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Factors Affecting Carbon Dioxide Release from Forest and Rangeland Soils in Northern Utah

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Laboratory and field CO_2 efflux measurements were used to investigate the influence of soil organic C (SOC) decomposability and soil microclimate on summer SOC dynamics in seasonally dry montane forest and rangeland soils at the T.W. Daniel Experimental Forest in northern Utah. Soil respiration, soil temperature, and soil moisture content (SMC) were measured between July and October 2004 and 2005 in 12 control and 12 irrigated plots laid out in a randomized block design in adjacent forest (aspen or conifer) and rangeland (sagebrush [*Artemisia tridentata* Nutt.] or grass–forb) sites. Irrigated plots received a single water addition of 2.5 cm in July 2004 and two additions in July 2005. The SOC decomposability in mineral soil samples (0–10, 10–20, and 20–30 cm) was derived from 10-mo lab incubations. The amount of SOC accumulated in the A horizon (16 Mg ha^{-1}) and the top 1 m (74 Mg ha^{-1}) of the mineral soil did not differ significantly among vegetation type, but upper forest soils tended to contain more decomposable SOC than rangeland soils. The CO_2 efflux measured in the field varied significantly with vegetation cover (aspen > conifer = sagebrush > grass–forb), ranging from 12 kg CO_2–C ha^{-1} d^{-1} in aspen to 5 kg CO_2–C ha^{-1} d^{-1} in the grass–forb sites. It increased (~35%) immediately following water additions, with treatment effects dissipating within 1 wk. Soil temperature and SMC, which were negatively correlated (r = −0.53), together explained ~60% of the variability in summer soil respiration. Our study suggests that vegetation cover influences summer CO_2 efflux rates through its effect on SOC quality and the soil microclimate.

Abbreviations: SMC, soil moisture content; SOC, soil organic carbon.

Soils represent the largest C storage reservoir in terrestrial ecosystems, and soil respiration is a major release mechanism of previously fixed C to the atmosphere (Schlesinger and Andrews, 2000). Changes in the ability of soils to store SOC may have positive or negative feedbacks on atmospheric CO_2 levels (Rustad et al., 2000; Davidson and Janssens, 2006) and can be linked to plant characteristics (De Deyn et al., 2008). Shifts from grass- to tree-dominated systems have been associated with a loss of SOC from the mineral soil (Jackson et al., 2002; Thuille and Schulze, 2006; Risch et al., 2008) as well as with net gains (McCulley et al., 2007; McKinley and Blair, 2008). The efflux of CO_2 from the soil, which is the combination of rhizosphere respiration and microbial decomposition, is controlled by several factors, including temperature (Kätterer et al., 1998), moisture (Davidson et al., 2000; Orchard and Cook, 1983), and substrate quality (Tewary et al., 1982; Rustad et al., 2000; Janssens et al., 2001). Changes in climate and in substrate with different vegetation cover can thus impact SOC dynamics (e.g., De Deyn et al., 2008).

Numerous laboratory and field studies have shown the influence of temperature and soil moisture on soil CO_2 efflux rates from wildland soils (e.g., Lloyd and Taylor, 1994; Emmett et al., 2004). Soil respiration generally increases with temperature (Kätterer et al., 1998; Pietikainen et al., 1999; Rustad et al., 2000), but moisture deficits during the growing season (Vogel et al., 2005; McCulley et al., 2007) or during wetting and drying cycles (Borken et al., 2003) can constrain the temperature response and may account for large differences in soil respiration between wet and dry years (Davidson et al., 2002; Sulzman et al., 2005).

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Organic matter turnover is also affected by vegetation type and substrate quality (e.g., Murphy et al., 1998; Trofymow et al., 2002), often acting in conjunction with climate. Several studies have found differences in soil CO_2 efflux among vegetation types (Raich and Tufekcioglu, 2000; Palmroth et al., 2005) and even under different vegetation covers within the same forest type (Janssens et al., 2001), attributed, in part, to differences in SOC composition as well as to the influence of vegetation on the soil microclimate (Raich and Tufekcioglu, 2000).

Compared with humid forest soils, fewer studies have investigated CO_2 efflux in arid and semiarid ecosystems (i.e., Wildung et al., 1975; Parker et al., 1983; Mielnick and Dugas, 2000; McCulley et al., 2004). Conant et al. (2004) noted that while soil respiration in semiarid systems increases with increasing temperature, soil moisture can override this effect, especially during the dry, warm portion of the year. Similarly, Fernandez et al. (2006) showed soil temperature and moisture to be major abiotic controls of soil respiration in xeric landscapes, with temporal offsets between temperature and moisture optima causing seasonal patterns in respiration.

Relatively little is known about the soil C sink strength and SOC dynamics in montane ecosystems of the semiarid West despite their areal extent (Schimel et al., 2002). In the nonmonsoonal part of the Intermountain West, most precipitation falls as snow, and many biogeochemical processes slow down in summer when moisture is limiting (e.g., Charley, 1977; Burke, 1989). Future climate scenarios for this region predict changes in the precipitation pattern, including reduced snowpack accumulation and duration in the winter and a possible northward movement of monsoonal rains, resulting in greater summer precipitation input (Wagner, 2003). Such changes in site hydrology are likely to alter the SOC dynamics, and potentially more so in some ecosystems than others.

Prior studies of montane forest and rangeland ecosystems at Utah State University's T.W. Daniel Experimental Forest in northern Utah have shown that the presence of trees attenuates summer soil temperature and moisture extremes relative to surrounding grass–forb meadows (Van Miegroet et al., 2000) and that vegetation cover further affects the distribution and the quality of SOC in the mineral soil (Van Miegroet et al., 2005). Thus, the turnover of SOC and its response to climatic drivers are expected to vary spatially within this forest–rangeland mosaic. Our working hypothesis was that in seasonally moisture-limited forest and rangeland soils, small increases in the SMC in summer will stimulate soil respiration, but the response will be vegetation specific and controlled by SOC decomposability. Our objective was to test this hypothesis in adjacent forest (conifer and aspen) and rangeland (grass–forb and sagebrush) ecosystems through a combination of laboratory and field assays.

MATERIALS AND METHODS

Study Site

The T.W. Daniel Experimental Forest is located at an elevation of 2600 m, approximately 30 km northeast of Logan, UT (41.86° N, 111.50° W). The average annual precipitation at the site is 950 mm, 80% as snow. Snowmelt typically occurs from mid-May to mid-June. Monthly rainfall is low between May and October, with the lowest monthly precipitation (<2 cm) typically in July. The mean annual temperature is around 7°C (Scott Jones, unpublished data, 2008). The average low temperature is around −10°C in January; the highest mean monthly temperature (14.5°C) occurs in July (Schimpf et al., 1980; Skujins and Klubek, 1982). Cattle and sheep grazing has occurred since the late 1800s (Schimpf et al., 1980) but has been greatly reduced coincident with fire suppression since 1910 (Wadleigh and Jenkins, 1996). Following an increase in fire frequency during the 1856 to 1909 settlement period, fire frequencies have declined, and there is no evidence of fire in the area since 1910 (Wadleigh and Jenkins, 1996).

