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Michael C. Amacher

US Forest Service, Rocky Mountain Research Station

Cheryl L. Mackowiak

North Florida Research and Education Center, University of Florida

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Cover Page Footnote

In Monaco, T.A. et al. comps. 2011. Proceedings – Threats to Shrubland Ecosystem Integrity; 2010 May 18-20; Logan, UT. Natural Resources and Environmental Issues, Volume XVII. S.J. and Jessie E. Quinney Natural Resources Research Library, Logan Utah, USA.

Seasonal Soil CO₂ Flux Under Big Sagebrush (*Artemisia tridentata* Nutt.)

Michael C. Amacher US Forest Service, Rocky Mountain Research Station, Logan, Utah; and **Cheryl L. Mackowiak** North Florida Research and Education Center, University of Florida, Quincy, Florida

ABSTRACT

*Soil respiration is a major contributor to atmospheric CO₂, but accurate landscape-scale estimates of soil CO₂ flux for many ecosystems including shrublands have yet to be established. We began a project to measure, with high spatial and temporal resolution, soil CO₂ flux in a stand (11 x 25 m area) of big sagebrush (*Artemisia tridentata* Nutt.) at the Logan, Utah, Forestry Sciences Laboratory. Beginning on Nov. 1, 2009, hourly soil CO₂ flux measurements were made at a single location in the stand using the Li-Cor LI-8100 soil CO₂ flux instrument and 20-cm long-term chamber. Beginning in April, 2010, monthly soil CO₂ flux measurements were made on a grid of 11 locations within the stand using the LI-8100 equipped with the 20-cm survey chamber. Hourly soil temperature (10-cm depth) and volumetric soil water content data were also collected. Soil CO₂ flux, temperature, and water content were highly temporally and spatially variable in the sagebrush stand. Mean (std dev) soil CO₂ flux, temperature, and water content for the measurement period (November 1, 2009 - October 31, 2010) were 0.96 (0.81) $\mu\text{mol m}^{-2} \text{s}^{-1}$, 10.59 (10.11) deg C, and 0.101 (0.062) $\text{m}^3 \text{m}^{-3}$, respectively. Calculated annual soil CO₂ flux obtained by summing all the hourly measurements was 328 g C $\text{m}^{-2} \text{y}^{-1}$. For semi-arid or arid sites where precipitation is less than evapotranspiration, measured total annual soil CO₂ flux will be less than the potential maximum because of dry season suppression of soil respiration when soil water content is very low.*

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INTRODUCTION

Potential changes in the global climate are closely linked with changes in the global carbon (C) cycle (Denman and others 2007). An important part of that cycle is soil respiration returning CO₂ to the atmosphere. Autotrophic (e.g., plant roots) and heterotrophic (e.g., soil microbes) respiration in soils is a major contributor to atmospheric CO₂ and the predominant one in terrestrial ecosystems. Many factors contribute to the high spatial and temporal variability of soil respiration. In the local soil environment, temperature, water content, porosity, atmospheric pressure fluctuations, and substrate quantity and composition control soil CO₂ flux with the atmosphere. At broader landscape scales, soil CO₂ flux varies with overlying plant community types (primary productivity), regional climate, topographic (elevation, aspect) gradients, and geographic (latitude, longitude) gradients that reflect climatic variation. Although soil CO₂ flux data are now available for many biomes (Bahn and others 2010), accurate landscape-scale estimates of soil CO₂ flux

for many ecosystems, including some important shrublands, have yet to be established.

Accurate soil CO₂ flux measurements require costly instrumentation (e.g., Li-Cor LI-8100). To get an accurate annual total soil CO₂ flux at a site, frequent measurements are needed. To obtain accurate landscape-scale estimates of annual total soil CO₂ flux, adequate spatial coverage is needed. Cost constraints and trade-offs between spatial and temporal resolution (Savage and Davidson 2003) drive attempts to find proxies for estimating total annual soil respiration. Examples of such proxy data sets include air temperature and precipitation (Raich and others 2002), litterfall (Davidson and others 2002), primary productivity (Bahn and others 2008), and soil respiration at mean annual temperature (MAT) (Bahn and others 2010).

Big sagebrush (*Artemisia tridentata* Nutt.) is one of the most common and widespread shrub species in the Interior West (McArthur 2000). Given the relatively large land area (50 to 54 million ha as estimated by McArthur and Ott 1996) of sagebrush-dominated

ecosystems, soils under sagebrush may be a large yet relatively unknown contributor to annual soil CO₂ fluxes in the Interior West. To provide some guidance on the spatial and temporal scales needed to more fully characterize soil respiration under big sagebrush, we began a project to measure soil CO₂ flux, temperature, and water content with a high degree of temporal and spatial resolution. Our objectives were to 1) characterize soil respiration under big sagebrush at multiple temporal scales, 2) determine local-scale spatial variability, 3) quantify relationships of soil temperature and water content to soil respiration, and 4) determine N and C substrate limitations on soil microbial respiration.

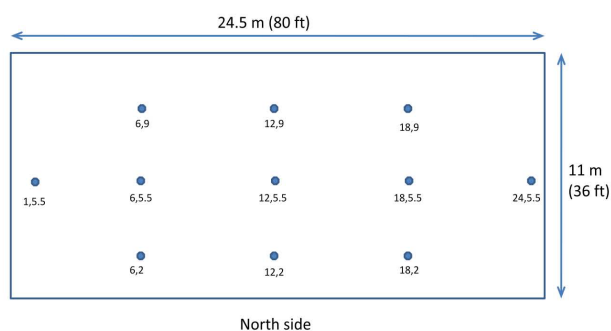


Figure 1. Map of sample points in the sagebrush stand at the Logan Forestry Sciences Laboratory. Numbers refer to distance (m) west and south from lower left corner.

MATERIALS AND METHODS

The sagebrush stand studied (latitude 41° 44.815', longitude 111° 48.453', elevation 1450 m) is on level land at the Logan Forestry Sciences Laboratory (FSL). The Logan FSL is on the ancient Lake Bonneville bench (Provo level) on the west side of the Bear River Range on the eastern edge of the Great Basin. Mean annual air temperature is 8.9 deg C and mean annual precipitation is 450 mm (1893-2005) (data from Utah State University Climate Center). The stand measures 11 m x 25 m (0.0275 ha) and was planted in the mid-1990s in a site formerly occupied by desert wheatgrass (*Agropyron desertorum* (Fisch. ex Link) Schult.). Today the site consists entirely of a closed (no significant gaps) big sagebrush canopy (0.5 to 2 m height) with some minor forb and grass (chiefly cheatgrass (*Bromus tectorum* L.)) components along the edges.

A grid of 11 sample points was established within the stand for soil core sampling and soil respiration

measurements under the sagebrush canopy (figure 1). A PVC soil respiration collar (20-cm diameter x 11.5-cm in height) was installed adjacent to each sample point leaving about half the collar height above ground. The above-ground median height of each soil collar (known as the chamber offset) was determined by measuring the soil collar height at the north, south, east, and west edges and in the middle (from soil surface to a straight edge placed across the top of the soil collar) and taking the median of the 5 readings.

