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# Net carbon exchange and evapotranspiration in postfire and intact sagebrush communities in the Great Basin

**Abstract** Invasion of non-native annuals across the Intermountain West is causing a widespread transition from perennial sagebrush communities to fire-prone annual herbaceous communities and grasslands. To determine how this invasion affects ecosystem function, carbon and water fluxes were quantified in three, paired sagebrush and adjacent postfire communities in the northern Great Basin using a 1-m$^3$ gas exchange chamber. Most of the plant cover in the postfire communities was invasive species including *Bromus tectorum* L., *Agropyron cristatum* (L.) Gaertn and *Sisymbrium altissimum* L. Instantaneous morning net carbon exchange (NCE) and evapotranspiration (ET) in native shrub plots were greater than either intershrub or postfire plots. Native sagebrush communities were net carbon sinks (mean NCE 0.2–4.3 μmol m$^{-2}$ s$^{-1}$) throughout the growing season. The magnitude and seasonal variation of NCE in the postfire communities were controlled by the dominant species and availability of soil moisture. Net C exchange in postfire communities dominated by perennial bunchgrasses was similar to sagebrush. However, communities dominated by annuals (cheatgrass and mustard) had significantly lower NCE than sagebrush and became net sources of carbon to the atmosphere (NCE declined to −0.5 μmol m$^{-2}$ s$^{-1}$) with increased severity of the summer drought. Differences in the patterns of ET led to lower surface soil moisture content and increased soil temperatures during summer in the cheatgrass-dominated community compared to the adjacent sagebrush community. Intensive measurements at one site revealed that temporal and spatial patterns of NCE and ET were correlated most closely with changes in leaf area in each community. By altering the patterns of carbon and water exchange, conversion of native sagebrush to postfire invasive communities may disrupt surface-atmosphere exchange and degrade the carbon storage capacity of these systems.

**Keywords** *Artemisia tridentata* · *Bromus tectorum* · Invasion · Carbon flux · Water flux

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## Introduction

Ecosystem processes are tightly linked to the structure and function of plant communities; therefore changes in the dominant vegetation will have important consequences for ecosystem function. Species vary widely in the utilization of available resources and response to the environment (Chapin et al. 1997; Chapin 2003). Changes in species composition and diversity caused by altered land use practices and invasive species may have important feedbacks on ecosystem processes by altering atmosphere-surface exchange of carbon (Shukla et al. 1990), and water (Sala et al. 1996), nutrient cycling (Schlesinger et al. 1990), and disturbance patterns (D'Antonio and Vitousek 1992).

Non-native grasses, including cheatgrass (*Bromus tectorum* L.), have aggressively invaded the sagebrush steppe ecosystem of the Western United States over the last century (Mack 1981; Young et al. 1987). In addition to this invasion, management and restoration practices have resulted in a mosaic of community types, dominated by non-native species including annual grasses, forbs and perennial bunchgrasses. However, repeated fires may cause cheatgrass to become dominant in most postfire communities (Young et al. 1972).

Promoted by overgrazing and fire, this invasion has rapidly converted large expanses of native sagebrush shrubland to successional postfire communities. Cheatgrass, a non-native winter annual grass, has become the most widespread noxious weed in Western North America (Lacey and Olson 1991), invading over 80% of public lands in Nevada (Pellant 1994). Senescing earlier in the summer than most native vegetation, cheatgrass expanses become tinder for large fires. Following fire, cheatgrass depletes soil moisture early in the growing season before native vegetation germinates or has broken dormancy (Melgoza et al. 1990; Blank et al. 1994). By exploiting vital soil moisture reserves and promoting repeated fires, cheatgrass inhibits postfire germination and growth of native vegetation (Harris 1967; Blank et al. 1994) and alters postfire succession (Young et al. 1972; Young and Evans 1978). As a winter annual, the phenology of cheatgrass is unlike native shrubs or grasses. Therefore, this cheatgrass-driven landscape transformation may impact the timing and magnitude of carbon and water exchange in the Great Basin.

While much research has focused on the effects of human-induced land cover change on ecosystem function (e.g. Bonan 1999; Houghton 1999; Eastman et al. 2001), fewer studies have examined how invasive species, as vectors of landscape transformation, impact ecosystem processes such as water and nutrient cycling (Vitousek and Walker 1989; Busch and Smith 1995). Shrubs tightly control the spatial distribution of soil nutrients (Charley and West 1975; Halvorson et al. 1997) and these patterns persist following postfire conversion to cheatgrass communities (Schlesinger et al. 1996). While the legacy of removed shrubs continues to influence nutrient distribution, fluxes of carbon and water are largely determined by physiologically active vegetation (e.g. Chapin et al. 1997; Law et al. 2002); therefore, these fluxes may be altered in invasive communities. Obrist et al. (2003) found surprisingly small differences between ecosystem carbon and water exchange measured in sagebrush communities and those measured in a recently established non-native postfire community during periods of low precipitation. When differences were detectable, net carbon uptake and evapotranspiration were higher in the postfire community than the native sagebrush at a single site. These differences, as well as the spatial variation in fluxes and vegetation, may be quite different when soil moisture is more readily available.

The objectives of this study were to determine how replacement of sagebrush with alien postfire communities alters spatial and temporal patterns of ecosystem carbon and water exchange in the northern Great Basin Desert, and to investigate how biotic and environmental factors control these fluxes. We predicted that the patterns of carbon and water exchange would follow the phenology of the different dominant species in each community. Using a large static gas-exchange chamber, we quantified the surface fluxes of carbon and water in adjacent sagebrush and postfire communities at three sites where the dominant non-native species and cover of cheatgrass in the postfire community varied.

## Materials and methods

### Site descriptions

The main location for this research (Golden Valley site) was a recent postfire community and adjacent sagebrush community located 10 km north of Reno, Nevada (39°38′N, 119°48′W, 1,600 m elevation). This was the same site used by Obrist et al. (2003); it was chosen for intensive measurements of ecosystem net carbon exchange (NCE) and evapotranspiration (ET) to discern seasonal variation and to determine the components that control these fluxes. In 1999, one year before measurements were initiated, a fire burned a large intermountain saddle of native sagebrush, leaving adjacent patches of burned and unburned vegetation. Since the fire was not controlled, it was assumed that the intact unburned vegetation was representative of the preburn vegetation and that there were no intrinsic differences between the burned and unburned areas (e.g. soil properties).