Our study was located at and around Sunshine Meadow, a 10-ha fenced research area characterized by similar elevation, aspect, climate, geomorphology, and noncalcareous geology (Van Miegroet et al., 2005). Forested communities include aspen forest (*Populus tremuloides* Michx.) and conifer forest, predominantly Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and subalpine fir [*Abies lasiocarpa* (Hook) Nutt.]. Non-forest communities include open meadows consisting of a mixture of grasses and forbs (here referred to as grass–forb), and areas dominated by sagebrush. The soils in the study area are carbonate free and generally well drained, formed in eolian deposits overlying residuum and colluvium from the Wasatch formation (Tertiary: middle and lower Eocene) dominated by roughly stratified, poorly sorted conglomerate a few hundred meters thick (Dover, 1995).

Experimental Design

In June 2004, 36 plots were laid out in a randomized block design with three blocks per vegetation type (aspen, conifer, sagebrush, and grass–forb). Each block contained three 5- by 5-m plots each surrounded by a >1-m buffer zone, randomly assigned to control, summer irrigation, or future snowmelt treatments. Only the results of control and summer-irrigated plots were used for this study.

Soil Sampling and Classification

One pedon (1 m wide, >1 m deep) was manually excavated at the outside of the center plot in each block (n = 12, three per vegetation type) in summer 2004, described in the field following standard methods (Soil Survey Division Staff, 1993), and classified. Samples from each pedogenic horizon were air dried, sieved (<2 mm), and analyzed for selected physical and chemical characteristics, including total C concentration using a Leco CHN analyzer (CHN 1000, Leco Corp., St. Joseph, MI). Bulk density was determined for each horizon by removing a known volume of soil from the pedon face using a brass ring (50-mm diameter, 50-mm height), oven drying the sample at 105°C, and weighing the coarse (>2-mm) and fine (<2-mm) fractions.

Laboratory Incubation

The SOC decomposability was assessed from long-term aerobic laboratory incubations (Paul et al., 2001) of fresh upper mineral soil samples taken in October 2005 from all control plots (n = 12, three per vegetation type). Several soil cores (0–30 cm) were taken in each plot, cut into three sections (0–10, 10–20, and 20–30 cm), and composited

in the field by plot and depth. Large rock fragments were manually removed from the samples. Approximately 50 g of field-moist soil was placed in a 120-mL cup, brought to 20 to 30% gravimetric soil moisture content (~60% of the water holding capacity) by adding distilled water, and incubated in glass jars for 10 mo at 25°C ($n = 36$ total). Three blanks (incubation jars without soil) were included in the design. The incubation jars were aerated weekly and the soils were periodically weighed and water added to maintain the initial soil moisture contents. Carbon dioxide evolution was measured periodically (biweekly for the first 8 wk, monthly thereafter) using 20 mL of 2 mol L^{-1} NaOH as a trapping agent, followed by backtitration with 2 mol L^{-1} HCl. Pre-incubation subsamples were analyzed for C concentration using a Leco CHN analyzer. All CO_2 release values were expressed on a soil dry-weight basis.

Field Irrigation

Summer irrigation began in the summer of 2004, with the intent of increasing summer precipitation by ~25% in two applications of 2.5 cm each to mimic a monsoonal rainfall pattern. Water was pumped from the irrigation canal at Utah State University's Greenville Farm in Logan into 1600- to 2000-L water tanks, transported by truck to holding tanks at the sites, and pumped through a portable irrigation system onto each irrigation plot at 138 to 165 kPa for ~30 min, delivering ~625 L of water to each plot (McBride, 2006). In 2004, only a single irrigation treatment of 2.5 cm was applied to all vegetation types on 12 to 13 August. In 2005, the plots were irrigated twice (~2.5 cm per irrigation) in the periods 13 to 14 July and 27 to 28 July.

Field Soil Respiration

Soil respiration was measured in all control and irrigation plots in each vegetation type using static chambers (Raich et al., 1990) ($n = 2$ per plot) with NaOH as a trapping agent. Two blanks were located in the buffer zone in each block by covering the soil with plastic underneath the chamber. To avoid a CO_2 flush associated with the soil disturbance and root damage, soil collars were installed at least 2 wk before our first 2004 respiration measurement and left in the field thereafter. At the time of measurement, the collars were removed and 20 mL of 1 mol L^{-1} NaOH was placed inside a circular respiration chamber (height, 23 cm; diameter, 20 cm) for 24 h, followed by backtitration with 1 mol L^{-1} HCl within 2 d. In 2004, measurements were taken 3 d, 20 d, 1 mo, and 2 mo (fall measurement) after irrigation ($n = 4$). Based on the first-year results, respiration was measured 1 d, 7 d, and 11 to 12 d after the first irrigation ($n = 3$) and 1 d, 7 d, 12 to 13 d, and 46 d (fall measurement) after the second irrigation ($n = 4$) in 2005.

Temperature and Moisture

Soil temperature was measured in all control and irrigation plots with Onset Tidbit dataloggers (Onset Computer Corp., Bourne, MA) installed between the 10- and 15-cm depths ($n = 24$). One set of dataloggers was installed in late July 2004 in the control and irrigated plots of one block per vegetation type; the remainder were installed in July 2005. Temperatures were recorded every 1 to 1.5 h.

Temperatures recorded during the 24-h period of respiration measurement were averaged into one temperature value per respiration measurement. Except for those plots where the temperature loggers were installed in 2004, we had no actual temperature data for Day 1 after the first irrigation in 2005. They were estimated from the measured temperature data for that period in the same vegetation type using correlations ($R^2 \geq 0.70$, $P \leq 0.0001$) of available 2004 and 2005 data from plots in the same vegetation type. Due to a download malfunction, the 2005 temperature data were missing from one aspen control plot, and temperatures were estimated from data from the other plot within the same block.

Soil moisture was measured before and after irrigation and during every respiration measurement in 2005 using Decagon ECH_2O probes, Model EC-20 (Decagon Devices, Pullman, WA), installed in July 2005 between the 0- and 20-cm soil depths. Periodic readings were made in the field using a hand-held device (ECH_2O Check, Decagon Devices) and converted to volumetric soil moisture content from vegetation-specific laboratory calibrations. Soil samples collected in each vegetation type ($n = 2$ for each forest type, $n = 1$ for each range type) were placed in polyvinyl chloride collars (4 by 25.1–27.4 cm) with mesh on the bottom (two replicates per soil sample), and subjected to a series of wetting and drying cycles while core weights and ECH_2O readings were recorded. Calibration curves were then constructed for each vegetation type ($R^2 = 0.90$–0.99, $P \leq 0.0001$) and used to convert our field ECH_2O readings into soil moisture contents.

