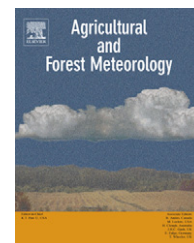


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Spring drought regulates summer net ecosystem CO₂ exchange in a sagebrush-steppe ecosystem

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ABSTRACT

Climate, as reflected by seasonal variations in precipitation and temperature, plays a critical role in ecosystem productivity and composition in the Western US and other arid regions. This study was conducted in the sagebrush-steppe ecosystem co-dominated by mountain big sagebrush (*Artemisia tridentata* var. *vaseyana*) and perennial grasses in south-central Wyoming across two growing seasons (2004 and 2005). A dry spring in 2004 and a wet spring in 2005 provided an opportunity to evaluate the influence of precipitation timing on the magnitudes and patterns of net ecosystem CO₂ exchange (NEE) and its environmental drivers. Summer weather conditions (light, temperature, and vapor pressure deficit) for the 2 years were similar but deep soil moisture content was lower in 2004. Daily rates of NEE demonstrated a net carbon source in 2004 and a net carbon sink in 2005. Midday depression of NEE frequently occurred in both measurement years (June–August in 2004 and mid July–August in 2005) due to stomatal control restricting water loss from the system under low soil moisture and high temperature and vapor pressure deficit conditions. Across different soil moisture regimes, the controlling factors on NEE differed. Under water limitation, soil water availability (soil drought) was the main driving factor of growing season NEE regardless of weather conditions while vapor pressure deficit (atmospheric drought) was the main driver of NEE when the ecosystem was not limited by soil moisture. Nighttime NEE showed strong non-linear relationship with soil moisture but no relationship with soil temperature, demonstrating that respiratory processes in the sagebrush-steppe ecosystem were limited by soil moisture during summer. The dynamic response of NEE to two summer seasons with dissimilar spring precipitation indicates that intra-seasonal variability in precipitation and subsequent impact on deep soil moisture should be taken into consideration to explain magnitudes and patterns of NEE at diurnal to seasonal time scales.

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1. Introduction

Sagebrush-steppe ecosystems dominate the Intermountain West, covering about 36 million ha in North America (West, 1983). These ecosystems are located in high elevation (above 1200 m) basins and consist of mosaics of shrubs, forbs, and grasses, which are utilized for livestock production (Knight,

1994). Semi-arid regions with woody vegetation, such as sagebrush rangelands, may sequester increasing amounts of anthropogenic carbon in the future because increasing atmospheric CO₂ is likely to stimulate productivity and enhance plant–water relations (Allen-Diaz et al., 1996; Jackson et al., 2002). Despite the extensiveness and potential for carbon sequestration of sagebrush-steppe ecosystems, they have

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received less research attention than forests (MacMahon, 2000).

Studies in sagebrush rangelands have emphasized assessment of changes in plant species abundance, biodiversity, and productivity (West, 1983; Anderson and Inouye, 2001; Boyd and Svejcar, 2004), vegetation development and structure (Anderson and Holte, 1981; Ewers and Pendall, 2008), and management (Watts and Wambolt, 1996). Recently the USDA's Agricultural Research Service (USDA-ARS) established a network of 11 study sites to quantify carbon balance on major rangeland ecosystems of the western US using chamber and Bowen ratio methods (Svejcar et al., 1997; Angell et al., 2001; Gilmanov et al., 2003, 2006). Remote sensing and modeling approaches have also been employed to estimate regional spatial and temporal relationships between CO₂ fluxes and environmental conditions (e.g., light and normalized difference in vegetation index; Wylie et al., 2003; Gilmanov et al., 2005).

Previous measurements using chamber and Bowen ratio methods show that the sagebrush-steppe ecosystem is a carbon sink over the growing season (Angell and Svejcar, 1999; Angell et al., 2001; Gilmanov et al., 2006). Studies on annual carbon budgets showed that inter-annual variability of carbon balance was dependent on the variability of herbaceous production (Gilmanov et al., 2003) and precipitation timing and amount (Gilmanov et al., 2006). Although these studies provide insights on the dynamics of carbon flux, the mechanisms driving the dynamics (e.g., the influence of soil and atmospheric drought on photosynthetic and respiratory processes) remain under-characterized.

It is expected that pattern, amount, and frequency of regional precipitation will be altered under future climate change (National Assessment Synthesis Team, 2000). Adequate precipitation, in the form of snow or rain, during winter and spring periods can recharge the entire soil profile. Spring precipitation provides additional water for shallow rooted plants (grass and forbs) and determines productivity of herbaceous biomass. The deeper soil, which is recharged during winter and spring, supplies soil moisture to deep rooted shrubs throughout the growing season (Knight, 1994). Heitschmidt and Haferkamp (2003) reported that a shift in spring drought impacts the structure and function of grasslands more than the summer/fall drought for the region of the Northern Great Plains of the U.S. It was also suggested that precipitation timing may be the critical factor affecting productivity and carbon sequestration of semi-arid regions (Knapp et al., 2002; Fay et al., 2003; Huxman et al., 2004; Gilmanov et al., 2006; Potts et al., 2006).

Understanding responses of ecosystems to the environment drivers is essential for predictive modeling of potential short- and long-term changes in carbon storage and feedback to climate (Law et al., 2002; Weltzin et al., 2003). However, there are only a few representative sites for shrub ecosystems in FLUXNET (<http://www.daac.ornl.gov/FLUXNET/>; Luo et al., 2007). This study was conducted in a sagebrush-steppe ecosystem in Wyoming, USA using eddy covariance during 2004 and 2005. The data collection rates were low during the winters due to difficult accessibility to the site so the data analysis in this study was limited to the growing season (June 1–August 31) which included the major

period of plant growth. The objective of this study was to assess the functional responses of NEE to changing environmental conditions in a sagebrush-steppe ecosystem. Because NEE in sagebrush-steppe ecosystem is controlled by water availability, we hypothesized that spring drought influenced the magnitude and responses of NEE by regulating availability of soil moisture during summer seasons.

