

Non-native grasses alter evapotranspiration and energy balance in Great Basin sagebrush communities

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Received 19 April 2006; accepted 23 August 2006

Abstract

Over the last century non-native plants have invaded sagebrush communities of the American West. The widespread transformation from native sagebrush to invasive grassland communities as a result of wildfire will likely alter key ecosystem processes in the Great Basin, including hydrology and energy balance. To determine how this invasion may be disrupting ecosystem function, we coupled measurements of evapotranspiration (ET) and energy fluxes using the Bowen ratio-energy balance method with measurements of normalized difference vegetation index (NDVI) and plant cover in native sagebrush and adjacent post-fire bunchgrass communities in the northern Great Basin Desert over the growing season of 2003. Soil heat flux and soil temperatures were generally greater and sensible heat flux and net radiation were lower in the post-fire community compared to sagebrush. These differences increased through the summer. The post-fire community had greater ET than sagebrush in early May, likely driven by relatively high volumetric soil moisture (>20%) and greater transpiration by the developing vegetation. In June and July, ET was correlated with surface soil moisture (top 20 cm) in both communities. During late May and June, surface soil moisture was greater in the sagebrush; however, there was no difference after mid-June when soil moisture declined below 10%. By disrupting surface-atmosphere exchange in the early growing season, conversion of native sagebrush to post-fire invasive communities may disrupt hydrologic patterns in this semi-arid ecosystem.

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Keywords: *Agropyron cristatum*; *Artemisia tridentata*; Bowen ratio-energy balance; Invasive plants

1. Introduction

Invasion of non-native plants is causing drastic changes in community composition and function in a variety of ecosystems (e.g. Vitousek et al., 1997). Non-native plants, such as cheatgrass (*Bromus tectorum* L.), have been aggressively invading the native sagebrush communities of the Great Basin Desert over the last century (Mack, 1981; Young et al., 1987). Abundant dry litter produced by non-native herbaceous species

provides tinder for widespread and frequent fires (Whisenant, 1994). Following fire, these plants are superior competitors for the limited water resources (Link et al., 1996) and displace native vegetation (Young et al., 1972). This replacement has significantly altered the structure of the landscape and has impacted important ecosystem processes, such as carbon and water cycling (Obrist et al., 2003; Prater et al., 2006).

The multiple stresses of invasions and recurring fires have caused the sagebrush ecosystem to shift to alternate, seemingly irreversible, post-fire communities dominated by a suite of non-native species. Additionally, land managers often reseed fire scars with a mixture of native and non-native seeds in an effort to reduce the establishment of noxious species (Pellant,

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1994). However, these reseeding practices often result in persistent communities of non-native species, such as crested wheatgrass (*Agropyron cristatum*), with native shrubs and grasses largely absent. With different phenology, non-native species often utilize soil water and nutrients at different times than natives (Holmes and Rice, 1996; Obrist et al., 2004; Prater et al., 2006). This widespread replacement of native communities with functionally different plant communities may severely alter ecosystem resource utilization.

Energy partitioning and evapotranspiration in sagebrush steppe ecosystems are markedly affected by seasonal patterns of water availability and plant phenology, and the relative magnitude and seasonality of energy and water fluxes may be very different from persistent post-fire communities dominated by herbaceous vegetation (Scott et al., 2000a). While most available energy in sagebrush steppe is allocated to sensible heat flux, latent heat flux can be as much as 25% of total net radiation during the early growing season (Wight et al., 1996; Malek and Bingham, 1997).

In sagebrush ecosystems, annual evapotranspiration (ET) often exceeds precipitation (Malek et al., 1997) as shrubs access deep soil moisture reserves to sustain growth during the summer drought (Link et al., 1990; Donovan and Ehleringer, 1992). More shallow-rooted bunchgrasses may not access these same resources when they become dormant or senescent as surface moisture is depleted (Link et al., 1990); thus, annual ET from grass communities in the same environment may equal precipitation inputs (Malek et al., 1997). Using a static chamber, Prater et al. (2006) found that when soil moisture was relatively abundant, instantaneous rates of ET can be substantially greater in a well-established perennial bunchgrass community compared to an adjacent sagebrush community, but the relative magnitude of these fluxes between sites varied strongly with time of year and with the composition of the post-fire community. These changes in water use throughout the season may render conditions unfavorable for the growth and establishment of native species and therefore reinforce the altered ecosystem state.

