



Original Research

Biophysical Factors and Canopy Coupling Control Ecosystem Water and Carbon Fluxes of Semiarid Sagebrush Ecosystems[☆]David E. Reed^{a,b,*}, Brent E. Ewers^{b,c}, Elise Pendall^{c,d}, Kusum J. Naithani^e, Hyojung Kwon^f, Robert D. Kelly^{b,g}^a University of Wisconsin, Department of Atmospheric and Oceanic Science, Madison, WI 53706, USA^b University of Wyoming, Program in Ecology, Laramie, WY 82071, USA^c University of Wyoming, Department of Botany, Laramie, WY 82071, USA^d Western Sydney University, Hawkesbury Institute for the Environment, Penrith, NSW 2571, Australia^e University of Arkansas, Department of Biological Sciences, Fayetteville, AR 72701, USA^f Oregon State University, Department of Forest Ecosystems and Society, Corvallis, OR 97331, USA^g University of Wyoming, Department of Atmospheric Science, Laramie, WY 82071, USA

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ABSTRACT

The sagebrush-steppe ecosystem covers much of western North America, and its productivity is sensitive to warming and increasingly variable precipitation. Interannual variation in precipitation has been shown to be the most significant factor controlling biogeochemical cycling while both soil and atmospheric drought are dominant factors of ecosystem fluxes. We show that plant canopies can also act to limit water losses through stomatal and aerodynamic control. We use 4 data-yr from 2 sites (2 069 and 2 469 m above sea level elevation, respectively) to evaluate control of carbon and water fluxes and to calculate the degree to which the ecosystem canopy and atmosphere are decoupled. Environmental conditions were similar between the two sites, although the lower elevation site was slightly warmer (1.8°C higher temperature) and drier (0.2 kPa higher vapor pressure deficit). Ecosystem responses of net ecosystem exchange (NEE) and evapotranspiration (ET) to environmental drivers were similar between sites and years, with the wet site-yr 2009 having the largest ET and NEE fluxes. Canopy leaf area led to divergent behavior of the canopy-atmosphere decoupling parameter under high (> 11% by volume) soil moisture conditions. During low (< 11%) soil moisture periods, both sites had tight ecosystem stomatal control on ET with little NEE activity. This study highlights how semiarid ecosystems can alter their canopy leaf area in order to control how decoupled semi-arid canopies are to the atmosphere, potentially moderating impacts of climate change.

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Introduction

Shrublands and mixed shrub/grasslands combine to cover 29% of North America and 8% of the global land surface (Loveland et al., 2000). Biological processes in these steppe ecosystems are controlled by water availability; they are characterized by long dry periods with relatively small amounts of carbon respiration balanced by short periods of potentially strong carbon uptake during the growing season (Svejcar et al., 2008). Ecosystem flux observations that quantify net ecosystem exchange (NEE) of carbon dioxide show that semiarid systems

may switch between net carbon sources and sinks based on the timing and amount of precipitation (Gilmanov et al., 2006; Luo et al., 2007). Different semiarid ecosystems such as shrublands, savannas, and desert scrub have individual annual precipitation thresholds that regulate when NEE switches between negative and positive (Scott et al., 2015).

Climate variability in the Rocky Mountain region is expected to increase, including more frequent temperature and precipitation extremes (Stocker, 2014). Responses of NEE and evapotranspiration (ET) fluxes to this increased variability in semiarid ecosystems are more dependent on the timing and amount of precipitation and the depth of available moisture than other ecosystem types (Huxman et al., 2004; Ivans et al., 2006; Kwon et al., 2008; Svejcar et al., 2008; Sanchez-Mejia et al., 2014; Scott et al., 2015). Small precipitation pulses in semiarid ecosystems have been shown to maintain leaf and canopy area (Yan et al., 2000), and there is a correlation between precipitation timing and amount with canopy growth in sagebrush (Ivans et al., 2006). When the net effects of climate change on both plant species (Anderson and Inouye, 2001) and plant functional type (Ewers and Pendall, 2008) are

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considered in sagebrush ecosystems, it is possible that these ecosystems will lose more carbon than otherwise expected (Jackson et al., 2002), potentially acting as a positive feedback to climate change.

Canopy-atmosphere studies in semiarid ecosystems show that canopies influence biophysical processes across large scales. Canopy leaf area acts to modify how efficiently plants use precipitation during dry conditions (McLendon et al., 2008) while photosynthesis and respiration rates can be modified during periods of brief water availability (Huxman et al., 2004). Fractional plant cover and albedo (Sanchez-Mejia et al., 2014), as well as overall site energy balance (Alfieri and Blanken, 2012), can moderate water use through changing the partitioning of heat fluxes between latent and sensible components. However, biophysical processes at small spatial scales might be more important than previously realized in sagebrush ecosystems. In a recent study by Alfieri and Blanken (2012), large differences were noted in the partitioning between sensible and latent heat fluxes on the scale of tens of meters in sagebrush that were previously considered horizontally uniform. This would lead to variations in the vertical soil water profile across similar scales, in turn affecting aboveground canopy properties such as canopy biomass and albedo (Sanchez-Mejia et al., 2014).

While canopy leaf area index in semiarid ecosystems can be difficult to quantify (White et al., 2000), small canopy structure changes can cause proportional changes to hydrological cycling components, which, in semiarid ecosystems, could lead to large changes in the carbon balance (Scott et al., 2015). Scott et al. (2015) show that water availability in semiarid ecosystems is a primary driver of productivity and that leaf area differences may contribute to the speed at which ecosystem carbon cycling adjusts to large-scale climatic shifts. In more mesic regions, ecosystem water conductance (Monteith and Unsworth, 2008) and canopy coupling (Jarvis and McNaughton, 1986) studies have also highlighted the connection between vegetation biomass changes and ecosystem fluxes; however, studies on canopy coupling in semiarid systems are less commonplace. In this study, we aim to use the canopy coupling parameter outlined by Jarvis and McNaughton (1986) as a means to quantify how ecosystems can act to control NEE, ET, and ecosystem water use under variable climate conditions.

