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Carbon pools and fluxes along an environmental gradient in northern Arizona

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Abstract. Carbon pools and fluxes were quantified along an environmental gradient in northern Arizona. Data are presented on vegetation, litter, and soil C pools and soil CO_2 fluxes from ecosystems ranging from shrub-steppe through woodlands to coniferous forest and the ecotones in between. Carbon pool sizes and fluxes in these semiarid ecosystems vary with temperature and precipitation and are strongly influenced by canopy cover. Ecosystem respiration is approximately 50 percent greater in the more mesic, forest environment than in the dry shrub-steppe environment. Soil respiration rates within a site vary seasonally with temperature but appear to be constrained by low soil moisture during dry summer months, when approximately 75% of total annual soil respiration occurs. Total annual amount of CO_2 respired across all sites is positively correlated with annual precipitation and negatively correlated with temperature. Results suggest that changes in the amount and periodicity of precipitation will have a greater effect on C pools and fluxes than will changes in temperature in the semiarid Southwestern United States.

Introduction

It is generally accepted that global climate will change due to increasing atmospheric CO_2, although the magnitude of change and different regional effects are still uncertain (Washington & Meehl 1989; Schneider 1995; Houghton et al. 1996). Rates of soil respiration are highly sensitive to changes in 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). If warming yields even a small increase in the rate of soil respiration and CO_2 release from the large terrestrial soil C pool, the result may be a positive feedback on climate (Post 1993; Schimel 1995).

Many climate models predict that the southwestern United States will get warmer, the amount of precipitation will decrease, and the proportion of precipitation delivered as rainfall will increase (e.g., Neilson et al. 1990; Douglas 1995). Additionally, several analyses suggest that semiarid systems will increase in areal extent due to climate changes predicted with a doubling of atmospheric CO_2 (Emanuel et al. 1985; Pastor & Post 1988). If temperature were the primary or only factor affecting soil respiration rates as in some other studies investigating potential effects of climate change on soil respiration (e.g. Schlentner & Van Cleve 1985; Anderson 1991; Townsend et al. 1992), we would expect increased temperature to lead to increased soil respiration. However, other research has emphasized the importance of changes in soil moisture on soil processes (Pastor & Post 1988; Ojima et al. 1993). In arid and semiarid systems, soil moisture is a key factor controlling biogeochemical processes including microbial and plant respiration, decomposition, and nutrient uptake and release (Wildung et al. 1975; Bottner 1985; Fisher et al. 1987; Paul & Clark 1989; Parton et al. 1994; Klopatek et al. 1995).

We examined C storage and soil respiration across several semiarid ecosystem types in northern Arizona along a temperature and precipitation gradient. The objectives of the research were (1) to measure variation in C storage and soil respiration in some dominant semiarid vegetation types in the Southwest, (2) to evaluate differences in soil C storage and soil respiration between cover types within a vegetation type, and (3) to determine the relative importance of precipitation, temperature, and soil C on temporal patterns of soil respiration within these communities.

Materials and methods

Study area

The research area is located along Deadman's Wash in the Coconino National forest, due north of Flagstaff, Arizona on the leeward side of the San Francisco Mountains (between 35°25′ N, 111°34′ W and 35°26′ N, 111°40′ W). The area covers a seven-kilometer 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 yrs) of moderate to light grazing. Domestic livestock have not grazed in the area since summer 1993.

Five one hectare study plots, one representative of each vegetation type, were established in May 1993. The desert scrub site (DS) is dominated by winterfat (*Ceratoides lanata*), snakeweed (*Gutierrezia sarothrea*), rubber rabbit brush (*Chrysothamnus nauseosus*) and blue grama grass (*Bouteloua gracilis*). The pinyon-juniper woodland (PJ), contains one-seed juniper (*Juniperus monosperma*) and pinyon pine (*Pinus edulis*), with blue grama in the interspaces. Maximum tree age on this site ranges between 150–180 years

Table 1. Elevation, tree canopy cover and model estimates of mean annual temperature and annual precipitation for five sites along an environmental gradient.

Name	Description	Elevation (m)	Annual precipitation (mm)	Mean annual temperature (°C)	Tree canopy cover[*] (%)	Litterfall (g C m^{-2} yr^{-1})
DS	Great basin desert scrub	1987	310	8.5	0	4.1
DS-PJ	Transition zone 1	2040	350	7.9	15	28.5
PJ	Pinyon-juniper woodland	2126	410	7.1	42.4	79.6
PJ-PP	Transition zone 2	2179	450	6.3	36.6	57.8
PP	Ponderosa pine forest	2295	530	5.5	30.5	54.7

[*] from Francis and Klopatek, submitted manuscript

old indicating a history of disturbance in the area. The ponderosa pine forest site (PP), is an open, park-like stand of ponderosa pine (*Pinus ponderosa*) trees of several age classes, with mutton grass (*Poa fendleriana*), mountain muhly (*Muhlenbergia montana*) and buck brush (*Ceanothus fendleri*) in the understory. The ponderosa pine site contains several trees more than 250 years old containing a number of fire scars. Ecotones between the above sites (DS-PJ and PJ-PP) contain a mixture of the vegetation at adjoining sites.