2. Materials and methods

2.1. Sites

This study was conducted in a sagebrush-steppe ecosystem located in the northwestern Sierra Madre mountains of Wyoming at 2260 m elevation (N41°19'51.9":W107°24'02.4"). The study site is moderately grazed and contains both recently burned sagebrush (approximately 5 years since fire) and mature sagebrush (approximately 40 years since fire) in equal proportions. The dominant shrub, forb, and grass at the site are mountain big sagebrush (*Artemisia tridentata* var. *vaseyana* (Rydb.)), phlox (*Phlox* spp.), and Idaho fescue (*Festuca idahoensis*), respectively. The total vegetation cover (i.e., shrub and non-shrub covers) was 27% for the recently burned area and 39% for the mature sagebrush area. The recently burned area was dominated by herbaceous cover while the mature area primarily supported co-dominant herbaceous plants and shrubs. The height of the sagebrush was about 1 m and leaf area index (LAI) was 1.2 (Ewers and Pendall, 2008). The climate at the site is semi-arid with long, cold winters and dry, warm summers. The annual temperature was 6.2–7.2 °C and annual precipitation was 259–341 mm, 50% of which occurs in April, May, and June (Ewers and Pendall, 2008). Soil at the site has sandy loam texture and was classified as a Calcic Pachic Argicryoll with a 40-cm deep, C-rich A horizon (Cleary et al., in review).

2.2. Eddy covariance measurements

Measurements of NEE were conducted using eddy covariance technique (Baldocchi et al., 1988) from a tower height of 3 m using a 3D sonic anemometer (Model CSAT3, Campbell Scientific, Logan, Utah, USA) to measure wind (vertical, streamwise, and lateral wind) and temperature fluctuation, and an open-path infrared gas analyzer (IRGA; Model LI-7500, LI-COR, Lincoln, Nebraska, USA) to measure carbon dioxide and water vapor fluctuations. Half-hour eddy covariances and associated statistics were calculated from raw data stored on a datalogger (4 Hz stored on a Model CR23X in 2004 and 10 Hz stored on a CR5000 in 2005, Campbell Scientific). The sonic anemometer data set was rotated to force the mean vertical wind speed to zero and to align the horizontal wind speed onto a single horizontal axis. CO₂ and water vapor fluxes were corrected for the variation in air density due to simultaneous transfers of water vapor and sensible heat according to Webb et al. (1980). The effect of surface heating on the open-path IRGA (Burba et al., 2006) was found to be extremely small ($<0.0001 \text{ g C m}^{-2} \text{ h}^{-1}$) and we did not apply the correction to the CO₂ flux data. The effect of friction

velocity (u^*) was evaluated using the data collected during nocturnal periods when photosynthetically active radiation (PAR) was less than $20.0 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Goulden et al., 1996). To reduce the scatter in the data set, the nighttime NEE data were bin-averaged at the interval of $0.05 \text{ ms}^{-1} u^*$ (Aubinet et al., 2000) and then plotted against u^* . At our study site, the u^* threshold was 0.17 ms^{-1} (data not shown). Due to the calm conditions at night, about 85% of nighttime flux data were below the u^* threshold and these data were excluded. This paper mainly focuses on functional response of the sagebrush-steppe ecosystem to environmental conditions and gap-filling methods were not applied to the NEE data set.

2.3. Meteorological measurements

Net radiation (R_n) was measured with a net radiometer (Model CNR 1, Kipp & Zonen, Delft, the Netherlands) at a height of 2.5 m. Photosynthetically active radiation was measured with a quantum sensor (Model LI-190SZ, LI-COR) at a height of 2.5 m. Air temperature (T_{air}) and relative humidity (RH) were measured with a T_{air}/RH probe (Model HMP45C, Vaisala, Helsinki, Finland) at a height of 2.5 m. Soil heat flux (G) was measured at a depth of 4 cm with two heat flux plates (Model HFP01SC, Hukseflux, Delft, the Netherlands). Soil temperatures (T_{soil}) were measured using T-type thermocouples at four different levels (2, 5, 6, and 10 cm below the surface). Some measurements of T_{soil} in June and August, 2004 (about 23% of the total data collection) showed very high T_{soil} values (e.g., above 60°C) due to thermocouple malfunction. This problem was resolved and the soil temperature data collected in 2005 did not show any symptoms of malfunction. Soil moisture was measured at four different depths using soil moisture probes (Model CS616, Campbell Scientific). Two soil moisture probes were buried horizontally at 4 and 15 cm depth while the other two probes were buried vertically from 15 and 45 cm and 45 to 75 cm depths. Precipitation was measured with a tipping-bucket rain gauge (Model TE525MM, Texas Electronics, Texas, USA). The relationship between soil water potential and soil water content was measured using a dewpoint potentiometer (Model WP4-T, Decagon Devices, Pullman, WA, USA) from soil samples collected at different soil depths (0–120 cm) at the study site.

Because the measurements of eddy covariance and meteorological variables in this study were conducted from late June 2004, spring precipitation data were absent in 2004; winter precipitation data were absent for both years. In order to compare the general patterns of the precipitation and the total annual precipitation for both years, the precipitation data collected at Glacier Lakes Ecosystem Experiments Site (GLEES) from 1989 to 2005 were used in this study (Korfmacher & Hulstrand, 2006, http://www.fs.fed.us/rm/data_archive/dataaccess/GLEES_meteorology.html). The GLEES site is located in the Snowy Range near Centennial, Wyoming (3200–3500 m elevation) and is 100 km from the Sierra Madre site. Despite the distance between the two locations, the timing of the precipitation at the GLEES coincided with that at the Sierra Madre site. Therefore, it is acceptable to use the data from GLEES to regionally generalize the pattern and timing of precipitation at the Sierra Madre site.