Changes in energy partitioning that accompany changes in land cover have been found in other systems. Large changes in the partitioning of sensible and latent heat occur immediately following fire (Bremer and Ham, 1999; Amiro, 2001). In grasslands, alterations in surface albedo, litter depth and vegetation cover controlled water and energy balance such that net radiation and surface conductance were greater in recently burned sites compared to intact prairie (Bremer and Ham, 1999). Evapotranspiration increased through

the season with increased vegetation cover as the post-fire community recovered from the burn. Conversely, in boreal forest ecosystems, post-fire tree communities had reduced net radiation and latent heat flux compared to the mature forests (Amiro, 2001). These differences disappeared in the decade following the fire when surface energy fluxes of successional communities became similar to the intact system (Amiro, 2001; Chambers and Chapin, 2002). Scott et al. (2006) found that ET was greater in arid communities that were invaded by woody species compared to native grass-dominated communities. However, few of these studies have investigated land cover changes as a result of invasive species replacing natives on a widespread basis.

The objective of this research was to investigate how the combined disturbance of fire and invasion may impact energy partitioning and evapotranspiration in intact sagebrush and an adjacent post-fire grassland community using the Bowen ratio-energy balance method. Measurements of plant cover and soil water content were used to determine the driving forces and interpret the effects of the plant community on the surface energy fluxes.

2. Methods

2.1. Research site

This research was conducted at Bedell Flats, located 35 km north of Reno, NV (39°51'N, 119°49'W, 1500 m elevation). Areas of the valley burned in 1984, leaving a large fire scar that was seeded by the Bureau of Land Management (BLM) with crested wheatgrass (*Agropyron cristatum* (L.) Gaertn.) immediately following the fire. Nearly 20 years after the fire, sagebrush was still largely absent and the post-fire community was a mixture of cheatgrass and perennial bunchgrasses (*A. cristatum* and *Stipa comata*) with occasional rabbitbrush (*Chrysothamnus viscidiflorus* [Hook.] Nutt.), which re-sprouts after fire. Across the road that served as a firebreak was a vast (>1 km²) continuous expanse of intact sagebrush, with infrequent individuals of rabbitbrush and smooth horsebrush (*Tetradymia glabrata* Gray). Mean shrub height was 0.75 m. Soils are a shallow sandy loam belonging to the Acrelane series (Baumer, 1983).

2.2. Bowen ratio theory

Bowen ratio-energy balance (BREB) towers were installed in both the intact sagebrush and in the bunchgrass communities to measure energy fluxes and

estimate evapotranspiration. The BREB method is an effective tool for measuring ET over landscapes in other similar ecosystems (Ortega-Farias et al., 1996; Bremer and Ham, 1999; Angell et al., 2001) and has been shown to correspond with lysimeter measurements of water loss under nonadvective conditions (Denmead and McIlroy, 1970).

The components of surface energy balance are: $R_n = \lambda E + H + G + S$, where R_n is the net radiation, λE the latent heat flux composed of latent heat of vaporization (λ) and rate of evaporation (E), H the sensible heat flux, G the soil heat flux and S is the heat stored in the system. Since soil moisture and vegetation cover are major determinants of how incoming radiation is partitioned into sensible and latent heat (e.g. Baldocchi, 1994; Kustas et al., 1996; Scott et al., 2000b; Baldocchi et al., 2004), the components of the energy balance change over the growing season. In spring, with increasing vegetation cover and soil moisture, more energy is utilized for ET, thereby decreasing the sensible heat loss. This variation in energy partitioning was quantified through BREB measurements, where the Bowen ratio, β is defined as (Bowen, 1926):

$$\beta = \frac{H}{\lambda E} = \frac{C_p \Delta T}{\lambda \Delta q}$$

where C_p is the specific heat of moist air at constant pressure, ΔT the temperature difference between two reference heights and Δq is the humidity difference over the same height interval. This equation assumes the eddy diffusivity of water is equal to the eddy diffusivity for heat (Monteith and Unsworth, 1990), which holds in the turbulent boundary layer under unstable conditions. Given the above ratio, λE and H can be calculated by

$$\lambda E = \frac{R_n - G}{1 + \beta}, \quad H = \beta \lambda E$$

While the BREB method works well when R_n is large, λE becomes undefined as β approaches -1 . These conditions typically occur only around sunrise and sunset.