Statistical Analysis

To evaluate the differences in SOC decomposability among vegetation types, cumulative CO_2 release after 150 and 300 d of incubation (absolute and normalized for soil C) was tested using one-way ANOVA for each soil depth (three replicates per vegetation type and soil depth), followed by post hoc means comparisons (Tukey–Kramer), with differences considered statistically significant at $P \leq 0.10$.

The effects of vegetation type, irrigation treatment, and time since irrigation on field respiration were assessed using a three-way factorial design in a mixed model design. The experimental unit for vegetation type was the block, irrigation treatment was assigned to plots nested within blocks, and time since irrigation treatment was a repeated measure on each plot. Post-hoc pairwise comparisons between vegetation means (Tukey–Kramer) were performed with Type I error controlled at $\alpha = 0.10$. To test significant treatment × day interactions, treatment means at each time were compared using multiple *t*-tests, with means adjusted for experimentwise Type I error. In evaluating vegetation and treatment effects, separate analyses were run for 2004, the period following the first irrigation in 2005, and the period following the second irrigation in 2005. In addition, the influence of soil temperature and moisture on soil respiration was assessed using simple correlations (Proc CORR) and nonlinear regressions (Proc REG) applied to the summer 2005 data set across all measurement days and separately by date. For reasons that were not clear, the respiration data from 4 August were not significantly correlated with either temperature or moisture data; therefore, results of the statistical analyses are reported with and without the 4 August data. Finally, we conducted multiple linear regressions (Proc REG) of soil respiration against both temperature and moisture to evaluate their combined effect on soil respiration. For all analyses, the soil respiration data were logarithmically transformed to meet assumptions of normality and homogeneity of variance. In addition, nonlinear regressions across measurement dates also required a logarithmic transformation of the independent variables

(temperature and moisture). All statistical analyses were performed using SAS/STAT Version 9.1 for Windows (SAS Institute, 2003).

RESULTS AND DISCUSSION

Soil Characteristics

Selected physical and chemical soil properties are summarized in Table 1. Vegetation type, especially forest vs. rangeland cover, influenced soil development. Forest soils (aspen and conifer) were classified as fine to coarse-loamy to loamy-skeletal Haplocryalfs, with some pedons in the aspen vegetation type showing mollic characteristics. The temperature regime was classified as cryic and the moisture regime as udic. Rangeland soils (sagebrush and grass–forb) were classified as fine-loamy to loamy-skeletal Haploxeralfs (with one Dystroxerept in the grass–forb vegetation type). These soils were slightly warmer (frigid) and drier (xeric moisture regime).

In all ecosystems, the highest SOC concentrations were measured near the soil surface in the A horizon, and SOC concentrations declined with depth to a low of ~3 g kg^{-1} at around 1 m (Table 1). There was no statistically significant difference among

Table 1. Selected soil physical and chemical properties of mineral soils at the different sites.

Horizon	Depth	Bulk density	Coarse fraction	Texture†	C	N	Field pH
	cm	g cm^{-3}	kg kg^{-1} soil		g kg^{-1} soil		
ASPEN							
Block A, fine-loamy, mixed, superactive Mollic Haplocryalf							
A1	0–8	0.72	0.04	GR L	27.01	2.03	6.5
A2	8–15	0.70	0.04	L	12.00	0.82	6.4
A3	15–33	0.79	0.04	L	9.30	0.55	5.6
ABt	33–50	0.78	0.08	SiL	6.31	0.39	5.5
Bt1	50–76	1.16	0.00	CL	3.20	0.26	5.5
Bt2	76–103	1.04	0.00	CL	2.91	<0.1	5.3
Bt3	103–127	1.04	0.00	C	2.90	<0.1	5.3
Block B, fine-loamy, mixed, superactive Pachic Argicryoll							
A1	0–9	0.82	0.07	L	34.52	2.51	5.8
A2	9–19	0.78	0.04	L	26.76	2.08	5.6
ABt	19–33	0.87	0.05	ST SiL	16.67	1.38	5.6
BAt	33–53	0.75	0.06	VST CL	11.92	0.96	6.0
Bt	58–88	1.11	0.00	CL	4.60	0.22	7.5
Btk	88–105	1.26	0.00	GR CL	12.95	0.29	7.6
Crtk	105–119	1.20	0.00	CL	15.06	0.11	8.1
Block C, coarse-loamy, mixed, superactive Inceptic Haplocryalf							
A1	0–8	0.88	0.58	VGR L	42.08	2.73	6.2
A2	8–18	0.69	0.33	GR L	21.50	1.57	6.2
Bt	18–40	0.82	0.09	GR L	9.30	0.52	5.7
Ab	40–58	0.93	0.36	GR L	8.29	0.58	5.4
BAb	58–80	0.82	0.11	CB L	5.93	0.33	5.0
Bwb	80–114	0.80	0.10	CB SL	3.41	<0.1	4.8
SAGEBRUSH							
Block A, loamy-skeletal, mixed, superactive, frigid Ultic Haploxeralf							
A1	0–8	0.74	0.10	GR SL	42.83	2.78	5.0
A2	8–16	0.79	0.20	SL	31.65	2.25	5.2
BA	16–33	0.80	0.11	L	17.69	1.59	5.2
Bw1	33–47	0.89	0.15	L	13.67	1.33	5.0
Bw2	47–61	0.75	0.07	VCB L	10.02	1.43	4.8
Bt1	61–86	0.99	0.33	XGR L	6.17	0.87	4.6
Bt2	86–105	0.78	0.25	VGR SL	4.07	0.69	4.6
CBt	105–128	ND‡	ND	CB SL	3.40	0.48	4.6
Block B, fine-loamy, mixed, superactive, frigid Ultic Haploxeralf							
A1	0–8	0.81	0.09	GR L	26.64	2.02	5.4
A2	8–21	0.75	0.15	GR SL	14.93	1.47	5.4
Bw1	21–33	0.86	0.03	GR SiL	12.54	1.32	5.4
Bw2	33–48	0.79	0.05	L	11.65	1.31	5.4
Bt1	48–76	0.69	0.04	SiL	11.33	1.29	5.2
Bt2	76–95	0.72	0.10	GR SL	4.55	0.59	4.8
Bt3	95–115	0.94	0.00	CL	3.36	0.46	4.4
Block C, fine-loamy, mixed, superactive, frigid Ultic Haploxeralf							
A1	0–7	0.74	0.19	GR SiL	25.67	2.06	6.2
A2	7–18	0.74	0.25	SiL	18.55	1.52	5.4
A3	18–33	0.80	0.17	SiL	13.77	1.38	5.4
AB	33–46	0.88	0.29	SL	13.40	1.46	5.5
Bw	46–62	0.74	0.08	SL	11.26	1.16	5.2
Bt1	62–73	0.62	0.20	SCL	7.97	0.85	5.3
Bt2	73–89	0.97	0.34	GR SCL	4.22	0.58	5.3
Bt3	89–107	0.95	0.12	SCL	4.09	0.53	5.1
Bt4	107–120	1.00	0.00	SCL	2.99	0.51	4.6