2.4. Energy budget

The performance of eddy covariance measurements was evaluated by energy budget closure. Soil heat flux was calculated by adding the measured soil heat flux to the energy stored in the soil layer above the soil heat flux plates (Gao, 2005). The heat storage was estimated using an equation, $\Delta T C_s d / \Delta t$, where ΔT is difference in T_{soil} between soil temperatures at 2 and 6 cm, C_s is the heat capacity of soil, d is the depth of the soil heat flux plates (4 cm), and Δt is the time interval (1800 s). During the period of temperature probe malfunction (June–August, 2004), the heat storage was not calculated and the soil heat flux data were not used to estimate energy balance closure. Energy balance closure was tested by a linear regression between the amount of the available energy ($R_n - G$) and the sum of sensible heat (H) and latent heat (LE) fluxes ($H + LE$) using the half-hourly data collected for two summer seasons. The energy balance closure indicated 70% agreement (i.e., $H + LE = 0.70 \times (R_n - G) + 5.01$, $r^2 = 0.90$, $P < 0.0001$) in 2004 and 75% agreement (i.e., $H + LE = 0.75 \times (R_n - G) + 22.12$, $r^2 = 0.91$, $P < 0.0001$) in 2005. When the data for the two summers were combined, the energy balance closure was 74% (i.e., $H + LE = 0.74 \times (R_n - G) + 16.79$, $r^2 = 0.90$, $P < 0.0001$). A possible cause for the lack of energy closure may arise from source scales of measurements in R_n and G compared to H and LE (Schmid, 1997; Foken, in press). The sagebrush-steppe ecosystem is heterogeneous on scales of meters (Ewers and Pendall, 2008) and within the scale of the source areas, albedo, soil temperature and soil moisture may differ. Horizontal advection of H and LE , which may be generated by temperature and water vapor gradients along the heterogeneous fetch, may be another reason for the observed energy imbalance (Paw et al., 2000).

2.5. Statistics

A multiple regression analysis was performed to assess the relationship of NEE with concurrent changes in environmental variables (PAR, T_{air} , T_{soil} , vapor pressure deficit, and soil moisture) using half-hourly data in SAS (Version 9.1.3, SAS Institute, Cary, NC, USA) (Table 1). The interaction terms among PAR, T_{air} , T_{soil} , D , and soil moisture were included to understand relative importance of the joint effect of two or three variables on NEE (Table 1). Although time lags were found between NEE and environmental variables (0.5–3.0 h lags), the results of the multiple regression analysis with time lag correction were very similar with the results of the analysis without time lag in terms of r^2 and coefficient values. Thus, the results corrected with time lags were not shown in this study.

3. Results

3.1. Weather conditions

The values of daily integrated PAR were similar for the two summers (Fig. 1). Daily average T_{soil} and T_{air} gradually increased and reached their maxima in July for both years. Comparison between T_{soil} and T_{air} indicated that T_{soil} was consistently higher than T_{air} in 2004 while the values of T_{soil} and T_{air} were similar in 2005. Vapor pressure deficit (D)

Table 1 – Statistical information (regression correlation coefficient (r^2), regression coefficient (Coef.), standard error (S.E.), and partial correlation coefficient (partial r^2) for the relationship between NEE and changes in PAR, T_{air} , D , T_{soil} , and SM[†] using a stepwise multiple regression model: $Y_i = \beta_0 + \beta_1 X_{\text{PAR}i} + \beta_2 X_{T_{\text{air}}i} + \beta_3 X_{Di} + \beta_4 X_{T_{\text{soil}}i} + \beta_5 X_{SMi} + \beta_6 X_{\text{PAR}i} X_{T_{\text{air}}i} + \beta_7 X_{\text{PAR}i} X_{Di} + \beta_8 X_{\text{PAR}i} X_{T_{\text{soil}}i} + \beta_9 X_{\text{PAR}i} X_{SMi} + \beta_{10} X_{\text{PAR}i} X_{T_{\text{air}}i} X_{Di}$

Year	Effect	Coef.	S.E.	Partial r^2	P	Year	Coef.	S.E.	Partial r^2	P
2004	CONS [†]	−0.018	0.014		*	2005	0.023	0.008		**
$r^2 = 0.30$	PAR [†]	<0.0001	<0.0001	0.06	***	$r^2 = 0.64$	<0.0001	<0.0001	0.07	***
	T_{air} [†]	0.011	0.001	0.06	***		−0.005	0.002	0.05	***
	D [†]	−0.073	0.012	0.04	***		−0.046	0.006	0.09	***
	T_{soil} [†]	−0.002	0.001	0.02	***		0.007	<0.0001	0.20	***
	SM [†]	0.375	0.149	0.01	*		0.076	0.045	0.00	*
	PAR \times T_{air} ^{††}	<0.0001	<0.0001	0.01	***		<0.0001	<0.0001	0.02	***
	PAR \times D ^{††}	0.001	<0.0001	0.03	***		−	−	0.00	−
	PAR \times T_{soil} ^{††}	<0.0001	<0.0001	0.01	***		−	−	0.00	−
	PAR \times SM	−0.001	<0.0001	0.03	***		−0.001	<0.0001	0.20	***
	PAR \times T_{air} \times D ^{††}	<0.0001	<0.0001	0.04	***		<0.0001	<0.0001	0.01	***

Significance of the regressions (P) are (*), (**), or (***) for $P < 0.05$, 0.01, and 0.001, respectively.
[†] CONS, PAR, T_{air} , D , T_{soil} , and SM indicate constant (intercept), photosynthetically active radiation, air temperature, vapor pressure deficit, soil temperature, and soil moisture, respectively.
^{††} Symbol (\times) indicates cross-product of the variables.

followed the same patterns as T_{air} during the summer seasons and D in 2004 was slightly greater than in 2005.

3.2. Precipitation anomaly

Precipitation anomaly, defined as the difference between observed and 10-year average precipitation, indicated below average precipitation in winter and spring 2004 (DOY 1–150) followed by more precipitation in late June (DOY 170–180; Fig. 2). From July to mid August, 2004 (DOY 180–230), the precipitation anomaly was again below average. In 2005, several long winter (DOY 70–90) and late spring (DOY 115–160) precipitation events resulted in a large positive precipitation anomaly. After mid June (DOY 170), the magnitude of the precipitation anomaly was low until around DOY 300. The precipitation anomaly indicates

that winter precipitation in 2004 was less than that in 2005, and that 2004 had a dry spring while 2005 had an unusually high amount of precipitation in late spring.