Temporal Soil CO₂ Flux

To measure temporal variability of soil CO₂ flux, the Li-Cor LI-8100-104 long-term chamber (Li-Cor, Lincoln, Nebraska) was installed at the west end of the sagebrush stand with the collar under the sagebrush canopy. The long-term chamber was connected to the LI-8100 automated control unit (ACU), which houses the infra-red gas analyzer (IRGA) that measures changing CO₂ efflux from the soil. The ACU was housed in an instrument shelter. The system was powered by three 98 A/hr Pb-acid gel-cell batteries connected in series. These were re-charged with two 40-watt solar panels.

Beginning at midnight on November 1, 2009, hourly soil CO₂ flux readings were collected for an entire year and continue to be collected. There were some brief periods (from hours up to about 2 days) during winter months when solar re-charge was insufficient to power the system. In such cases, we waited until battery re-charge was sufficient to operate the system. Occasional data gaps during summer months (up to 2 days) were due to operation of the LI-8100 with the survey chamber at other forest, shrub, and meadow ecosystems. In all, 7211 hourly readings were collected from November 1, 2009 through October 31, 2010. The IRGA was calibrated monthly using zero air (zero CO₂ and H₂O content) for baseline calibration and 1000 umol CO₂/mol air for the span calibration. Drift was typically less than 5 umol/mol CO₂ per month.

Annual total soil CO₂ flux was obtained by summing all the measured and interpolated (for missing values) hourly values from November 1, 2009 through

October 31, 2010. To obtain this value, total values for each hour were calculated by multiplying the LI-8100-calculated soil CO₂ flux in $\mu\text{mol CO}_2 \text{ flux m}^{-2} \text{ s}^{-2}$ by 3600 seconds in an hour. Then after summing all the measured and interpolated hourly values, total $\mu\text{mol of CO}_2$ for the year was converted into the more commonly reported grams of C.

Ancillary soil temperature and soil moisture data also were collected on an hourly basis during long-term chamber operation. Soil temperature at 5-cm depth was collected with the soil temperature probe included with the LI-8100. A separate channel logged soil temperature at a 10-cm depth using a thermistor connected to the LI-8100 interface box. Volumetric soil moisture content (8-cm depth) was measured with a Delta-T ML2x thetaprobe (frequency domain type capacitance sensor) connected to the LI-8100 interface box.

Spatial Soil CO₂ Flux

Spatial soil CO₂ flux was measured monthly at all 11 soil collars beginning in April, 2009 using the LI-8100 20-cm survey chamber and ACU. Soil temperature (5-cm depth) and soil moisture (8-cm depth) were also measured adjacent to the spatially distributed collars.

Soil Sampling and Characterization

Soil cores (5-cm diameter x 10-cm depth) were collected at each sample point in November, 2009 to provide soil characterization information. Soil probe (1-cm diameter x 10-cm depth) samples were collected monthly on days when survey-chamber soil CO₂ fluxes were measured.

Soil cores were air-dried at ambient temperature. A subsample was analyzed for gravimetric residual moisture content by oven-drying at 105 C and soil-core bulk density was calculated. The air-dried soil samples were then sieved through a 2-mm stainless-steel screen and the less-than and greater-than 2-mm fractions were weighed. The <2-mm fraction was analyzed for particle-size distribution (sand, silt, and clay) (Klute 1986), soil pH, total organic and inorganic C and total N by Leco TruSpec and RC-412 combustion analyzers, and 2 M KCl-extractable NH₄-N and NO₃-N by flow-injection colorimetric analysis (Sparks 1996).

Microbial Respiration by BD Oxygen Biosensor (BDOBS)

Oxygen consumption by native soil microbes was measured with a 96-well microplate platform containing an O₂-sensitive fluorophore (4,7-diphenyl-1,10-phenanthroline ruthenium chloride) in a silicone gel matrix permeable to O₂ (BD Biosciences, Franklin Lakes, New Jersey). The fluorescence of the ruthenium dye is quenched by O₂. The fluorescence signal from the fluorophore-gel complex embedded in the bottom of microplate wells increases in response to respiration (O₂ consumption) in overlying microbial samples (e.g., soil slurries). Results are expressed in normalized relative fluorescence units (NRFU) calculated as the ratio of fluorescence of soil sample plus any amendments in each well to the fluorescence of each empty well. Microbial respiration in response to nutrient limitations, substrate composition, or other environmental influences can be measured with this method. In this study, microbial respiration in soil slurries (1: 2.5 ratio of soil to sterile deionized water) was measured. Microbial response to added N (10 mg/L NH₄-N from (NH₄)₂SO₄), C substrate (50 mg/L C from glucose), and added N + C was also measured (Zabaloy and others 2008). Control wells contained amendment solutions (sterile deionized water, (NH₄)₂SO₄, glucose) but no soil.

RESULTS

Soil Characteristics

The top 10 cm of soil under the sagebrush stand is sandy with about 20 percent coarse fragment content (table 1). The bulk density is considered optimal for growing plants. This soil is highly calcareous with a strongly alkaline pH and total inorganic C (from carbonates) exceeds total organic C. At the end of the growing season in November, the soil had concentrations of available N below 10 mg kg⁻¹, mostly as NO₃-N.

Hourly Soil CO₂ Flux, Temperature, and Water Content

Early November, 2009, was relatively warm and dry and hourly soil CO₂ flux generally exceeded 0.5 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ (figure 2). In late November the top 10 cm of soil began to freeze (soil temp decreased to about 0 deg C), soil water content decreased as free water in the soil profile froze, and soil CO₂ flux decreased overall. The top 10 cm of soil remained frozen throughout December, January, and February, and soil respiration slowly declined and eventually ceased

when no measureable soil respiration was recorded throughout February. In early March, soil water content sharply increased as the soil surface began to thaw, although overall surface soil temperature remained at freezing. A corresponding large increase in soil CO₂ flux was associated with soil surface thawing. Throughout spring, soil water content remained high via replenishment from spring storms. As the soil slowly warmed, hourly soil CO₂ flux generally increased, but hourly flux showed large changes on most days. With arrival of the dry season in July, soil temperature continued to warm, but soil water content decreased substantially. Soil CO₂ flux decreased along with the decreasing soil water content. Major storms in mid-June, early September, and mid and late October produced large increases in soil water content and attendant pulses of soil respiration. Annual total soil CO₂ flux obtained by summing all the measured and interpolated (for missing values) hourly values was 328 g C m⁻² y⁻¹.

Table 1. Physical and chemical properties of the sagebrush stand soil (0-10 cm). Values shown are the means ± std errs of 11 soil cores collected at the sample points shown in figure 1.