Soils at all sites are derived from volcanic material and are classified as Typic Argiborolls at the upper elevations grading into Aridic Argiustolls at the lower elevations. Soils are sandy loams and are slightly basic to slightly acidic. Soil carbonate (indicated by reaction with 1N HCl) was present in only one location (PJ site under juniper canopy at 100 cm depth).

A microclimate model, based on the Mountain Climate Model of Hungerford, et al. (1989), was used to estimate temperature for each site. Our model, written in C^{++}, calculates daily site minimum temperatures, dew point, and vapor pressure deficit based on data from nearby weather stations. Daily maximum temperatures were calculated as a function of minimum temperature and total solar insolation. Total solar radiation was determined by modifying transmittance as a function of elevation and corrected for slope and aspect at each site. Temperature estimates were cross-checked with spot maximum-minimum measurements taken periodically at each of the five study sites.

Precipitation is bimodal in this region. Intense convectional precipitation during the summer months is highly spatially variable. Low intensity precipitation in winter months often falls as snow and displays a high degree of interannual variability. Similar to examples of Hanson (1984) and Rowlands (1983), we employed a linear regression model based on elevation to estimate monthly precipitation. However, we used a seasonally adjusted regression model to more accurately represent the bimodal differences found at our sites. We based our regression models on long-term data from three meteorological stations located within 25 km of the sites.

Surface organic horizon C pools

Organic C and nutrients are often concentrated under canopies in semiarid woodlands in ‘islands of fertility’ (Klopatek 1987; Schlesinger et al. 1990; McDaniel & Graham 1992). Quantifying C pools and fluxes in these systems requires explicit recognition of the spatial variation of resources and microclimate. Therefore, we treated interspaces (I) and each of the three canopy types, juniper (J), pinyon (P), and ponderosa (PP), as separate cover types and sampled each independently within each site.

Twelve replicate 0.0625 m^2 samples from L and H horizons (organic horizons consisting of recognizable and non-recognizable litter material, respectively) were taken under each cover type at all five sites. Sampling points were distributed in a stratified random manner, with three sampling points under each cover type in each quadrant at all sites. Samples were returned to the laboratory, dried at 60 °C, weighed, and ground. Subsamples of L and H horizon material were ashed to determine loss by ignition. Additional subsamples were analyzed for C and N on a Perkin-Elmer 2400 CHN analyzer.

Soil C

Soil samples from three depths (5, 20, and 100 cm) were taken from three randomly located soil pits under each cover type at each site. Soil cores of known volume were also extracted from the sides of each pit at each depth, dried at 60 °C, and weighed to determine bulk density. In addition to the above samples, eight shallow (0–10 cm and 10–20 cm) soil samples, each a composite from three locations, were collected using a soil auger. All soil samples were returned to the lab, sieved (2 mm mesh), ground, and analyzed for C content. Total organic matter was determined using a Walkley-Black digest (Nelson & Sommers 1982). Organic matter was assumed to be 58% C (Schlesinger 1977; Nelson & Sommers 1982). Soil C concentrations were verified by analyses with a Perkin-Elmer 2400 CHN analyzer. Carbon pool sizes under each cover type were calculated by multiplying bulk density by percent C.

Vegetation C pools

Cover values for tree species at each site were calculated using a stem map with associated canopy dimensions (Francis and Klopatek submitted manuscript). Shrub cover was obtained using the point-quarter method on four 100 m transects. Mean cover of each herbaceous species was determined by averaging values obtained at one random point for every ten meters on the same transects. Above- and belowground biomass values were calculated using synthetic measurements taken for each woody species within the 1 ha exclosures and allometric equations for each tree and shrub type (Grier et al. 1992; DeLucia et al. 1994; Klopatek et al., unpublished manuscript). Carbon content of wood, leaves (needles), and roots were determined for all woody species using a Perkin-Elmer 2400 CHN analyzer.

Soil respiration

Soil respiration was measured using the static absorption technique (Van Cleve et al. 1990; Freijer & Bouton 1991; Raich & 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 diameter = 15.5 cm) enclosing a container (diameter = 5.9 cm) with 20 ml of 1N KOH were left in place for 24 hours, then titrated with 1N HCl using phenolphthalein indicator. Blanks consisted of a sealed chamber of the same volume also enclosing a container of 1N KOH. Alkali absorption methods are inaccurate if the surface area of the absorbent solution covers less than 6% of the soil surface area (Raich & Schlesinger 1992; Nay et al. 1994); our absorptive surface covered 14% of soil surface area inside the chamber.

Soil respiration sampling was performed twice per month between May 1994 and September 1994, once per month between October 1994 and April 1995 and twice per month May 1995 through August 1995. Measurements were taken in randomly located non-vegetated interspaces, and under randomly chosen canopies of each of the dominant cover types (pinyon pine, juniper, and ponderosa pine) in each of four quadrants at each site.