3.3. Soil moisture and daytime NEE

The magnitude and patterns of soil moisture at depths of 4 and 15 cm were similar for both summers (Fig. 3A). There was a gradual decrease in soil moisture from DOY 150 to 170, followed by a peak ($0.25 \text{ m}^3 \text{ m}^{-3}$) coinciding with intermittent rainfall around DOY 180, and then a rapid decrease (about $0.10 \text{ m}^3 \text{ m}^{-3}$) to around DOY 230.

There was a prominent difference in the magnitude and patterns of soil moisture in the deeper soil layers between 2004 and 2005 (Fig. 3B). Soil moisture in 2004 remained low and relatively constant through the season at both depths. In 2005, the maximum of soil moisture at both depths occurred near DOY 150 and declined slowly as the season progressed. Throughout both summers, there was a constant difference ($0.15 \text{ m}^3 \text{ m}^{-3}$) in soil moisture between the two depths. The high soil moisture in the deeper soil layers in 2005 reflected percolation of winter and late spring precipitation.

Seasonal pattern of daytime sum of NEE in 2004 remained relatively constant, showing net carbon source throughout the season (Fig. 3C). The daytime sums of NEE were calculated using the data collected when PAR was above $20.0 \mu\text{mol m}^{-2} \text{ s}^{-1}$ over 24 h period. Daytime sum of NEE in 2005 showed a strong net carbon uptake (about $5.5 \text{ g C m}^{-2} \text{ day}^{-1}$) in early June and gradual decrease throughout the season, indicating that the active growing season of the sagebrush-steppe ecosystem occurred early in the summer. The seasonal patterns of daytime sum of NEE reflected well those of deeper soil moisture in both years. In general, the growing season in 2005 had greater net carbon uptake than in 2004 over the same period of the measurement.

3.4. Diurnal variation of NEE

The diurnal pattern of NEE averaged over 15-day periods demonstrated sharp contrasts between 2004 and 2005 (Fig. 4).

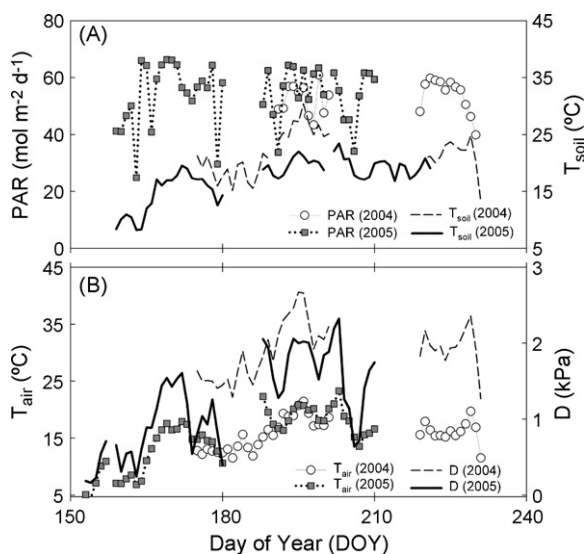


Fig. 1 – Seasonal patterns of daily integrated photosynthetically active radiation (PAR), air temperature (T_{air}), soil temperature at 2 cm (T_{soil}), and vapor pressure deficit (D) during the two summer seasons. Daily average was calculated over 24 h period.

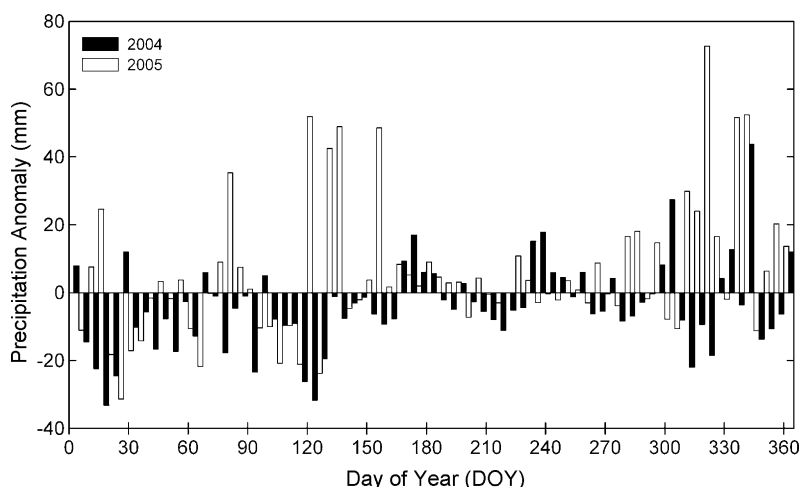


Fig. 2 – Precipitation anomalies measured at Glacier Lakes Ecosystem Experiments Site (GLEES) in 2004 and 2005. The values of precipitation anomalies were integrated over 7 days.

NEE in 2004 exhibited a small range of variation (-0.1 to $0.1 \text{ g C m}^{-2} \text{ h}^{-1}$) with net carbon uptake during morning and net carbon loss during midday (i.e., midday depression). The

magnitude of midday depression slowly declined in late afternoon and NEE remained a net carbon source at night. As the season progressed, net carbon loss during midday increased. The diurnal patterns of NEE in 2005 showed a strong net carbon uptake during midday and the magnitudes of net carbon uptake gradually decreased during the late season.