Soil property	mean ± std err
Bulk density, g/cm ³	1.28 ± 0.05
Coarse fragments, %	20.0 ± 1.8
Sand, %	58.7 ± 2.3
Silt, %	30.3 ± 1.8
Clay, %	11.0 ± 0.7
Soil pH	7.80 ± 0.03
Total organic C, %	1.97 ± 0.13
Total inorganic C, %	2.95 ± 0.17
Total C, %	4.92 ± 0.16
Total N, %	0.151 ± 0.012
2 M KCl-extractable NH ₄ -N, mg/kg	2.2 ± 0.5
2 M KCl-extractable NO ₃ -N, mg/kg	6.3 ± 2.9

Daily Mean Soil CO₂ Flux, Temperature, and Water Content

Hourly soil CO₂ flux can be highly variable throughout any given day (figure 2) and tend to be more erratic than soil temperature which is associated with daytime heating and nighttime cooling. To dampen the amplitude of the measured quantities versus time plots, daily mean ± std err values of soil CO₂ flux, temperature, and water content were calculated (figure 3). Day to day changes throughout the seasons are more easily discerned with daily means plots. Daily mean soil CO₂ flux ceased (February) after the soil was frozen for an extended period (December through February). Soil CO₂ flux increased linearly with soil temperature during the spring and early summer up to about 20 deg C, but then decreased with continued soil warming as soil

drying occurred (figure 4). Thus a peak shaped distribution relationship between soil CO₂ flux and soil temperature was found.

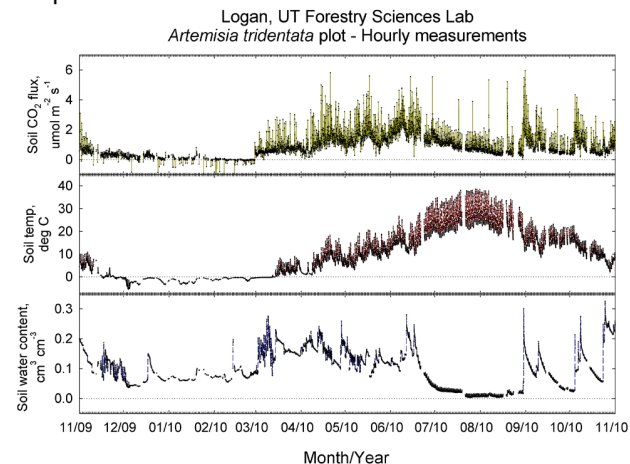


Figure 2. Hourly soil CO₂ flux (top), temperature (middle), and water content (bottom) from November 1, 2009 through October 31, 2010 in a sagebrush stand at the Logan Forestry Sciences Laboratory.

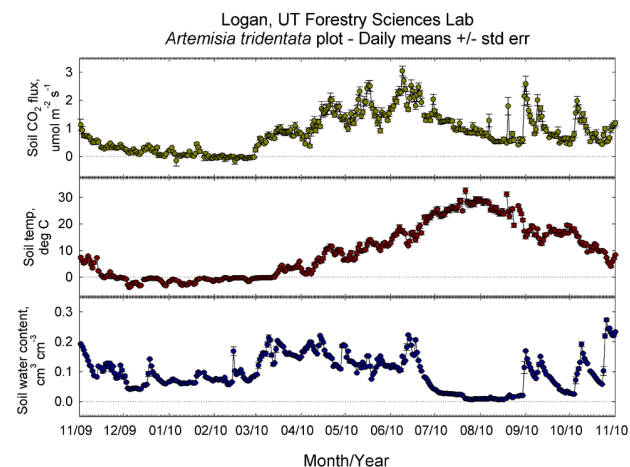


Figure 3. Daily mean ± std err soil CO₂ flux (top), temperature (middle), and water content (bottom) from November 1, 2009, through October 31, 2010, in a sagebrush stand at the Logan Forestry Sciences Laboratory.

The relationship between soil CO₂ flux and soil water content is more complex. In general, soil respiration was greater with increasing soil moisture (figure 4), but there was a hysteresis effect. Pulses of CO₂ flux were seen during and immediately after passing rainstorms (e.g., mid-June, early September, mid and late October) as soil microbial activity was stimulated (figure 3). As the soil dried, soil respiration again decreased. At times, soil water content during wetting had a different associated soil CO₂ flux value than soil CO₂ flux at the same numerical water content value during drying.

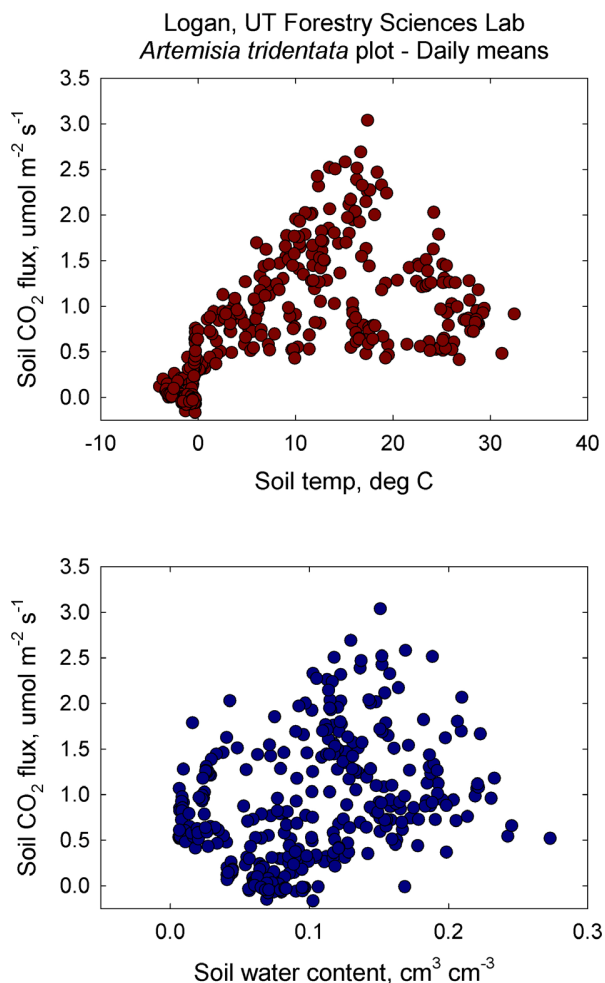


Figure 4. Relationship between daily mean soil CO₂ flux and daily mean soil temperature (top) and between daily mean soil CO₂ flux and daily mean soil water content (bottom) from November 1, 2009, through October 31, 2010, in a sagebrush stand at the Logan Forestry Sciences Laboratory.

Monthly Mean Soil CO₂ Flux, Temperature, and Water Content

Seasonal changes in mean soil CO₂ flux, temperature, and water content are apparent in the monthly mean plots (figure 5). Even though July and August mean soil temperatures were higher than that in June, soil CO₂ flux was less because the soil was drier. The soil remained frozen throughout December, January, and February in the 2009-2010 winter season with no significant thaw period. As a result, mean soil CO₂ flux entirely ceased during February. Thus, a two-month lag was observed between onset of soil freezing and cessation of measurable soil respiration.

