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Soil respiration in the cold desert environment of the Colorado Plateau (USA): abiotic regulators and thresholds

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Abstract. Decomposition is central to understanding ecosystem carbon exchange and nutrient-release processes. Unlike mesic ecosystems, which have been extensively studied, xeric landscapes have received little attention; as a result, abiotic soil-respiration regulatory processes are poorly understood in xeric environments. To provide a more complete and quantitative understanding about how abiotic factors influence soil respiration in xeric ecosystems, we conducted soil-respiration and decomposition-cloth measurements in the cold desert of southeast Utah. Our study evaluated when and to what extent soil texture, moisture, temperature, organic carbon, and nitrogen influence soil respiration and examined whether the inverse-texture hypothesis applies to decomposition. Within our study site, the effect of texture on moisture, as described by the inverse texture hypothesis, was evident, but its effect on decomposition was not. Our results show temperature and moisture to be the dominant abiotic controls of soil respiration. Specifically, temporal offsets in temperature and moisture conditions appear to have a strong control on soil respiration, with the highest fluxes occurring in spring when temperature and moisture were favorable. These temporal offsets resulted in decomposition rates that were controlled by soil moisture and temperature thresholds. The highest fluxes of CO_2 occurred when soil temperature was between 10 and 16 °C and volumetric soil moisture was greater than 10%. Decomposition-cloth results, which integrate decomposition processes across several months, support the soil-respiration results and further illustrate the seasonal patterns of high respiration rates during spring and low rates during summer and fall. Results from this study suggest that the parameters used to predict soil respiration in mesic ecosystems likely do not apply in cold-desert environments.

Introduction

Soil respiration (SR) is the emission of CO_2 from plant roots and soil organisms involved in the decomposition of soil organic matter (SOM) and is the primary pathway by which carbon is transferred from the soil to the atmosphere (Schimel 1995). In contrast to numerous soil-respiration studies from mesic ecosystems, there is a paucity of research from xeric ecosystems (e.g.,

Raich and Schlesinger 1992). Research from mesic environments shows that soil temperature, moisture, and texture are the major abiotic controls of decomposition. These three factors constitute the primary controls of SR and decomposition in ecosystem models such as Century, GEM, and TEM (Parton et al. 1987; Raich et al. 1991; Rastetter et al. 1991). Considerable uncertainty, however, remains as to how these factors interact to control soil respiration and decomposition in xeric ecosystems.

Temperature exerts both indirect and direct effects on decomposition, but the effects may differ between mesic and xeric ecosystems. Temperature indirectly controls decomposition by influencing the rate at which soil moisture is lost and directly controls decomposition by affecting the efficiency of enzymes involved in decomposition. In both mesic and xeric ecosystems, low temperatures inhibit SR (e.g., Carlyle and Than 1988; Conant et al. 1998). As temperature increases, however, an exponential increase in SR rate occurs. (Lloyd and Taylor 1994; Fang and Moncrieff 2001). The exponential response of SR relative to temperature peaks at 25 °C and remains relatively constant to 35 °C, at which point SR rate generally declines because enzymes used by soil microfauna denature and become less efficient Paul and Clark 1989). In seasonally hot, xeric environments, SR inhibiting temperatures are common, but temperature induced declines in SR are not commonly represented in conceptual and quantitative models of soil processes (e.g., Parton et al. 1987; Kittel et al. 1995). Data collected by O'Connel (1990) in a mesic environment and by Parker et al. (1983) in a hot desert environment suggest different SR inhibiting temperatures for mesic and xeric environments. O'Connel found the optimal temperature before SR-rate decline to be between 32 and 34 °C, whereas Parker et al. reported a temperature of 41 °C. Differences in the temperature-SR relation between mesic and xeric environments may be further complicated by differences in soil-moisture regime for each environment.

Precipitation inputs in xeric ecosystems are highly variable in occurrence and magnitude (Noy-Meir 1973). As a consequence, biological activity is driven primarily by discontinuous and discrete pulses of precipitation large enough to activate biota. The timing of precipitation pulses is also important because biological activities, such as SR, are temperature dependent. Between precipitation pulses, edaphic factors may also be important in the regulation of biological activity. For example, soil characteristics influencing water retention may affect SR.

Soil texture, determined by the relative proportion of clay, silt, and sand, is an important regulator of SR and decomposition in most environments. Soil texture influences the accumulation of SOM and nutrients that promote decomposition and also determines water-holding capacity of soil (Jenny 1980). Fine-textured soils, high in silt and clay, tend to have higher SOM content and decomposition rate than do coarse-textured soils (e.g., Schimel et al. 1985). Fine-textured soils also have a higher water holding capacity than do coarse-grained soils. In mesic environments, this higher moisture availability in fine-textured soil leads to greater productivity. However, this is not

the case in xeric lands where the low-water holding capacity of sandy soil allows water to infiltrate deeper into the soil column, reducing evaporative loss. As a result higher productivity in xeric ecosystems may occur on coarse textured soil relative to finer soil. This phenomenon of textural influence on water holding capacity and productivity in xeric environments is known as the Inverse Texture Hypothesis (ITH) (Noy-Meir 1973). According to the ITH, higher levels of plant productivity should occur in fine-textured soil when precipitation is greater than a threshold of 300–500 mm per year. When annual precipitation is below this precipitation threshold, however, higher productivity may occur in sandy soils. Numerous studies conducted in the semi-arid Great Plains of North America support the ITH (Sala et al. 1988; Dodd and Lauenroth 1997; Epstein et al. 1997; Lane et al. 2000); however, it is not known whether the moisture-texture relations described by the ITH influence SR. According to the ITH, greater soil moisture will occur deep within the soil profile when annual precipitation is less than 300–500 mm, but in these environments SOM and nutrient pools vital to decomposers are found near the surface (West 1981).

Abiotic controls on decomposition are central to carbon exchange and nutrient-release processes in all ecosystems. Knowledge of how these controls operate is well established for mesic ecosystems but not for xeric ones. Qualitative and quantitative differences in soil moisture, temperature, and textural relations between mesic and xeric landscapes may bring about differences in how abiotic variables influence soil respiration. To provide a more complete and quantitative understanding of how abiotic factors influence SR in xeric ecosystems, we conducted SR and decomposition-cloth measurements along soil textural gradients in southeastern Utah, USA, a cold desert environment with strong seasonal precipitation and temperature gradients. In this study we examine (1) when and to what extent SR is influenced by soil-texture, moisture, temperature, organic carbon, and nitrogen, (2) whether the ITH applies to decomposition, and (3) the effect of an artificial monsoonal precipitation pulse on SR.