Horizon	Depth	Bulk density	Coarse fraction	Texture†	C	N	Field pH
	cm	g cm^{-3}	kg kg^{-1} soil		g kg^{-1} soil		
CONIFER							
Block A, fine-loamy, mixed, superactive Typic Haplocryalf							
A	3–12	0.77	0.15	L	29.80	0.98	5.2
E	12–22	0.77	0.04	CB L	6.85	0.35	4.8
BEt	22–35	0.94	0.12	VGR CL	5.17	0.15	5.2
Bt1	35–51	0.74	0.26	GR C	4.10	0.18	4.8
Bt2	51–66	1.09	0.00	C	3.32	<0.1	5.2
Bt3	66–84	0.98	0.00	C	2.76	<0.1	4.8
Bt4	84–107	1.18	0.00	C	2.63	<0.1	5.0
BCt	107–124	0.92	0.00	CL	2.87	<0.1	5.2
Block B, loamy-skeletal, mixed, superactive Typic Haplocryalf							
A1	3–10	0.70	0.15	GR SL	49.96	2.70	5.3
A2	10–23	0.83	0.12	GR SL	17.74	0.83	5.2
BA	23–38	0.67	0.18	VCB L	15.11	0.71	5.0
Bt1	38–52	0.86	0.20	GR CL	7.39	0.36	5.2
Bt2	52–76	0.83	0.18	VCB SCL	4.52	0.18	5.2
Bt3	76–98	0.60	0.15	XGR SCL	3.97	< 0.1	5.0
2Bt4	98–112	0.79	0.01	C	3.87	< 0.1	4.4
2Bt5	112–124	ND	ND	GR SCL	3.26	< 0.1	5.1
Block C, fine, mixed, superactive Umbric Haplocryalf							
Oe/A	4–10	0.67	0.11	SiL	52.64	2.93	5.5
A1	10–18	0.80	0.12	VGR SiCL	15.22	0.96	4.8
A2	18–41	0.81	0.14	SiL	11.21	0.57	5.4
Bt1	41–61	1.01	0.01	C	5.33	0.64	5.4
Bt2	61–109	1.15	0.00	C	3.31	0.66	5.3
Bt3	109–125	1.06	0.00	C	2.73	0.40	4.8
GRASS–FORB							
Block A, loamy-skeletal, mixed, superactive, frigid Typic Dystroxerept							
A	0–7	0.91	0.27	VGR SL	17.97	2.36	4.8
E	7–20	0.75	0.15	L	14.70	1.71	4.8
Bt1	20–40	0.77	0.24	L	11.27	1.31	4.6
Bt2	40–57	0.79	0.18	VGR L	9.71	0.96	4.6
Bt3	57–70	0.87	0.19	VCB L	8.39	1.08	5.2
Bt4	70–84	0.70	0.17	VCB L	6.68	0.97	4.8
BCt	84–106	0.70	0.34	VCB SL	4.92	0.77	4.8
C	106–128	0.70	0.53	SL	3.14	0.49	5.2
Block B, fine-loamy, mixed, superactive, frigid Ultic Haploxeralf							
A1	0–10	0.71	0.06	GR SiL	19.60	1.52	5.2
A2	10–20	0.72	0.06	GR SiL	17.07	1.56	5.2
A3	20–33	0.79	0.10	SiL	15.02	1.56	5.0
E	33–45	0.83	0.12	SiL	11.51	1.26	5.0
BEt	45–64	0.82	0.05	CB L	8.53	0.96	5.2
Bt1	64–81	0.89	0.07	CB L	4.99	0.69	4.8
2Bt2	81–100	1.02	0.17	L	3.92	0.54	5.4
2Bt3	100–118	0.94	0.23	CL	3.11	0.50	5.2
2Bt4	118–129	0.94	0.08	CL	2.92	0.43	4.8
Block C, fine-loamy, mixed, superactive, frigid Ultic Haploxeralf							
A1	0–8	0.74	0.16	GR SiL	22.85	1.68	5.6
A2	8–16	0.87	0.11	SiL	17.99	1.55	4.8
A3	16–27	0.91	0.07	GR SiL	12.89	1.41	4.8
Bt1	27–39	0.73	0.19	SiL	11.95	0.54	4.8
Bt2	39–52	0.83	0.04	L	14.26	1.42	5.2
Bt3	52–81	0.88	0.05	CL	4.59	0.54	4.8
2Bt4	81–106	1.08	0.20	SCL	3.59	0.62	4.8
2Bt5	106–135	0.99	0.14	SCL	2.88	0.34	4.8

† C, clay; L, loam; CL, clay loam; SCL, sandy clay loam; SL, sandy loam; SiL, silt loam; CB, cobbly; GR, gravelly; ST, stony; VCB, very cobbly; VGR, very gravelly; VST, very stony; XGR, extremely gravelly.

‡ ND, not determined.

vegetation types in total SOC content in the top 1 m of the mineral soil: 79.1 Mg ha^{-1} for aspen, 63.6 Mg ha^{-1} for conifer, 83.8 Mg ha^{-1} for sagebrush, and 70.2 Mg ha^{-1} for grass–forb (mean = 74.2 ± 18.2 Mg ha^{-1}). The latter value is slightly lower than the 85 Mg ha^{-1} reported earlier for the site (Van Miegroet et al., 2005), but our results were consistent with the previous observation that vegetation type did not significantly affect SOC accumulation in the mineral soil at this site. Even in the top A horizon, where the SOC concentration is highest and vegetation is expected to have the greatest impact on SOC accumulation and C dynamics (Jobbagy and Jackson, 2000; McCulley et al., 2007), we did not detect a significant difference in SOC content among the vegetation types (16.9 Mg ha^{-1} for aspen, 19.1 Mg ha^{-1} for conifer, 16.5 Mg ha^{-1} for sagebrush, 10.9 Mg ha^{-1} for grass–forb; overall mean of 15.9 ± 4.95 Mg ha^{-1}). This is contrary to the observations of McCulley et al. (2004) for semiarid grassland–woodland savannas in Texas, where woodland encroachment was associated with a significant increase in the SOC content in the upper 20 cm of the mineral soil.