Using multiyear (from 2006 to 2009) data from two shrubland eddy covariance sites, we will address the following questions: 1) What are the relationships of NEE and ET with biophysical variables at annual and seasonal scales? 2) Does canopy structure and canopy-atmosphere coupling change between research sites that are relatively close in space (80 km) and in elevation (400 m)? and 3) Are ecosystem fluxes in semiarid ecosystems a function of canopy coupling? Evaluation of these questions will increase the understanding of feedbacks between canopies and water relations of semiarid plant communities.

Methods

Site Description

Two eddy covariance towers, one located in Saratoga, Wyoming (41.3966°N, 106.8024°W at 2 069-m elevation) and the other located in Walden, Colorado (40.7838°N, 106.2618°W at 2 469-m elevation), were installed in 2005 to understand the influence of elevation on ecosystem NEE and ET fluxes in big sagebrush (*Artemisia tridentata*) ecosystems. Big sagebrush is common in semiarid ecosystems throughout the intermountain western United States, and these steppe ecosystems are characterized by greater potential evapotranspiration than precipitation. In the Northern Rockies, summers are hot and dry while winters are cold with most of the yearly precipitation occurring as snow. Vegetation was primarily mountain big sagebrush (*Artemisia tridentata vaseyana*) at Walden and black sagebrush (*Artemisia tridentata nova*) at Saratoga with several perennial grasses (e.g., *Festuca idahoensis* and *Poa secunda*, *Koeleria macrantha*) and forbs (e.g., *Stenotus acaulis*, *Eriogonum umbellatum*, *Phlox* spp.), with sagebrush cover averaging 18% and a total vegetation cover of 36% (Mitra et al., 2014). Soil at

both sites was sandy loam texture to a depth of at least 150 cm; the soil type at Saratoga was McFadden sandy loam and at Walden it was Bosler sandy loam (Natural Resource Conservation Service).

Annual air temperatures averaged 5.1°C (range of daily averages: –14.9 to 34.4°C) at the Saratoga site and 3.3°C (–19.6 to 32.3°C) at the Walden site during this study. Summer precipitation was recorded at each site via TE525WS rain gauges (Texas Electronics Inc., Dallas, TX). Because these steppe ecosystems are snow dominated by high winds, the required high-maintenance snow gauges were not used. Annual precipitation data from the Wyoming Water Resources Data System (WRDS, 2016) were used for regional climate data from the Upper Platte Basin. The growing season for this study was defined as 1 May – 30 September, which was determined by average snow-free periods.

Eddy Covariance Data

Both sites had near-level topography (< 1%) and were instrumented with CSAT3 (Campbell Scientific Inc., Logan, UT); LI-7500 (LI-COR, Lincoln, NE); and a CNR-1 four-component net radiometer (Kipp and Zonen, Delft, The Netherlands). Sensors were mounted on short tripod towers at approximate heights of 3.0 m at Saratoga and 2.3 m at Walden. Slow-response temperature and relative humidity sensors (HMP45C; Vaisala, Finland) were also present at each site (2 m). Thirty-cm-long soil moisture probes (CS616; Campbell Scientific Inc., Logan, UT) were installed at depths of 0–15, 15–45, and 45–75 cm to measure soil water content, with the sensors at the shallow depth installed at approximately 30 degrees from the soil surface to give a measurement depth of 15 cm, allowing for higher-measurement resolution near the surface. Analysis was done using the 15- to 45-cm depth layer soil due to the fact that the 0-to 15-cm layer was predominantly dry. Two soil heat flux plates (HFP01SC; Hukseflux, Netherlands) were collocated at a depth of 5 cm to measure soil heat flux (G). Both 10 Hz (CSAT3 and LI-7500), and slow-response (HMP45, CS616, and HFPs) instruments were logged on a CR5000 data logger (Campbell Scientific Inc., Logan, UT) with slow-response sensors sampled once per minute and averaged to 30-min time scales.

Ecosystem fluxes were computed from the 10-Hz data and output as 30-min averages (Lee et al., 2004), and the 10-Hz data were despiked (Frank et al., 2014). Calibration drifts were addressed using the slow response HMP45 relative humidity sensor (Loescher et al., 2009). Wind data were rotated and planar fitted (Finnigan et al., 2003), and time lags between spatially separate sensors were corrected (Horst and Lenschow, 2009). Spectral corrections were applied following the methods of both Horst (2000) and Massman and Lee (2002). Finally, the WPL correction was applied to 30-min fluxes (Webb et al., 1980).

Vapor pressure deficit (VPD) was calculated as described by Murray (1967) and Monteith and Unsworth (2008) as:

$$VPD = \left(\frac{0.611e^{17.27 T_a}}{T_a + 273.3} \right) - (\rho_a 461.5 \square) \quad (1)$$

Here T_a is air temperature and ρ_a is water vapor mass density, both recorded as 30-min averages. Ecosystem water use efficiency (eWUE) was calculated as the ratio of weekly average NEE to weekly average ET (Emmerich, 2007; VanLoocke et al., 2012). Atmospheric momentum flux was calculated and recorded as the Reynolds stress (τ) (Lee et al., 2004).

Leaf Area Index Measurements

Canopy leaf area index (LAI) measurements were recorded with LAI-2000 Plant Canopy Analyzers (LI-COR, Lincoln, NE) on 23 July 2005 and 17 August 2005 at Walden and 23 July 2005 and 16 August 2005 at Saratoga. Measurements were taken along a 10-m linear transect with observations taken every 1 m. Data from both sampling times were

grouped by field site for statistical analysis. Due to the limitations of the sensor, canopy leaf area cannot be distinguished from canopy woody biomass. Therefore, the observed LAI is only an approximation to true leaf area and will be referred to as effective LAI_e. Saratoga had a non-significantly lower average LAI_e at 0.67 m² m⁻² compared with Walden at 0.80 m² m⁻² ($P > 0.05$). However, Saratoga also had a larger variability of LAI_e, with a standard deviation of 1.15 m² m⁻² compared with a standard deviation at Walden of 0.96 m² m⁻². Average canopy height was 1 m at Walden and 0.5 m at Saratoga.