Materials and methods

Study design

We divided our study into two components. In the first component we measured SR fluxes to evaluate immediate biological decomposition activity as a function of soil texture, temperature, moisture, organic carbon, and nitrogen. In the second component we examined seasonal changes in decomposition-cloth tensile strength as a means to understand how soil texture, depth, and season affect decomposition over a long period of time and to determine whether the ITH applies to decomposition.

Site description

The research sites for this study were located on the Colorado Plateau, approximately 100 km south of Moab, Utah, USA, in the Needles district of Canyonlands National Park (CNP). The area of CNP is characterized as a cold-desert environment approximately 1500 m above sea level with mean annual precipitation of 207 mm. Data collected daily and averaged on a monthly basis from 1965 to 2004 indicate that the mean annual maximum temperature is 20 °C and mean minimum annual temperature is 3 °C (http://www.wrcc.dri.edu/summary/climsmut.html). The soils of the study area were derived from the Cedar Mesa Sandstone of the Cutler Group.

For the study we set up two transects, 2 km apart, with a coarse-to-fine soil textural gradient from hill-top to toe slope with an incline of approximately of 4°. One transect was located at Squaw Flat (SF), the other in an area called Mustard Patch (MP). Each transect was on coarse-loamy mixed soil having kaolinitic clays. The soil of SF is classified as Begay fine sandy loam occurring on mixed, mesic Typic Torrripsamments, whereas the soil of MP is classified as Sheppard fine sand occurring on superactive, mesic Ustic Haplocambids (U.S. Department of Agriculture Soil Conservation Service 1991). Percent fines (silt + clay) for the SF and MP soils ranged from 14 to 52 and 3 to 37%, respectively (Table 1). The soil for both transects was devoid of gravel and rock. Mean soil organic carbon and nitrogen for SF was 296.4 g m^{-2} (SE 36.4) and 28.2 g m^{-2} (SE 5.5), respectively, and that of MP was determined to be 153.2 g m^{-2} (SE 26.2) and 7.2 g m^{-2} (SE 0.17), respectively (Table 1). The area containing the two transects was grazed by domestic livestock until becoming part of CNP in 1974 (Neff et al. 2005).

Two transects were used to obtain a greater spatial representation of soil texture, organic carbon, and nitrogen, and increase the number of study plots. Each transect was established by following a compass bearing parallel to the slope and setting up a study plot every 15 m. Nine plots were set up at SF and 16 at MP. Both transects were closely similar in vegetation and geochemistry and were thus treated as one site in study analyses. At each study plot, a 5-cm-tall, circular 80 cm^2 PVC soil respiration collar (SRC) was permanently inserted 5 cm into the soil. Additionally, extra SRCs were installed at the top, middle, and bottom of the MP transect in order to observe how SR was affected by simulated monsoonal precipitation. We positioned all SRCs in the interspaces between plants to avoid root respiration as much as possible. In close proximity to each SRC, a decomposition-cloth was vertically inserted 30 cm into the ground. Soil from each plot was analyzed for texture, organic carbon, and nitrogen.

Both transects were in grasslands with scattered shrubs, but the density of shrub cover was higher in the Mustard Patch transect. The dominant plant species within each transect were *Stipa comata*, *Stipa hymenoides*, *Hilaria jamesii*, *Coleogyne ramosissima*, *Ephedra trifurca*, and *Atriplex canescens*. The grasses within the study area are predominantly shallow rooted, but *Hilaria*

Table 1. Particle-size distribution (% sand, silt, and clay) of the 0–50 cm section of the soil profile and grams organic carbon per kilogram of soil and grams nitrogen per kilogram of soil of the 0–10 cm section of the soil profile from SF and MP transect plots.

Transect	Plot number	Percent sand	Percent silt	Percent clay	Carbon g/kg	Nitrogen g/kg
SF	1	83	12	5	2.50	0.28
SF	2	81	13	6	1.76	0.15
SF	3	82	14	5	2.00	0.20
SF	4	86	11	3	1.91	0.18
SF	5	75	18	7	1.09	0.07
SF	6	55	34	12	2.23	0.27
SF	7	62	26	12	2.51	0.29
SF	8	48	37	15	3.22	0.44
SF	9	49	35	16	4.85	0.65
MP	A	96	3	1	2.18	0.06
MP	B	94	4	3	0.95	0.06
MP	C	74	22	4	0.81	0.05
MP	D	97	2	1	0.39	0.04
MP	E	86	8	5	0.91	0.12
MP	F	81	15	4	0.68	0.01
MP	G	96	3	1	0.90	0.04
MP	H	65	30	5	0.88	0.05
MP	I	66	30	5	1.06	0.11
MP	J	78	19	3	1.87	0.10
MP	K	91	7	2	1.58	0.17
MP	L	71	25	3	1.85	0.15
MP	M	77	18	5	1.39	0.11
MP	N	77	17	6	1.77	0.19
MP	O	86	10	4	2.37	0.28
MP	P	63	27	11	2.43	0.16

Plots 1 and A are situated at hilltops with subsequent plots located down slope and plots 9 and P at the toe slopes.

jamesii can extend a small portion of its roots beyond 1 m (West et al. 1972; Schwinning et al. 2003). The shrubs of the study area have deep rooting morphology. Though our measurements likely include some contribution from both root and soil respiration, examination of the area beneath the SRCs indicated few fine roots in the interspace areas.

Field respiration measurements

Soil respiration was measured with a Licor 6400 infrared gas analyzer (Licor industries Omaha, NE, USA) fitted with a 6400-09 soil respiration chamber attachment. Soil respiration measurements were conducted at least once a month over a 2-year period. Measurements were taken in February, March, May, June, July, September, October, and November. Soil-respiration measurements were taken in February only during the first year of the study. No efflux measurements were taken within 15 days of a preceding precipitation

pulse. During each sampling session, two SR measurements were taken at each plot and averaged. For each SR measurement the Licor pumped the soil chamber to 5 ppm below ambient CO_2. Once ambient CO_2 concentrations were reached within the soil chamber, we measured CO_2 efflux for 2 min or a CO_2 concentration change of 10 ppm. Mean soil temperature and moisture of the top 10 cm of the soil profile were also recorded at each plot when conducting SR measurements. Soil-surface temperature was taken with a soil-temperature probe that is a component of the Licor 6400, and soil-surface moisture was measured with a Hydosense Sensor (Campbell Scientific, Australia) calibrated to nearby TDR soil installations located at Squaw Flat.