2.3. Tower measurements

Surface energy fluxes were measured continuously in each community type from the time of maximum physiological activity (May, 2003) to the time when most herbaceous vegetation became dormant (July; Prater et al., 2006). Measurements were made at one permanent sampling location in each community at least 300 m

away from the road that served as a fire break. The post-fire and adjacent sagebrush communities extended for at least 1 km on either side of the road, providing sufficient fetch for tower measurements (Heilman et al., 1989). The Bowen ratio was calculated from measurements of the temperature (ΔT) and humidity gradients (Δq) over the surface using an instrumented tower. The temperature gradient was measured with sheltered and aspirated 0.08-mm diameter copper-constantan thermocouples at 1 and 3 m heights above the ground. To measure atmospheric water vapor, air samples at these two heights were drawn through separate mixing volumes and then sampled with a single HMP35C Temperature/RH Probe (Campbell Scientific Inc., Logan, UT) enclosed in a sealed, tee-shaped pipe fitting. Every two minutes the airflow sampled by the temperature/RH probe was switched from one height to the other. The instrument was allowed to stabilize (<45 s) before samples were recorded. Net radiation was measured directly with a Q-7.1 net radiometer (Radiation and Energy Balance Systems, Seattle, WA) oriented to the south and was corrected for variations in wind speed. The radiometer was mounted 2 m above the ground on an arm extending away from the tower, thus minimizing obstruction from the tower while providing sufficient footprint for the instrument. Wind speed and direction were measured at 2 m using a three-cup anemometer and wind vane (03001-L R.M. Young Wind Sentry Set; Campbell Scientific Inc.). Soil heat flux was measured with four heat-flux plates (REBS HFT-3, Campbell Scientific Inc., Logan, UT) installed at a depth of 8 cm at each tower location. To account for horizontal variation in soil heat flux, plates were located in open unshaded locations as well as underneath the vegetation canopy. Above each soil heat flux plate, 0.25-mm diameter copper-constantan thermocouples were installed at 2 and 6 cm below the soil surface. Soil moisture was measured with a reflectometer (CS615 Water Content Reflectometer, Campbell Scientific Inc.) installed between the soil heat flux plates. Total soil heat flux at the surface (G) was calculated using the soil heat flux measured at 8 cm, soil water content and temperature measurements as in Malek (1993). At each tower data were collected with a datalogger (CR10, Campbell Scientific Inc.) at 5-s intervals and averaged over a 20-min time period.

Surface soil moisture (top 20 cm) was measured weekly using a hand-held time domain reflectometer (TDR) probe (Hydrosense, Campbell Scientific Inc., Logan, UT). Moisture was measured at 20 random locations in each community. Measurements were taken under shrub canopies and in the inter-shrub spaces in the sagebrush community.

All sensors were factory calibrated prior to installation. Tower instrumentation was cross-calibrated for 3 days under greenhouse conditions. The towers were then installed adjacent to each other in the post-fire grass community. Calculated flux data (e.g. sensible, latent and soil heat fluxes) collected by the two towers over 3 days in the field did not differ by more than 4% during daylight and not more than 10% during nighttime hours. Following these calibrations, towers were installed in their respective plant communities.

Measurements of surface reflectance (normalized difference vegetation index; NDVI) were taken with a narrow band spectrometer (Unispec Spectral Analysis System, PP Systems, Inc., Haverhill, MA) along four 50 m transects in each community type approximately every 2 weeks. The spectrometer measured from 400 to 1100 nm wavelengths at 3 nm intervals. The end of the standard fore-optic was held 1.7 m above the ground, allowing a field of view of approximately 1 m diameter of ground area. Ambient full sunlight illuminated the canopy during each measurement and a standard white reference was scanned prior to each measurement. Canopy reflectance was calculated by comparing the sample reflectance to a standard reflectance. NDVI was calculated as a ratio of reflectances of near-infrared (R_{NIR}) and red (R_R) wavebands using the equation: $(R_{NIR} - R_R)/(R_{NIR} + R_R)$ as in Gamon et al. (1995). Measurements were taken at 50 random locations along four 50 m transects in each community type. Percent cover of green vegetation (grouped into categories of either forb, bunchgrass, shrub or *Bromus tectorum*) also was determined by the point-transect method (Elzinga et al., 1998) along the NDVI transects.

2.4. Data analysis

Tower data were analyzed following the criteria of Ohmura (1982) and Perez et al. (1999) that eliminated measurements when the direction or magnitude of the energy fluxes are unreasonable and inaccurate. Days in which more than 40% of the measurements failed were dropped from further analysis. Data were retained from each tower for 62 and 52% of a total of 73 days in the sagebrush and post-fire communities, respectively. Integrated daily values of each energy component were calculated by fitting a high degree polynomial to the diurnal curve and determining the area under the curve using SAS (PROC EXPAND; SAS, Version 7.1, The SAS Company, Cary, NC). To compare the two communities, days on which data were available from both towers were selected and means were calculated for blocks of days that had similar weather conditions

(total R_n and mean air temperature differed by <10%). Comparisons between communities were not examined with inferential statistics since measurements were not independent.