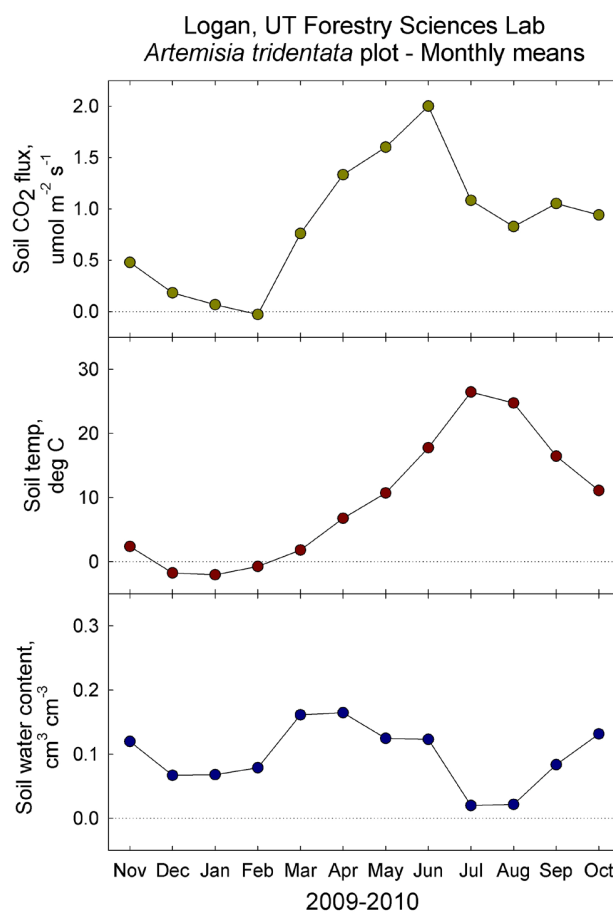


Figure 5. Monthly mean \pm std err soil CO₂ flux (top), temperature (middle), and water content (bottom) from November, 2009, through October, 2010, in a sagebrush stand at the Logan Forestry Sciences Laboratory.

Seasonal Mean Soil CO₂ Flux, Temperature, and Water Content

Mean nighttime soil CO₂ fluxes were slightly less (0.05 to 0.16 umol CO₂ m⁻² s⁻¹) than those during daylight hours during fall and winter (table 2). During spring and summer, mean nighttime soil CO₂ flux averaged about 0.35 umol CO₂ m⁻² s⁻¹ less than the daytime mean. Nighttime soil CO₂ flux averaged 78, 82, 78, and 72 percent of daytime values for the fall, winter, spring, and summer seasons, respectively. The decrease in nighttime CO₂ flux compared to daytime was probably related to soil temperature differences since there was no difference in mean soil water content between daylight and nighttime hours. Daytime and nighttime soil temperature contrasts in terms of absolute temperature differences were greater in spring, summer, and fall than in winter (1.2 to 1.5 deg C in spring, summer, and fall versus only 0.3 deg C in winter). On a relative basis, nighttime soil

temperatures averaged 82, 63, 85, and 94 percent of daytime values for the fall, winter, spring, and summer seasons, respectively.

Overall, mean soil CO₂ flux under sagebrush was found to be highest during the spring when the soil water content was relatively high and the soil temperature was high enough to promote root respiration and vigorous soil microbial activity in terms of organic substrate decomposition (table 3). Mean soil temperature more than doubled in summer compared to spring, but mean soil water content was less than a third as much leading to a significant decrease in mean soil respiration.

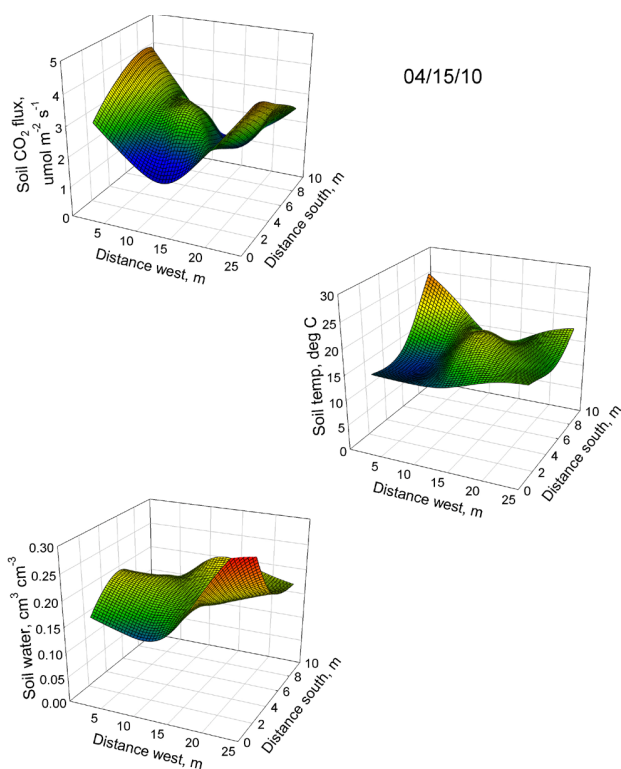


Figure 6. Spatial distribution of soil CO₂ flux (top), temperature (middle), and water content (bottom) on April 15, 2010, in a sagebrush stand at the Logan Forestry Sciences Laboratory.

Spatial Distribution of Soil CO₂ Flux, Temperature, and Water Content

Soil CO₂ flux, temperature, and water content were spatially variable within the 11 x 25 m sagebrush stand and the extent and complexity of spatial variability changed with the seasons (figures 6 and 7). In the spring (e.g., on April 15, 2010), soil respiration was highest at the east and west ends of the stand, soil temperature was highest in the

southeast corner, and soil water content was highest in the northwest corner. In the summer (e.g., on August 16, 2010), soil respiration tended to be uniformly low, soil temperatures were high throughout the plot, and soil water content was low throughout the plot. Overall, the west side of the stand was wettest during spring months, but during the summer, the east side tended to remain the wettest as the west side dried.

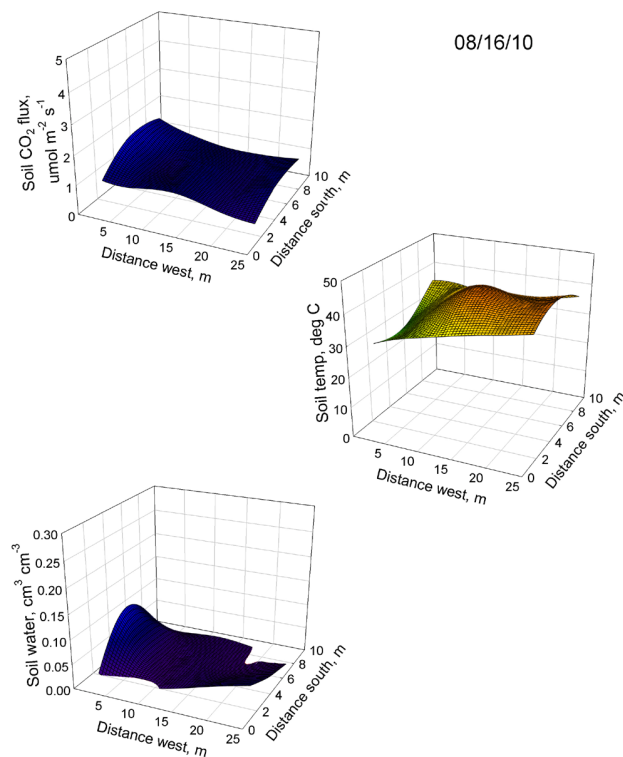


Figure 7. Spatial distribution of soil CO₂ flux (top), temperature (middle), and water content (bottom) on August 16, 2010, in a sagebrush stand at the Logan Forestry Sciences Laboratory.