Simulated monsoonal precipitation experiment

A series of SR measurements, with a simulated precipitation pulse, were also taken once during the study. This series of measurements occurred over a 33-h period in June 2002. For this series of measurements, 1 cm of precipitation was added to six extra SRCs within the MP transect. These extra SRCs (two per plot) were located in the top, middle, and bottom of the MP transect (plots A, K, and P Table 1). One of the extra SRCs in each plot was used exclusively for SR measurements and the other was used for monitoring moisture throughout the simulation. With each SR measurement, soil moisture and temperature were recorded as done with the other SR measurements. Two SR measurements were taken on the SRC having the simulated precipitation and an additional two SR measurements were taken on an adjacent SRC, without the addition of water. Measurements were done in this way to determine how long and by how much the simulated precipitation pulse elevated SR rate.

Seasonal, soil-texture, and soil-depth effects on decomposition and the influence of the Inverse Texture Hypothesis

Decomposition cloths (30-cm long strips of unbleached cotton fabric) were inserted vertically into the soil to 30 cm next to SRCs to evaluate the influence of soil depth, texture, and season on decomposition. The decomposition-cloth method uses loss of cloth tensile strength through tensiometer analysis as a proxy for cellulose decomposition by comparing breaking load (kN) of unburied cloths to buried cloths. Decomposition cloths were installed twice, once to determine spring/summer decomposition and once to determine fall/winter decomposition. The first batch of cloths were inserted spring 2002 and removed at the beginning of fall 2002, and the second batch of cloths were inserted fall 2002 and removed at the beginning of spring 2003. Cloths were autoclaved within 1 week of removal, and then cut into 2-cm long strips representing the following depth increments: 0–2, 4–6, 12–14, and 22–24 cm.

Soil chemistry and texture analysis

Analyses for soil texture, organic carbon, and nitrogen were done to determine the influence of each property on SR and decomposition. Soils adjacent to SRCs were sampled for texture, organic carbon, and nitrogen. Soil from the top 50 cm of the soil was used to determine texture and soil from the 0–10 cm section was used for determining organic carbon and nitrogen. Prior to chemical analysis, soil samples from each plot were oven dried, weighed, and passed through a 2 mm sieve and then homogenously split, using a splitter, to obtain a sub-sample.

Soil carbon and nitrogen content were measured using a Leco high-temperature combustion instrument (St George, MI, USA) at the Natural Resource Ecology Laboratory, Colorado State University. Prior to analysis, soils were ground and carbonate was removed by adding 15% HCl solution until effervescence was no longer observed.

Soil texture was determined on a volume percentage basis with a Mastersizer 2000 (Malvern Instruments Ltd., Southborough, MA, USA). The Mastersizer 2000 uses a laser-light scattering method capable of measuring particles between 0.05 and 3480 μm and has an accuracy and reproducibility of ±1%. Prior to analysis, organic matter and carbonates were removed from the soil. Large organic particles were mechanically removed with tweezers, and small particles were removed with the use of a 30% hydrogen peroxide solution. Carbonate was removed with the use of a 15% HCl solution. The Wentworth scale was used to assign each soil sample its class percentage breakdown for sand, silt, and clay.

Continuous monitoring of soil moisture and temperature

Soil moisture and temperature were continuously monitored throughout the study with time-domain reflectometer (TDR). Campbell Scientific (Logan, Utah, USA) soil-moisture (CS 616) and temperature (CS 106) probes were installed to understand how soil texture, depth, temperature, and moisture influence SR and decomposition. These probes were located at the SF transect in soil pits of differing texture at 10 and 30 cm below the surface. One set of probes was installed at the top of the transect where sand makes up 82% of the soil, and one set was located at the bottom of the transect where the soil is 48% sand. A Campbell CR 10× data logger was used to record soil moisture and temperature every 10 min. The moisture probes were calibrated in the lab to known masses, volumes, and soil textures of soil from the SF transect. This calibration was done by adding a known volume of water to the soil and using the change in mass to calculate and record the correct volumetric water content (VWC). The known VWC was compared to the output of the moisture probe, and calibration coefficients were calculated and incorporated into the CR 10× program (Campbell Scientific, Logan, Utah, USA).

Statistical analyses

The Statistica software package (Tulsa, OK, USA) was used for all statistical analyses. Classification and regression-tree analysis (CART) (Breiman et al. 1985; De' Anth and Fabricus 2000) was used for determining the significance of soil texture, organic carbon, nitrogen, moisture, and temperature in relation to SR rate. Classification and regression-tree analysis was chosen because of its ability to reliably deal with auto-correlated data, and because it explains the significant influence of predictor variables based on interactions with the dependent variable. This method uses multiple predictor variables (continuous or categorical) to explain a dependent response variable, in this case SR, by generating an explanatory tree by repeatedly splitting independent variables into dichotomous homogeneous groups. The resulting tree splits (nodes) explain the greatest possible proportion of variance for the dependent-response variable on the basis of predictor variable interactions that predict the dependent variable.

Effects of soil texture, depth, and season on decomposition cloths were evaluated with the use of factorial ANOVA. The occurrence of significant interactions, between effects, was evaluated with Tukey's *post hoc* test for highly significant differences (HSD) at an alpha of 0.05. Prior to the factorial ANOVA analysis, soil-texture groups were determined with classification and regression-tree analysis by using percent loss of cloth tensile strength as the dependent variable and percent soil fine fraction (silt plus clay) as an independent variable. This analysis produced a tree with three non-terminal nodes and four terminal nodes. The mean and maximum decomposition variances within each node were 0.01 and 0.02, respectively. The four terminal nodes were used to demarcate four soil-texture groups and used as categorical factors in the factorial ANOVA analysis of decomposition-cloth tensile strength loss.

Time-domain reflectivity data relative to SR respiration was evaluated on a seasonal basis by using the calendar year as reference. For example, spring occurs from vernal equinox to summer solstice, and fall occurs from autumnal equinox to winter solstice. These demarcations were used to determine the julian days in each season.

