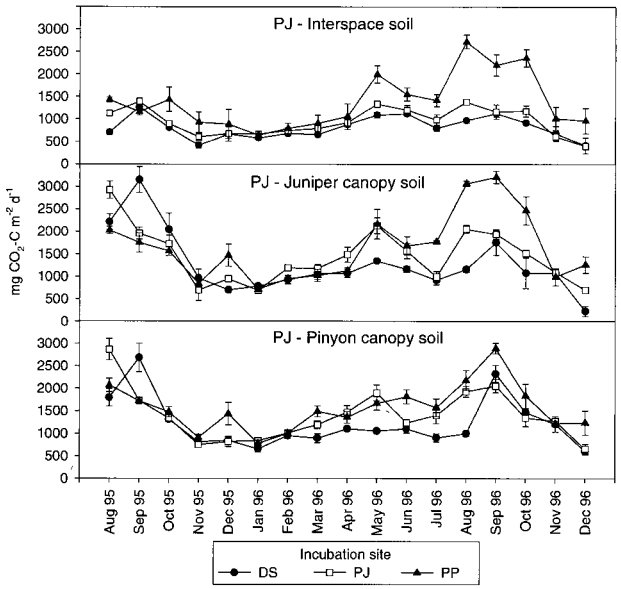

Fig. 3. Seasonal pattern of soil respiration for the three PJ mesocosm types incubated at each of the three incubation sites (DS, desert scrub; PJ, pinyon–juniper; PP, ponderosa pine). Values are the average of four replicate measurements (±95% confidence intervals).

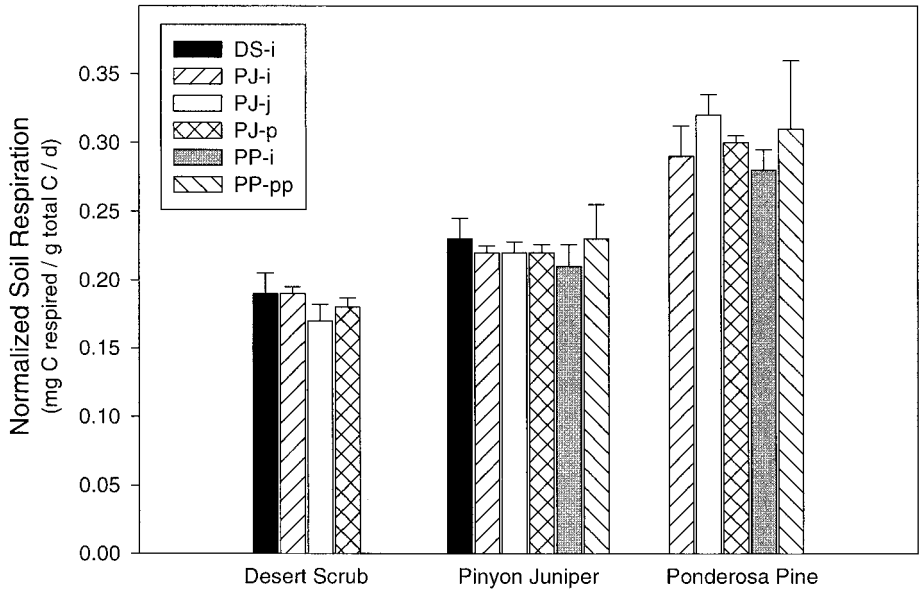

Fig. 4. Average soil respiration (±95% confidence intervals) for six mesocosm types at the desert scrub (DS), pinyon–juniper woodland (PJ), and ponderosa pine forest (PP) Sites. Soil respiration values are normalized per unit C in each mesocosm (including soil, litter, and duff). Names of mesocosms indicate the site of origin and cover type (interspace [i], juniper canopy [j], pinyon canopy [p], or ponderosa canopy [pp]).

The overall effect of moving mesocosms downslope was to increase temperature and decrease soil moisture, while moving mesocosms upslope decreased temperature and increased soil moisture. Mesocosms moved upslope respired more C and those moved downslope generally respired less. Warmer temperatures were linked to higher soil respiration rates only during periods of high soil moisture. Thus decreases in precipitation, or a decrease in the proportion of precipitation delivered during the warm summer months when soil respiration rates are greatest, will likely result in decreased soil respiration. Similar to the results of Harte and Shaw (1995), our results suggest that decreased soil moisture as a result of increased temperature may be the most important effect of increased temperature in this region.

These results differ from results of other research performed in the field (e.g., Billings et al., 1982; Van Cleve et al., 1990; Peterjohn et al., 1994) and in the laboratory (Kirschbaum, 1995), possibly because those studies focused on more mesic systems. Our results show that significant incubation site effects tended to be concentrated during the dry summer months. Higher soil respiration rates at lower temperature but high soil moisture indicate that soil respiration was moisture limited during this period. Since a large portion of annual soil respiration occurs during the summer months, soil moisture exerts significant control on annual soil respiration rates. Preliminary laboratory analyses for soils collected at these sites indicate that at any particular soil moisture content, soil respiration is directly related to temperature, but that the magnitude of response is influenced by soil moisture.

Though all mesocosms located at the same incubation site experienced the same climatic conditions, we expected process rates to differ between different meso-

Table 4. Initial mesocosm organic C pools, annualized soil respiration rates, portion of total mesocosm organic C lost through soil respiration, and laboratory estimates of the active C as a percent of mineral-soil organic C.