Boxplots of monthly soil CO₂ flux, temperature, and water content for the 11 sample points in the stand reveal how the magnitude of spatial variability changed through the seasons (figure 8). The spatial distribution of soil temperature tended to follow a statistically normal distribution each month. The contrast between highest and lowest temperatures was greatest during July and August. Soil water content spatial distribution was more skewed during the summer since some points in the stand were wetter than most of the other points. Although soil CO₂ flux tended to be spatially normally distributed in the spring, outlier values skewed the statistical distribution in the summer.

Table 2. Seasonal daytime and nighttime mean \pm std err soil CO₂ flux, temperature, and water content. Because hourly measurements did not begin until November 1, 2009, the fall season data includes November 1 through December 20, 2009 and September 23 through October 31, 2010.

2009-10 Season	Photoperiod	Soil CO ₂ flux, umol m ⁻² s ⁻¹	Soil temperature, deg C	Soil water content, m ³ m ⁻³
			mean \pm std err	
Fall	Day	0.71 \pm 0.02	6.77 \pm 0.26	0.106 \pm 0.002
	Night	0.55 \pm 0.01	5.56 \pm 0.21	0.108 \pm 0.002
Winter	Day	0.28 \pm 0.02	-0.48 \pm 0.07	0.108 \pm 0.002
	Night	0.23 \pm 0.01	-0.76 \pm 0.05	0.103 \pm 0.002
Spring	Day	1.70 \pm 0.03	10.33 \pm 0.16	0.146 \pm 0.001
	Night	1.33 \pm 0.02	8.81 \pm 0.16	0.146 \pm 0.001
Summer	Day	1.21 \pm 0.02	23.73 \pm 0.20	0.043 \pm 0.001
	Night	0.87 \pm 0.02	22.20 \pm 0.18	0.042 \pm 0.002

Soil Microbial Respiration

Native soil microbial respiration in the sagebrush stand expressed as peak oxygen consumption (normalized relative fluorescence units or NRFU) was high (figure 9). Without adding any additional nutrients and relying strictly on native substrate C levels, native soil microbe communities showed an almost six-fold increase in peak oxygen consumption over control wells (no soil), which had an NRFU value of 1. Adding 10 mg/L extra N (from (NH₄)₂SO₄) produced a slight increase in microbial respiration indicating that this sagebrush stand soil is not N deficient for microbial utilization. Adding extra C substrate (50 mg/L C as glucose), produced a large increase in microbial respiration compared to unamended soil (more than 8-fold the O₂ consumption compared to controls). Adding N and C together did not increase O₂ consumption more than the added glucose alone. Although there is adequate C substrate in the soil for the native microbial communities, an additional positive response was obtained to added substrate (more food in the form of glucose).

DISCUSSION

Soil CO₂ flux data for sagebrush-dominated areas of the Great Basin and adjacent physiographic areas are sparse and limited to select sites and years. Furthermore, most estimates of soil CO₂ flux in this region are based on net ecosystem exchange (NEE) measurements rather than chamber-based methods. For example, Gilmanov and others (2004) measured NEE of CO₂ using the Bowen ratio energy balance method during winter (November 1 - March 15) at two sagebrush sites in Idaho and one in Oregon. During winter months, autotrophic respiration is at or very near zero so NEE would tend to be heterotrophic CO₂ respiration from soil. They obtained mean (std dev)

daily CO₂ flux values of 0.68 (0.56) (Burns, Oregon, in 2000/2001), 1.23 (1.19) (INEEL, Idaho, in 1999-2001), and 1.31 (0.80) (Dubois, Idaho, in 2000) g CO₂ m⁻² day⁻¹. Our mean chamber-based measurement of soil CO₂ flux for the same November to March time period in 2009-2010 was 0.32 umol CO₂ m⁻² s⁻¹, which is equivalent to a daily mean of 1.22 g CO₂ m⁻² day⁻¹, a value very much in line with the wintertime Bowen ratio estimated values for sagebrush-steppe areas given by Gilmanov and others (2004). Gilmanov and others (2004) also summarized average wintertime soil CO₂ fluxes for a range of biomes from published values. These values ranged from a low of 0.23 g CO₂ m⁻² day⁻¹ in an arctic tundra in ALASKA to a high of 4.4 g CO₂ m⁻² y⁻¹ for a lowland grassland in Switzerland. Wintertime soil CO₂ flux values in sagebrush-steppe soils from the Gilmanov and others (2004) NEE estimates and our chamber-derived value are within the range of wintertime values for other biomes.

In a different plant community type (cheatgrass) in southwest Idaho, on the boundary between the Snake River Plain and Great Basin, Myklebust and others (2008) measured a combined NEE estimate from eddy covariance, soil CO₂ gradient, and soil chamber (LI-8100) methods for annual soil CO₂ flux during 2005 of 406 \pm 73 g C m⁻². Our annual soil CO₂ flux under sagebrush during 2009-2010 was 328 g C m⁻² y⁻¹, which is similar, but a little lower than the cheatgrass site in Idaho. Differences in vegetation type, soil properties, and climatic conditions during the measurement periods could account for the relatively small difference between these annual totals.

Bahn and others (2010) summarized calculated annual total soil CO₂ flux for 15 Mediterranean, subhumid, and semi-arid forests, savannas,

shrublands, and grasslands. These ranged from 345 g C m⁻² y⁻¹ for intershrub microsites in a semi-arid Mediterranean shrubland with prickly burnet (*Sarcopoterium spinosum* (L.) Spach) to 1456 g C m⁻² y⁻¹ for a holly oak (*Quercus ilex* L.) forest. The mean (std dev) annual total soil respiration for all 15 biomes was 684 (68) g C m⁻² y⁻¹. Mean annual soil temperature (MAT) in these 15 biomes ranged from 8.5 to 22.9 deg C while mean annual precipitation (MAP) ranged from 280 to 844 mm. Most of these biomes are wetter and warmer than our sagebrush site so it is not surprising that they had higher annual total soil CO₂ flux values. The biome with annual total soil respiration closest to our calculated value (328 g C m⁻² y⁻¹) was a semi-arid Mediterranean prickly burnet shrubland (345 g C m⁻² y⁻¹). Relative to our sagebrush site, this prickly burnet shrubland was warmer (MAT = 22.9 deg C), which favors increased soil respiration, and drier (MAP = 300 mm), which favors respiration inhibition. In contrast, the biome with the closest MAT (10.4 deg C) and MAP (460 mm) to our site had an annual total soil respiration more than double that of our site (726 g C m⁻² y⁻¹). This was a Canary Island pine (*Pinus canariensis* C.Sm.) forest on the island of Tenerife, Spain and most likely has a much thicker forest floor layer to provide more substrate for heterotrophic respiration during organic matter decomposition.

Table 3. Seasonal mean ± std err soil CO₂ flux, temperature, and water content. Because hourly measurements did not begin until November 1, 2009, the fall season data includes November 1 through December 20, 2009 and September 23 through October 31, 2010. Total annual soil CO₂ flux was 328 g C m⁻² s⁻¹.