Stand-level calculations and statistical analyses

Estimates of total site soil, surface, and vegetation C pools and site soil respiration were calculated based on measurements for each canopy type and the amount of coverage for each canopy type. Total site C pool sizes were calculated by multiplying relative cover values and mean C pool size for each cover type and summing at each site. Total site soil respiration was calculated in the same manner by multiplying soil respiration rates and percent cover of each cover type and summing for each of the five sites. Standard errors for site C pools and soil respiration rates were calculated by weighting the data according to proportion of each cover type (sensu Cochran 1977). Since unequal sampling intervals were used, annual site CO_2 efflux was calculated by summing measurements weighted according to the duration of time represented by each.

Analysis of variance was used to compare C pool measurements and soil respiration for each cover type (SAS 1989). The relative influence of cover values and flux rates (by canopy type) in determining site soil respiration and soil C storage were distinguished by comparing mean soil respiration rates between sites without accounting for cover differences. Multiple linear regressions, generated in a step-wise fashion, were used to develop equations correlating monthly rates of soil respiration with mean monthly temperature and monthly precipitation. Simple linear regressions were used to relate annual soil respiration across all five sites with mean annual temperature, mean annual precipitation, and soil C. Regressions of annual site-level soil respiration rates against mean annual temperature and mean annual precipitation were carried out despite the fact that they have very low statistical power due to few degrees of freedom (d.f. = 4). Significant regression equations are reported at the 0.05 level. Independence of residuals was confirmed by the Durbin Watson test (SAS 1989) and no trends were apparent in residuals.

Results

Climate

We used 30 years of climatic data (1967–1996) to determine that mean annual temperatures ranged from 8.5 to 5.5 °C at the lowest and highest sites, respectively (Table 1). Temperatures modeled using differences in elevation and minimum daily temperature at one climate station explained 85% of the variation observed at other stations during the experimental measurement period. Tests against temperature data from data loggers at each study site showed that monthly estimates were within 1.0% of actual site temperatures for those periods measured. Actual data showed that while the model predictions were reasonably accurate, occasional periods of cold air drainage resulted in overestimates of minimum daily temperatures at the lower two sites. This is a typical phenomenon occurring in western mountainous regions (Baker 1944). Predicted mean monthly precipitation tested against a number of independent regional recording stations explained 89 and 77% of the variation in monthly summer and winter precipitation, respectively. Our model estimates of mean annual precipitation ranged from approximately 320 mm yr^{-1} at the lower elevations to 530 mm yr^{-1} at the upper elevation (Table 1).

Carbon pools

Vegetation coverage at all sites was dominated by interspaces between woody plant canopies (Table 2). Tree canopy coverage was lowest at the DS-PJ site (15%) and highest at the PJ site (33%). Woody shrub canopies covered 10.3% of the surface at the DS site. Juniper was the dominant tree at DS-PJ and PJ. At the PJ-PP site pinyon and juniper coverage are nearly equal and ponderosa canopies cover only a small portion of the site (3.5%).

Patterns of C concentration in interspaces varied between sites. The concentration of C in surface mineral soil horizons in the interspaces is significantly greater at the ends of the gradient (DS and PP) than at the middle three

Table 2. Relative cover for interspace and three tree canopy types at five sites along an environmental gradient.

Site	Interspace	Juniper	Pinyon	Ponderosa
DS	90			
DS-PJ	85	10	5	
PJ	58	24	18	
PJ-PP	63.5	16	17	3.5
PP	69			31

sites (DS-PJ, PJ, and PJ-PP; Figure 1; $p < 0.05$). However, at 20 cm depth, soil C concentration in interspaces at the middle three sites was significantly higher than at the most mesic (PP) and xeric sites (DS; Figure 1; $p < 0.05$) possibly indicative of rooting depth of interspace grasses. Carbon concentrations under juniper, pinyon and ponderosa pine canopies did not differ significantly between sites. For all cover types, except the interspaces of the middle three sites, the soil C concentration decreased with depth ($5>20>100$ cm); C concentration was always lowest at 100 cm. With the exception of the PJ-PP site, C concentrations in surface soils under canopies were significantly greater than in surface interspace soils (Figure 1; $p < 0.05$).

Site C storage in the L horizon, H horizon, mineral soil, and above- and belowground vegetation pools generally increased with elevation (Figure 2). The soil compartment contained the largest pool of C at all sites, ranging from 65% (PP) to 87% (DS-PJ) of the total C storage. Total mineral soil C storage at the ponderosa pine forest site was nearly twice that at the desert scrub site. The portion of C in L and H horizons increased from the desert scrub site (1%) to the ponderosa forest site (>10%). The portion of C in aboveground biomass is much larger at the upper three sites than at the lower two, with an abrupt transition between the DS-PJ site and the PJ site, where tree coverage increases.

Total site C storage was significantly influenced both by differences in canopy coverage and soil C concentration between sites. Low total soil C storage (Figure 2) at the DS-PJ site reflects relatively low canopy coverage and low soil C concentrations. The PJ site had much more canopy coverage than the DS-PJ site (Table 2), but the total soil C pool was relatively small due to low soil C concentrations (Figure 2). Tree canopy coverage was lower at the top two sites (Table 2), but significantly greater mean soil C concentrations (Figure 1) resulted in greater site soil C storage. Thus the trend of increasing C storage along the gradient is due both to increased canopy coverage (lower sites) and soil C concentration.