Soil Organic Carbon Decomposability

During the laboratory incubations, surficial soils generally released more CO_2 (10 cm > 20 cm, P = 0.0059; 10 cm > 30 cm, P = 0.0014; 20 cm = 30 cm, P = 0.7005), and this depth pattern was especially pronounced in the forest soils (Fig. 1A). After 300 d of incubation, 5.1 g CO_2–C kg^{-1} soil was released from the upper (0–10 cm) conifer soil and 3.8 g CO_2–C kg^{-1} soil from the aspen soil compared with 2.2 and 2.5 g CO_2–C kg^{-1} soil from the sagebrush and grass–forb soils, respectively (Fig. 1A); due to high variability, the differences were nonsignificant (P = 0.105) among vegetation types. At the 10- to 20-cm depth, there was a significant vegetation effect (P = 0.079) associated with greater CO_2–C release from the conifer soils (2.9 g CO_2–C kg^{-1} soil) compared with the other substrate types (1.6–1.8 g CO_2–C kg^{-1} soil), although individual means were not always statistically different. The CO_2 release rates converged among vegetation types (1.5–1.8 g CO_2–C kg^{-1} soil) between the 20- and 30-cm soil depths (P = 0.94). Rate differences and depth patterns among vegetation types partly reflected differences in the soil C concentration (Table 1); therefore, CO_2 release rates were normalized for soil C content to more clearly indicate the relative decomposability of the SOC (Fig. 1B). Although not all differences were statistically significant, our data suggest that the SOC in the conifer soils was turning over more rapidly than the SOC from the other vegetation types (16–20% after 300 d in conifers vs. 8.5–14.5% across other vegetation types and depths). Also, cumulative CO_2–C efflux curves largely overlapped during the first 100 d of incubation (data not shown) and statistically significant differences in daily CO_2–C efflux rates among vegetation types did not emerge until the second half of the incubation (Table 2), suggesting differences in SOC with longer residence time (months

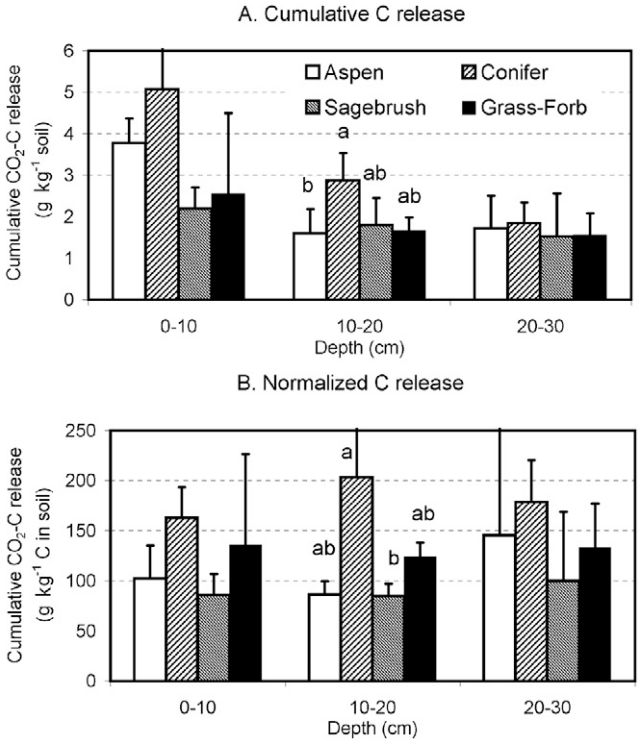

Fig. 1. (A) Total CO_2–C release after 300 d of incubation and (B) cumulative CO_2–C release per unit of C from mineral soils collected under different vegetation types and three soil depths. Error bars represent standard deviations about the mean (n = 3); different letters indicate significant differences between vegetation types for a given soil depth (Tukey–Kramer test, P = 0.10).

Table 2. Average daily CO_2–C release during aerobic incubation of mineral soils taken at various depths under four vegetation types.

Period	Soil depth	Average daily C release rate				P value, vegetation effect
		Aspen	Conifer	Sagebrush	Grass–forb	
d	cm	mg CO_2–C kg^{-1} soil d^{-1}				
0–150	0–10	13.9 ± 6.9	18.7 ± 7.0	8.2 ± 2.9	10.2 ± 6.3	0.230
	10–20	5.3 ± 2.5	8.9 ± 4.5	6.6 ± 1.7	5.9 ± 2.1	0.489
	20–30	3.6 ± 0.4	5.6 ± 1.9	7.5 ± 7.0	7.2 ± 3.7	0.572
150–300	0–10	11.3 ± 2.4 ab†	16.3 ± 5.1 a	6.5 ± 1.0 b	6.9 ± 6.5 ab	**0.076‡**
	10–20	5.2 ± 1.5 b	10.4 ± 3.6 a	5.4 ± 2.4 ab	5.1 ± 0.7 b	**0.062**
	20–30	7.4 ± 4.6	6.8 ± 3.6	3.0 ± 0.5	3.4 ± 1.9	0.360
		Average daily normalized C release rate				
		mg CO_2–C kg^{-1} C d^{-1}				
0–150	0–10	390 ± 246	591 ± 86	320 ± 114	543 ± 290	0.380
	10–20	283 ± 69	652 ± 516	314 ± 43	437 ± 124	0.381
	20–30	274 ± 118	585 ± 294	492 ± 477	610 ± 297	0.526
150–300	0–10	294 ± 32	530 ± 124	253 ± 32	366 ± 306	0.262
	10–20	285 ± 27 b	725 ± 341 a	251 ± 68 b	383 ± 47 ab	**0.039**
	20–30	644 ± 645	627 ± 208	197 ± 39	293 ± 173	0.460

† Means with different letters indicate significant differences among vegetation types for a given soil depth at $P \le 0.10$.

‡ Bold type indicates statistical significance at $P \le 0.10$.

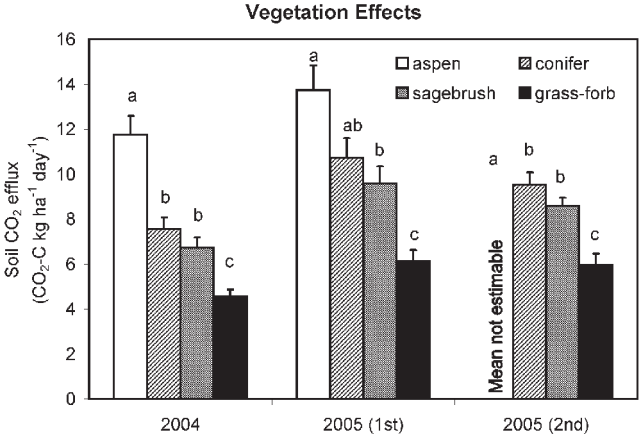

Fig. 2. Mean field respiration rates by vegetation type and treatment period, averaged across control and irrigation plots. Different letters indicate significant differences between vegetation types for each sampling period (Tukey–Kramer test, $P = 0.10$). Due to missing values for Day 1 post-irrigation for aspen in the second treatment period in 2005, the aspen mean for that period could not be estimated.

to a few years) rather than differences in very labile SOC among the vegetation types. We did not observe an initial flush followed by a gradual decline in CO_2 release rates with time as proposed by Paul et al. (2001), so it is possible that we missed some highly decomposable C by starting the incubation between 10 and 14 d after sampling. Nevertheless, our average daily CO_2–C release rates in the upper 10 cm (8.4 mg kg^{-1} soil d^{-1} for grass–forb and 7.2 mg kg^{-1} soil d^{-1} for sagebrush vs. 12.4 mg kg^{-1} soil d^{-1} for aspen and 17.3 mg kg^{-1} soil d^{-1} for conifers) are very close to the average short-term (10-d) C mineralization rates reported in McCulley et al. (2004) in semiarid grasslands (8.0 mg kg^{-1} d^{-1}), woody clusters in grassland (13.8 mg kg^{-1} d^{-1}), and woodlands (14.9–16.8 mg kg^{-1} d^{-1}) in Texas.