Atmosphere-Canopy Decoupling Parameter

The rate of evaporation (Jarvis, 1976; Jarvis and McNaughton, 1986) can be written in the form described in Monteith and Unsworth (2008):

$$E = \Omega E_q + (1 - \Omega)E_i \quad (2)$$

Where E is the ecosystem-level evapotranspiration as measured by eddy covariance, Ω is the canopy decoupling coefficient, E_q is the equilibrium evapotranspiration rate, and E_i is the imposed evapotranspiration rate. The equilibrium evapotranspiration rate is calculated by Priestley and Taylor (1972) as:

$$\lambda E_q = \alpha \frac{\Delta R_n}{\Delta + \gamma} \quad (3)$$

Where λ is the latent heat of vaporization of water, α is the fitted Priestley-Taylor coefficient, Δ is the change of saturation pressure with temperature, R_n is ecosystem net radiation, and γ is the psychrometric constant.

The imposed evapotranspiration rate represents the flux from a surface that is decoupled from the saturation deficit of the atmosphere (Monteith and Unsworth, 2008):

$$\lambda E_i = \rho C_p VPD / (\gamma r_s) \quad (4)$$

Here ρ is dry air density, C_p is the specific heat of air, and r_s is total ecosystem resistance to water flux. r_s is fitted to data at the ecosystem level using inverse Penman-Monteith modeling (Monteith and Unsworth, 2008). Together these equations allow calculation of Ω , which measures the extent of ecosystem canopy decoupling with the atmosphere. It varies between 0 (full ecosystem/stomatal control of ET) and 1 (no ecosystem/stomatal control of ET).

Soil r_s was calculated as an empirical function developed from similar dry sandy loam soils:

$$\text{Soil } r_s = 1000 e^{0.3563 (\theta_{min} - \theta)} \quad (5)$$

Here soil moisture, θ , and the yearly minimum of soil moisture, θ_{min} , was measured at the 15- to 45-cm layer. Plant r_s was calculated as the difference of total ecosystem r_s and soil r_s .

Statistical Analysis

Data collection started in 2005 (2 November start date at Saratoga and 21 December at Walden) and ended in 2009. Flux data were not reliable in 2006 from Saratoga due to large gaps from intermittent power and failure of instruments and thus were not included in this analysis. The rate of missing data was 57% at Saratoga and 54% at Walden. Flux data processing and statistical analyses were done using MATLAB (R2010a, Mathworks Inc., Natick, MA).

Within the LAI_e dataset, outliers were defined as being larger than the 75th percentile. For linear regression, results are shown if the regression P value was < 0.05 . Soil moisture at 15- to 45-cm depth from both sites was pooled, and the median soil moisture value of 11% was used to bin data into high and low soil moisture periods. When averaged

to weekly timescales, the 11% value was also used to define low or high soil moisture conditions.

Results

Regional Climate

The North Platte River basin experienced long-term drought during the study period of late 2005 through early 2010 (Fig. 1) relative to the long-term (1895–2011) annual average precipitation of 308 mm. The 5-yr running average of precipitation over the basin was below average for about a decade, with near-average precipitation in both 2003 (301 mm annual precipitation) and 2004 (300 mm), but much drier years from 1999 to 2008 (255 mm). The drought ended in 2009 with the next 3 yr having average or above-average precipitation. For the purpose of this work, site yr 2006–2008 can be classified as dry yr with 210, 269, and 272 mm of annual precipitation, respectively, and 2009 as a wet year with 386 mm of precipitation.

Time series of growing season data from both sites are shown in Figure 2 as averaged daily values. Net radiation (Fig. 2a and b) was similar between sites. Air temperature (Fig. 2c and d) was on average 3.2°C higher at the lower-elevation Saratoga site, which in turn caused VPD (Fig. 2e and f) to be 0.2 kPa higher on average at Saratoga. Soil moisture values between depths of 15 and 45 cm are shown in Fig. 2g and h and show responses to late summer/early fall rain patterns at the end of the growing season, as well as the expected seasonal drying pattern. The increased precipitation of 2009 was not observed in the soil moisture record, due to a data gap in the early parts of the 2009 growing season.

The ET at the Saratoga site (Fig. 2i) showed a clear wet year and higher average flux in 2009 compared with 2007 and 2008. ET was similarly low in 2006 through 2008 at Walden (Fig. 2j). Ecosystem NEE (Fig. 2k and l) is related to ET with higher carbon uptake (more negative) in 2009 at Saratoga and lower uptake values throughout the study period at Walden.

Interannual and Intersite Differences

Overall energy closure was 67.7% at Walden and 68.8% at Saratoga. Energy closures shown in Figure 3 did not include energy storage terms and are comparable to other short canopy sites within the Ameriflux Network.

The relationships of ecosystem NEE and ET to environmental drivers of VPD and air temperature for both sites combined are plotted by year in Figure 4, with regression results in Table 1. The two sites are grouped by year, with data averaged by week during the growing season. Due to the weekly averaging, net radiation was not used as it showed small week-to-week variations.

Regression results of ET to both VPD (Fig. 4a) and air temperature (Fig. 4c) are statistically significant ($P < 0.05$) in 2008 and are not significant ($P > 0.05$) in all other years. NEE regressions are statistically significant ($P < 0.05$) in 2008 for VPD (Fig. 4b) and air temperature (Fig. 4d) and in 2007 for soil moisture (Fig. 4f).

Ecosystem ET and NEE are compared between sites in Figure 5 and Table 1. Data from all site years are averaged together over 1-wk periods. In order to remove periods of ecosystem dormancy from the data, regression results were computed only on weeks with $\geq 11\%$ soil moisture. As expected, there is a positive correlation between air temperature and ET for both sites (Fig. 5c), but air temperature and NEE were correlated only at Walden (Fig. 5d). Neither ecosystem flux had significant regressions for VPD (Fig. 5a, b) or soil moisture (Fig. 5e, f).