Soil moisture data was analyzed with analysis of variance (PROC MIXED, SAS) to test for community effects, using linear contrasts for post hoc comparisons. Regressions were calculated using PROC GLM (SAS).

3. Results

Particularly early in the growing season, the pattern of energy exchange in the post-fire and sagebrush communities was markedly different (Fig. 1). In May and June the loss of sensible heat to the atmosphere was the dominant component of energy exchange in the sagebrush community, and latent heat fluxes showed a well-defined mid-day peak. In contrast, latent heat flux to the atmosphere was the dominant

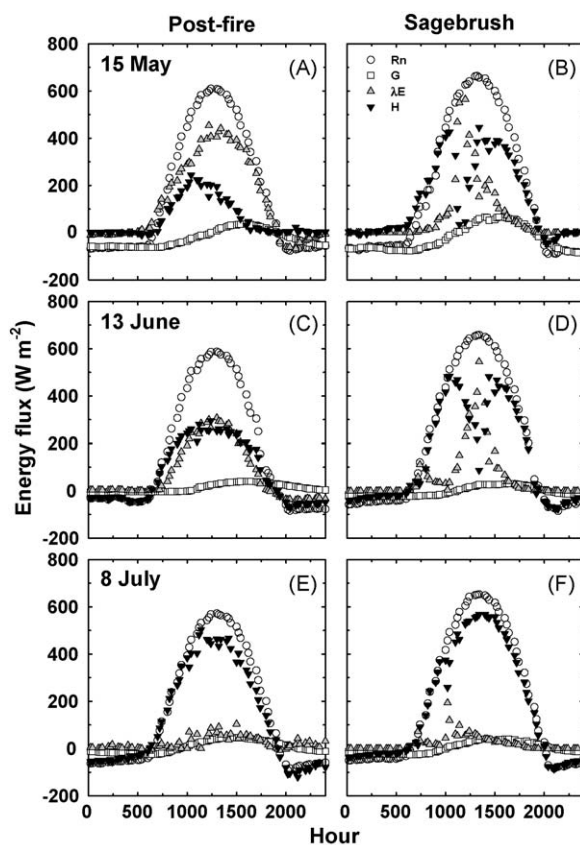


Fig. 1. Representative diurnal pattern of net radiation (circles), soil heat flux (squares), latent heat flux (grey triangles) and sensible heat flux (solid triangles) over post-fire bunchgrass (A, C and E) and native sagebrush (B, D and F) communities in 2003. Positive net radiation indicates incoming energy towards the land surface; all other positive fluxes indicate energy fluxes away from the land surface.

component of energy exchange in the bunchgrass community and the diurnal pattern of latent heat closely followed the change in net radiation during the day (Fig. 1). By July, the form of energy and its daily pattern of exchange were similar across community types; the major flux of energy to the atmosphere was sensible heat and it varied during the day in concert with net radiation (Fig. 1).

Net radiation consistently was greater in sagebrush than in the post-fire community (Fig. 2, Table 1). There was no seasonal pattern in the difference, but values of net radiation were $\sim 5\%$ to more than 17% greater in the sagebrush than bunchgrass community. As these communities were adjacent to one another, this difference presumably stems from differences in albedo.

At its maximum in May and early June, the percentage vegetation cover was similar in the sagebrush and post-fire communities ($\sim 80\%$) and beginning in June it declined strongly in both communities (Fig. 3). Cover in post-fire community was comprised primarily of forbs, bunchgrasses and *Bromus*, and shrubs were a minor component. Shrubs dominated cover in the sagebrush community, but *Bromus* contributed significantly from late May through June during its peak activity. NDVI values were highly correlated with percentage cover in both communities from June onward ($R^2 = 0.85$, $P < 0.01$), but underestimated actual cover early in the growing season. Dormant foliage from the previous growing seasons in the post-fire community and sparsely vegetated branches in the sagebrush contributed to estimates of percentage cover, but would not have made a substantial contribution to NDVI because of low reflectance in the red and infrared portions of the spectra.