Other studies have reported similar differences in SOC decomposability between forest and rangeland soils or among forest types. For example, Ross et al. (1996) found greater C decomposability in montane *Nothofagus* forest soils than in tussock grassland soils, and Kammer et al. (2009) also found greater decomposability of SOC under conifers than in tundra soils in the Ural Mountains. Our findings do not agree with McCulley et al. (2004), who concluded that the SOC in semiarid woody communities was more recalcitrant than that in grasslands. The CO_2 release patterns per unit C for aspen and conifer agree with Giardina et al. (2001), who similarly found during long-term incubations that upper soils under aspen contained SOC that was less mineralizable than the SOC found in pine stands in northern Colorado.

Field Soil Respiration

There were significant differences in the overall soil CO_2 efflux among vegetation types, irrespective of treatment or sampling date (Fig. 2; 2005 first irrigation: $P < 0.0005$; 2004 and 2005 second irrigation: $P < 0.0001$). Consistent with the laboratory assays, the rangeland soils generally emitted less CO_2 in the field than the forest soils. Aspen had the highest CO_2 efflux rates (~12 kg CO_2–C ha^{-1} d^{-1}), grass–forb the lowest (5–6 kg CO_2–C ha^{-1} d^{-1}), while conifer and sagebrush rates were intermediate (7–10 kg CO_2–C ha^{-1} d^{-1}) and not statistically different from one another (Fig. 2).

Adding water in the summer generally increased soil respiration in all ecosystems (Table 3; treatment effect $P < 0.05$ in 2005, nonsignificant in 2004). Treatment effects were not persistent with time, as indicated by the significant treatment × time interaction (2004: $P < 0.10$; 2005 first irrigation: $P < 0.05$; 2005 second irrigation: $P < 0.001$). Immediately after irrigation, there was a significant CO_2 pulse in all sites (~35% increase over control plot values), but differences between irrigation and control were no longer statistically significant within 1 wk of adding 2.5 cm of water. The largest treatment response was observed in the grass–forb and aspen sites, the smallest in the conifer site (Table 3). Such transient response in CO_2 efflux to soil wetting has been reported in the literature for a variety of ecosystems (Illeris et al., 2003; Liu et al., 2002; Lee et al., 2004), and several researchers have suggested that this phenomenon reflects a microbial response to the alleviation of drought stress, leading to an increased turnover of a small labile soil C pool possibly of microbial origin (Fierer and Schimel, 2003; Saetre and Stark, 2005).

Our field respiration rates (50 mg C m^{-2} h^{-1} for aspen, 40 mg C m^{-2} h^{-1} for conifers, 36 mg C m^{-2} h^{-1} for sagebrush, and 24 mg C m^{-2} h^{-1} for grass–forb) are within the range of values measured with similar methodologies in Mediterranean ecosystems in Spain (20–70 mg C m^{-2} h^{-1}, Romanya et al., 2000) and in semiarid systems at similar elevation in Arizona (32–65 mg C m^{-2} h^{-1}, Conant et al., 2000; Kaye and Hart, 1998), but lower than the averages obtained for grassland, scrub clusters, and woodland systems in Texas (80–110 mg C m^{-2} h^{-1}; McCulley et al., 2004, 2007) and for prairie soils in North Dakota (145–180 mg C m^{-2} h^{-1}; Frank et al., 2002) using infrared gas analyzers (IRGAs). Since it has been demonstrated that alkali traps underestimate CO_2 efflux rates relative to IRGA measurements (Kaye and Hart, 1998; Knoepp and Vose, 2002), we compared both techniques on a subset of field measurements in 2006 and concluded that we had accurately captured relative site differences (Van Miegroet, unpublished data, 2006).

Soil Microclimate

Each vegetation type had a distinct soil microclimate in the summer. Based on the summer 2005 data, the grass–forb sites had the highest average soil temperature (17.8 ± 3.4°C), sagebrush and aspen intermediate (14.5 ± 2.6 and 13.1 ± 1.7°C, respectively), while the lowest and temporally least variable soil temperatures were measured under conifer (10.4 ± 1.3°C). Soil temperatures showed the greatest temporal variability in the more exposed grass–forb soils and the least in the forest soils. The moisture data from ECH$_2$O readings in 2005 indicated that volumetric SMC in the forest soils was higher than in the rangeland soils, with conifer soils generally the least dry and the grass–forb soils consistently the driest in summer 2005, even when irrigated (Fig. 3). The observed differences in soil microclimate were consistent with the taxonomic classification (Table 1). In

Table 3. Average field respiration rates in control vs. irrigated plots (n = 3) and for the different measurement periods in 2004 and 2005 in each of the four ecosystems.