Canopy-Atmosphere Decoupling

The canopy decoupling parameter (Ω) was calculated on a weekly basis and varied during the study between 0.1 and 0.7 for both sites (Fig. 6). During the growing season and at low soil moisture values

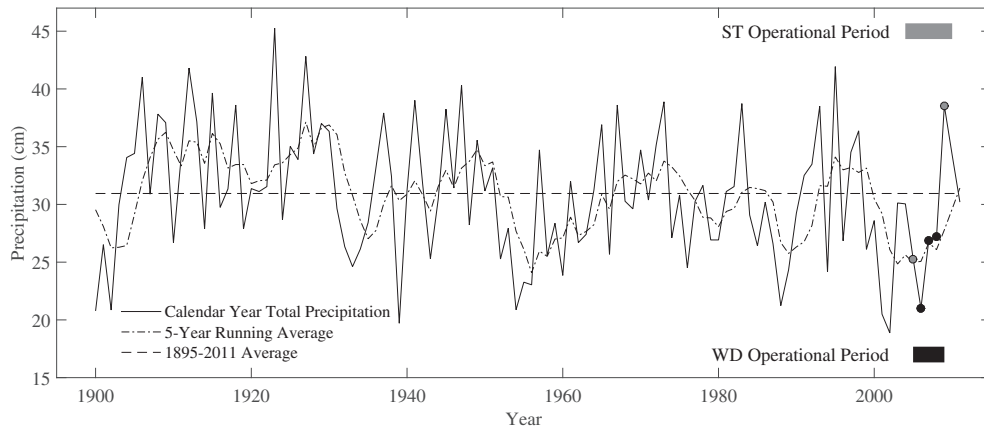


Figure 1. Long-term regional (Upper North Platte Basin) climate precipitation used for the Saratoga (ST) and Walden (WD). Active flux measurement periods at field sites are shown as gray circles for Saratoga and overlaid with black circles for the shorter measurement period at Walden. Climatological data are produced by the Wyoming Water Resources Data System (<http://www.wrds.uwyo.edu>) and the National Climatic Data Center (<http://www.ncdc.noaa.gov/oa/ncdc.html>).

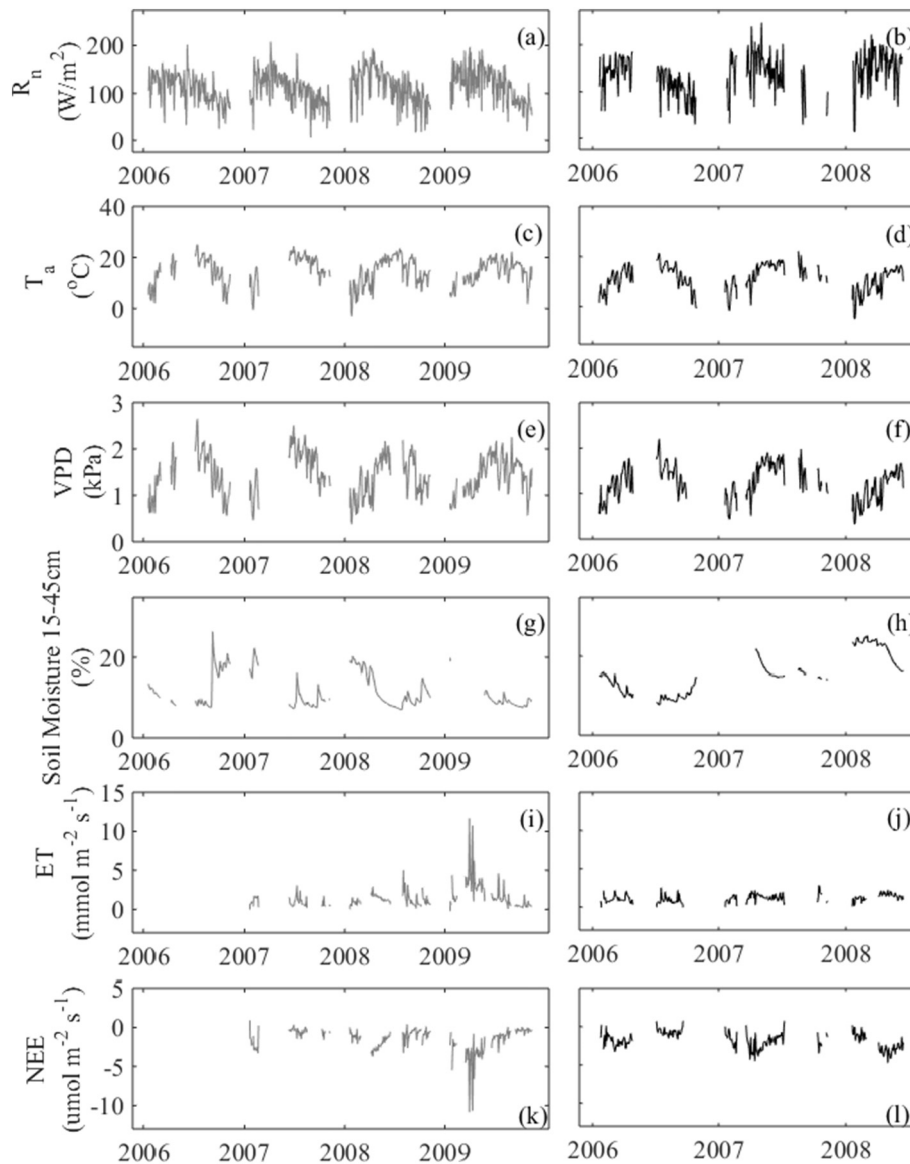


Figure 2. Time series of environmental conditions and ecosystem fluxes at both Saratoga (2006–2009) and Walden (2006–2008). Environmental daily averages of net radiation (a and b), air temperature above canopy (c and d), above-canopy vapor pressure deficit (e and f), and soil moisture at 15–45 cm depth (g and h). Ecosystem fluxes of water (evapotranspiration [ET]) (i and j) and carbon (net ecosystem exchange [NEE]) (k and l) are shown from 2006 to 2009, but 2006 data from Saratoga are not shown here due to data issues.