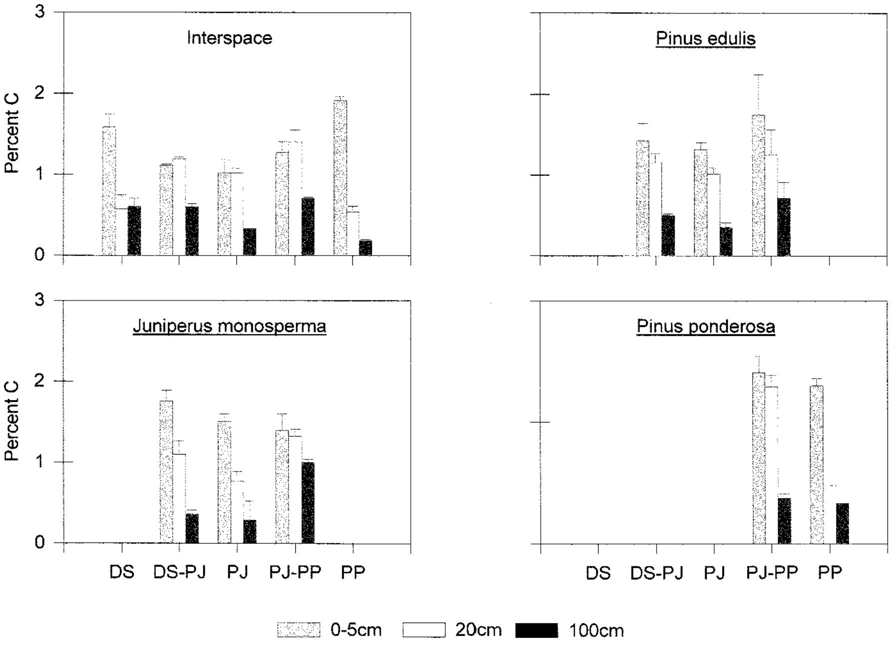

Figure 1. Mean % C of soil at three depths for four cover types at five sites along an environmental gradient (+1 SE; $n = 3$).

Soil respiration

Soil respiration rates for the four different cover types are shown in Figure 3. Soil respiration in interspaces increased from the xeric to the more mesic sites (Figure 3); soil respiration under juniper and ponderosa pine canopies followed the same trend, though differences were not significant. Though soil respiration under canopies was generally higher than in interspaces, differences were not significant at any site.

Total site soil respiration rates (Figure 4) followed C storage trends, increasing with C storage and annual precipitation and decreasing with mean annual temperature. Soil respiration at the upper two sites was significantly greater than at the bottom two sites. Similar to C storage, total site soil respiration was a function of both soil respiration rates and amount of canopy coverage. Combined mean soil respiration rates of all cover types were significantly different between the PJ, PJ-PP, and PP sites. Thus, differences in total site soil respiration rates between the upper three sites were primarily due to differences in soil respiration rates whereas differences between the lower sites were linked to changes in canopy coverage.

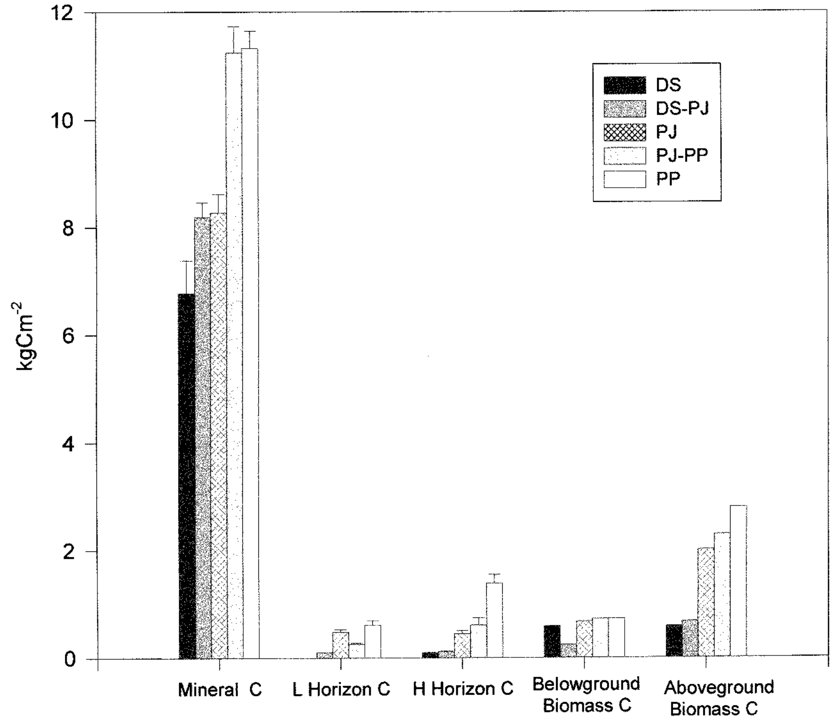

Figure 2. Total mineral soil C (0–100 cm), L horizon C, H horizon C, and above- and belowground C pools at five sites along an environmental gradient (±1 SE).