Incubation site	Mesocosm type	Initial organic C			Soil respiration		Initial active C
		O_iC	O_aC	Mineral soil C	Rate for each mesocosm	Proportion C respired	
		kg C mesocosm^{-1}			g C yr^{-1}	%	%
DS	DS-i	0.02	0.00	4.88	285	5.8	4.7
DS	PJ-i	0.00	0.00	4.39	296	6.7	4.5
DS	PJ-j	0.21	0.36	6.77	464	6.3	2.9
DS	PJ-p	0.40	0.26	6.81	444	5.9	2.8
PJ	DS-i	0.02	0.00	4.48	323	7.2	4.7
PJ	PJ-i	0.00	0.00	4.36	345	7.9	4.5
PJ	PJ-j	0.21	0.36	7.19	533	6.9	2.9
PJ	PJ-p	0.40	0.26	5.98	512	7.7	2.8
PJ	PP-i	0.16	0.00	6.09	381	6.1	1.7
PJ	PP-pp	0.49	0.25	6.11	551	8.0	2.5
PP	PJ-i	0.00	0.00	4.86	505	10.4	4.5
PP	PJ-j	0.31	0.36	7.24	604	7.7	2.9
PP	PJ-p	0.40	0.26	5.22	573	9.7	2.8
PP	PP-i	0.16	0.00	6.80	423	6.1	1.7
PP	PP-pp	0.49	0.25	7.42	564	6.9	2.5

cosm types. We did not expect to see significant differences in soil moisture between mesocosms, which occurred within each of the three sites. Observed differences in soil moisture appear to be influenced by the amount of litter and duff on the soil in the mesocosms. Surface organic matter, especially accumulations of duff, slowed water loss from mineral soil. Interspace soils, with no duff and little litter, were always driest and had the lowest rates of soil respiration. Canopy soils with more organic matter in litter and duff were wetter and had slightly greater soil respiration rates. Comparison of soils originating from different locations incubated under identical conditions is especially important in semiarid systems where microsite differences, such as those between canopy and interspace, have dramatic effects on microclimate, soil processes, and soil characteristics, including the accumulation of surface organic matter (Klopatek, 1987; Schlesinger et al., 1990; McDaniel and Graham, 1992).

Soil respiration is widely believed to follow first-order kinetics, wherein the rate of soil respiration is directly related to the size of the soil C pool (e.g., Parton et al., 1988; Paul and Clark, 1989). The fact that normalized soil respiration rates were not significantly different within each of the three incubation sites suggest that soil C pool size is the most important factor associated with soil respiration in this study as well. Though there were differences in litter quality, active C pool size, texture, soil moisture, and organic matter quality (C/N ratios), these factors did not appear to influence soil respiration as strongly as total C. Between sites, annual soil respiration rates, normalized for total mesocosm organic C, were always least at the warmest, driest site at which a mesocosm was incubated and greatest at the coolest, wettest site. This illustrates the importance of soil moisture in influencing soil respiration rates, regardless of soil C content. Differences between incubation sites within sampling periods followed the same pattern. Based on multiple regression analysis, it appears that when soil respiration is normalized for soil C content, temperature is the primary factor controlling soil respiration under only the wettest conditions.

Under natural conditions, soil respiration is a function of the decomposition of organic matter, root respiration, and root-associated respiration. Since all live roots and most dead roots were excluded, the soil respiration we measured was derived from organic matter decomposition, which is dominated by turnover of the large intermediate soil C pool and from the smaller pool of active C (Townsend et al., 1995; Parton et al., 1988). While it was not surprising that we were unable to measure a change in total organic C over the short duration of this experiment, our estimates indicate that between 6 and 10% of total soil C was respired. Based on data from laboratory incubations, we estimate that the amount of soil C lost in the field was greater than the size of the mineral–soil active C pool. Significant losses of soil C suggest that observed changes in soil respiration rates due to climate change will persist for only a limited time without continual replenishment of the active soil C pool, which may not occur under increased temperatures (West et al., 1994). Smaller losses of active C for warmer, drier soils suggest that decreased soil respiration due to warmer, drier conditions may persist longer. These expectations assume that the source of respired CO_2 does not shift in response to changes in climate, though this may not be the case (Zogg et al., 1997).

This study shows that soil respiration in these semiarid ecosystems is largely controlled by soil C pool size and soil moisture. Unlike results from more mesic systems, increases in temperature (with corresponding decreases in soil moisture) led to net decreases in soil respiration throughout the duration of the experiment. Only during periods when soil moisture was >200 g H_2O kg soil^{-1} (usually during the fall and winter) was soil respiration strongly related to temperature. As much as 75% of all soil respiration occurs during late spring, summer, and early fall in these systems (Conant et al., 1998) and differences between incubation sites were often significant most often during this time period. Thus, changes in precipitation, rather than temperature, during this active portion of the year will have the greatest potential to affect total soil respiration rates. Furthermore, the spatial patterning and extent of plant canopies and interspaces (and associated microclimatic and soil differences) will play a critical role in ecosystem response to climate change, since the influence of canopies is both significant and persistent. While long-term decreases in aboveground and belowground detrital inputs may ultimately be greater than decreased soil respiration, initial response to increased temperature in these systems appears to be a net decrease in soil C release.

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