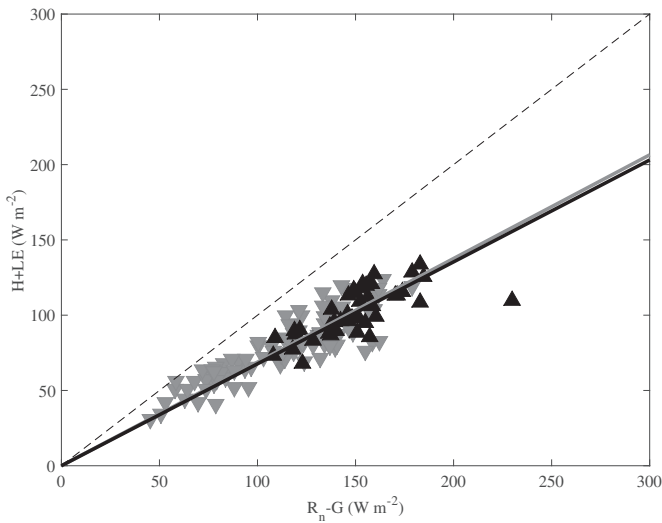


Figure 3. Energy closure, calculated at daily time scales for the growing season, from Saratoga (gray downward pointing triangle, lower elevation site) was 69% and Walden (black, upward pointing triangle, higher elevation site) was 68%. Only data with zero gaps per day were used for energy closure calculations. Dashed line is a 1:1 line.

(< 11%), there was little difference in Ω between sites. Only at relatively high soil moisture levels (> 11%) did values of Ω begin to diverge on the basis of site. Average Ω at soil moisture above 11% at Saratoga was 0.42 (SD \pm 0.11) while Walden was 0.30 (SD \pm 0.09). At soil moisture values > 11%, Ω did not vary significantly between years (results not shown),

implying that Ω was not connected to differences in interannual water availability.

Plant and soil r_s is shown in Figure 7a and b, respectively. Canopy decoupling is shown for both sites as related to ecosystem fluxes of NEE, ET, and momentum (Fig. 8). Regressions were valid ($P < 0.05$) between Ω and all variables at Saratoga, due in part to Ω values over a larger range (ST Ω range = 0.11–0.64, WD Ω range = 0.09–0.5). Both sites showed similar relationships between canopy decoupling and eWUE; however, significant differences in slopes ($P < 0.05$) between sites were noted for momentum fluxes, with the regression slope at Saratoga not differing from zero ($P > 0.05$).

Discussion

During the dry yr of 2006–2008, there were only small differences in the ecosystem NEE and ET fluxes, as well as the environmental controls of those fluxes between sites, supporting a prior study where dry periods led to small ecosystem fluxes in sagebrush steppe (Kwon et al., 2008). In the wet yr of 2009, a large increase in ET and NEE uptake was noted during the growing season at Saratoga, although the Walden site was not operational that year. Our work thus supports previous studies demonstrating that water availability is the dominant control of ecosystem carbon fluxes in semiarid ecosystems (Gilmanov et al., 2003; Gilmanov et al., 2006; Ivans et al., 2006; Kwon et al., 2008; Svejcar et al., 2008; Schlaepfer et al., 2012; Scott et al., 2015; Villarreal et al., 2016).

We observed strong relationships between ET and VPD during 1 yr (2008) of this study. Due to the interdependency of VPD and air temperatures, we also noted a significant relationship between ET and air temperature at both sites. Recent studies in the same region have indicated

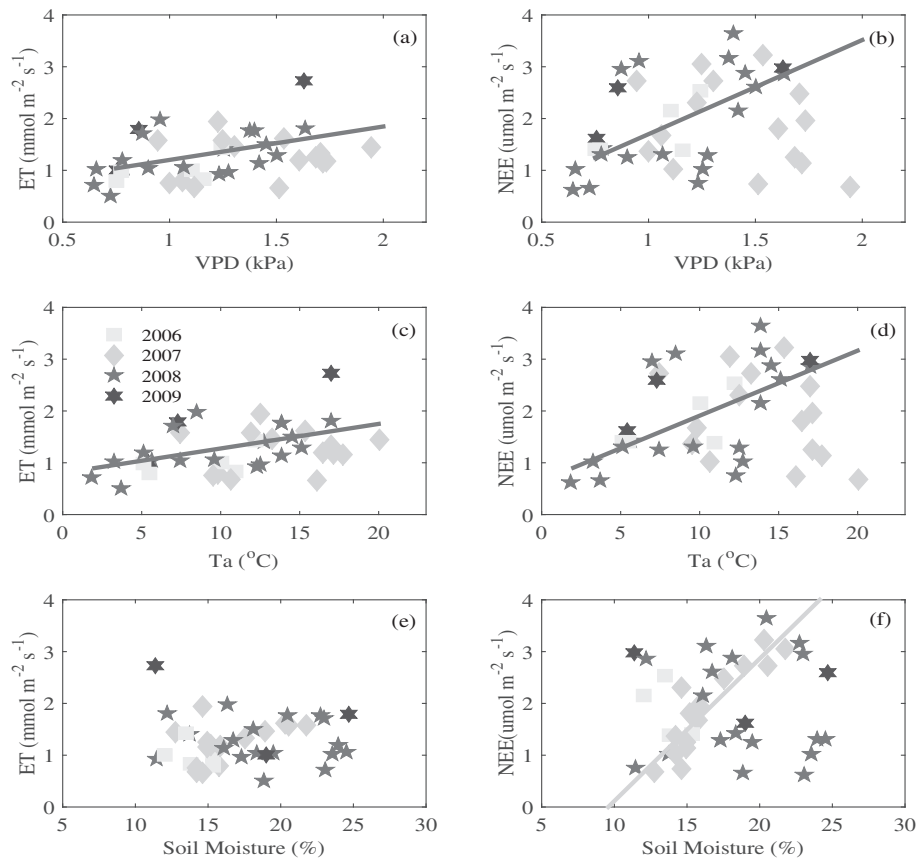


Figure 4. Water (evapotranspiration [ET]) and carbon (net ecosystem exchange [NEE]) fluxes as functions of vapor pressure deficit (VPD; **a** and **b**), air temperature (T_a ; **c** and **d**), and soil moisture (**e** and **f**). Data were combined from both sites. Regression line was only significant for soil moisture (NEE $P < 0.01$) in 2007 and for VPD (ET $P = 0.03$, NEE $P = 0.01$) and T_a (ET $P = 0.02$, NEE $P = 0.01$) in 2008.