Soil respiration was highly seasonal at all sites (e.g. Figure 5a–e). Peak rates of soil respiration occurred in June and August of 1994 and in June and August of 1995 at all sites. Seasonal patterns of soil respiration rates at all sites show a departure from those of temperature (Figure 5a–e); differences are more distinct at the lower, drier sites (Figure 5a,b,c). Respiration rates did, however, decrease with temperature during the winter months (Figure 5a–e). Monthly rates of soil respiration within each site were positively correlated with both mean monthly temperature and monthly precipitation. Regression equations relating monthly rates of soil respiration to mean monthly temperature and monthly precipitation relied primarily on temperature and secondarily on precipitation at all sites (Table 3). These equations explained much of the variability of measured soil respiration rates, with r^2 values between 0.74 and 0.90 (Table 3).

Table 4 shows the amount of variation in annual soil respiration across all five sites explained using linear regressions based on mean annual temperature, mean annual precipitation, and soil C. Though the regressions represent

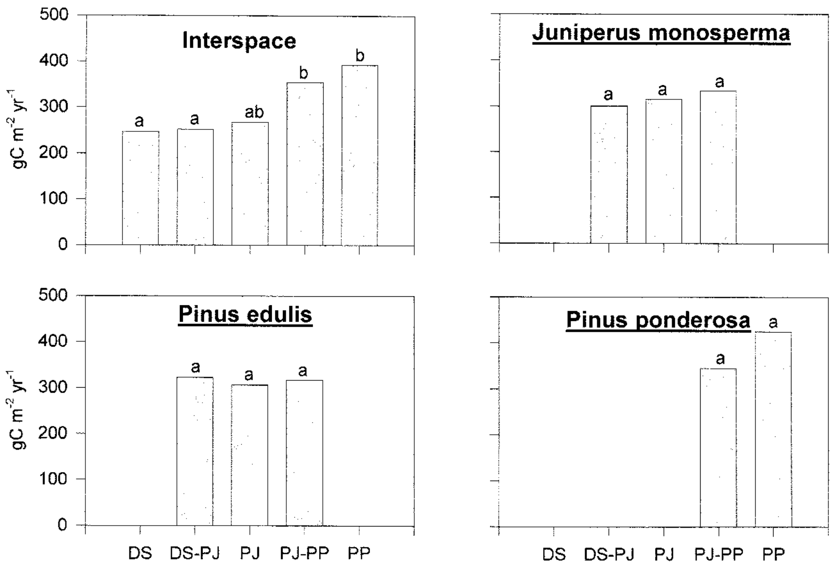

Figure 3. Mean (+1 SE; *n* = 4) soil respiration by cover type at five sites along an environmental gradient.

Table 3. Statistics for stepwise linear regression equations between soil respiration (y) and mean monthly temperature (T) and monthly precipitation (P) for each of the five study sites.

Site	r^2	Prob>f	Equations
DS	0.77	0.006	$y = (43.1 \times T) - (3.0 \times P) + 369$
DS-PJ	0.85	0.001	$y = (46.3 \times T) - (131.0 \times P) + 356$
PJ	0.90	0.001	$y = (50.0 \times T) - (1.7 \times P) + 467$
PJ-PP	0.74	0.012	$y = (68.9 \times T) - 6.6 \times P) + 738$
PP	0.75	0.010	$y = (84.7 \times T) - (9.2 \times P) + 901$

only five data points, soil respiration is strongly positively correlated with both precipitation and soil C ($r^2 = 0.91$, 0.84, respectively; soil C and precipitation are correlated), and strongly negatively related to mean annual temperature ($r^2 = 0.90$; Table 4).