Year	Time since irrigation	Treatment†	Respiration rate					*P* value, treatment effect
			Aspen	Conifer	Sagebrush	Grass-Forb	Overall treatment mean	
	d		CO_2–C kg ha^{-1} d^{-1}					
2004	3	C	11.77 ± 2.36	10.85 ± 1.76	8.02 ± 1.30	4.94 ± 0.80	8.43 ± 0.70	**0.0292‡**
		I	17.94 ± 2.91	8.30 ± 1.35	10.78 ± 1.75	8.08 ± 1.31	10.67 ± 0.83	
	20	C	14.93 ± 2.43	11.46 ± 1.86	7.62 ± 1.24	4.63 ± 0.75	8.81 ± 0.69	0.5082
		I	15.90 ± 2.58	9.91 ± 1.61	8.68 ± 1.41	5.74 ± 0.93	9.41 ± 0.74	
	30	C	10.12 ± 1.64	6.79 ± 1.10	4.75 ± 0.77	3.91 ± 0.63	5.98 ± 0.47	0.1790
		I	8.95 ± 1.45	4.00 ± 0.65	5.50 ± 0.89	3.76 ± 0.61	5.22 ± 0.41	
	60	C	8.10 ± 1.62	6.41 ± 1.04	5.56 ± 0.90	3.19 ± 0.52	5.51 ± 0.46	0.6024
		I	9.96 ± 1.62	6.06 ± 0.98	5.01 ± 0.81	3.78 ± 0.61	5.81 ± 0.45	
2005, 1st irrigation	1	C	13.28 ± 1.74	10.81 ± 1.42	9.07 ± 1.19	4.82 ± 0.76	8.90 ± 0.59	**0.0005**
		I	19.10 ± 2.51	13.01 ± 1.71	12.43 ± 1.63	7.34 ± 1.15	12.27 ± 0.82	
	7	C	11.04 ± 1.45	9.63 ± 1.26	9.09 ± 1.19	5.41 ± 0.71	8.50 ± 0.54	0.1363
		I	13.23 ± 1.74	10.75 ± 1.41	8.89 ± 1.17	6.47 ± 0.85	9.51 ± 0.60	
	11	C	12.30 ± 1.61	9.61 ± 1.26	9.80 ± 1.29	5.71 ± 0.75	9.02 ± 0.57	0.1120
		I	14.83 ± 1.95	11.04 ± 1.45	8.75 ± 1.15	7.47 ± 0.98	10.17 ± 0.65	
2005, 2nd irrigation	1	C	11.07 ± 1.27	8.82 ± 0.95	8.31 ± 0.89	4.44 ± 0.48	6.88 ± 0.42§	**0.0003**§
		I	NA¶	10.68 ± 1.15	12.02 ± 1.29	7.81 ± 0.84	10.01 ± 0.61§	
	7	C	13.81 ± 1.58	10.17 ± 1.09	10.37 ± 1.11	7.84 ± 0.84	9.39 ± 0.57	0.2108
		I	13.98 ± 1.60	12.46 ± 1.34	9.24 ± 0.99	9.84 ± 1.25	10.42 ± 0.67	
	12	C	12.94 ± 1.48	11.01 ± 1.18	9.68 ± 1.04	5.47 ± 0.59	8.35 ± 0.51	0.3274
		I	15.96 ± 1.83	11.86 ± 1.27	8.72 ± 0.94	7.14 ± 0.77	9.04 ± 0.55	
	46	C	10.98 ± 1.26	7.12 ± 0.77	6.26 ± 0.67	3.79 ± 0.41	5.53 ± 0.34	0.5925
		I	10.99 ± 1.26	6.18 ± 0.66	5.86 ± 0.63	4.11 ± 0.44	5.30 ± 0.32	

† C, control; I, irrigated.

‡ Bold type indicates statistical significance at $P \leq 0.10$.

§ Significance of treatment effect was tested using treatment × time since irrigation interaction; because Day 1 data were missing for the irrigated aspen plots, aspen data were excluded from this comparison in late 2005.

¶ Means could not be estimated due to missing data.

2005, SMC peaked immediately after irrigation (Fig. 3), coinciding with the peak respiration response (Table 3).

There was a positive correlation between respiration and SMC across the entire summer 2005 data set, or separated by vegetation type (except conifer, which showed no pattern), treatment, or individual measurement date (except 4 August, which showed no statistically significant correlation between respiration and SMC). Soil moisture explained 43 to 52% of the variation in soil respiration on separate measurement days. Across all summer 2005 respiration data, a second-order polynomial ($\ln(\text{Resp}) = 1.459 + 17.921[\ln(\text{SMC})] - 74.308[\ln(\text{SMC})]^2$) explained 29% of the variation in respiration ($P = 0.0002$) and indicated an optimum between 8 and 13% volumetric SMC. Exclusion of the 4 August data increased the explanatory power of SMC to 43% ($P = 0.0001$).

Summer soil respiration was negatively correlated with soil temperature, and this relationship held across the entire data set or when data were separated by treatment or measurement day (except for 4 August). For individual measurement dates, R^2 ranged between 0.45 and 0.68, with respiration rates peaking between 10 and 16°C. Regression analysis of log-transformed respiration rates yielded a second-order polynomial as the best fit ($R^2 = 0.44$, $P < 0.0001$), with an inflection point between 12 and 14°C, and significantly lower soil respiration rates at higher soil temperatures (Fig. 4). There was a slight increase in explanatory power (to 47%) when the 4 August data were excluded ($P < 0.0001$). Not much additional explanatory power could be

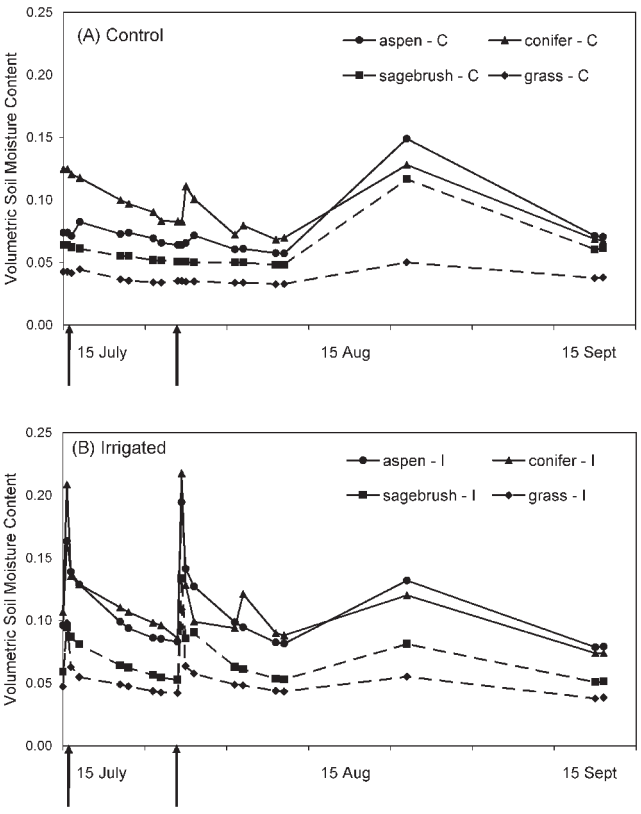

Fig. 3. Volumetric soil moisture content under different vegetation covers in summer 2005 in (A) control plots, and (B) irrigated plots. Solid lines represent forest soils, dashed lines rangeland soils. Arrows indicate dates of irrigation treatment.

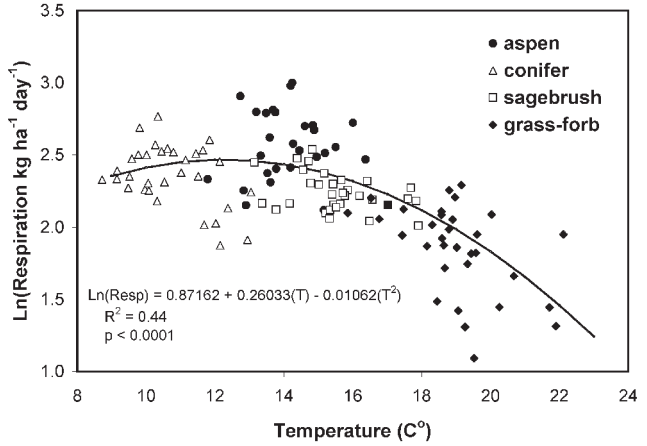

Fig. 4. Relationship between soil respiration across all vegetation types and soil temperatures in summer 2005.

gained by including SMC in a multiple regression, as the combination of temperature and SMC explained 58 to 64% of the variation in the summer 2005 soil respiration rates ($P < 0.0001$) with or without the 4 August data, respectively. This was partly due to the fact that soil temperature and SMC were negatively correlated (Pearson's $r = -0.53$, $P < 0.001$). Individual regressions were thus not true independent evaluations of the effect of either temperature or SMC on soil respiration, but rather various representations of a combined microclimate effect, with the highest respiration rates in cooler, more mesic soils, and respiration rates declining as soils became simultaneously drier and hotter.