Results

Mean monthly SR rates during this study period were generally low, except during March (Figure 1). During May and June the mean monthly SR rate decreased as soil temperature increased and soil moisture decreased. Soil respiration in July was higher than in May and June though mean monthly soil moisture was lowest and temperature was highest. Mean monthly SR rates for the late growing season months of September through November were also lower than in July. However, soil moisture was higher during the late growing season months than in July.
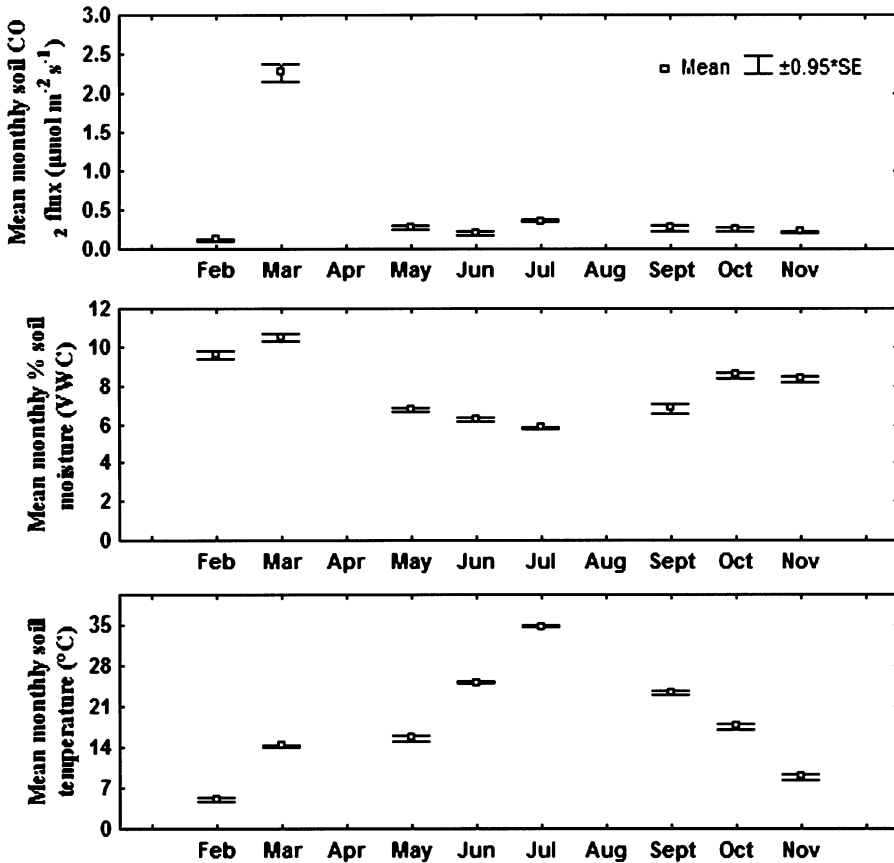
Figure 1. Monthly means for data collected during soil-respiration measurements for both transects combined. Error bars demarcate standard error.

The influence of soil texture, temperature, moisture, organic carbon, and nitrogen on soil respiration

Regression-tree analysis incorporated soil temperature, moisture, percent organic carbon, and percent nitrogen into a descriptive tree model predicting SR rate on the basis of independent variable threshold measures (Figure 2). Regression-tree analysis did not find a correlation between SR and soil texture. This non-correlative result was also verified when tested with simple linear regression. The overall R^2 of this regression tree is 0.47. Soil temperature and moisture explain the greatest amount of variance in SR rate in this model (Table 2). Soil temperature splits the regression tree into left and right branches at a threshold of 15.7 °C. The left branch (starting at node ID #2) incorporates all SR measurements with temperature $\leq$15.7 °C whereas the right branch (starting at node ID #3) consists of all SR measurements with soil temperature > 15.7 °C.
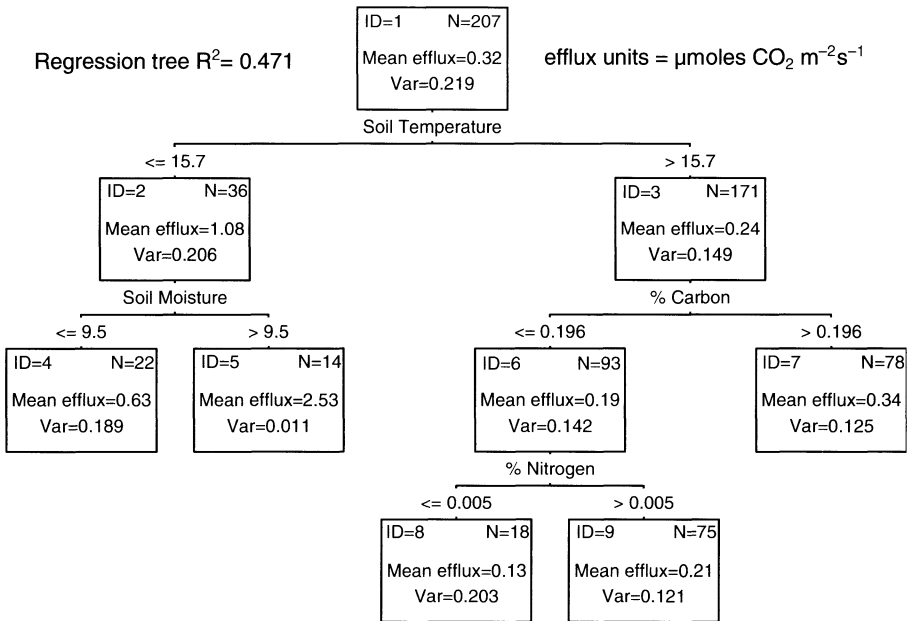
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Figure 2. Regression-tree results. Boxes (nodes) show mean efflux in μmol CO_2 m^{-2} s^{-1}, variance, and number of observations for each node. Horizontal lines below each node demarcate thresholds at which explanatory variables are significant.

Table 2. Results from regression tree analysis. The table shows node p values, R^2s, and regression-line equations for each node.

Node ID #	p	R^2	Regression line equation
2	$p < 0.01$	0.46	$y = -0.65 + 0.15\ (X)$
4	$p < 0.01$	0.43	$y = -3.24 + 51.14\ (X)$
5	$p < 0.01$	0.12	$y = -1.00 + 32.56\ (X)$
3	$p < 0.05$	0.39	$y = 0.20 + 0.01\ (X)$
6	$p < 0.05$	0.38	$y = 0.21 + 0.30\ (X)$
7	$p < 0.05$	0.36	$y = 0.35 + 0.29\ (X)$
8	$p < 0.06$	0.45	$y = 0.25 - 18.77\ (X)$
9	$p < 0.06$	0.35	$y = 0.24 + 1.61\ (X)$

p-values and regression-line equations were obtained with linear regression.