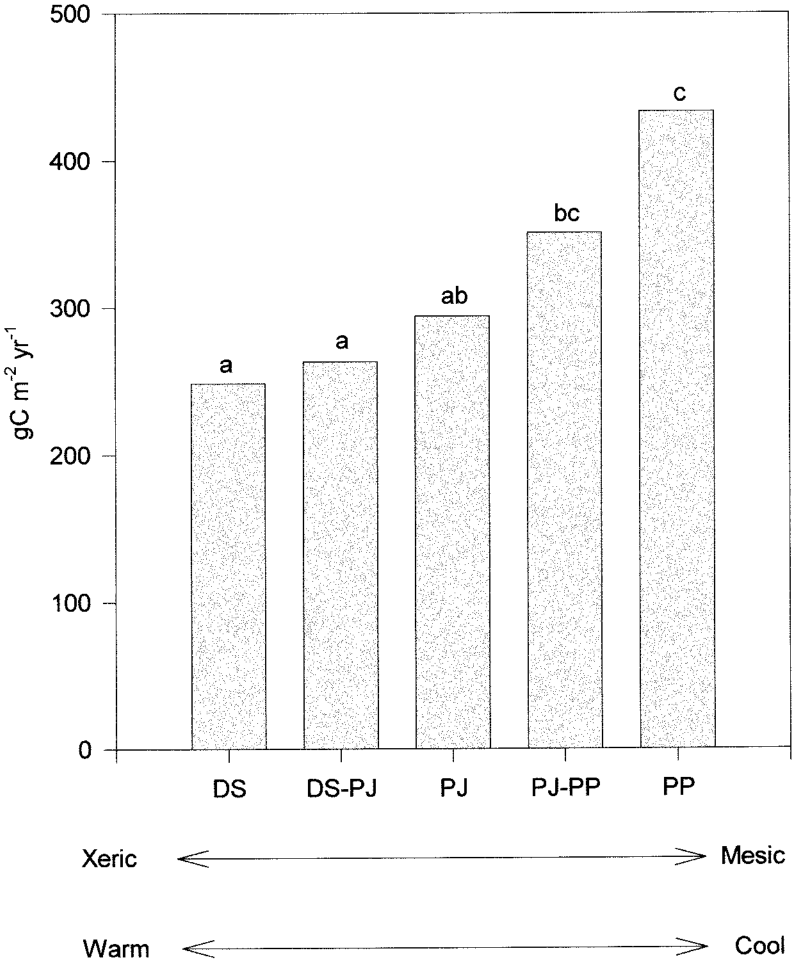

Figure 4. Yearly rates of soil respiration for five sites along an environmental gradient (±1 SE; $n = 4$).

Table 4. Amount of variation explained, f-values, and regression equations relating yearly rates of soil respiration (y) at five sites with three different independent variables (temperature, precipitation, and total soil C).

Variable	r^2	Prob>f	Equation
Temperature	0.90	0.0035	$y = 899.5 - (T \times 60.69)$
Precipitation	0.91	0.0037	$y = (P \times 0.887) - 45.44$
Soil Carbon	0.84	0.0287	$y = (SC \times 25.822) + 79.4$