The pattern of change in surface soil moisture (top 20 cm) during the growing season was different between communities (Fig. 4). The post-fire bunchgrass

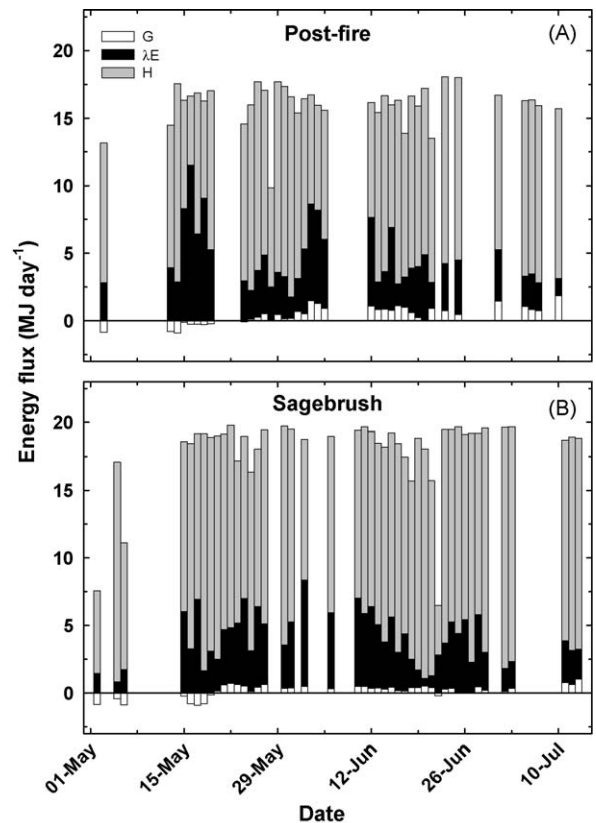


Fig. 2. Total integrated daily energy fluxes of soil heat flux (open bars), latent heat flux (solid bars) and sensible heat flux (grey bars) for post-fire bunchgrass (upper panel) and native sagebrush (lower panel) communities in 2003. Height of the bars represents the total incoming net radiation. Missing bars indicate times of unsuitable weather or instrument failure.

community had significantly greater soil moisture in early May but declined more rapidly than the adjacent sagebrush community, resulting in significantly lower soil moisture in late May and June. The two communities did not differ late in the season when surface soil moisture was largely depleted. ET was

Table 1

Partitioning of energy components (net radiation, R_n ; latent heat flux, λE ; sensible heat flux, H ; soil heat flux, G) for adjacent sagebrush and post-fire bunchgrass communities in the Great Basin Desert

Date	n	Sagebrush				Post-fire			
		R_n	λE	H	G	R_n	λE	H	G
15 May	5	18.3 (0.2)	4.2 (0.9)	15.2 (1.0)	-1.1 (0.3)	16.3 (0.2)	8.0 (1.2)	8.6 (1.7)	-0.7 (0.3)
24 May	4	18.2 (0.7)	5.0 (0.8)	12.0 (0.8)	0.8 (0.2)	17.3 (0.8)	3.5 (0.5)	13.3 (1.1)	0.7 (0.2)
30 May	3	19.3 (0.3)	5.4 (1.4)	13.2 (1.7)	0.8 (0.1)	16.8 (0.3)	3.2 (0.9)	13.0 (1.2)	0.6 (0.2)
12 June	5	18.7 (0.3)	4.5 (0.6)	13.6 (0.5)	0.7 (0.1)	16.1 (0.2)	3.9 (1.0)	10.5 (1.0)	1.8 (0.1)
21 June	3	18.3 (1.3)	2.9 (1.0)	14.9 (0.4)	0.5 (0.2)	16.9 (1.7)	3.2 (0.6)	12.1 (1.1)	1.4 (0.2)
5–11 July	3	18.8 (0.1)	2.7 (0.3)	14.9 (0.4)	1.6 (0.2)	16.0 (0.2)	2.0 (0.3)	11.6 (0.5)	2.3 (0.7)

Data are means (\pm S.E.) of integrated daily fluxes (in MJ day^{-1}), calculated for each date and n subsequent similar days when both towers were operating.