Following the fire, the Bureau of Land Management (BLM) seeded the site with native and non-native grasses and shrubs. The early postfire community was composed of a mixture of early successional annuals, dominated by an invasive mustard (*Sisymbrium altissimum* L.). Cheatgrass was present but not dominant, and other forbs included *Lupinus caudatus* Kellogg, *Stephanomeria spinosa* Tomb, *Descurainia sophia* L., *Eriastrum sparsiflorum* (Eastw.) H. Mason, *Gayophytum ramossisimum* T. & G., and *Eriogonum* sp., although none of these species had cover values > 5%. Shrubs and native bunchgrasses were mostly absent from the postfire community. The adjacent unburned community was dominated by sagebrush (*Artemisia tridentata wyomingensis* Beetle), with sporadic bitterbrush (*Purshia tridentata* Pursh, DC, USA) and rabbitbrush (*Chrysothamnus nauseosus* Pall., Britton). Shrub cover was 29%, and cheatgrass was present mostly under shrubs in the unburned sagebrush community.

Two other sites with different fire histories and dominant vegetation were chosen to investigate how these fluxes may vary across types of postfire communities common in the Great Basin. The postfire communities at these sites were dominated by a different non-native species and varied in cheatgrass cover.

Bedell Flats is a northwest-to-southeast intermountain valley 35 km north of Reno (39°51′N, 119°49′W, 1,500 m elevation) with large, continuous expanses of undisturbed sagebrush vegetation, adjacent to a restored postfire community of perennial grasses and cheatgrass. A road that served as a break during the most recent fire in 1984 bisects the valley. The fire removed all sagebrush south of the road and immediately following the fire the scar was seeded by the BLM with crested wheatgrass (*Agropyron*

*cristatum* (L.) Gaertn). Nearly twenty years after the fire, no sagebrush had become established, and this area was a mixture of cheatgrass and bunchgrasses (*A. cristatum* and *Stipa comata*) with occasional rabbitbrush (*Chrysothamnus viscidiflorus* [Hook.] Nutt.). Cheatgrass cover in the postfire community varied spatially from 10 to >50%. Across the road was a vast expanse of intact sagebrush, with occasional individuals of bitterbrush and smooth horsebrush (*Tetradymia glabrata* Gray). Shrub cover declined at this site over 3 summers from approximately 38% in 2000 to 15% in 2002 (personal observation). Cheatgrass cover was 15–20% both under shrub canopies and in intershrub spaces.

The Dun Glen site (40°43′N, 117°59′W, 1,800 m elevation) was a large expanse of cheatgrass with remnant unburned patches of sagebrush shrub communities. The area was subject to repeated fires. Following the most recent fire in 2000, the fire scar was seeded by the BLM with a mixture of native and non-native species; however, the postfire community was strongly dominated by cheatgrass (>70% cover), with other forbs and grasses comprising <1% cover. The adjacent sagebrush community was similar to that of the other two sites (25% shrub cover), dominated by *Artemisia tridentata*, with a few individuals of *Chrysothamnus nauseosus* occurring mostly under mature sagebrush canopies.

Ecosystem gas exchange

Net carbon exchange (NCE) and ET were measured with a single closed, static gas-exchange chamber at each site. The 1-$m^3$ chamber was made of an aluminum frame supporting transparent Lexan® and Propafilm® C (ICI Americas, Chicago, IL, USA) plastic sides, similar to the chamber used by Vourlitis et al. (1993), but modified to accommodate an average-sized shrub (as in Angell and Svejcar 1999). The 4-cm aluminum bottom edge of the chamber penetrated the soil to form a seal and eliminate leaks. Small fans rapidly circulated air inside the chamber. Initially, carbon dioxide and water vapor concentrations in the chamber were measured with a closed path gas exchange system (LI-6200, LI-COR, Inc., Lincoln, NE, USA). In June, 2001, the closed path system was replaced with an open path infra-red gas analyzer (LI-7500, cf. Arnone and Obrist 2003) to reduce the duration and improve the accuracy of measurements. Two ventilation ports and a large fan were installed on the outside wall of the chamber to increase mixing with ambient air between measurements.

The chamber was used to rapidly quantify surface fluxes of individual community elements (shrub, intershrub, postfire) without significantly affecting air temperature, which typically increased in the chamber by less than 1°C per min at midday. Measurements were completed in less than 2 min. After an initial mixing period (<10 s) the concentration of $CO_2$ and water vapor changed linearly with time (initial $CO_2$ concentrations of ~380 μmol $mol^{-1}$ did not decline by more than 20 μmol $mol^{-1}$ and $H_2O$ concentrations of ~10 mmol $mol^{-1}$ did not increase more than ~3 mmol $mol^{-1}$ during the measurement period) and fluxes as low as 0.1 μmol $mol^{-1}$ $CO_2$ and 0.1 mmol $mol^{-1}$ $H_2O$ were detectable. The calculation of $CO_2$ and water vapor fluxes were corrected to the initial chamber temperature to account for warming during the measurement (Hooper et al. 2002). Net C exchange was defined as positive when fluxes were toward the land surface and indicated net uptake by the vegetation.

At the Golden Valley site, ecosystem gas exchange was measured twice a month at the onset and middle of the summer drought in 2000 and throughout the spring and summer of 2001 and 2002. Less frequent (monthly) measurements were made during the 2003 growing season and once during the winter of 2001. Thirty 1-$m^2$ plots (ten in each community element: shrub, intershrub, postfire) were established randomly throughout each community. Measurements were made using the single chamber between 0800 and 1200 pacific standard time (PST) when photosynthetic rates were highest and chamber air temperature remained close to ambient (based on diurnal data not shown). Beginning in July 2000, monthly diurnal measurements were conducted approximately every 4 h on five plots in each community element to estimate integrated NCE and ET over the course of a 24-h period. Net carbon exchange and ET for the sagebrush community were calculated as the weighted sum (by relative cover) of fluxes measured in the shrub and intershrub plots.

The 1-$m^3$ chamber permitted us to measure the relative contributions of each community element to overall NCE and ET, and to investigate how the phenology of the dominant vegetation in each community element influenced the seasonal patterns fluxes. The fluxes calculated by scaling measurements made with the 1-$m^3$ chamber agreed with fluxes made with a larger chamber that simultaneous measured all elements of each community (Obrist et al. 2003).