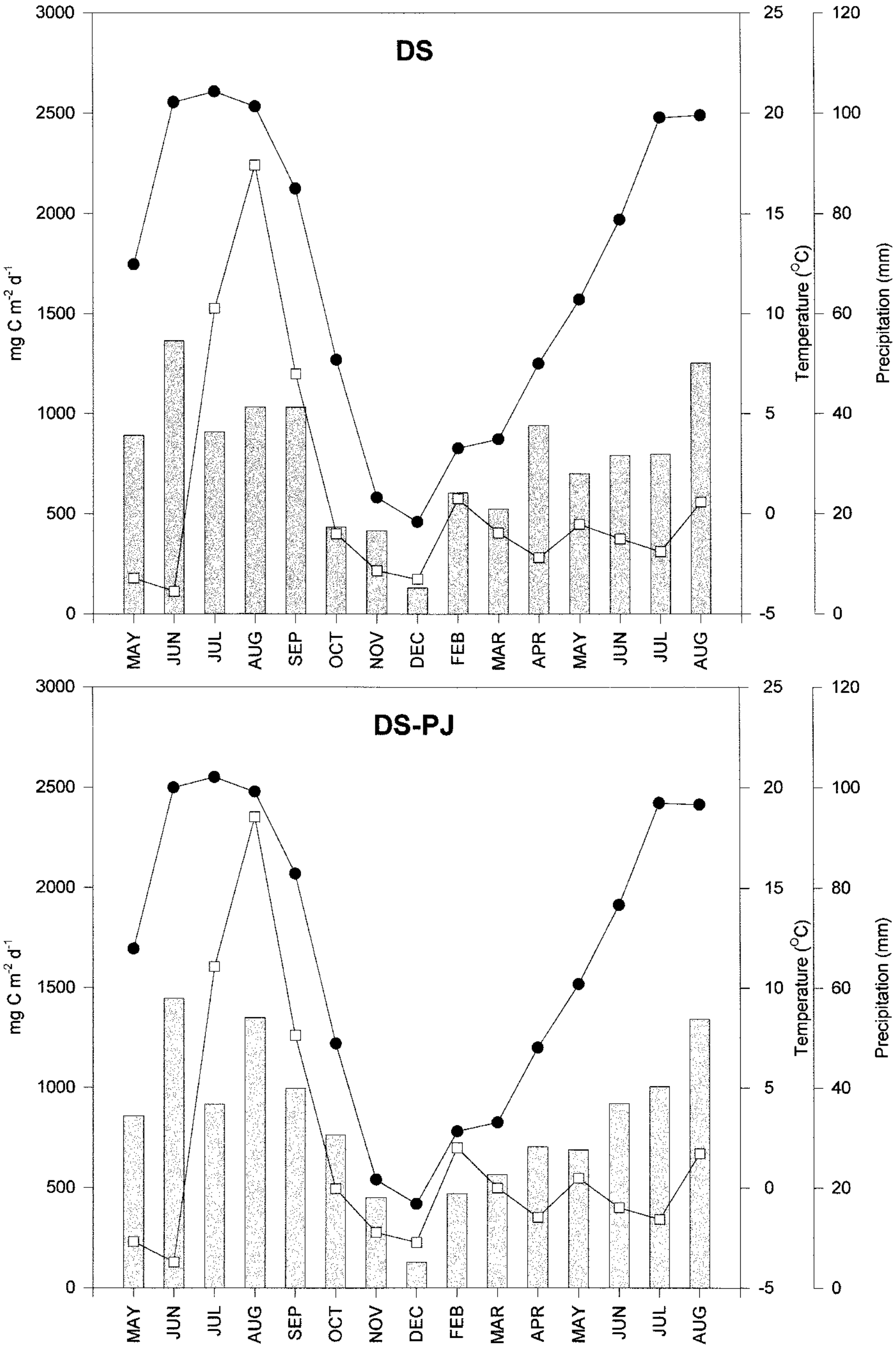

Figure 5a–e. Seasonal patterns of monthly soil respiration rates (bars), mean monthly temperature (closed circles), and total monthly site precipitation (open squares) for five sites along an environmental gradient. a) DS; b) DS-PJ; c) PJ; d) PJ-PP; e) PP.

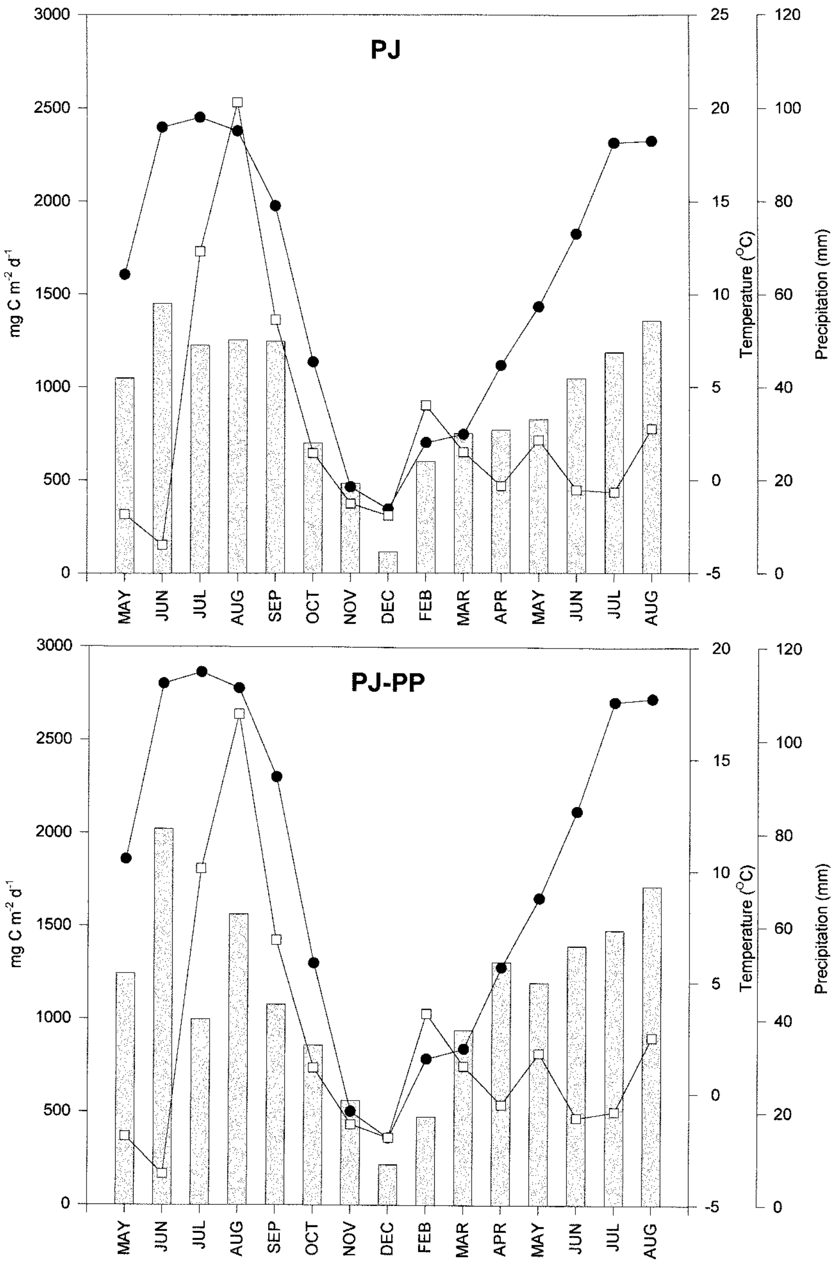

Figure 5a–e. Continued.