2009-10 Season	Soil CO ₂ flux, umol m ⁻² s ⁻¹	Soil temperature, deg C	Soil water content, m ³ m ⁻³
	mean ± std err		
Fall	0.62 ± 0.01	6.07 ± 0.16	0.107 ± 0.002
Winter	0.25 ± 0.01	-0.64 ± 0.04	0.105 ± 0.001
Spring	1.55 ± 0.02	9.69 ± 0.012	0.146 ± 0.001
Summer	1.07 ± 0.02	23.09 ± 0.14	0.043 ± 0.001
2009-10	0.96 ± 0.01	10.59 ± 0.12	0.101 ± 0.001

Autotrophic respiration by sagebrush roots would occur only during the growing season (about 7 months) for this species at our location and is temperature related (Bahn and others 2010). Heterotrophic respiration is strongly controlled by soil

temperature, moisture, and substrate availability in semi-arid soils (Conant and others 2004). Wintertime soil respiration is related to freeze/thaw cycles and wind events (Gilmanov and others 2004). During the 2009-2010 winter season at our site, the typical wintertime freeze/thaw cycles that often occur here were not observed since the shallow soil froze in early December and remained frozen until early March (figure 2).

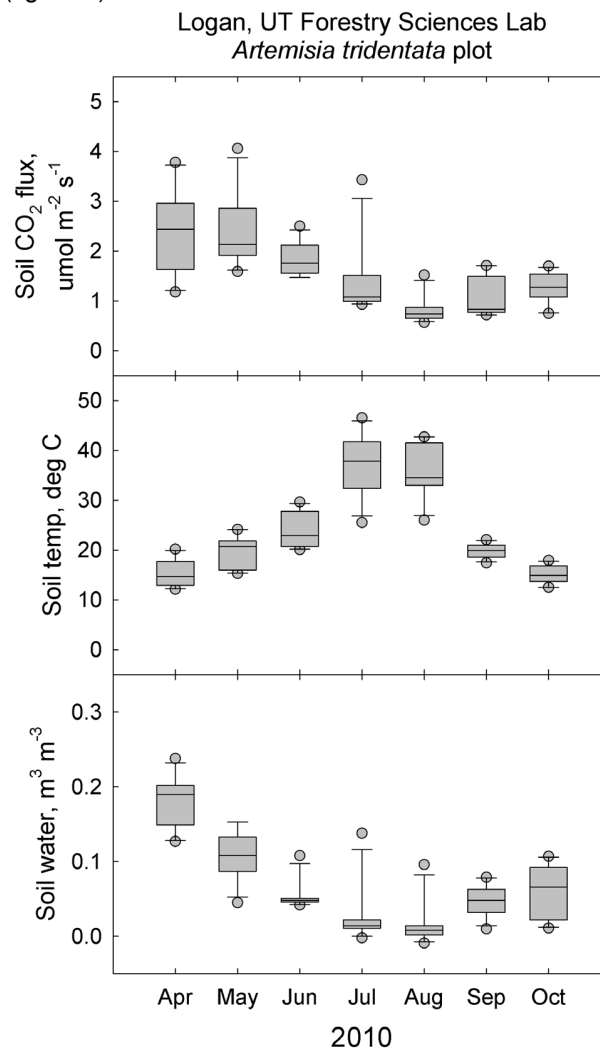


Figure 8. Boxplots of monthly (April through October, 2010) soil CO₂ flux (top), temperature (middle), and water content (bottom) for all 11 sample points in a sagebrush stand at the Logan Forestry Sciences Laboratory. Median spatial values are shown as a horizontal line surrounded by a box representing the 25 and 75 percentiles. Error bars represent the 10 and 90 percentiles and outliers are shown as points.

Aside from temperature effects, there are also resource limitations on heterotrophic respiration. The main resource limitations for heterotrophic soil

respiration under sagebrush at our location were water and C substrate. During or just after every spring through fall precipitation event, a significant, sometimes large increase in soil respiration was observed (for example, figure 3). The more immediate increase was probably due to a stimulation of microbial respiration in the upper few centimeters of soil. As water infiltrated the soil, respiration from plant roots deeper in the soil would then be stimulated. As the soil dried following a precipitation event, microbial respiration declined and perhaps even ceased at very low water contents. The stimulatory effect of summertime rainfall on soil respiration in semi-arid and arid plant communities is well known (for example, Austin and others 2004; Jin and others 2007, 2009; Sponseller 2007; Xu and others 2004).

Although many studies have attempted to separate root and microbial respiration in situ (e.g. Hanson and others 2000), we did not do so in this study since distinguishing between the two sources is blurred by the inseparable root-microbe associations within the rhizosphere (Baggs 2006). Nevertheless, the rapid response of soil respiration to the spring thaw and summer and fall precipitation events indicates a strong heterotrophic contribution to overall soil respiration. To provide additional insight on factors controlling heterotrophic respiration in sagebrush soils, we used the BD oxygen biosensor method to study C and N resource limitations on microbial respiration. Adding C substrate greatly stimulated microbial respiration, but adding extra N did not. This finding indicated that energy, not N, was more limiting to heterotrophic respiration in this soil (figure 9). The lack of microbial response to added N is not surprising given that the surface 10-cm of soil contained measureable levels of NH₄-N and NO₃-N at the end of the growing season (table 1), which indicates this soil contained adequate levels of N for sagebrush growth and microbial utilization.

Carbon substrate for heterotrophic decomposition appeared to be provided almost entirely by sagebrush leaf litter, which is very thin compared to appreciable and sometimes thick forest floor layers observed under deciduous and conifer forests. Carbon substrate and water limitations for heterotrophic respiration are probably common throughout shrublands so these results would be representative of other sagebrush stands under similar climatic conditions. During the dry season (mid-June through August in the Great Basin), rainfall events stimulate

pulses of soil respiration that characterize the highly skewed soil CO₂ spatial and temporal distributions found in our study. Thus, sufficient temporal measurements are needed to capture CO₂ respiration during and shortly after rainfall events. Infrequent measurements might result in underestimates of summertime soil CO₂ flux.

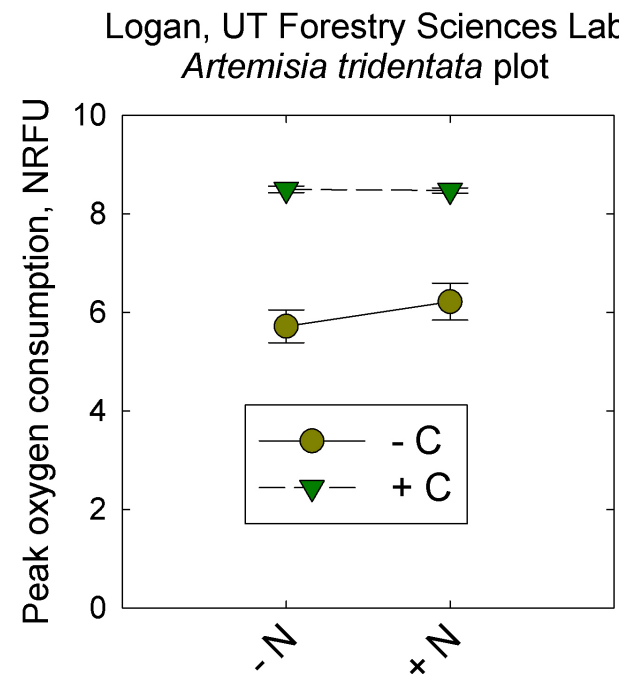


Figure 9. Effect of added N, C substrate (glucose), and N + C substrate on peak oxygen consumption by native microbe populations in a sagebrush stand at the Logan Forestry Sciences Laboratory.