During each chamber measurement, surface soil moisture (top 12 cm) was measured with a hand-held time domain reflectometer (TDR; Hydrosense, Campbell Scientific Inc, Logan, UT, USA). Photosynthetically active radiation (400–700 nm, PAR) was measured outside the chamber with a quantum sensor (LI-190SA, LI-COR, Inc.). The Propafilm® chamber top allowed >85% transmission of PAR. Air and soil temperatures (top 12 cm) were measured with copper-constantan thermocouples and chamber temperature was recorded with a thermocouple attached to the gas analyzer.

At Bedell Flats and Dun Glen, 21 plots (seven plots in each community element) were randomly established at each site. Because of the logistic challenges of moving and operating the chamber, diurnal measurements were not attempted and only instantaneous morning measurements were made at these sites. At the Golden Valley site, instantaneous morning measurements (made between 0800 and 1200 PST on cloud-free days) were highly correlated with integrated daily NCE ($y = 2.5 \ x + 0.4$,

$r^2 = 0.95$, $P < 0.01$, $n = 120$) and ET ($y = 1.1\ x\ -\ 0.1$, $r^2 = 0.85$, $P < 0.01$, $n = 120$). Therefore, morning measurements provided a reasonable measure of integrated daily fluxes in order to evaluate the spatial and temporal patterns of carbon and water fluxes in these communities.

## Leaf area index and plant cover

Leaf area index (LAI) and percentage plant cover were estimated in each community type coincident with ecosystem gas exchange measurements. Shrub LAI was estimated from the destructive harvest of at least 20 branches once a month at Golden Valley. Branch basal area was regressed against leaf area each month and these allometric relationships ($r^2$ values ranged between 0.68 and 0.92, $P < 0.01$) were used to estimate leaf area in each permanent chamber plot. Based on 20 branches harvested in July 2002, allometric relationships were not significantly different between sites, and relationships from Golden Valley were used to estimate leaf area of shrubs at all three sites. The percentage cover of green vegetation in each intershrub and postfire plot was determined from visual estimates by at least two independent observers as in (Anderson 1986).

## Respiration and photosynthesis measurements

To investigate the relative contributions of variation in respiration and photosynthesis to seasonal patterns of shrub NCE, nighttime ecosystem respiration and leaf level photosynthesis were measured at the Golden Valley site. Nighttime NCE, which included aboveground and belowground fluxes, was measured on all 30 plots between 2200 and 2400 PST using the chamber during diurnal measurements described above.

Leaf-level photosynthesis was measured with a closed gas-exchange system (LI-6200, LI-COR, Inc.) twice a month coincident with chamber measurements (mid-morning) at the Golden Valley site beginning in 2001. As sagebrush leaves were too small to be measured individually, we measured instantaneous leaf-level gas exchange of shrubs adjacent to each permanent chamber plot by placing small branches ($n = 10$) in a quarter-liter cuvette. Changes in $CO_2$ and water vapor concentrations were recorded for 2 min by the gas-exchange system and net C assimilation and evapotranspiration were calculated as in Hooper et al. (2002). The projected area of leaves in each sample (Smith et al. 1991) was determined from scanned images with an image analysis program (Scion Image, Beta Version 4.0.2, Scion Corp., Frederick, MD, USA).

## Statistical analysis

Chamber-based data were analyzed using repeated measures analysis of variance (PROC MIXED; SAS, The SAS Institute, Version 8.1, Cary, NC, USA) to test for treatment effects on NCE and ET. Each research site was analyzed separately. Plots within each site were considered replicates and therefore, inferences were limited to each site. Diurnal NCE and ET data were integrated using the trapezoidal method (PROC EXPAND; SAS) before being analyzed using repeated measures ANOVA. Leaf-level measurements were analyzed using analysis of covariance (PROC MIXED), with PAR and air temperature as covariates, to determine seasonal effects on leaf-level photosynthesis. All regressions were tested using PROC REG or PROC GLM. Post hoc analyses were performed using linear contrasts and considered significant when $P \leq 0.05$.

## Results

### Seasonal variability in fluxes at Golden Valley

Winter and spring precipitation was extremely low in 2000–2001 (November through May; 49 mm compared to the 30-year mean of 167 mm; http://www.wrcc.dri.edu), with only two rain events during the measurement period (both in early July totaling 2.5 mm). Winter precipitation (November through February) was below the 30-year mean of 142 mm in all study years, although the amount of spring rain was above average in all years except 2001 (23.1 mm in May 2000 compared to mean of 14 and 17.8 mm in April 2002 compared to April mean of 11 mm and 25.1 mm in May 2003).

Instantaneous morning net C exchange of shrub was significantly greater than either postfire or intershrub spaces across most of the four years (Fig. 1). However, the community elements (shrub, intershrub, postfire) were not different from each other in July 2000 or November 2001. Instantaneous NCE was lower in 2001 than in other years, and shrub NCE declined during the growing season in all years. In most years, postfire and intershrub NCE were not significantly different from each other. Late May and early June of 2002 were the only times when postfire NCE was significantly greater than intershrub spaces but both were still lower than shrubs. During 2001, postfire and intershrub NCE increased slightly into July because of the dry spring and subsequent precipitation. In 2002 and 2003, postfire NCE increased until May and then gradually declined.

Instantaneous NCE of the sagebrush and postfire communities, calculated by multiplying the rates for each community element by the area of that element, were not different during the drought of 2001 (hatched bars and solid bars, respectively; Fig. 1). In all other years, the sagebrush community had significantly greater carbon uptake than the postfire community early in the season. Although shrubs comprised only 29% cover, sagebrush community-level NCE was 40–90% greater than the postfire community uptake during April and May.