Table 1

Regression results of slope and intercept for environmental drivers (vapor pressure deficit [VPD], air temperature [Ta]) and ecosystem fluxes. Nonsignificant regressions are left blank. 95% confidence levels are noted in brackets.

Y-axis	ET			NEE			ET			NEE		
X-axis	VPD			VPD			Air temperature			Air temperature		
	Slope	Intercept	R ² value	Slope	Intercept	R ² value	Slope	Intercept	R ² value	Slope	Intercept	R ² value
Units	(mmol m ⁻² s ⁻¹)/(kPa)	(mmol m ⁻² s ⁻¹)		(μmol m ⁻² s ⁻¹)/(kPa)	(μmol m ⁻² s ⁻¹)		(mmol m ⁻² s ⁻¹)/(C)	(mmol m ⁻² s ⁻¹)		(μmol m ⁻² s ⁻¹)/(C)	(μmol m ⁻² s ⁻¹)	
Site												
Saratoga	–	–	–	–	–	–	0.06 (0.00, 0.12)	0.76 (0.04, 1.47)	0.24	–	–	–
Walden	–	–	–	–	–	–	0.03 (0.00, 0.06)	0.91 (0.52, 1.30)	0.11	0.07 (0.00, 0.14)	1.18 (0.27, 2.09)	0.13
Yr												
2006	–	–	–	–	–	–	–	–	–	–	–	–
2007	–	–	–	–	–	–	–	–	–	–	–	–
2008	0.65 (0.06, 1.23)	0.56 (–0.13, 1.23)	0.25	1.82 (0.46, 3.17)	–0.12 (–1.67, 1.44)	0.34	0.05 (0.01, 0.09)	0.80 (0.37, 1.23)	0.28	0.13 (0.03, 0.22)	0.65 (–0.36, 1.67)	0.34
2009	–	–	–	–	–	–	–	–	–	–	–	–
Y-axis	ET			NEE			ET			NEE		
X-axis	Soil moisture			Soil moisture			Soil moisture			Soil moisture		
	Slope	Intercept	R ² value	Slope	Intercept	R ² value	Slope	Intercept	R ² value	Slope	Intercept	R ² value
Units	(mmol m ⁻² s ⁻¹)/(%)	(mmol m ⁻² s ⁻¹)		(μmol m ⁻² s ⁻¹)/(%)	(μmol m ⁻² s ⁻¹)		(mmol m ⁻² s ⁻¹)/(%)	(mmol m ⁻² s ⁻¹)		(μmol m ⁻² s ⁻¹)/(%)	(μmol m ⁻² s ⁻¹)	
Site												
Saratoga	–	–	–	–	–	–	–	–	–	–	–	–
Walden	–	–	–	–	–	–	–	–	–	–	–	–
Yr												
2006	–	–	–	–	–	–	–	–	–	–	–	–
2007	–	–	–	–	–	–	0.27 (0.19, 0.36)	–2.63 (–4.03, –1.23)	0.79	–	–	–
2008	–	–	–	–	–	–	–	–	–	–	–	–
2009	–	–	–	–	–	–	–	–	–	–	–	–

ET, evapotranspiration; NEE, net ecosystem exchange.

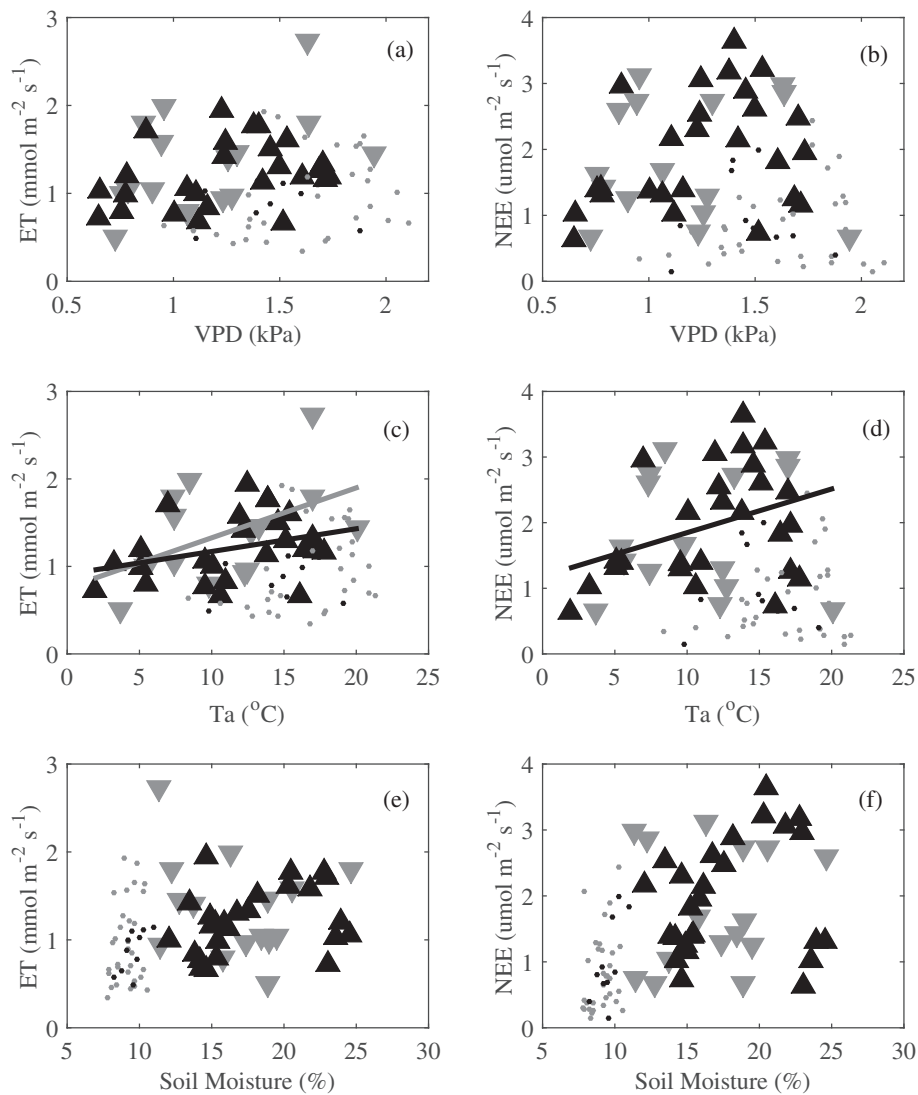


Figure 5. Intersite variability regressions of ecosystem fluxes and environmental conditions: Saratoga (gray) and Walden (black). Water flux (evapotranspiration [ET]; **a**) and carbon flux (net ecosystem exchange [NEE]; **b**) as functions of vapor pressure deficit (VPD), air temperature (T_a ; **c**, **d**), and soil moisture (**e**, **f**). Large symbols are weekly average values with soil moisture > 11%, small symbols are weeks with < 11% soil moisture. Regressions were performed only on high soil moisture dataset with low soil moisture data shown for completeness. Significant regression slopes between sites were not statistically different from each other (**c**).

