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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:

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

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

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