The temporal patterns of morning ET were similar to the patterns of carbon flux (Fig. 2). Shrubs were the
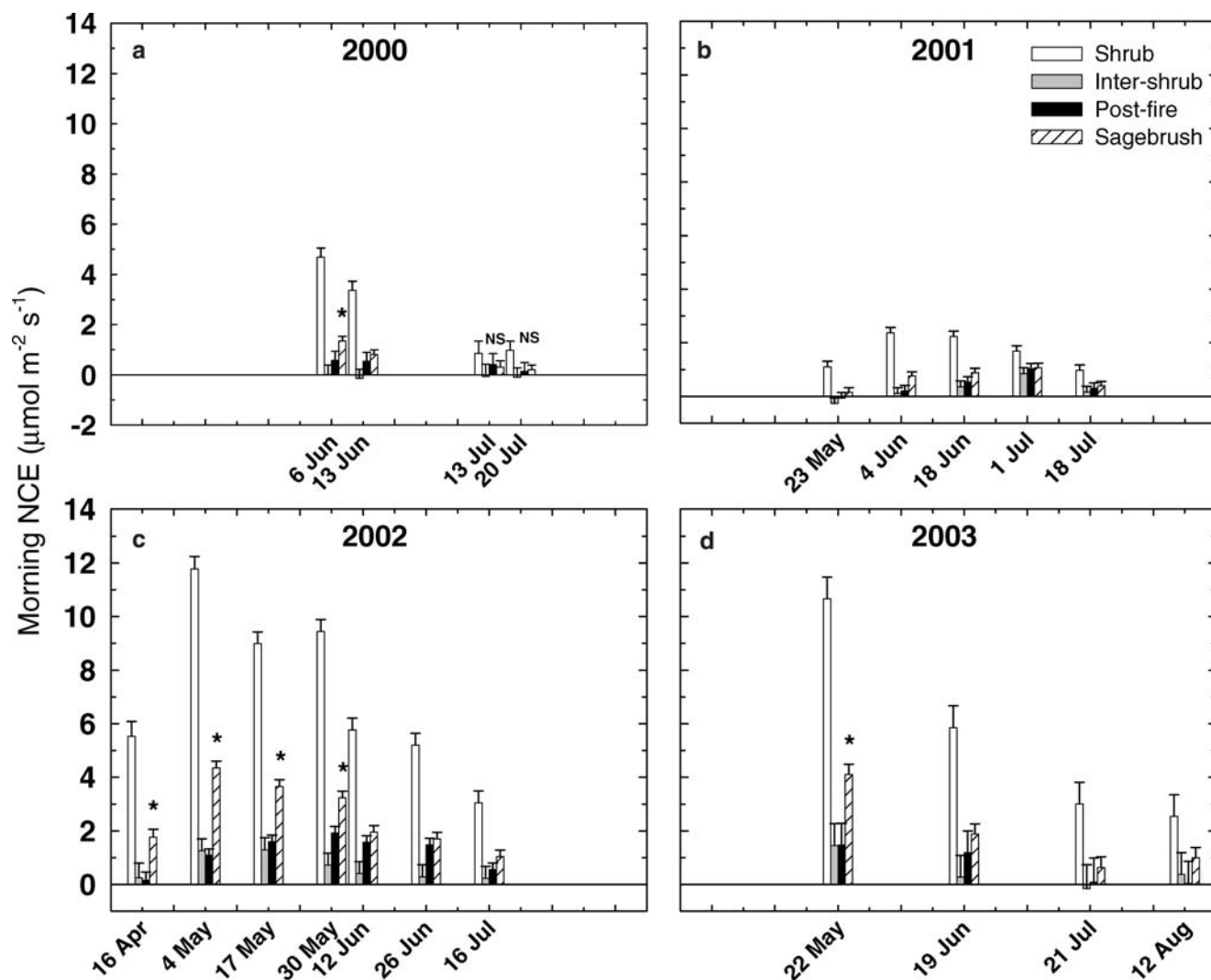
**Fig. 1** Instantaneous morning net carbon exchange (NCE) from shrub (*open*), intershrub (*gray*) and postfire (*solid bars*) plots in 2000–2003 at the Golden Valley site. Sagebrush community exchange (*hatched bars*) was calculated as a weighted sum of values from shrub and intershrub plots based on percent ground cover of each. *Positive values* indicate net flux from the atmosphere to the land surface and *negative values* indicate net flux to the atmosphere. *Bars* are least square means ± SE (*n* = 10). *Asterisks* (*) indicate significant (*P* < 0.05) difference between postfire and sagebrush community-level fluxes. *NS* indicates no significant difference between community elements (shrub, intershrub or postfire)

major source of ET throughout the growing season in all years, except in July 2000. Fluxes across all community elements were extremely low in 2001; therefore, no seasonal pattern was apparent and fluxes from the two communities were not different.

Instantaneous shrub ET was significantly greater than for postfire and intershrub spaces, and declined during the summer in all years except 2001 (Fig. 2). Postfire ET was greater than in intershrub plots in late May through June, when postfire vegetation was most active, but decreased sharply in July when postfire vegetation senesced. In 2002 and 2003, the composite ET from the sagebrush community was significantly greater than the postfire community early in the season but declined steadily thereafter. This decline resulted in significantly lower ET in sagebrush than in the postfire community in June. Instantaneous morning ET of the

two communities did not differ when soil moisture was low (as in 2001 and late July of all years, Figs. 2 and 3). Total daily ET from the sagebrush and postfire communities followed a similar pattern (Table 1).

While instantaneous morning NCE was not statistically distinguishable between the two communities later in the summer, postfire communities had lower total daily carbon uptake (Table 1). Postfire plots had greater system-level respiration (mean NCE $-0.2 \pm 0.1$ μmol mol$^{-1}$) than sagebrush plots (mean NCE $0.4 \pm 0.02$ μmol mol$^{-1}$) in the afternoon (based on diurnal data not shown), resulting in the community having little or no C gain in July of all years.