Bahn and others (2010) showed that regardless of biome, total annual measured soil CO₂ flux is closely related to soil CO₂ flux measured at mean annual temperature (MAT). They based this finding on analysis of 80 site-years of soil respiration, temperature, and moisture data from 57 forests, plantations, savannas, shrublands, and grasslands from boreal to tropical climates. However, there were no sagebrush-dominant sites in their database. Their derived relationship is

$$\text{Annual soil CO}_2 \text{ flux} = 436.2 (\text{Soil CO}_2 \text{ flux at MAT})^{0.926}, r^2 = 0.94 (p < 0.001) \quad (\text{equation 1})$$

Mean annual temperature for our site from November 1, 2009 through October 31, 2010 was 10.59 ± 0.12 deg C. We used all the soil measurements collected when soil temperature was between 10.1 and 11.1 deg C to provide a larger pool of values (241

measurements) to calculate soil respiration at our MAT ± 0.5 deg C. We obtained a mean soil respiration value of 1.41 ± 0.04 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at our MAT. This value is similar to calculated soil respiration values from other biomes with similar MAT values (Bahn and others 2010). This MAT soil respiration value predicts an annual total soil CO₂ flux of $598 \text{ g C m}^{-2} \text{ y}^{-1}$ using the Bahn and others (2010) equation 1 shown above. Actual annual total soil CO₂ flux calculated by summing all the measured and interpolated (for missing values) hourly values was $328 \text{ g C m}^{-2} \text{ s}^{-1}$ for our site, about half the predicted value from the Bahn and others (2010) equation.

However, for semi-arid and arid sites in which precipitation is less than potential evapotranspiration ($P < \text{PET}$), Bahn and others (2010) had to derive an aridity index based on P/PET to accurately estimate annual total CO₂ flux from soil respiration measured at MAT:

$$\text{Annual soil CO}_2 \text{ flux predicted/observed} = 1.278 - 0.601 \ln(P/\text{PET}), r^2 = 0.82 (p < 0.001) \quad (\text{equation 2})$$

Logan, Utah, is in a semi-arid region with a mean annual precipitation of 450 mm (1893-2005). Soil respiration at MAT tends to occur during the spring wet season. Throughout the summer months, precipitation is substantially less than ET so the predicted annual total soil CO₂ flux must be adjusted downward to account for suppression of soil respiration during dry periods when soil water content is very low. Bahn and others (2010) used PET to calculate their aridity index. However, PET is not easy to derive and depends on many factors. The Utah State University Climate Center reports daily precipitation and reference evapotranspiration (ET₀) values. Using that dataset we calculated a 30-year average (1980-2010) P/ET_0 for our site of 0.488 (504 mm/1033 mm). For the November 1, 2009 through October 31, 2010 period when we measured soil CO₂ flux, P/ET_0 was 0.396 (385 mm/972 mm), which was drier than the most recent 30-year period. Using a P/ET_0 of 0.396, the ratio of predicted to observed annual soil CO₂ flux from equation 2 is expected to be 1.83. The ratio of predicted (calculated from equation 1) to observed annual soil CO₂ flux was 1.82 ($598/328 \text{ g C m}^{-2} \text{ y}^{-1}$). Thus, equation 2 accurately calculated the correction factor needed to adjust predicted annual soil CO₂ flux to match the observed value for a semi-arid sagebrush site. Dividing the predicted annual soil CO₂ flux of $598 \text{ g C m}^{-2} \text{ y}^{-1}$ by the 1.83

correction factor calculated from equation 2, a corrected value of $327 \text{ g C m}^{-2} \text{ y}^{-1}$ is obtained for the predicted annual CO₂ flux, a number virtually identical to the observed result from summing the hourly measurements. Thus, annual soil respiration can be accurately calculated using 1) soil CO₂ measurements at or near MAT, 2) hourly soil temperature measurements throughout the year to calculate MAT, and 3) daily precipitation and ET₀ data from a nearby weather station.

Since soil temperature and water content are often routinely measured with soil respiration, it might be possible to develop a relationship between measured soil CO₂ flux and measured soil temperature and water content. Figures 3 and 4 reveal that the relationships among soil CO₂ flux, soil temperature, and soil moisture are complex. During dry summer months, soil temperature continues to increase, but soil respiration decreases as soil water content decreases. We found that the product of soil temperature and soil water content (soil temperature x soil water content), which we call the soil environment index (SEI), is linearly related to soil CO₂ flux (figure 10), although there is significant scatter. Only when soil temperature and water content are high does soil respiration reach its peak. Any combination of low temperatures or low soil moisture will tend to decrease soil respiration.

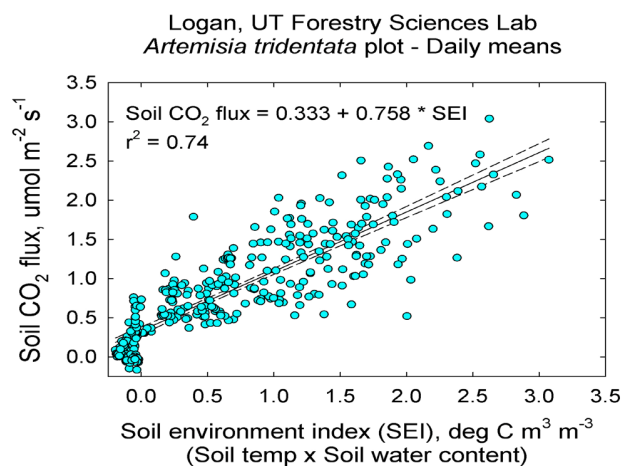


Figure 10. Relationship between soil CO₂ flux and soil environment index (defined as soil temperature x soil water content) for a sagebrush stand at the Logan Forestry Sciences Laboratory.

At times, large hourly variations in soil respiration in the sagebrush stand were observed. Although hourly soil respiration does not follow a predictable pattern,

monthly and seasonal values are strongly related to seasonal changes in soil temperature and soil water content and are therefore more predictable than short-term temporal changes. Once the seasonal relationship of soil CO₂ flux to soil temperature and water content is established for a given plant community and site combination (e.g., figure 10 for a sagebrush site), that relationship can be used to estimate soil CO₂ flux for areas or times with few soil respiration measurements provided soil temperature and moisture are measured frequently. We only have a single year of temporal variation in soil CO₂ flux at this site. Additional years of data are needed to determine variability across years as climatic conditions change from year to year.