Soil temperature and moisture are the only significant variables within the left branch. This branch has a mean soil CO_2 efflux of 1.08 μmol m^{-2} s^{-1} and is split into left and right nodes (node ID #4 and 5) on the basis of a VWC threshold of 9.5%. The left side of this split (node Id #4) is made up of measurements with a VWC $\leq$ 9.5% and is characterized by an average soil CO_2 efflux of 0.63 μmol m^{-2} s^{-1}, soil temperature of 10.1 °C, and a VWC of 8.2%. Examination of node ID #4 indicates that SR values below 10.5 °C are substantially lower than those with temperature above 10.5 °C. The SR measurements in node ID #4 with temperature < 10.5 °C average 0.157 μmol m^{-2} s^{-1}

with a standard deviation (SD) of 0.81 and those with temperature $> 10.5\ °C$ have an average CO_2 efflux of 1.22 μmol m^{-2} s^{-1} (SD = 0.94). The right node of this split (node ID #5) has a mean SR rate of 2.53 μmol m^{-2} s^{-1}, soil temperature of 14.1 °C, and a VWC measure of 11.6%. All SR measurements within this node have a soil temperature $> 10.5\ °C$.

The right branch of the regression tree (starting at node ID #3) has soil temperature, organic carbon, and nitrogen as significant predictors and consists of 60% summer and 40% fall measurements. Relative to the left branch of the tree, the right branch represents conditions that are 77.4% lower in CO_2 efflux, are 70% warmer, and 50.8% drier. The average SR rate, temperature, and VWC for this branch are 0.24 μmol m^{-2} s^{-1}, 29.9 °C, and 6.3% respectively. This branch is split twice into left and right nodes: first at a threshold of 1.96 g organic carbon per kilogram of soil (node ID #6 and 7) and then at a threshold of 0.05 g nitrogen per kilogram of soil (node ID #8 and 9).

Node ID #6 consists cases having ≤ 1.96 g organic carbon per kilogram of soil and has a mean soil CO_2 efflux of 0.19 μmol m^{-2} s^{-1}. Node ID #7 consists of cases having > 1.96 g organic carbon per kilogram of soil and has an average SR rate of 0.34 μmol m^{-2} s^{-1}, 76.4% higher relative to node ID #6.

Node ID #8 and 9 are made up of cases having ≤ 1.96 g organic carbon per kilogram of soil. Node ID #8 has cases with ≤ 0.05 g nitrogen per kilogram of soil and has a mean CO_2 efflux of 0.13 μmol m^{-2} s^{-1}. Node ID #9 has a mean SR rate of 0.21 μmol m^{-2} s^{-1} and is made up of cases having > 0.05 g nitrogen per kilogram of soil.

Seasonal patterns of soil respiration in relation to soil moisture, temperature, and regression tree results

During the study period, values of soil SR decreased annually from spring to winter. Surface soil moisture and temperature measures for the 0–10 cm interval taken at the time of SR measurements are variable as correlates of SR. Soil CO_2 efflux was highest in the spring (0.91 μmol m^{-2} s^{-1}, SD = 0.99). Mean surface-soil moisture during spring-time SR measurements was 8.6% (SD = 2.0) and average surface-soil temperature was 11.8 °C (SD = 4.1). Average summer SR rate was 0.36 μmol m^{-2} s^{-1} (SD = 0.29). During the summer average surface-soil temperature was highest (34.2 °C, SD = 6.1), and soil-surface moisture was lowest 5.7% (SD = 1.0). Average fall SR rate was 0.24 μmol m^{-2} s^{-1} (SD = 0.13), lower than in summer. This result was surprising considering that the average surface-soil temperature was higher than in spring (15.5 °C, SD = 6.4), and average surface-soil moisture was similar to that of spring-time (8.1%, SD = 1.3). Mean SR rate during winter was lowest (0.09 μmol m^{-2} s^{-1}, SD = 0.10). Mean soil temperature for winter SR measurements was also lowest (5.0 °C, SD = 2.6), but winter soil moisture was highest (9.6%, SD = 1.1), suggesting that SR was limited by temperature during winter.

Continuous monitoring of soil moisture and temperature with the Campbell instruments shows that there are large seasonal differences in the number of days with temperature and soil-moisture suitable for high efflux rates. Data from the Campbell instruments helps explain seasonal SR patterns in relation to the regression-tree results. Winter has the fewest days with soil temperatures > 10.5 °C but has the highest soil moisture (Figure 3 and Table 3). During spring, soil moisture ≥ 9.5% most often coincides with a soil temperature between 10.5 and 15.7 °C, helping explain high flux rates during this season. Soil-climate conditions 30 cm below the surface with soil-moisture > 9.5% and temperature > 10.5 °C occurred more often in summer than fall, but at 10 cm these conditions occurred more often in fall.

Effect of season, soil texture, and soil depth on decomposition and significance of the Inverse Texture Hypothesis

Time domain reflectivity data show that soil-moisture content follows the pattern suggested by the ITH and that soil-moisture recharge occurs during the cooler part of the year as would be expected in a cold desert. At 10 cm below
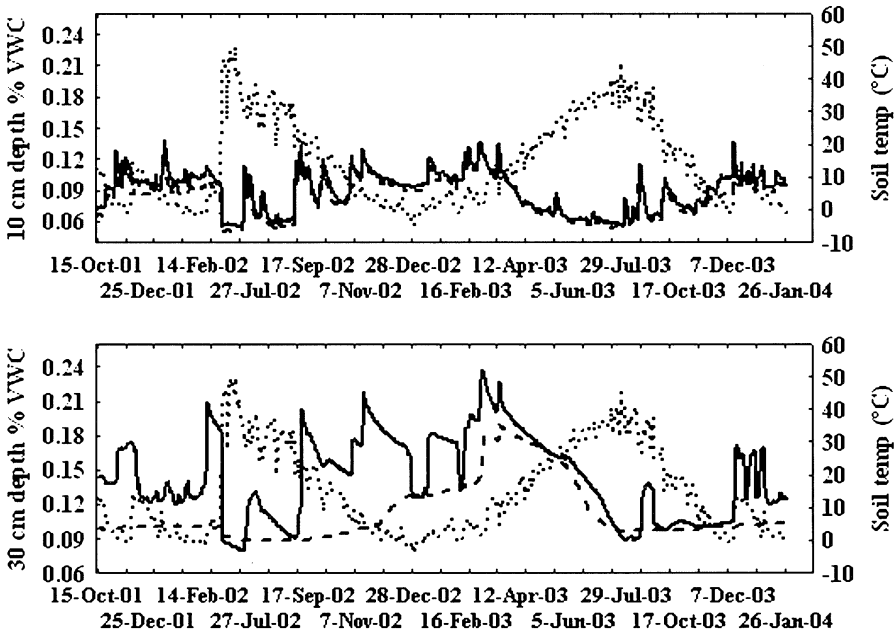

Figure 3. TDR soil-moisture and temperature data for soils at the Squaw Flat site. The top graph shows percent soil moisture (VWC) and temperature in °C at 10 cm below the surface. The bottom graph shows percent soil moisture and temperature at 30 cm below the surface. Both graphs have the same line symbology; (— VWC 82% sand), (- - - VWC 48% sand), (...... soil temperature). Data from March 2002 through June 2002 are not shown.