Daytime soil temperature (top 12 cm) did not differ between community elements at the Golden Valley site (data not shown), but mean volumetric soil moisture (top 12 cm) was consistently greater in sagebrush than in
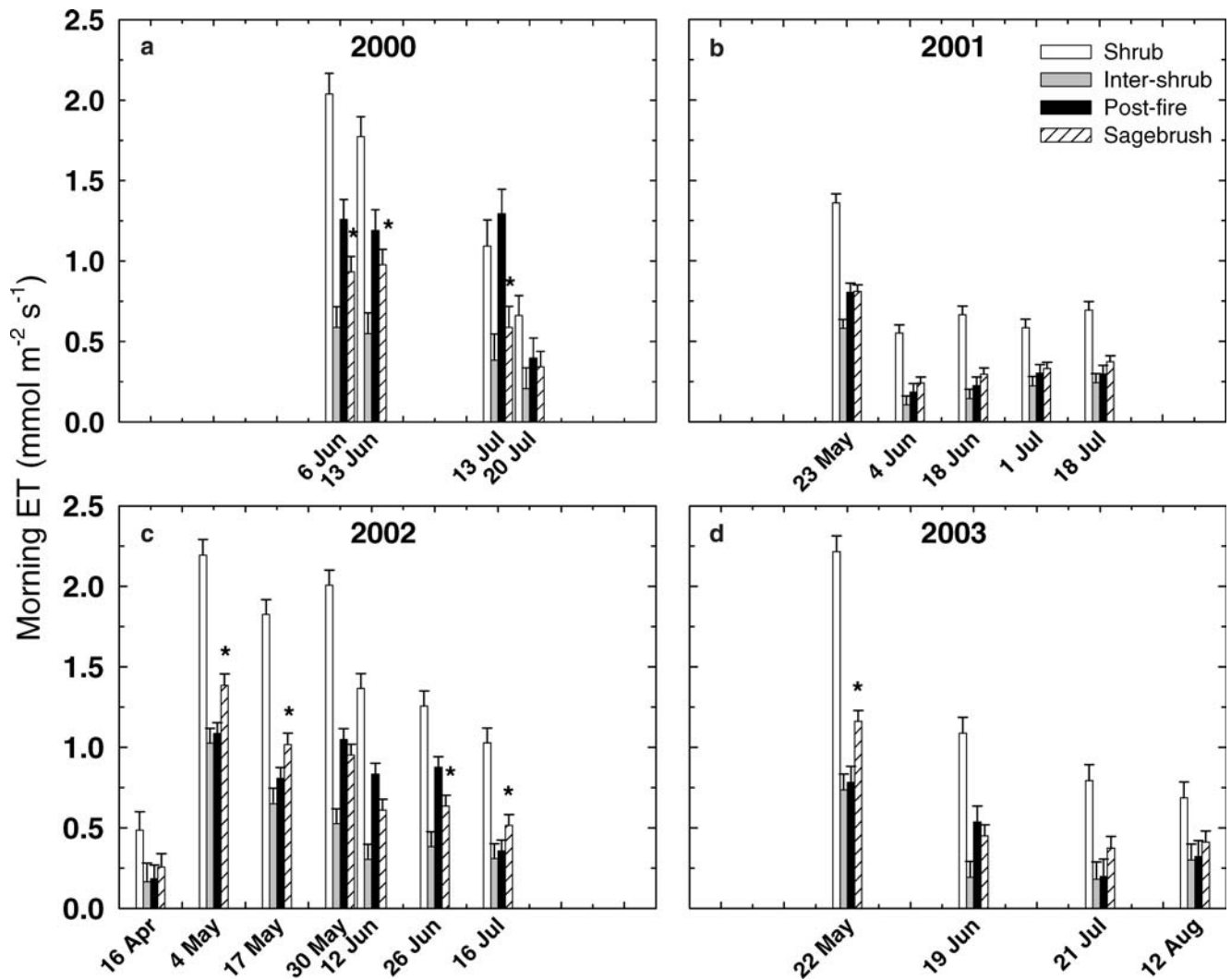
**Fig. 2** Instantaneous morning evapotranspiration (ET) from shrub (*open*), intershrub (*gray*) and postfire (*solid bars*) plots in 2000–2003 at the Golden Valley site. Sagebrush community exchange (*hatched bars*) was calculated as a weighted sum of values for shrub and intershrub plots based on percent ground cover of each. *Positive values* indicate net flux from the atmosphere to the land surface and *negative values* indicate net flux to the atmosphere. *Bars* are least square means ± SE ($n = 10$). *Asterisks* (*) indicate significant ($P < 0.05$) difference between postfire and sagebrush community-level fluxes

the postfire community early in the season (Fig. 3). This difference disappeared as soil moisture dropped below 15%. Shrub and postfire NCE were positively correlated with soil moisture across sites and years ($y = 0.4x - 0.6$, $r^2 = 0.46$, $P < 0.01$; $y = 0.1x - 0.6$, $r^2 = 0.51$, $P < 0.01$, respectively). Intershrub NCE showed only a weak correlation with soil moisture ($y = 0.05x - 0.2$, $r^2 = 0.30$, $P = 0.01$). ET also was positively correlated with soil moisture across sites and years (shrub: $y = 0.06x - 0.3$, $r^2 = 0.43$, $P = 0.01$; intershrub: $y = 0.03x - 0.1$, $r^2 = 0.48$, $P < 0.01$; postfire: $y = 0.04x - 0.06$, $r^2 = 0.46$, $P < 0.01$).

### Respiration and photosynthesis - Golden Valley

The seasonal pattern of nighttime NCE (respiration) generally followed changes in soil moisture across all