The relatively small and fairly constant observed difference between daytime and nighttime mean soil respiration at this site indicates that it would be sufficient to characterize soil respiration at other sagebrush sites using daylight measurements with the survey chamber. Nighttime values could be modeled based on relative differences from more complete datasets at a limited number of sites. Because monthly and seasonal differences tend to be larger than daily differences, daytime survey type measurements at other sites during spring through fall months (e.g., weekly or even biweekly) may be sufficient to estimate seasonal soil CO₂ fluxes with the caveat that missing rainfall event effects on soil respiration would result in underestimation. Soil CO₂ flux can be estimated at times between survey measurements using soil temperature and moisture data collected hourly via dataloggers connected to the sensors and relationships such as that shown in figure 10.

An indication of the ability of monthly survey chamber (local spatial scale) measurements to represent monthly means from the long-term chamber can be seen in figure 11. Survey chamber soil CO₂ flux measurements at mid-month during the growing season overlapped with monthly means from the long-term chamber except in the spring (April and May) when monthly means were lower than survey-chamber means. Rapid changes in soil CO₂ flux occur at this time of year in response to large temperature and moisture changes. Thus, survey chamber measurements on a single day may differ substantially from monthly means measured with the long-term chamber. Soil temperatures measured during survey chamber soil CO₂ flux measurements

were always greater than monthly mean temperatures because monthly means includes lower nighttime soil temperature readings. Soil water content measured during survey chamber measurements were similar to monthly mean values since soil water content had little diurnal variation.

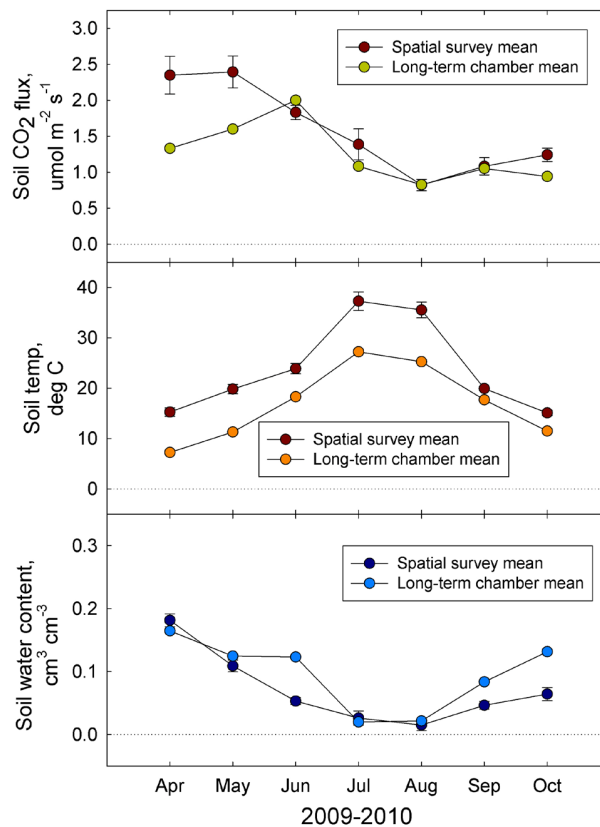


Figure 11. Monthly (April through October, 2010) survey (11 points) and long-term chamber (one point) mean \pm std err soil CO₂ flux (top), temperature (middle), and water content (bottom) in a sagebrush stand at the Logan Forestry Sciences Laboratory.

Within site variability in soil respiration can be large (figure 9). Sufficient local-scale measurements are needed to fully characterize a given locale and reduce uncertainty about a site mean. Bradford and Ryan (2008) provided guidelines on the number of soil collars needed per site to adequately estimate local spatial variability to detect differences among sites due to plant community types, land use activities, or vegetation treatments that could influence soil respiration. Bradford and Ryan (2008) also provided guidelines for seasonal temporal sampling.

For landscape-scale estimates of soil CO₂ flux in shrublands in general or sagebrush-dominated lands in particular, small-scale spatial variance is of less

concern than having enough sites across the landscape to provide large-scale estimates of soil CO₂ fluxes. Unfortunately, landscape-scale estimates of soil CO₂ flux in sagebrush-dominated plant communities are largely unknown. Given the large spatial extent of sagebrush in the Great Basin and elsewhere, spatial variability of soil respiration under sagebrush is probably as great as or perhaps even greater than temporal variability as documented herein. A Forest Inventory and Analysis (FIA)-type sampling (Amacher and Perry 2010) of soil CO₂ flux across sagebrush-dominated plant communities in the Great Basin and other physiographic areas could provide the most accurate landscape-scale estimate. Stratification of sampling based on plant community types, landscape position, and topographic and geographic gradients (elevation, latitude, and longitude) would provide the most efficient sampling scheme to reduce uncertainties. A broad-scale survey would need to include plant communities with other sagebrush species (e.g., black sagebrush (*Artemisia nova* A. Nelson), plant communities in which sagebrush co-occurs with herbaceous species such as grasses (e.g., sagebrush-steppe ecosystems), and other types of shrublands (e.g., desert communities dominated by salt shrubs). Work is underway to try to determine large-scale spatial variability of soil CO₂ flux in a variety of plant community types across geographic gradients in the Interior West.

SUMMARY

Soil CO₂ flux, temperature, and water content exhibited large temporal and spatial variability in a sagebrush stand at the Logan FSL. Mean (std dev) soil CO₂ flux, temperature, and water content for the measurement period (November 1, 2009 - October 31, 2010) were 0.96 (0.81) $\mu\text{mol m}^{-2} \text{s}^{-1}$, 10.59 (10.11) deg C, and 0.101 (0.062) $\text{m}^3 \text{m}^{-3}$, respectively. Measured soil CO₂ flux within 0.5 deg of the mean annual soil temperature (10.6 deg C) averaged $1.41 \pm 0.04 \mu\text{mol m}^{-2} \text{s}^{-1}$. Using an equation from Bahn and others (2010) to predict annual soil CO₂ flux from measured soil CO₂ flux at MAT, our predicted annual soil CO₂ flux was $598 \text{ g C m}^{-2} \text{ y}^{-1}$ for the sagebrush stand at the Logan FSL. The actual measured total obtained by summing all the hourly measurements was about half that ($328 \text{ g C m}^{-2} \text{ y}^{-1}$). For semi-arid or arid sites where precipitation is less than evapotranspiration, measured total annual soil CO₂ flux will be less than the potential total because of dry season suppression of soil respiration when soil water content is very low. A correction factor based on local climate station P/ET₀ datasets correctly calculated

that the ratio of predicted to observed annual soil CO₂ flux was 1.83. Dividing the predicted annual soil CO₂ flux ($598 \text{ g C m}^{-2} \text{ y}^{-1}$) by the correction factor (1.83) yielded an accurate prediction ($327 \text{ g C m}^{-2} \text{ y}^{-1}$) of the measured annual soil respiration ($328 \text{ g C m}^{-2} \text{ y}^{-1}$).

This study provides guidelines for capturing the temporal variability of soil CO₂ flux. Although our site is representative of other sagebrush sites under similar climatic conditions, a landscape-scale spatial survey is needed to estimate large-scale soil CO₂ flux for sagebrush-dominated landscapes.

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