3.5. Controlling environmental factors

The influence of the environmental controlling variables (e.g., PAR, D , and soil moisture) on NEE is often complex and correlated. To analyze the effect of each variable, half-hourly data for 2004 and 2005 were combined and categorized under three different PAR ranges and six different soil moisture ranges (Fig. 5). The relationship between D and T_{air} was strong ($Y_D = 0.6113 \exp(0.0656X_{T_{\text{air}}})$, $r_2 = 0.99$ in 2004, $Y_D = 0.1407 \exp(0.1152X_{T_{\text{air}}})$, $r_2 = 0.89$ in 2005). The results of the relationship between NEE and T_{air} were very analogous with those between NEE and D shown in Fig. 6 and thus were not shown. Under low light conditions, NEE was not affected by D over different soil moisture ranges (Fig. 5A and D). At moderate and high light levels with low soil moisture, there was no clear relationship between NEE and D (Fig. 5B and C). Above $0.1 \text{ m}^3 \text{ m}^{-3}$ of soil moisture, net carbon uptake increased with soil moisture content and decreased with D (Fig. 5E and F). The response of NEE to PAR and D was relatively independent under soil water-limited conditions (below $0.1 \text{ m}^3 \text{ m}^{-3}$ of soil moisture) whereas it was dependent on these components at higher soil water conditions. The relationship between half-hourly NEE and D using different ranges of soil moisture ($0.28\text{--}0.50 \text{ m}^3 \text{ m}^{-3}$) measured at deeper soil layer ($15\text{--}45 \text{ cm}$) under same ranges of PAR was examined. The results illustrated very similar patterns with those shown in Fig. 5 (data not shown).

The effects of concurrent changes in all environmental variables (PAR, T_{air} , T_{soil} , D , and soil moisture) on NEE varied with year (Table 1). The multiple regression model suggested

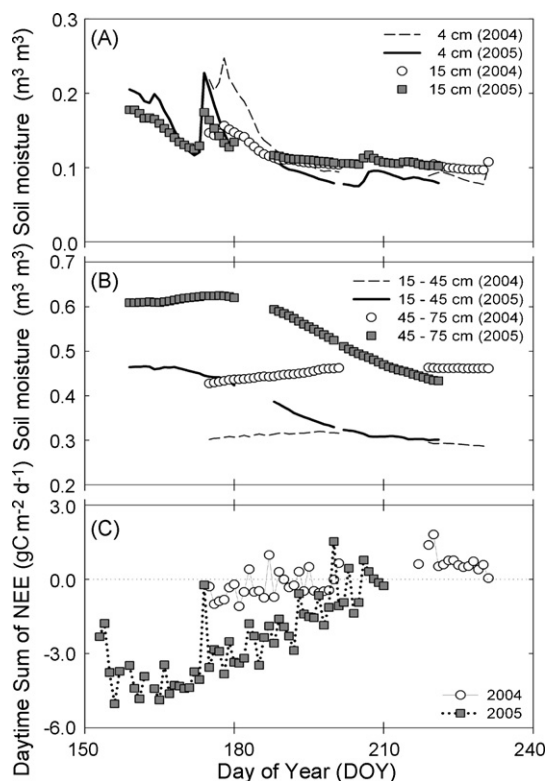


Fig. 3 – Seasonal patterns of soil moisture at four different depths (A and B) and daytime sum of net ecosystem CO_2 exchange (NEE: C) during the two summer seasons: (A) soil moisture from horizontally buried soil moisture probes and (B) soil moisture from vertically buried soil moisture probes. Note difference in scale between panels A and B. Positive sign indicates carbon source while negative sign indicates carbon sink in panel C.

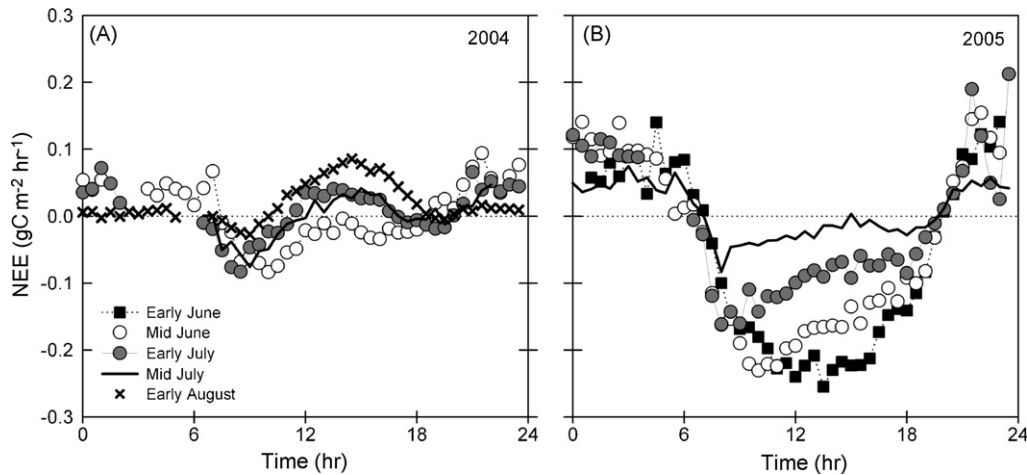


Fig. 4 – Diurnal variations of 15-day average net ecosystem CO₂ exchange (NEE) in 2004 (A) and 2005 (B). Positive sign indicates carbon source while negative sign indicates carbon sink.

that the environmental variables were more strongly related to NEE in 2005 ($r^2 = 0.6$) than in 2004 ($r^2 = 0.3$). The values of partial correlation coefficient (partial r^2), which was computed from type III sums of squares, were low (<0.1) for all variables in 2004. In 2005, the values of partial r^2 ranged from 0.01 to 0.2 with maximum values of T_{soil} and $\text{PAR} \times \text{SM}$. The coefficients of all the variables including the interaction terms were statistically significant in 2004, and all except two

interaction terms ($\text{PAR} \times D$ and $\text{PAR} \times T_{\text{soil}}$) were significant in 2005.

3.6. Effect of soil temperature and soil moisture on nighttime NEE

The relationship between nighttime NEE and T_{soil} was examined using average nighttime NEE and T_{soil} (Fig. 6A).