community elements in all years (Fig. 3) but regressions of nighttime NCE and soil moisture content were not statistically significant ($P > 0.05$). Nighttime NCE of shrub plots showed a weak correlation with soil moisture ($y = -0.09x + 0.1$, $r^2 = 0.35$, $P < 0.01$). Respiration from shrub plots was significantly greater (more negative NCE) than postfire or intershrub spaces when soil moisture was relatively high (November 2001 through all of 2002 and early 2003). The rates of respiration from postfire and intershrub plots were not different from one another. Respiration rates were greatest when soil moisture was greatest, except in November, when low soil temperature may have limited respiration. During the extreme drought in 2001, respiration rates across all plots were low and there was no difference between community elements. During all, the years except 2001, aboveground shrub respiration contributed 75% or
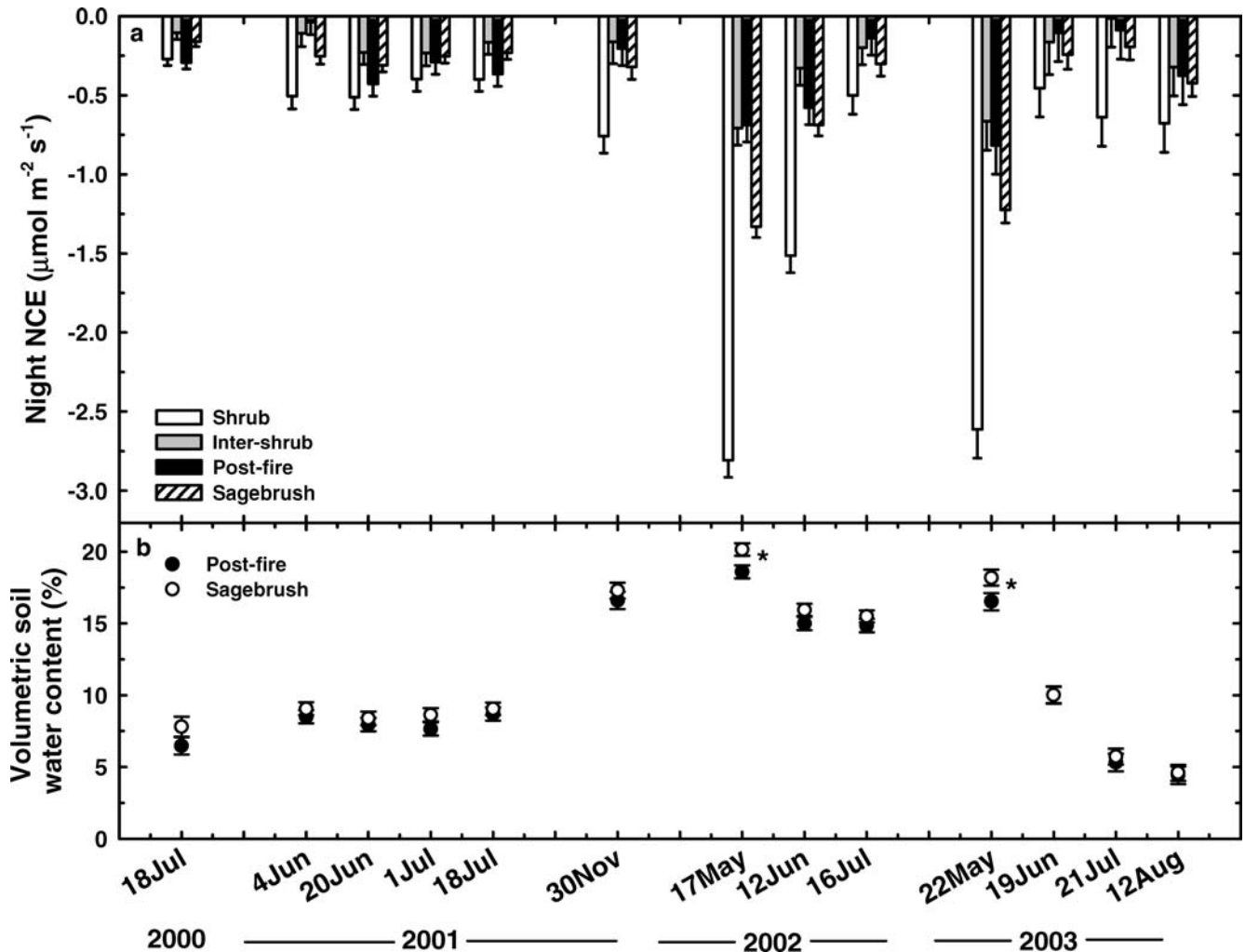
**Fig. 3 a** Nighttime NCE from shrub (*open*), intershrub (*gray*) and postfire (*solid bars*) plots in 2000–2003 at the Golden Valley site. *Negative values* indicate net flux to the atmosphere. *Bars* are least square means ± SE (*n* = 5). **b** Mean soil moisture content (top 12 cm) of postfire (*solid circles*) and sagebrush (*open circles*) plots during respiration measurements (n = 5 ± SE). *Asterisks* (*) indicate significant (*P* < 0.05) difference between postfire and sagebrush community-level fluxes or moisture content

more of total ecosystem respiration (data not shown), which may have accounted for the differences between community elements.

There was no seasonal trend in leaf-level photosynthesis of sagebrush during the extreme drought in 2001 (mean between 2.0 ± 0.9 and 2.4 ± 1.0 μmol m$^{-2}$ s$^{-1}$). Soil moisture and photosynthetic rates in 2002 generally were greater than in 2001. Large spring ephemeral leaves were present in May and June of 2002 and photosynthetic rates were significantly greater (5.3 ± 0.7 and 7.0 ± 0.6, respectively) than at other times of the year. As spring leaves senesced and were replaced by smaller leaves, late season photosynthesis in 2002 (mean ranged between 3.2 ± 1.0 and 4.6 ± 0.9) decreased and was not significantly different from 2001 rates.

Flux patterns at Bedell Flats: 2002

Morning NCE of shrubs was significantly greater than either postfire or intershrub spaces at Bedell Flats

throughout the season (Fig. 4 a–c). Shrub NCE was similar in May and June but values declined later in the season. In the postfire plots composed mostly of non-native bunchgrasses, NCE reached its maximum in May and was significantly greater than intershrub spaces. Differences in carbon fluxes among the three community elements disappeared in June and July as bunchgrasses in the intershrub spaces senesced.

When scaled to the community level, the postfire community at Bedell Flats had significantly greater NCE than sagebrush early in the season but there was no difference between the two communities in June or July (solid bars and hatched bars, respectively; Fig. 4 a–c).

Evapotranspiration from individual community elements (shrub, intershrub, postfire) and scaled values for the sagebrush and postfire communities reached their maximum values in June (Fig. 4 d–f). ET from the postfire plots was significantly lower than from the shrubs and generally greater than from the intershrub spaces. When scaled to the entire community, the post-