Table 3. Number of days during which temperature and soil volumetric water content (VWC) regression tree thresholds were met seasonally.

Season	# Days sampled	Soil depth (cm)/ % sand of each installation	Mean % soil VWC	# of days <10.5 °C and > 9.5% VWC	# of days > 10.5 °C and <15.7 °C and > 9.5% VWC	# of days >15.7 °C and > 9.5% VWC
Winter	196	10/80	10.8	147	9	0
		30/80	17.7	187	9	0
		10/50	10.5	89	8	0
		30/50	14.7	187	9	0
Spring	112	10/80	7.4	5	25	23
		30/80	16.7	5	87	72
		10/50	7.26	3	20	19
		30/50	12.9	5	87	72
Summer	182	10/80	7.2	0	6	0
		30/80	11.2	0	91	87
		10/50	6.8	0	9	0
		30/50	8.9	0	52	50
Fall	162	10/80	9.7	84	31	6
		30/80	14.2	123	82	25
		10/50	8.9	56	9	1
		30/50	11.6	120	58	21

Data were obtained from two continuously logging (seasonally averaged) soil-temperature and TDR installations along the SF transect. Each installation had a different percentage of sand. Each installation had a set of instruments at 10 and 30 cm below the surface. Data shown are from October 2001 to January 2004; however, data between March 2002 and June 2002 were not available and as a result number of days sampled for each season are unequal. Demarcations for season are based on the calendar-year equinox and solstice.

the surface, soil moisture is similar in soils composed of 48 and 82% sand, but at 30 cm below the surface moisture is greater in soil with more sand (Figure 3). However, decomposition-cloth experiments indicate that coarse-textured soil did not support higher decomposition activity than fine-textured soil (Table 4).

The factorial ANOVA model used to determine the significance of season, soil depth, and soil texture on decomposition-cloth tensile strength had an overall F-value of 10.06 and a p-value < 0.01. Season, depth, and texture all were significant and each had a p-value of < 0.01 (Table 4). Season had the greatest effect ($F = 96.14$) with the average spring/summer and fall/winter tensile strength losses of 95.7% and 82.7%, respectively. Depth had the second greatest effect ($F = 43.04$). With depth as the effect, the greatest average losses in tensile strength were 95.3 and 95.0% at the depths of 4–6 and 12–14 cm, respectively, followed by 89.6% at a depth of 22–24 cm and 79.9% at a depth of 0–2 cm. Soil texture had the smallest effect on percentage loss of cloth tensile strength ($F = 6.77$). With soil texture as the effect, the highest average loss in tensile strength was 93.22% in soil with the highest amount of soil fines (37–51%). Soil cloths placed in soils with 13–22% fines lost 91.1% of their tensile strength, whereas those placed in soils with 25–35% and 1–10% fines lost 86.9% and 85.6% of their tensile strength, respectively.

The two-way interactions of season-by-soil-depth, season-by-soil-texture, and soil-depth-by-soil-texture were also significant (Table 5). The season and depth interaction had the greatest F-value (12.43), with a $p < 0.01$; season and soil texture exhibited the second largest F-value (8.02) with $p < 0.01$. Depth and texture had the smallest F-value (2.14) with $p < 0.03$.

Effect of a precipitation pulse on soil respiration

Simulated monsoonal precipitation influenced SR for approximately a day and a half. During this wet-up simulation event, VWC increased by 3% in plots A and P and 4% in plot K (Figure 4). However, elevated VWC was short in duration. During the simulation, the rate at which elevated soil-moisture decreased correlated positively to the percent soil fine fraction of each plot. Plot

Table 4. Decomposition-cloth results for factorial ANOVA one-way effects with season, soil depth, and soil texture as categorical variables and percent loss of decomposition-cloth tensile strength (kN) as the dependent variable.

Effect	Spring/ summer	Fall/ winter	Depth 0–2	Depth 4–6	Depth 12–14	Depth 22–24	1–10% Fines	13–22% Fines	25–35% Fines	36–51% Fines
Season	95.7a	82.7b								
Depth			79.9a	95.3b	95.0b	89.6c				
Texture							85.6a	91.1b	86.9a	93.22b

Values with the same letter within an effect have means that are not significantly different according to Tukey's *post hoc* test for HSD.

Table 5. Factorial ANOVA two-way interaction results for decomposition-cloths.

Interaction	F-value	p-value	Spring/summer		Fall/winter	
			Depth (cm)	Loss tensile strength % kN	Depth (cm)	Loss tensile strength % kN
(A) Season× depth	12.43	<0.01	0–2	89.6bc	0–2	64.3d
			4–6	99.2a	4–6	91.6ab
			12–14	97.2ab	12–14	92.8ab
			22–24	96.8ab	22–24	82.4c
			Soil fines % silt + clay		Soil fines % silt + clay	
(B) Season× texture	8.02	<0.01	1–10	96.2a	1–10	75.2c
			13–22	94.4b	13–22	87.5b
			25–35	94.7ab	25–35	79.0c
			37–51	96.7a	37–51	90.0bc

Season and depth as the interaction are shown in the top half (panel A) and season and soil texture as the interaction is shown in the bottom half (panel B). Percent losses with the same letter have means that are not significantly different according to Tukey's *post hoc* test for HSD.

P, which has the finest soil-texture, most rapidly lost soil moisture. Plot A, which has the coarsest soil-texture, relative to plots K and P (Table 1), retained soil-moisture longest. Before soil moisture returned to its pre-moisture addition level, SRCs with added moisture respired the same amount of CO_2 as SRCs without. Plot A, with an intermediate amount of carbon and the lowest nitrogen
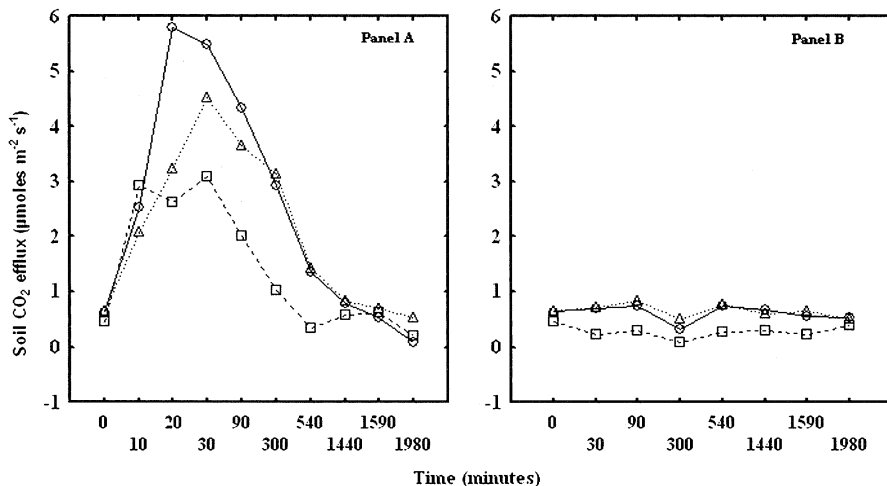