a connection between sagebrush canopies and the atmosphere by using a soil ecohydrologic model and have found that plant responses are strongly controlled by atmospheric dryness (Schlaepfer et al., 2012) and available soil moisture at depth (Sanchez-Mejia et al., 2014). Naithani et al. (2012) used ecosystem-scaled sap flux methods and observed that soil and atmospheric drought, as seen in VPD, controlled leaf transpiration and stomatal conductance. Previous work has shown that VPD is a driver of net carbon cycling only when soil moisture is not limiting (Kwon et al., 2008). The Priestley-Taylor coefficient relating potential ET to equilibrium ET, α , is normally globally assumed to be 1.26 (Priestley and Taylor, 1972). In this study α was found to be 0.24 at weekly, 0.23 at daily, and 0.15 at 30-min time scales. These are generally within the range of values from 0.2 to 0.8 of α values from semiarid rangelands lands as reported by Stannard (1993).

Sagebrush canopies can vary between 0.25 and 1 m in height, depending largely on the subspecies. Sagebrush communities also tend to form “islands” in circular to oval-shaped patterns (Knight, 1996). Both factors present a short yet horizontally complex canopy for ecosystem-level gas exchange (Ewers and Pendall, 2008). Considering the importance of atmospheric vapor pressure deficit we observed, the LAI_e differences noted between these study sites can act as a control

of canopy-atmosphere decoupling to varying degrees within each site and is a probable major mechanism regulating gas exchange. Other canopy-atmosphere decoupling studies have shown that low Ω values (between 0.1 and 0.2) typically apply to coniferous tree species (Jarvis and McNaughton, 1986) and intermediate values (0.3–0.6) for broad-leaf tree species (Martin et al., 1999). The Ω values calculated in this study, 0.4 and 0.3, are much more coupled than typical agriculture Ω values (0.6–0.7) and grassland ecosystem values (0.8), which have short canopy heights as with sagebrush. Low Ω values mean more ecosystem control of water loss, implying sagebrush are able to retain water where other agriculture or grass systems would be losing water under the same environmental conditions. Under similar canopy structure parameters with hedge-field ecosystems, a canopy-coupling study found an Ω value of 0.22 for a hedgerow bordering ecosystems of shorter canopy height, namely grassland and fields (Herbst et al., 2007). While there are clear environmental differences between this study and the work of Herbst et al. (2007), the strong canopy-atmosphere coupling of the hedgerow was related to the relatively compact canopy, with much higher Ω values found in nearby tree lines having similar LAI_e values as the hedgerow. At the small spatial scales (10s of m) of Alfieri and Blanken (2012), similar amounts of

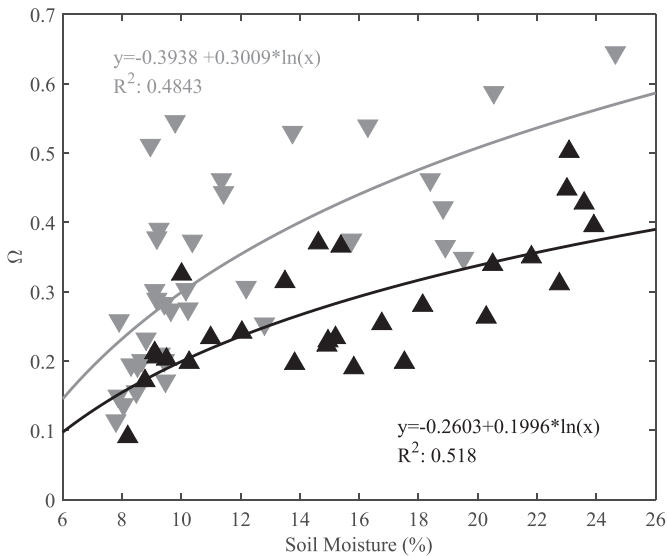


Figure 6. Weekly averaged atmosphere-canopy decoupling parameter Ω as a function of soil moisture at both sites; Saratoga in gray and Walden in black. Ω is plotted only for the growing season period.

canopy patchiness were observed, leading to differences in energy cycling across the small spatial scales. The connection between Ω values and the canopy is seen over one growing season in a maize canopy, where Ω was highly correlated with both leaf area and canopy height (Steduto and Hsiao, 1998).