**Table 1** Daily integrated net carbon exchange (NCE) and evapotranspiration (ET) for the Golden Valley site, 2000–2003

| | Date | Shrub | intershrub | postfire | Sagebrush |
|---|---|---|---|---|---|
| **Integrated NCE (g C m$^{-2}$ day$^{-1}$)** | | | | | |
| 2000 | 18 July | 0.29 (0.06) | −0.11 (0.05) | 0.01 (0.05) | 0.02 (0.07) |
| 2001 | 4 June | 0.43 (0.07) | − 0.08 (0.05) | −0.03 (0.08) | 0.20 (0.07) |
| | 1 July | 0.76 (0.09) | 0.11 (0.02) | 0.17 (0.03) | 0.40 (0.06) |
| | 21 July | 0.55 (0.06) | 0.06 (0.04) | 0.03 (0.02) | 0.28 (0.16) |
| | 30 Nov | −0.38 (0.10) | 0.11 (0.05) | −0.15 (0.11) | −0.06 (0.05) |
| 2002 | 17 May | 4.83 (0.57)[a] | 0.53 (0.06)[b] | 0.85 (0.09)[b] | 1.78 (0.16)[*] |
| | 12 June | 1.68 (0.17)[a] | 0.04 (0.10)[b] | 0.58 (0.12)[b] | 0.51 (0.08) |
| | 16 July | 1.23 (0.19)[a] | 0.00 (0.03)[b] | 0.05 (0.11)[b] | 0.35 (0.06)[*] |
| 2003 | 22 May | 3.63 (0.82)[a] | 0.11 (0.09)[b] | −0.02 (0.09)[b] | 1.13 (0.23)[*] |
| | 19 June | 2.73 (0.54)[a] | 0.01 (0.12)[b] | 0.35 (0.15)[b] | 0.80 (0.20)[*] |
| | 21 July | 1.06 (0.17)[a] | −0.05 (0.13)[b] | 0.03 (0.07)[b] | 0.27 (0.12) |
| | 12 Aug | 1.12 (0.26)[a] | −0.08 (0.10)[b] | −0.21 (0.07)[b] | 0.26 (0.12)[*] |
| **Integrated ET (mm day$^{-1}$)** | | | | | |
| 2000 | 18July | 0.08 (0.01) | 0.03 (0.00) | 0.07 (0.01) | 0.04 (0.00) |
| 2001 | 4 June | 0.26 (0.01) | 0.02 (0.01) | 0.09 (0.01) | 0.09 (0.01) |
| | 1 July | 0.44 (0.05)[a] | 0.17 (0.02)[b] | 0.21 (0.02)[b] | 0.22 (0.03) |
| | 21 July | 0.49 (0.04)[a] | 0.16 (0.02)[b] | 0.23 (0.01)[b] | 0.26 (0.02) |
| | 30 Nov | 0.40 (0.04) | 0.59 (0.04) | 0.53 (0.02) | 0.37 (0.09) |
| 2002 | 17 May | 2.56 (0.19)[a] | 0.96 (0.00)[b] | 1.11 (0.04)[b] | 1.42 (0.08)[*] |
| | 12 June | 1.23 (0.11)[a] | 0.32 (0.08)[b] | 0.83 (0.10)[c] | 0.58 (0.07)[*] |
| | 16 July | 0.96 (0.07)[a] | 0.31 (0.05)[b] | 0.38 (0.04)[b] | 0.49 (0.05) |
| 2003 | 22 May | 2.65 (0.30)[a] | 0.86 (0.10)[b] | 1.03 (0.08)[b] | 1.37 (0.15)[*] |
| | 19 June | 1.06 (0.15)[a] | 0.14 (0.04)[b] | 0.25 (0.05)[b] | 0.40 (0.07)[*] |
| | 21 July | 0.67 (0.08)[a] | 0.08 (0.03)[b] | 0.08 (0.02)[b] | 0.24 (0.04)[*] |
| | 12 Aug | 0.68 (0.05)[a] | 0.27 (0.02)[b] | 0.29 (0.01)[b] | 0.39 (0.03) |

Values are least square means of five independent measurements with standard errors of the means in parentheses. Integrated values were calculated from measurements taken every 4 h on each plot in each community element (shrub, intershrub, postfire). Sagebrush community level values were calculated as a weighted sum of values from shrub and intershrub plots based on percent ground cover.

Positive values indicate a net flux from the atmosphere to the land surface and negative values indicate a net flux to the atmosphere. Letters and asterisks (*) indicate significant treatment effects for each date ($P < 0.05$) for community elements and communities, respectively

fire bunchgrass community had greater ET than the sagebrush community throughout the entire season.

Soil temperature and soil moisture were generally not different between community elements, although small differences were observed in July when surface temperatures in the intershrub and postfire plots were slightly warmer ($< 1.5°C$) than in the shrub plots.

### Flux patterns at Dun Glen: 2002

As at other sites, morning NCE from shrubs at Dun Glen declined through the growing season but was greater than either postfire or intershrub spaces (Fig. 4 a–c). Postfire NCE was significantly greater than intershrub spaces in May but both declined and were not different as the cheatgrass senesced in June and July.

When scaled to the community level, sagebrush NCE was significantly greater than postfire NCE across the entire season (hatched bars and solid bars, respectively; Fig. 4 a–c). The cheatgrass community had only slightly but significantly lower NCE than the sagebrush community in May. However, this difference increased through the season such that the postfire cheatgrass community was a net source of carbon to the atmosphere (negative NCE) in July while the sagebrush community maintained positive carbon uptake.

Morning ET declined at the Dun Glen site in all plots across the season. Rates of community ET were not different from each other in May but sharp declines in postfire ET resulted in significantly lower values than sagebrush in June and July (Fig. 4 d–f).

Substantial variation in soil temperature or moisture among community elements (postfire, intershrub and shrub plots) was observed only at Dun Glen, where cheatgrass contributed heavily to the postfire community. The postfire community had significantly lower soil moisture than either shrub or intershrub plots in June (postfire: $12.1 \pm 1.3\%$, intershrub: $16.1 \pm 1.8\%$, shrub: $14.7 \pm 1.6\%$; $P = 0.03$) and July (postfire $9.7 \pm 1.4\%$, intershrub $14.2 \pm 1.3\%$, shrub $12.5 \pm 1.8\%$; $P = 0.02$), with greater morning soil temperatures compared to shrub and intershrub spaces in July (postfire $29.9 \pm 0.3°C$, intershrub $27.5 \pm 0.3°C$, shrub $26.8 \pm 0.3°C$; $P < 0.01$).