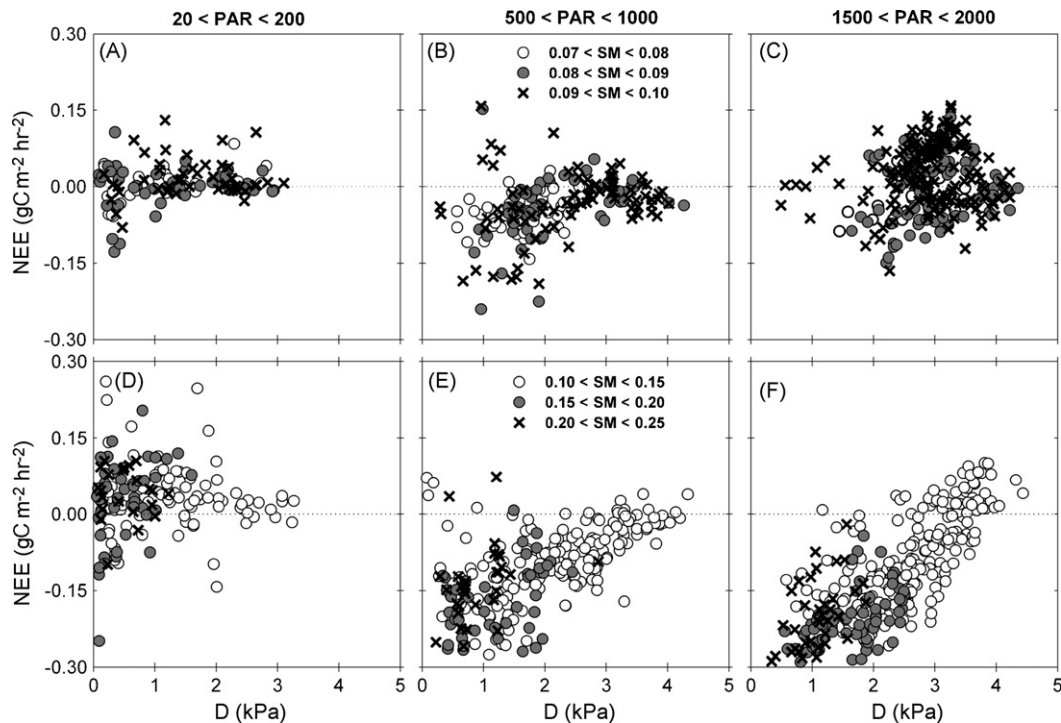


Fig. 5 – Relationship between half-hourly net ecosystem CO₂ exchange (NEE) and vapor pressure deficit (D) under different photosynthetically active radiation (PAR) and soil moisture (SM) range. Soil moisture collected at 4 cm was used in the analysis. PAR was categorized to low (20 < PAR < 200), moderate (500 < PAR < 1000), and high (1500 < PAR < 2000) light conditions while soil moisture categorized to low soil moisture (0.07 ≤ SM < 0.10) and high soil moisture (0.10–0.25). Units of PAR and soil moisture are $\mu\text{mol m}^{-2} \text{s}^{-1}$ and $\text{m}^3 \text{m}^{-3}$, respectively. Positive sign indicates carbon source while negative sign indicates carbon sink.

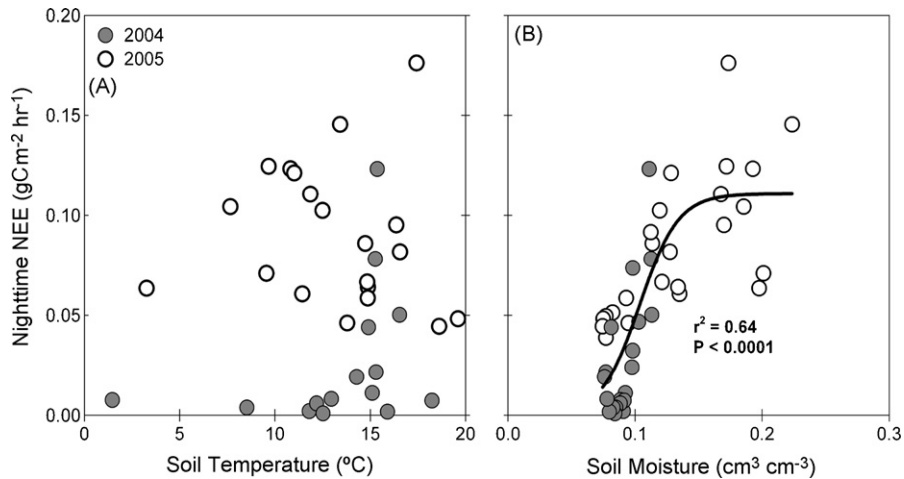


Fig. 6 – Effect of soil temperature (A) and soil moisture (B) on nighttime net ecosystem CO₂ exchange (NEE). Sigmoid curve fitting was used to fit nighttime NEE and soil moisture data: $y = a / (1 + e^{-(x - x_0)/b})$ where $a = 0.11$, $b = 0.02$, and $x_0 = 0.10$. Positive sign indicates carbon source while negative sign indicates carbon sink.

Average nighttime values were estimated using the data collected when PAR was below $20.0 \mu\text{mol m}^{-2} \text{s}^{-1}$. No relationship was found between average nighttime NEE and T_{soil} for both summers in this study. The relationship between the two variables was examined using the weekly binned data in order to scrutinize the effect of seasonal plant development on the relationship. Majority of the weekly binned data (about 83%) showed low correlations ($0.0 < r^2 < 0.25$), indicating that the seasonal plant development did not affect the relationship (data not shown). Average nighttime NEE and soil moisture at 4 cm had a non-linear relationship, showing sharp increase of average nighttime NEE above average nighttime soil moisture of about $0.13 \text{ m}^3 \text{m}^{-3}$ to a plateau at about $0.10 \text{ g C m}^{-2} \text{h}^{-1}$ (Fig. 6B). The relationship between average nighttime NEE and deeper soil moisture (15–45 cm) was similar with that at soil moisture at 4 cm (data not shown). No relationships were

found between average nighttime NEE and soil water potential for shallow (0–10 cm) or deep (15–45 cm) soil layers (data not shown).