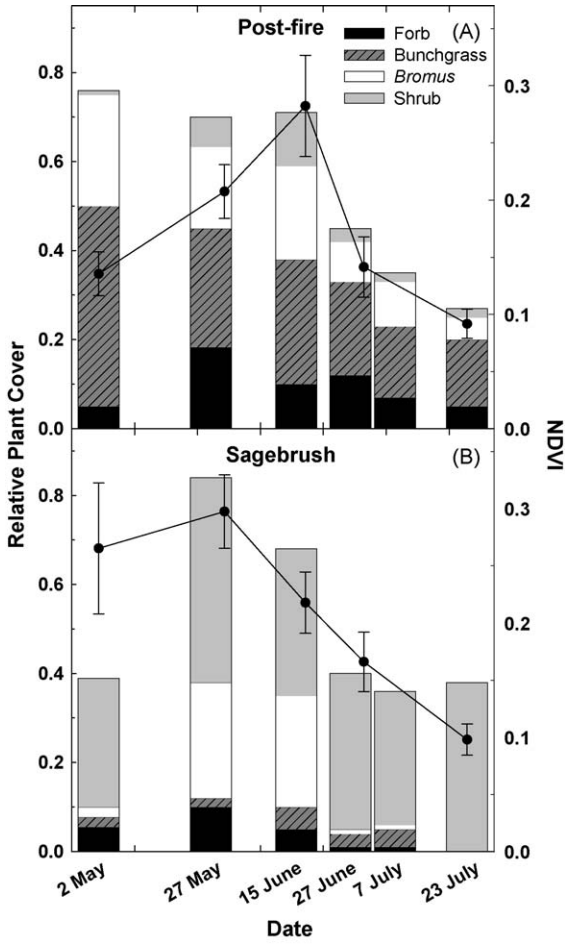


Fig. 3. Relative plant cover of forbs, bunchgrasses, *Bromus tectorum*, and shrubs (bars) and normalized difference vegetation index (NDVI) of post-fire bunchgrass (upper panel) and sagebrush (lower panel) communities. Points are means ($n = 50$) \pm S.E.

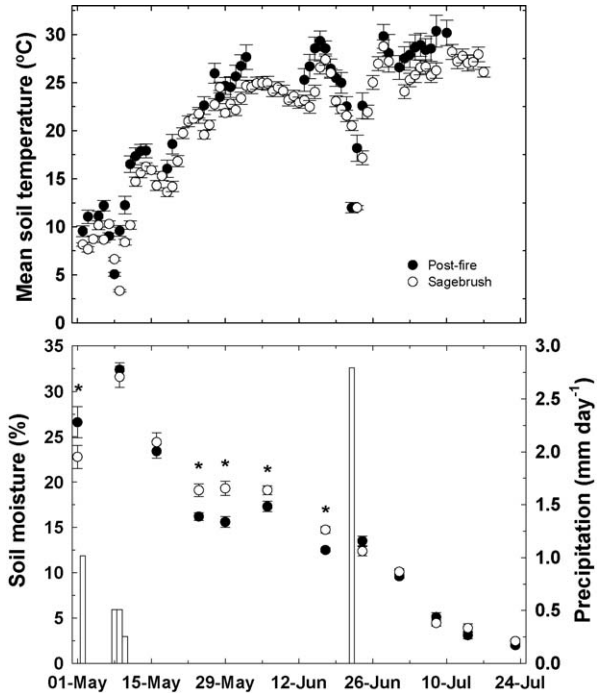


Fig. 4. Mean daily soil temperature in post-fire bunchgrass (solid symbols) and sagebrush (open symbols) communities. Each symbol is the mean ($n = 4$) averaged over a 24-h period. Mean volumetric soil moisture (top 18 cm) for post-fire bunchgrass (solid symbols) and sagebrush (open symbols) and total daily precipitation (bars). Each symbol represents the mean ($n = 20$) \pm S.E. Asterisks (*) indicate a significant difference between communities ($P \leq 0.05$).

correlated with surface soil moisture and NDVI across communities (individual regressions shown in Fig. 5; regression of soil moisture (x), NDVI (y) and ET (z): $z = 0.15x - 4.1y + 0.9$, $R^2 = 0.76$, $P < 0.01$).

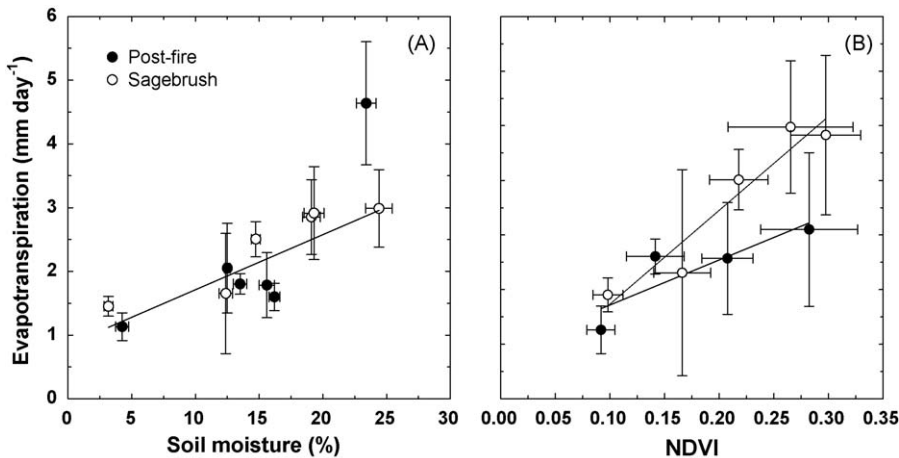


Fig. 5. Relationship of evapotranspiration and volumetric surface (top 20 cm) soil moisture (A) and normalized difference vegetation index (B; NDVI) of post-fire bunchgrass (solid symbols) and sagebrush (open symbols) communities. Soil moisture regression: $y = 0.11x + 0.5$, $R^2 = 0.64$, $P < 0.01$. NDVI regressions (sagebrush): $y = 8.6x + 0.5$, $R^2 = 0.92$, $P < 0.01$; post-fire after June: $y = 4.1x + 0.95$, $R^2 = 0.75$, $P < 0.01$.