Figure 4. Soil respiration measurements for a 1-cm precipitation simulation. Right panel corresponds to SR measurements for SRCs with added precipitation. Left panel corresponds to SRCs adjacent to panel (A) collars without the addition of precipitation. SR measurements for SRCs in both panels were taken at the same time. Solid line with circle markers is plot (A), dashed line with square markers is plot (K), and dotted line with triangles is plot (P).

relative to the other two plots, respired an extra 1.84 μmol m^{-2} s^{-1} during the simulation. Interestingly, SR in plot A with added water had lower SR than its control SRC at the end of the simulation. Plot K, with the lowest amount of carbon but highest nitrogen, respired an extra 1.11 μmol m^{-2} s^{-1} CO_2 with the addition of water. Plot P, with highest amount of soil carbon and nitrogen similar to that of plot K, respired an additional 1.42 μmol m^{-2} s^{-1} of CO_2.

Discussion

This study shows that temperature and moisture are the dominant abiotic controls on soil respiration at our cold desert study area. These variables do not influence SR in a continuous, predictable way; instead, thresholds determine their influence. The highest CO_2 fluxes occurred when soil temperature was between 10.5 and 15.7 °C, and when volumetric soil moisture was greater than 9.5%. These conditions primarily occurred during the spring. When soil temperature exceeds a threshold of 15.7 °C, SR in this cold desert ecosystem appears to be limited by a combination of high temperature and low moisture. For the set of SR measurements in this study, periods of high temperature generally coincided with periods of low moisture. For much of the summer and fall, average VWC was 6.3%, a level close to hygroscopic conditions for the soils within our study site (Fernandez, unpublished data) and therefore unavailable to microorganisms. At these low-moisture conditions, microorganisms experience dehydration and inhibition of enzyme activity Paul and Clark 1989). This combination of high temperature and low moisture resulted in low fluxes during the summer months.

   Although precipitation pulses help activate biotic processes in this xeric ecosystem, their influence upon SR depends on many factors (Austin et al. 2004). The monsoonal precipitation simulation conducted in July elevated soil CO_2 efflux substantially suggesting that moisture, rather than temperature, is the dominant control on summer-time CO_2 fluxes. This result also illustrates the limitations of regression-tree analysis of seasonal flux data. Additionally, during the wet-up experiment SR declined more rapidly than soil moisture, suggesting that substrate availability influences the duration of CO_2 fluxes. Results from this simulation also suggest that SR in coarse textured soil responds more positively to pulses of monsoonal precipitation than in fine soil. It remains unclear, though, whether the trend observed in the wet-up experiment relates to the dynamics of ITH or is solely an artifact of moisture infiltration. In hindsight, the addition of a second precipitation pulse could have been informative. Given that soil-moisture recharge and SOM inputs occur during the cool season in this region, we could benefit from further research into how pulses of warm-season precipitation affect warm-season SR dynamics.

   Low winter temperatures inhibit fluxes in this setting. The lowest fluxes in this study occurred during winter and fall, despite substantial soil-moisture recharge during this period (CLIM-MET). The seasonal patterns of high

spring fluxes and low summer and fall fluxes appear to be closely related to temperature as well as to the timing and depth of soil-moisture recharge. Time domain reflectrometer profiles show that higher average spring-time soil-moisture levels coincide with a higher percentage of days with temperatures between 10.5 and 15.7 °C (Table 3). During fall, soil-moisture content approaches spring-time values, but cold soil temperatures appear to inhibit SR (Figure 3). These seasonal patterns illustrate the strong interaction between temperature and soil moisture and help explain the threshold responses in respiration observed in this experiment. Decomposition-cloth results, which integrate decomposition processes across several months, support the results of the regression tree generated with soil-respiration data and further illustrate the seasonal patterns of high respiration rates during spring and low rates during summer and fall.

Given the threshold behavior of SR fluxes in this area, it would be reasonable to expect that soil texture would influence SR through its effect on soil-moisture content, with higher rates of emission on sandy soils. As predicted by the inverse texture hypothesis, subsurface soil moisture is higher in sandy vs. finer textured soil; however, these differences in subsurface moisture do not appear to influence SR fluxes.

The results of this study are strikingly different from those drawn from mesic ecosystems where SR fluxes are typically controlled in a continuous manner by soil texture, carbon, and nitrogen, and where fluxes are generally higher under warmer conditions (Schimel et al. 1994). Numerous studies show that soil respiration in mesic ecosystems is generally limited by either low temperature (e,g., Van Cleve et al. 1990; Peterjohn et al. 1994) or by a combination of soil moisture and temperature (Raich and Schlesinger 1992). In hot desert ecosystems it has been observed that SR increases when soil is warm and soil moisture increases. High rates of SR during periods of elevated soil moisture and warm soil temperature have been observed in the Chihuahuan Desert (Parker et al. 1983), northern Arizona (Conant et al. 1998), and northeasten Spain (Casals et al. 2000), regions where soil moisture inputs are greatest during the warm season. These studies contrast with the data presented here, but make clear that the seasonal timing of moisture inputs into xeric systems is likely to be a key control over SR.

Conclusions

This study shows temperature and moisture to be the dominant abiotic controls of soil respiration in the cold desert of southeastern Utah. The threshold behavior of SR observed in this study demonstrates the complexity of predicting fluxes from continuous variables such as temperature, moisture, and edaphic soil characteristics and illustrates the need to better understand SR and decomposition processes in cold-desert environments. Temporal offsets in temperature and moisture conditions appear to play a much stronger role in

the control of soil respiration in cold deserts compared to other ecosystems. For example, when temperatures are most favorable for SR, soil moisture is typically unavailable and does not predict SR. Additionally, when soil moisture and temperature are both favorable, soil organic carbon and nitrogen do not predict SR. Thus, the parameters used to predict soil respiration in mesic ecosystems likely do not apply in predicting soil respiration in cold-desert environments.