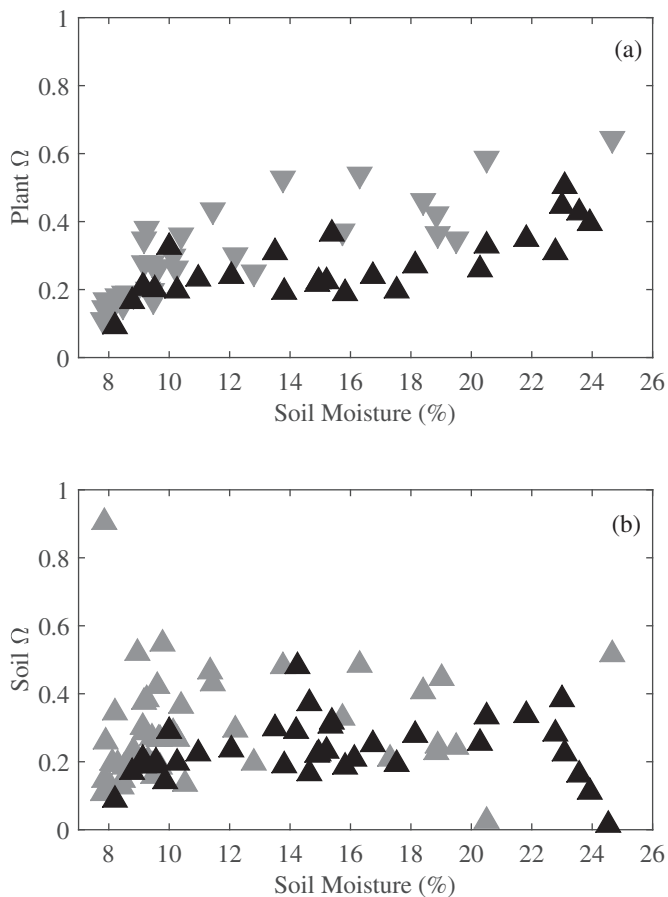


Figure 7. Weekly values of plant Ω (a) and soil Ω (b) as functions of soil moisture, at Saratoga (gray) and Walden (black).

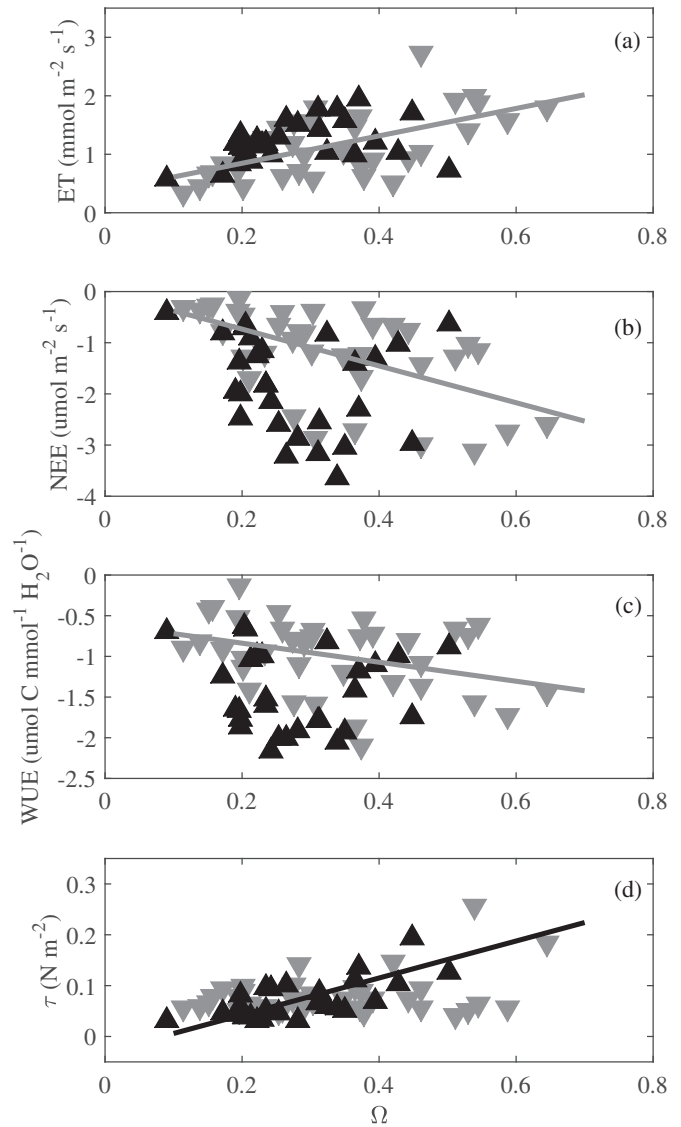


Figure 8. Weekly averaged evapotranspiration (ET) (a), net ecosystem exchange (NEE) (b), ecosystem water use efficiency (c), and momentum flux (d) as a function of atmosphere-canopy decoupling parameter Ω at both sites; Saratoga in gray and Walden in black. Ω is plotted only for the growing season period.

During dry ($< 11\%$ soil moisture) conditions, Ω values at both sites converged to small canopy-atmosphere decoupling. We attribute this to an overall lack of biological processes, with reductions of ecosystem water loss and carbon uptake occurring during periods of high soil drought. During these periods, we expect the ecosystem to behave more as a physically controlled system. As low Ω values normally signify stomatically controlled ecosystems where additional solar energy inputs leave the ecosystem via nonevapotranspiration pathways, in this case we suggest that a dry soil crust (Hillel, 2005) is acting to prevent soil evaporation from being greater than stomatal control of transpiration. While Ω values in this work are low, they are not zero due to available deeper soil moisture pools, which allow vegetation response during changing environmental conditions (Kwon et al., 2008; Sanchez-Mejia et al., 2014).

This canopy structure and decoupling mechanism helps to explain the lack of differences in carbon and water gas exchange measurements between sites. The less coupled site (Saratoga) experienced, on average, increased evaporative demand. Saratoga had less canopy leaf area and hence a reduced amount of stomatal control at the ecosystem level relative to the more coupled Walden site. ET fluxes at Saratoga were more

driven by environmental radiation. At Walden, with higher canopy leaf area and a more evenly distributed canopy, there was more leaf-level control over water losses. So while it would be expected that the higher-elevation Walden site would, on average, receive more precipitation and hence have larger ecosystem fluxes (Ivans et al., 2006), this was not observed during this study.

Conclusion

Although the two sagebrush study sites had similar environmental conditions and responses of ecosystem fluxes to those conditions during dry years, canopy-atmosphere decoupling was an important factor controlling ecosystem fluxes in both wet and dry years. These results support findings that soil and atmospheric drought are the dominant controls of biogeochemical cycling, with the interaction between canopy structure and the atmosphere enhancing or reducing plant control of water loss.

This study has important implications beyond water availability in semiarid ecosystems. Canopy-atmosphere interactions modulate ecosystem fluxes so that relatively small changes in canopy structure and leaf area can mitigate differences in ecosystem level fluxes from environmental changes. As climate predictions for the Northern Rockies include more variation in yearly precipitation amounts and timing, it is possible to envision a situation where canopy and LAI_c changes within these steppe ecosystems will moderate many potential impacts to biogeochemical cycling.

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