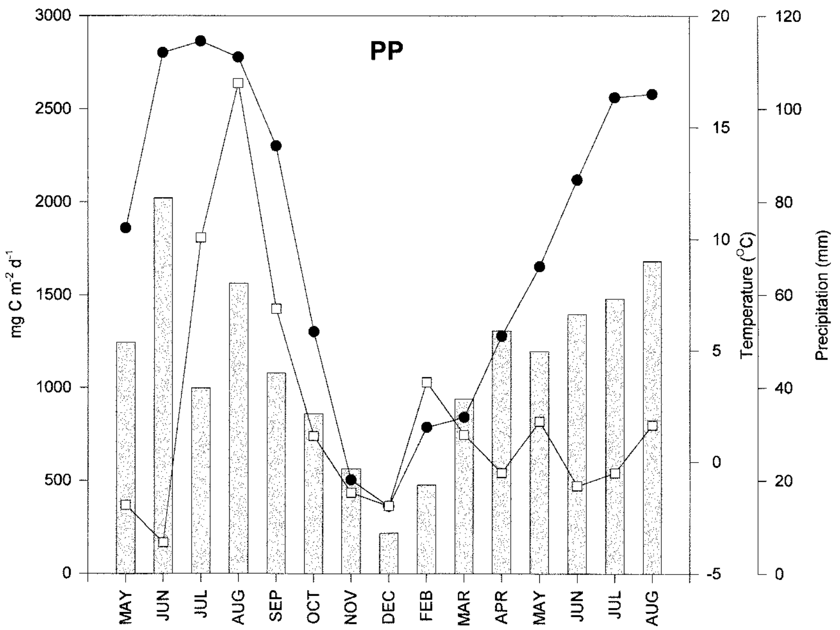

Figure 5a–e. Continued.

Discussion

Carbon pools

Total C increased with elevation and the soil fraction was the largest C pool at all sites. Site soil C pool values to 1m at the DS (6.3 kg C m^{-2}), PJ (9.2 kg C m^{-2}) and PP (12.3 kg C m^{-2}) sites are slightly larger than measurements for desert scrub systems (5.6 kg C m^{-2}), woodlands (6.9 kg C m^{-2}) and ponderosa pine forests (10.6 kg C m^{-2}) reported elsewhere (Klemmedson 1975; Schlesinger 1977).

Spatial differences in C distribution reflect the spatial arrangement of plant canopies as in other arid and semiarid systems (Klopatek 1987; McDaniel & Graham 1992; Schlesinger et al. 1996). The vegetation at the PJ site and the transition sites is highly spatially heterogenous (Klopatek et al. 1998) resulting in markedly greater soil C concentrations under canopies than in the interspaces. Greater soil C concentrations at 20 cm in interspaces at the middle sites may be due to significant belowground litter inputs from grasses. In contrast, the DS and PP sites have more homogenous cover (Klopatek et al. 1998); canopy and interspace C storage were not significantly different.

Schlesinger et al. (1990) concluded that the concentration of nutrients under shrub and tree canopies in desert systems result from a strong positive feedback that reinforces ‘islands of fertility’ in arid and semiarid systems. The influence of vegetative canopies on ecosystem properties is manifest at the lower three sites, where differences in soil C storage between sites are primarily due to differences in canopy coverage. Since the spatial patterning of C inputs to the forest floor has such a significant effect on C storage on the surface and in the soil, any changes in the amount and type of cover due to changes in land use or climate will result in different rates of C inputs to the soil system, and therefore soil C storage.

Soil respiration

Rates of soil respiration followed patterns similar to the distribution of C, increasing with elevation. Rates of soil respiration for the DS (249 g C m^{-2} yr^{-1}) and PJ (294 g C m^{-2} yr^{-1}) sites are comparable to measurements made by Caldwell et al. (1977) in a cold desert site in Utah (185 g C m^{-2} yr^{-1}) and by Holt (1987) in a Savannah system in Australia (381 g C m^{-2} yr^{-1}). The annual amount of soil respiration from the PP site, was lower than most measurements of soil respiration in temperate coniferous forests (Raich & Schlesinger 1992). This discrepancy at the PP site is likely due to the limitation of soil respiration for much of the year due to low soil moisture; predawn xylem potentials at this site can reach as low as -4.5 MPa (Toure 1995). Additionally, this site is not a well-stocked ponderosa pine stand, but exhibits a more open, park-like structure characteristic of many southwestern forests at the turn of the century (Fulé et al. 1997).

Monthly rates of soil respiration at all sites were highly correlated with temperature (Figure 5a–e), but exhibited seasonal patterns that departed from those of temperature. Though soil respiration increased during warmer months and decreased during colder months, increases in soil respiration during the summer months of both years were not concomitant with increases in temperature. It appears that during the summer months (May–Aug), the months with the highest rates of soil respiration, soil respiration is constrained by low soil moisture. Thus, monthly rates of soil respiration within each site are highly correlated with temperature, but annual rates of soil respiration are constrained by precipitation. This concurs with the concepts that greater temperatures prompt greater rates of soil respiration [the Q_{10} for soil respiration is around 2 for most soils (Schlesinger 1977; Anderson 1991)], but soil moisture limits decomposition rates in semiarid systems (Wildung et al. 1975; Richards 1987; Paul & Clark 1989; Murphy et al. 1998).

Although monthly soil respiration rates within each site are strongly correlated with mean monthly temperature, total annual soil respiration across all sites is highly positively correlated with annual precipitation and soil C pool size, and negatively correlated with mean annual temperature. Additionally, available moisture has been shown to limit the rate of leaf litter decomposition in our study area (Murphy et al. 1998) and litter inputs are related to the amount of precipitation (R.T. Conant unpublished data). Thus, precipitation may be more critical than temperature in controlling C dynamics in these semiarid systems suggesting that responses of C pools to changes in temperature may be constrained by changes in soil moisture.

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