Declines in ET corresponded to seasonal declines in cover and NDVI in both communities (Figs. 3 and 5), although the relationship was different between the two communities (slopes significantly different at $P < 0.05$). NDVI and ET were highly correlated in the sagebrush community (Fig. 5B; $y = 8.6x + 0.5$, $R^2 = 0.92$, $P < 0.01$). However, peak NDVI values occurred somewhat later than peak ET in the post-fire community. Early in May when post-fire NDVI was low, high rates of ET were likely caused by soil evaporation rather than plant transpiration. Therefore, there was no significant correlation between NDVI and ET for the post-fire community unless early season values were excluded (Fig. 5B; $y = 4.1x + 0.95$, $R^2 = 0.75$, $P < 0.01$).

4. Discussion

Conversion of sagebrush shrubland to non-native perennial grassland following fire altered surface energy partitioning in this semi-arid ecosystem during the growing season. Post-fire changes in the vegetation type and phenology resulted in decreased net radiation and sensible heat while increasing latent and soil heat fluxes at certain times during the growing season. The relationship between evapotranspiration (ET) and surface soil moisture was similar between communities; therefore, mid-season decreases in soil moisture and NDVI resulted in lower ET in the post-fire community compared to the sagebrush. These differences coupled with more rapid depletion of soil moisture by grasses will likely reinforce the new altered ecosystem state (Paine et al., 1998; Scheffer et al., 2001) and further inhibit re-establishment of native communities.

Actively growing post-fire vegetation early in the season resulted in a greater proportion of the available energy for evapotranspiration (Fig. 2). Crested wheatgrass is favored by a cool wet spring, as occurred in 2003, and typically has high water loss early in the summer (Trlica and Biondini, 1990). As soils dried and vegetation senesced, less total energy was devoted to latent heat than earlier in the season. The rapid depletion of surface soil moisture resulted in lower evaporation rates from the soil surface than early season rates (gas-exchange chamber data not shown). Additionally, transpiration from crested wheatgrass declines sharply after vegetation growth is completed for the season (Sala et al., 1981), which most likely accounted in part for the decrease in daily ET across the summer.

Seasonal decreases in soil moisture and leaf area corresponded to the decline in sagebrush ET (Fig. 5). Transpiration from sagebrush has been found to decline

linearly with soil water potential (Schlesinger et al., 1987) and decreases with vegetation cover (Prater et al., 2006). The magnitude and seasonal patterns of sagebrush ET were similar to those found in other Great Basin studies (Wight et al., 1996; Malek and Bingham, 1997; Wylie et al., 2003). Additionally, Wylie et al. (2003) found that while ET generally followed changes in NDVI throughout the year, peak rates of ET often do not correspond to peak values of NDVI. While there was a good relationship between sagebrush NDVI and ET in the current study (Fig. 5), peak ET did not correspond directly with peak NDVI. Spring rains that fell when LAI was relatively low and soil temperatures were periodically elevated were more likely to be lost through evaporation rather than infiltrating the soil (Huxman et al., 2004). These higher rates of soil evaporation, coupled with low transpiration rates, may have contributed to the disproportionately high rates of ET in early May than would be predicted for the lower leaf areas that occur before the larger spring leaves emerge.

Evapotranspiration increased linearly with surface (top 20 cm) soil moisture (Fig. 5), as found in other semi-arid systems (Kurc and Small, 2004). However, Kurc and Small (2004) found that ET was most closely controlled by surface (<5 cm) soil moisture in semi-arid shrublands and grasslands in New Mexico. The relationship was less significant with deeper soil layers and with total moisture in the rooting zone. In semi-arid regions, direct evaporation from bare soil is a large component of total flux and total moisture in deeper layers is more poorly correlated with ET than in temperate systems. In this study, ET was not correlated with surface soil moisture before mid-May, with relatively low rates of ET despite the highest soil moisture of the season. Transpiration from early season vegetation may have been temperature limited at this time. Post-fire evapotranspiration was greater than sagebrush ET in early May, corresponding with low soil and air temperatures (Fig. 4) and when soil moisture was also greater than in the post-fire bunchgrass. However, with rapid declines in soil moisture of the bunchgrass community in May, post-fire vegetation was unable to maintain high transpiration and evaporation rates, resulting in lower mid-season post-fire ET compared to sagebrush. ET was similar in both communities when surface soil moisture was depleted. Therefore, changes in ET associated with post-fire bunchgrass establishment were driven by altered soil moisture conditions in the bunchgrass community.