3.7. Response of daytime NEE to soil moisture

The response of daytime sum of NEE to soil moisture availability was investigated at two depths (4 and 15–45 cm; Fig. 7). Increased soil moisture at both depths enhanced the amount of daily net carbon uptake for both summer seasons. Deeper soil moisture explained the drought effect on daytime sum of NEE better than surface soil moisture, showing net carbon loss below $0.3 \text{ m}^3 \text{m}^{-3}$ of soil moisture and a net carbon sink above this value when the data for the two summers were combined. Due to a strong skewness of the soil water potential data at both shallow (0–10 cm) and deeper soil (15–45 cm),

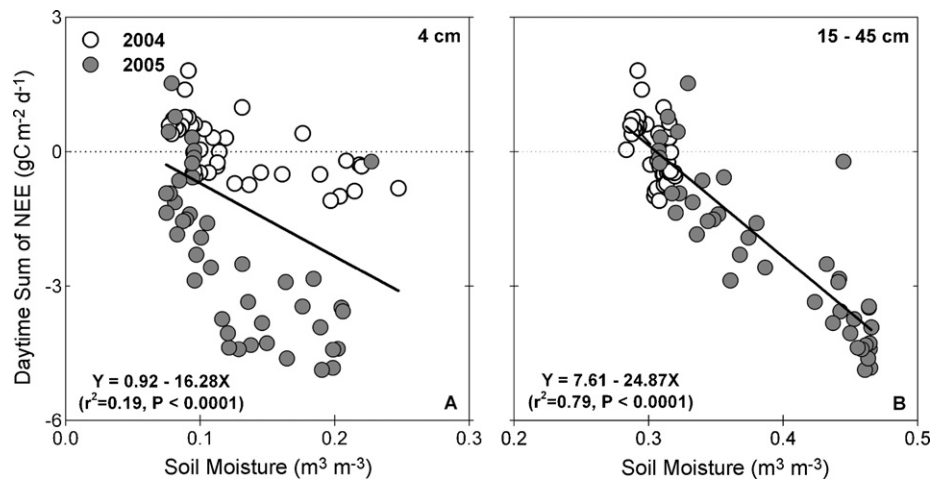


Fig. 7 – Response of daytime sum of net ecosystem CO₂ exchange (NEE) to soil moisture at two different depths (A and B). Liner regression in B was calculated using the combined data for 2004 and 2005. Note difference in scale between panels A and B. Positive sign indicates carbon source while negative sign indicates carbon sink.

there was no discernable relationship between daily NEE and soil water potential (data not shown).

4. Discussion

The results from this study support the hypothesis that spring drought drives the magnitude and response of NEE by regulating availability of soil moisture during the summer seasons. In particular, lack of recharge of deep soil moisture constrains biological activity and carbon uptake during the growing season to near-zero values in this shrub-dominated ecosystem.

4.1. Comparison of NEE between 2004 and 2005

The spring drought in 2004 substantially reduced NEE and changed its response to environmental drivers compared to 2005 (Figs. 3 and 4). This is likely due to lack of contribution from annual grasses and forbs to net carbon uptake and earlier dormancy of perennial grasses under dry early summer conditions (Campbell and Harris, 1977). Large winter and spring precipitation in 2005 likely provided additional water for shallow rooted plants early in the season (grasses and forbs; Knight, 1994; Bates et al., 2006) and recharged deep soil water, which was utilized by the deep sagebrush root system and allowed net carbon uptake until soil and air became dry in the late growing season (Miller, 1988; Knight, 1994). As shown in the precipitation patterns in 2005, the influence of winter precipitation can be significant on the amount of surface soil water and percolation into deep soil at the sagebrush-steppe ecosystem (Schwinning et al., 2003), and thus a lack of winter precipitation can enhance spring drought. Bates et al. (2006) suggested that shift of precipitation to spring/summer (April–July) has the highest potential to change productivity and composition at sagebrush-steppe ecosystem. Schwinning et al. (2005) suggested that growth of a shrub/grass community of the Colorado Plateau in North America is far more sensitive to spring drought than summer drought. As shown in Fig. 3 in this study, the most active period of plant growth, based on net carbon uptake, occurred in early June. This suggests that spring drought can be more critical to carbon dynamics than summer drought in the sagebrush-steppe ecosystem (Fay et al., 2003; Gilmanov et al., 2006).

4.2. NEE environmental drivers: light, temperature, soil moisture, and D

4.2.1. Light

Strong reduction in net carbon uptake and/or net carbon balance close to zero occurred under high light conditions, especially under water stress with high temperature and D (Fig. 4). Gilmanov et al. (2003) suggested that, in general, light conditions mostly determine the dynamics of photosynthesis, and a semi-empirical model based on a light-temperature response shows good predictability for estimating photosynthesis and respiration in sagebrush-steppe. Our results suggest that the light response relationship by Gilmanov et al. (2003) may not appropriately predict the dynamics of NEE in a water-stressed sagebrush-steppe because other environmen-

tal factors (e.g., soil moisture and D) play more important roles than light in controlling NEE.

4.2.2. Soil temperature

Soil temperature is often a critical factor in controlling respiration and is thus widely used to estimate respiration (e.g., Q_{10} function; Lloyd and Taylor, 1994; Janssens and Pilegaard, 2003; Gu et al., 2005; Chen and Tian, 2005) and gross primary production (GPP; Falge et al., 2001; Gilmanov et al., 2006). Because eddy covariance measurements cannot directly separate the contribution of photosynthesis and ecosystem respiration, nighttime NEE without photosynthetic activity is used to estimate daytime ecosystem respiration by employing the Q_{10} function (e.g., nighttime NEE versus T_{soil} ; Falge et al., 2001; Gu et al., 2005). The lack of correlation between nighttime NEE and T_{soil} in this study was due to soil water limitation (Fig. 6), which reduces root and soil microbial activity (Peterjohn et al., 1994; Luo et al., 2001). Measurements of soil respiration conducted at the same site indicate that soil respiration responds to temperature only above $0.10 \text{ m}^3 \text{ m}^{-3}$ of soil moisture (Cleary, 2007).

A major uncertainty in carbon cycle studies is associated with prediction of ecosystem respiration, in particular soil respiration. In ecological models, the Q_{10} value is either treated as a constant of 2 (Jenkinson et al., 1991; Schimel et al., 2000) or predicted as function of temperature (Arora, 2003). However, the complete lack of relationship between ecosystem respiration and T_{soil} in this study negates the application of Q_{10} to estimate respiration or perform gap filling. Therefore, understanding of the effect of soil water availability on respiration is essential for prediction of respiration in semi-arid ecosystems (Carlyle and Than, 1988; Xu and Qi, 2001).