What Controls Field Carbon Dioxide Efflux Rates?

The results from our lab and field measurements illustrate the complex interactions among vegetation-dependent differences in SOC decomposability, soil C concentrations, and soil microclimate. Field and laboratory results coincided in indicating lower CO_2 release rates from rangeland than forest soils, (i) because surface soils (0–10 cm) contained less decomposable SOC (the cumulative CO_2 efflux during incubation from rangeland soils [$\sim$2.3 g C kg^{-1} soil] were approximately half those from forest soils [$\sim$4.4 g C kg^{-1} soil], Fig. 1A) and (ii) because hotter, drier soils were less favorable for biological C turnover in the summer (Fig. 4). Within either forest or rangeland soils, field and lab results diverged, suggesting that microclimate was the major driver of soil respiration differences in the field, as the CO_2 release during incubation of surface soils (0–10 cm) was not statistically different within each group (Fig. 1A). Field respiration rates in the conifer soils, which generally had the highest SMC (Fig. 2), did not correlate well with SMC and showed the lowest response to water additions (Table 3), suggesting that SMC was less of a limiting factor to the SOC dynamics than perhaps temperature (which was slightly below optimum, Fig. 4).

For example, if we take the average summer field respiration rates under aspen in 2004 (11.76 kg CO_2–C ha^{-1} d^{-1}) and the first half of 2005 (13.75 kg CO_2–C ha^{-1} d^{-1}) and calculate the expected field CO_2 efflux under conifer based on lower average soil temperatures and applying an increase in the reaction rate with 10° temperature rise (Q_{10}) of 2, we obtain 9.10 kg CO_2–C ha^{-1} d^{-1} for 2004 and 10.75 kg CO_2–C ha^{-1} d^{-1} for 2005, which are close to the measured values of 7.57 and 10.64 kg CO_2–C ha^{-1} d^{-1} for 2004 and 2005, respectively. Likewise, in rangeland soils we can calculate a relative down-regulation of field respiration rates under grass–forb relative to sagebrush soils due to lower SMC. If summer field respiration rates in sagebrush soils (6.72, 9.6, and 8.6 kg CO_2–C ha^{-1} d^{-1} in 2004, the first period in 2005, and the second period in 2005, respectively) are divided by an average SMC ratio between sagebrush and grass–forb soils of $\sim$1.55, we obtain average CO_2 efflux rates from grass–forb of 4.34 kg CO_2–C ha^{-1} d^{-1} in 2004, 6.21 kg CO_2–C ha^{-1} d^{-1} in the first period of 2005, and 5.56 kg CO_2–C ha^{-1} d^{-1} in the second period of 2005, which again are similar to measured rates (4.56, 6.12, and 5.98 kg CO_2–C ha^{-1} d^{-1}, respectively). These findings suggest that field respiration rates in our study were controlled by a complex interaction between SOC quality and soil microclimate. Differences in the amount of decomposable SOC among vegetation types (forest > rangeland) were further modified by microclimate to create differences in soil respiration among and within vegetation types. Microclimatic controls may differ among vegetation types, however: temperature in the more mesic forest soils, SMC in the xeric rangeland soils. Another possible explanation for the lower field respiration and the limited irrigation response in the conifer forest soils compared with aspen could also lie in the presence of a thick O horizon, which may have absorbed some of the added water and reduced CO_2 diffusion out of the mineral soil.

The differences between field and lab respiration rates could also reflect different sources of CO_2. In this study, we were not able to separate microbial decomposition from root respiration in the field. Given that the latter may account for as little as 10% and as much as 80% of the total soil respiration (Hanson et al., 2000; Bond-Lamberty et al., 2004), applying an average ratio of 1 between heterotrophic and autotrophic respiration to all sites would not have fundamentally changed our interpretation. Furthermore, Högberg and Read (2006) recently argued that such separation is not meaningful because roots and microorganisms form a functional continuum. Finally, the wetting front could not penetrate very deeply into the soil ($\sim$5 cm at 50% pore volume), probably not reaching most of the active roots. We thus attributed most of the respiration response to heterotrophic processes, as also suggested by Fierer and Schimel (2003) and Saetre and Stark (2005).

Collectively, these findings suggest that at our site, changes in summer precipitation are more likely to elicit an immediate but short-term response in rangeland soils. Yet a prolonged response of these ecosystems may be limited by low SOC decomposability. Other studies have found lower respiration responses to wetting in grassland ecosystems compared with soils beneath woody canopies (Fierer and Schimel, 2002; Saetre and Stark, 2005), but it is not clear whether this was due to a depletion of readily decomposable substrate in soils subjected to more frequent wetting and drying cycles or to a shift toward more drought-resistant mi-

crobes. Conifer forest soils, on the other hand, are expected to be less responsive to small changes in summer precipitation but may instead be more sensitive to temperature increases.

CONCLUSIONS

The combination of laboratory and field respiration measurements and summer microclimate data give us some insight into the complex interactions between SOC quality and microclimate in controlling soil CO_2 efflux rates in these seasonally dry forest and rangeland soils and the critical role of vegetation as the driver of physical and biological soil characteristics. Forest soils tend to emit more CO_2 in the summer compared with adjacent rangeland soils because they contain more decomposable SOC near the soil surface and because the soil microclimate is more favorable for C turnover. Within forest and range soils, subtle differences in the soil microclimate can override or amplify intrinsic differences in SOC quality. Summer soil moisture and temperature regimes in these soils are not entirely independent and both appear to control soil respiration. A positive response of soil respiration to temperature is only expected above a certain threshold SMC. Likewise, increases in summer precipitation are likely to accelerate soil CO_2 efflux in these ecosystems, but the magnitude and the longevity of the response will probably depend on the decomposability of the SOC currently stored in these systems and the rate at which labile C is being depleted, as well as the combination of soil temperature and moisture regimes. Furthermore, predictions of respiration rates under future summer precipitation scenarios need to account for the transient and diminishing response of soil respiration to soil wetting so as to not overestimate the annual CO_2 efflux rates. Our study suggests that accurately modeling the effect of future climate change on soil CO_2 efflux patterns in these systems will be a complex task, as the changing role of SOC quality, SMC, and soil temperature in controlling soil respiration needs to be incorporated.

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