Acknowledgements

References

Austin A.T., Yahdjian L., Stark J.M., Belnap J., Porporato A., Norton U., Ravetta D.A. and Scheaffer 2004. Water pulses and biogeochemical cycles in arid and semiarid ecosystems. Oecologia 141: 221–245.

Breiman L., Friedman J.H., Olshen R.A. and Stone C.G. 1985. Classification and Regression Trees. Wadsworth International Group, Belmont, CA, USA.

Carlyle J.C. and Than U. 1988. Abiotic controls of soil respiration beneath an eighteen-year-old *Pinus Radiata* stand in south-eastern Australia. J. Ecol. 76: 654–662.

Casals P., Romanya J., Jordi C., Bottner P., Coûteaux M.M. and Vallejo V.R. 2000. CO_2 efflux from a semi-xeric forest soil. I. Seasonality and effects of stoniness. Biogeochemistry 48: 261–281.

CLIM-MET data obtained from Earth Surface Dynamics Program, U.S. Geological Survey. http://climchange.cr.usgs.gov/info/sw/clim-met/.

Conant R.T., Klopatek J.M., Malin R.C. and Klopatek C.C. 1998. Carbon pools and fluxes along an environmental gradient in northern Arizona. Biogeochemistry 43: 43–61.

De' Ath G. and Fabricus K.E. 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. Ecology 81: 3178–3192.

Dodd M.B. and Lauenroth W.K. 1997. The influence of soil texture on the soil water dynamics and vegetation structure of a short grass steppe ecosystem. Plant Ecol. 133: 13–28.

Epstien H.E., Burke I.C. and Lauenroth W.K. 1997. Effects of temperature and soil texture on ANPP in the US Great Plains. Ecology 78: 2628–2631.

Fang C. and Moncrieff J.B. 2001. The dependence of soil CO_2 efflux on temperature. Soil Biol. Biochem. 33: 155–165.

Jenny H. 1980. The Soil Resource: Origin and Behavior. Springer-Verlag, New York, NY, USA.

Kittel T.G.F., Rosenbloom N.A., Painter T.H., Schimel D.S. and VEMAP participants. 1995. The VEMAP integrated database for modeling United States ecosystem/vegetation sensitivity to climate change. J. Biogeog. 22: 857–862.

Lane D.R., Coffin D.P. and Lauenroth W.K. 2000. Changes in grassland canopy structure across a precipitation gradient. J. Veg. Sci. 11: 359–368.

Lloyd J. and Taylor J.A. 1994. On the temperature dependence of soil respiration. Funct. Ecol. 8: 315–323.

O'Connel A.M. 1990. Microbial decomposition (respiration) of litter in eucalyptus forests of South-Western Australia: an empirical model based on laboratory incubations. Soil Biol. Biochem. 22(2): 153–160.

Neff J.C., Reynolds R.L., Belnap J. and Lamothe P. 2005. Multi-decadal impacts of grazing on soil physical and biogeochemical properties in southeast Utah. Ecol. Appl. 15: 87–95.

Noy-Meir I. 1973. Desert ecosystems: environment and producers. Ann. Rev. Ecolog. Syst. 4: 25–51.

Parker L.W., Miller J., Steinberger Y. and Whitford W.G. 1983. Soil respiration in a Chihuahuan desert rangeland. Soil Biol. Biochem. 15: 303–309.

Parton W.J., Schimel D.S., Cole C.V. and Ojima D.S. 1987. Analysis of Factors controlling soil organic matter levels in the great plains grasslands. Soil Sci. Soc. Am. J. 51: 1173–1179.

Paul E.A. and Clark F.E. 1989. Soil Microbiology and Biochemistry. Academic Press Inc, San Diego, CA, USA.

Peterjohn W.T., Melillo J.M., Steudler P.A., Newkirk K.M., Bowles F.P. and Aber J.D. 1994. Response of trace gas fluxes and N availability to experimentally elevated soil temperatures. Ecol. Appl. 4: 617–625.

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

Raich J.W., Rastetter E.B., Melillo J.M., Kicklighter D.W., Steudler P.A., Peterson A.L., Grace B., Moore III and Vörösmarty C.J. 1991. Potential net primary production in South America: application of a global model. Ecol. Appl. 1: 399–429.

Rastetter E.B., Ryan M.G., Shaver G.R., Melillo J.M., Nadelhoffer K.J., Hobbie J.E. and Aber J.D. 1991. A general biogeochemical model describing the responses of C and N cycles in terrestrial ecosystems to changes in CO_2, climate, and N deposition. Tree Physiol. 9: 101–126.

Sala O.E., Parton W.J., Joyce L.A. and Lauenroth W.K. 1988. Primary production of the central grassland region of the United States. Ecology 69: 40–45.

Schimel D., Stillwell M.A. and Woodmansee R.G. 1985. Biogeochemistry of C, N, and P, in a soil catena of the shortgrass steppe. Ecology 66: 276–282.

Schimel D.S., Brasswell B.H., Holland E.A., McKeown R., Ojima D.S., Painter T.H., Parton W.J. and Townsend A.R. 1994. Climatic, edaphic, and biotic controls over storage and turnover of carbon in soils. Glob. Biogeochem. Cycles 8: 279–273.

Schimel D.S. 1995. Terrestrial ecosystems and the carbon cycle. Global Change Biol. 1: 77–91.

Schwinning S., Starr B.I. and Ehleringer J.R. 2003. Dominant cold desert plants do not partition warm season precipitation by event size. Oecologia 136: 252–260.

U.S. Department of Agriculture Soil Conservation Service 1991. Soil survey of Canyonlands Area, Utah: Parts of Grand and San Juan Counties. United States Department of Agriculture, Natural Resource Conservation Service, Salt Lake City, Utah, USA.

Van Kleve K., Oechel W.C. and Hom J.L. 1990. Response of black spruce (Picea mariana) ecosystems to soil temperature modification in interior Alaska. Can. J. For. Res. 20: 1530–1535.

West N.E., Moore R.T., Valentine K.A., Law L.A., Ogden P.R., Pinkney F.C., Tueller P.T., Robertson J.H. and Beetle A.A. 1972. Galleta: Taxonomy, Ecology, and Management of Hilaria jamesii on Western Rangelands. Utah Agricultural Experimental Station, Utah State University, Logan, Utah.

West N.E. 1981. Nutrient cycling in desert environments. In: Goodall D.W. and Perry R.A. (eds), Xeric-land Ecosystems: Structure, Functioning, and Management, Vol. 2. Cambridge University Press, Cambridge, UK, pp. 301–324.