4.2.3. Soil water availability and vapor pressure deficit

Soil water availability (soil drought) is the main driver of NEE in the sagebrush-steppe ecosystem under water-limited condition regardless of weather conditions while D (atmospheric drought) is the main driver of NEE in the absence of soil water limitation (Fig. 5). The analogous results of the correlations between NEE and soil moisture at different depths suggest that photosynthesis at the study site was controlled by both shallow and deeper soil moisture (Fig. 7). However, the stronger dependence of daily NEE on deeper soil moisture (Figs. 3 and 7) indicates that deep rooted sagebrush are primarily responsible for net carbon gain when it occurs. Perennial grasses that comprise a portion of the biomass probably contribute to net carbon gain when shallow soil moisture is adequate. Volumetric soil moisture had a better relationship with nighttime NEE and daily NEE than soil water potential, suggesting that volumetric soil moisture is a better predictor variable than soil water potential to NEE estimation at a sagebrush-steppe ecosystem. Although the effect of light, temperature, D, and soil moisture on NEE cannot be easily separated, this study shows that low soil moisture constrained the response of NEE more effectively than other factors at a lower soil moisture range.

The effect of D on NEE (i.e., less net carbon uptake with higher D) is consistent with findings of Fu et al. (2006) who reported a depression of net carbon uptake and eventually release of carbon at high D in a *Leymus chinensis* grassland in

Inner Mongolia of China. A reason for the depression of NEE at high D is that increasing D induces stomatal closure due to excessive loss of water by transpiration (Mott and Parkhurst, 1991), resulting in decreasing photosynthetic rates (Cowan, 1982; Dai et al., 1992). Half-hourly evapotranspiration and water use efficiency, defined as the ratio of NEE [mgC] to evapotranspiration [g H₂O], substantially decreased and reached near 30 mg m⁻² s⁻¹ and 0 mg g⁻¹, respectively, when D was larger than 1.5 kPa (data not shown). The portion of evaporation from soil would be small under extremely low soil moisture (Prater and DeLucia, 2006). Therefore, decline in evapotranspiration would mostly be due to reduction in transpiration. These results indicate that stomatal closure restricting water loss induces the decline in NEE at high D (Tang et al., 2006). Future work will evaluate the controls of stomata on transpiration and thus carbon uptake and quantify the contribution of transpiration to evapotranspiration through concurrent measurements of the eddy covariance and chamber methods.

The influence of atmospheric drought conditions expressed with D on NEE are often ignored in water-limited ecosystems. As shown in this study, D was a dominant control variable on NEE when soil moisture was not limiting. Understanding the mechanism of the role of D on the ecosystem process can be a useful tool (Fu et al., 2006) to predict the potential changes in the response of the sagebrush-steppe ecosystem to changing environments.

4.2.4. Implications for climate change

Precipitation has increased substantially in North America (IPCC, 2007) and its variability is projected to increase spatially and temporally (Katz and Brown, 1992; IPCC, 2007). In semi-arid ecosystems, annual precipitation amount has been emphasized to predict productivity and species composition. However, ecosystem response is relatively more dependent on variability of precipitation than on total annual precipitation (Knapp et al., 2002; Fay et al., 2003; Huxman et al., 2004; Bates et al., 2006).

Water (e.g., precipitation, soil water availability, and atmospheric dryness, D) is a primary environmental factor limiting productivity in rangeland ecosystems. General circulation models (GCMs) predict that changes in vegetation productivity are closely related to changes in precipitation over rangeland (Hanson et al., 1993). Although there has been disagreement in the prediction of precipitation amount in United States (National Assessment Synthesis Team, 2000; Daly et al., 2000), change in regional precipitation along with various climate change scenarios is expected to significantly affect rangeland ecosystem processes (Fay et al., 2003; Svejcar et al., 2003). This study shows that intra-seasonal variations in precipitation timing and amount have substantial ramifications in terms of the pattern and magnitude of NEE. The changes in precipitation will affect water balance via abiotic (e.g., drought, soil water recharge) and biotic (e.g., stomata control) processes, which are closely coupled with carbon balance. Jackson et al. (2002) indicated an increase in carbon storage with a decrease in precipitation in systems where shrub is replacing with grassland. In turn, the changes in vegetation composition will influence evapotranspiration, water recharge, and runoff through stomatal behavior (Skiles

and Hanson, 1994), leaf area (Kergoat, 1998), and phenology (Peel et al., 2001). Therefore, considering the interaction between carbon and water balances and paucity of studies connecting the two components, the feedback processes between the two components need to be assessed for semi-arid ecosystems.

Water limitation in arid and semi-arid regions can affect vegetation dynamics and ecosystem process on the scale of hours to decades (Westoby et al., 1989; Walker, 1993; Schwinning et al., 2004). Considering the complex non-linear processes and dynamics, any change in resource availability might create a wider range of variability in vegetation dynamics and consequently carbon budgets than many other ecosystems (e.g., forests).

5. Conclusion

This study has quantified the patterns and magnitudes of NEE and the relationship between NEE and major environmental factors across two summer seasons in a sagebrush-steppe ecosystem. The comparison of the response of NEE to environmental drivers over the two summers highlights (1) the strong effect of winter/spring precipitation on carbon flux dynamics and (2) the potential influence of altered precipitation patterns on carbon balance at the sagebrush-steppe ecosystem. Dependence of NEE on soil moisture and atmospheric drought eliminates the possibility of applying light response function to predict daytime NEE while dependence of ecosystem respiration (i.e., nighttime NEE) on soil moisture constrains the possibility of using a Q_{10} function to predict ecosystem respiration at the study site. Although the short-term data obtained in this study limit predictability of ecosystem response to climate change over longer-term, different responses of NEE with dissimilar spring precipitation suggests that intra-seasonal variability in precipitation can alter the magnitudes and patterns of NEE at diurnal to seasonal time scale over sagebrush-steppe ecosystems. Incorporating such mechanisms into ecosystem models of semi-arid shrub lands will thus improve predictive understanding.

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