Differences in rates of ET between post-fire and native sagebrush communities often are determined by

community composition. Using a static chamber, Prater et al. (2006) found that the perennial bunchgrasses at Bedell Flats had higher morning ET than sagebrush. Similarly, in the current study morning ET rates often were higher in bunchgrasses compared to sagebrush; however, daily-integrated rates were similar to sagebrush values (Fig. 1C and D). Prater et al. (2006) found that post-fire communities dominated by annual invasive species had even larger declines in ET during the summer compared to intact sagebrush. Therefore, it is possible that differences in ET may be magnified as the cover of annual cheatgrass increases in mixed post-fire grasslands.

Other comparisons of grass and shrub communities revealed little or no difference in rates of ET between shrub and bunchgrass communities (Obrist et al., 2003; Kurc and Small, 2004; Prater et al., 2006), although in some cases the two community types were not compared directly (Stannard et al., 1994). Kurc and Small (2004) found few differences between ET in native semi-arid grasslands and invaded shrublands. In a more arid system, Dugas et al. (1996) found differences in surface energy balance were small and mostly related to leaf area and water supply rather than vegetation type. Therefore, differences between rates of ET may be determined mostly by how the structure and composition of the vegetation affects soil moisture and resource utilization.

Differences in net radiation between community types varied during the growing season and were caused by vegetation cover and albedo. Since incoming radiation was not different between these adjacent communities, greater albedo in the non-native post-fire community likely caused a reduction in available energy to the system (Chambers et al., 2005). This difference between the two communities generally increased through the season, as bunchgrasses and annuals senesced. Greater vegetation density causes lower albedo resulting in higher net radiation at shrub sites compared to grasslands (Fig. 1, Table 1). Shrub-dominated communities often have higher net radiation than grasslands in arid and semi-arid systems (Malek et al., 1997; Laymon et al., 1998). In our system, more energy was partitioned into soil heat flux in the post-fire community and soil temperatures were greater than in the sagebrush community, which may have increased emitted longwave radiation, resulting in lower net radiation.

While few studies have investigated energy partitioning in invasive grasslands, energy balance in sagebrush ecosystems is relatively well documented. Malek et al. (1997) and Malek and Bingham (1997) found similar magnitude and seasonal patterns of sensible and latent heat fluxes of Nevada sagebrush as in

the current study. However, Wight et al. (1996) found a large percentage of net radiation was partitioned into latent heat early in the season (75% compared to this study's maximum of 40%) and also found somewhat higher ET rates than those measured in this study. Wight et al. (1996) used multiple sites in Idaho and greater precipitation in this region may account for the higher rates than those found in the drier basins of Nevada.

Multiple perturbations, such as invasion and frequent catastrophic fires, may lead to the establishment of a new, stable ecosystem state (Paine et al., 1998; Scheffer et al., 2001; Scheffer and Carpenter, 2003). Invasion of the Great Basin Desert by cheatgrass and other non-native species have increased the impact of fire as a disturbance in the native sagebrush ecosystem. Following fire, cheatgrass monopolizes soil moisture before native species can utilize this resource (Melgoza et al., 1990), thereby preventing native species from regenerating. This new grassland state changed surface energy and water fluxes. Alterations in surface energy partitioning, soil moisture and leaf area, such as those found in this study, reinforce this state change, such that native sagebrush communities may be permanently replaced by non-native grasslands. Cascading effects of changes in energy partitioning may alter other ecosystem processes such as litter dynamics (Chen and Stark, 2000), nutrient mineralization (Ogle et al., 2004), water resources (e.g. groundwater recharge) and even regional climate (e.g. Stohlgren et al., 1998; Asner and Heidebrecht, 2005).

Acknowledgements

We gratefully acknowledge D. Schorran for technical assistance in calibration and operation of field equipment, and E. Barrett, L. Beers, R. Bergin, M. Kernecker, C. Menkee, Y. Shulman and H. Weatherly for invaluable help in the field. We thank T. Ball for advice on the construction of the BR towers. We also thank T. Twine, O. Dermody, D. Moore, J. Tang and two anonymous reviewers for thoughtful criticisms of the manuscript. This research was funded by grants from the International Arid Lands Consortium (Project OOR-05 and O2R-03), with additional support provided by the University of Illinois Graduate College and the Francis M. and Harlie M. Clark Research Support Grant.

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