Ecosystem water-use efficiency was calculated as the slope of the linear regression of instantaneous morning NCE against ET for each of the communities (sagebrush or postfire) at each of the sites in 2002. The postfire annual communities at Golden Valley and Dun Glen both had significantly lower water-use efficiency ($y = 1.2x − 0.06$, $r^2 = 0.50$ and $y = 2.5x − 0.6$, $r^2 = 0.80$, respectively) than the adjacent sagebrush communities ($y = 2.4x − 0.12$, $r^2 = 0.69$ and $y = 3.8x − 0.8$, $r^2 = 0.66$, respectively). Ecosystem water-use efficiency of the
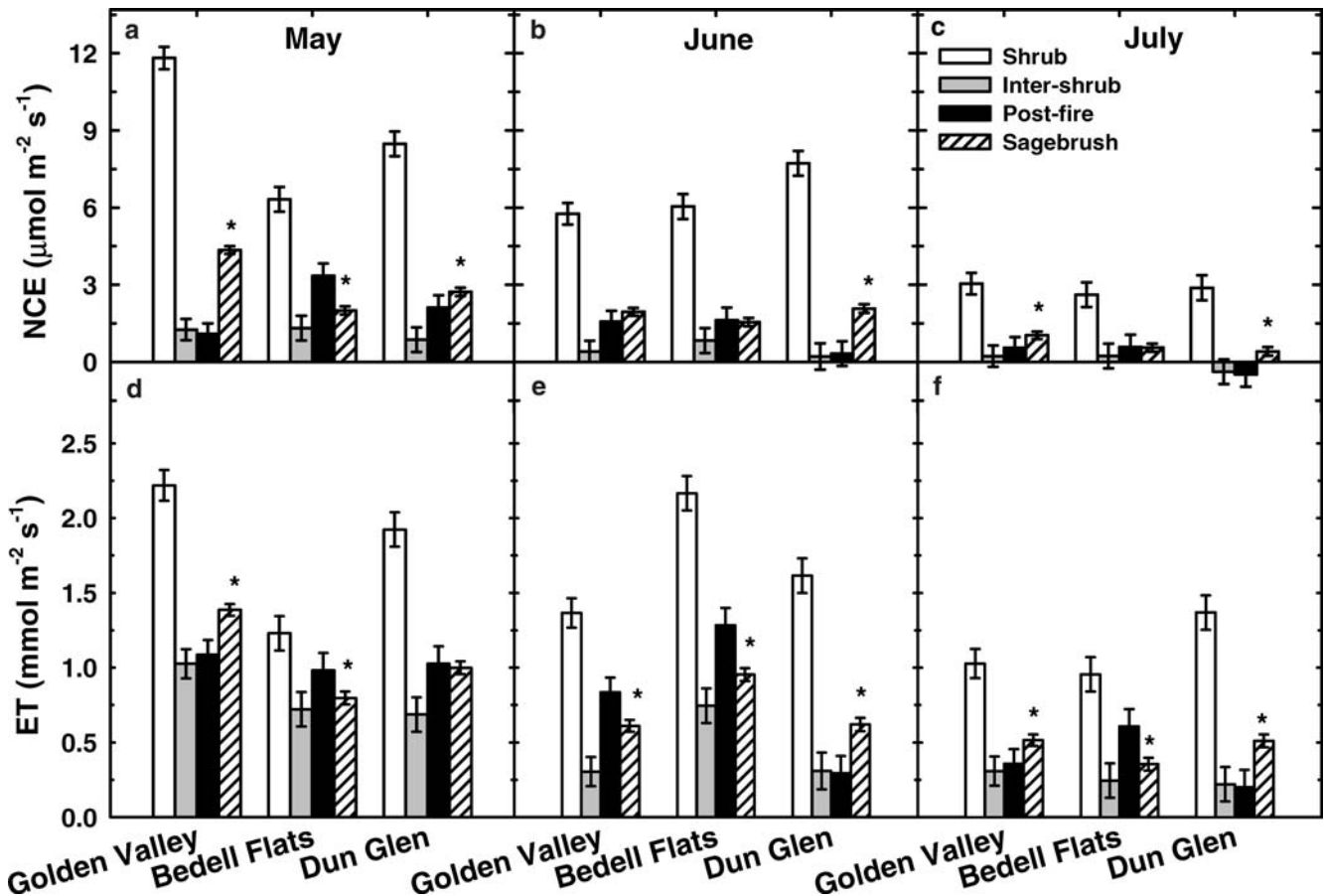
**Fig. 4** Instantaneous morning NCE (a–c) and ET (d–f) from shrub (*open*), intershrub (*gray*) and postfire (*solid bars*) plots in May (a, d), June (b, e) and July (c, f), 2002 at three sites (Golden Valley, Bedell Flats and Dun Glen) in the Great Basin Desert. Sagebrush community exchange (*hatched bars*) was calculated as a weighted sum of values from shrub and intershrub plots based on percent ground cover at each site. *Positive values* indicate net flux from the atmosphere to the land surface and *negative values* indicate net flux to the atmosphere. *Bars* are least square means ± SE ($n = 7$ at Bedell and Dun Glen and $n = 10$ at Golden Valley). *Asterisks* (*) indicate significant ($P < 0.05$) difference between postfire and sagebrush community-level fluxes

postfire bunchgrass and sagebrush communities were not different from each other at Bedell Flats ($y = 1.9 x - 0.2$, $r^2 = 0.28$).

### Leaf area index and plant cover

Shrub leaf area index (LAI) declined during the growing season in all years and at all sites. Compared to 2002 and 2003, average shrub LAI was low in June 2001 (Golden Valley site $0.42 \pm 0.4$) and declined by 33% by late July. In 2002, shrub LAI reached its maximum at all sites in May (Golden Valley site $3.5 \pm 0.6$, Bedell Flats $3.6 \pm 0.5$, Dun Glen $3.5 \pm 0.9$) but declined by approximately 75% by late July. In 2003, maximum shrub LAI occurred in May ($3.6 \pm 0.6$) and declined by approximately 65% by mid-August. The decrease in carbon uptake and ET during the growing season in all years and at all sites was related to changes in leaf morphology and the decline in leaf area of sagebrush (Fig. 5).

The percent cover of green vegetation in the intershrub spaces was < 5% during all years at the Golden

Valley site (data not shown). Maximum cover was 30 and 75% in some plots at Bedell Flats and Dun Glen, respectively, but most of the cover was cheatgrass, which senesced later in the season. Since seasonal variation was relatively low, no significant relationship was found between intershrub cover and NCE or ET for any site or year.

Decreases in postfire NCE and ET during the growing season appeared to correspond with decreases in cover at all sites; however, the relationship between cover and fluxes appeared different at each site (Fig. 6). At the Golden Valley site, cover was linearly related to mean NCE ($y = 0.2x - 0.3$, $r^2 = 0.65$, $P < 0.01$). There were insufficient data to establish a relationship between surface fluxes and plant cover for the other two sites.

### Discussion

After fire, the replacement of sagebrush by herbaceous communities substantially altered ecosystem carbon and water exchange, but the nature of this change varied
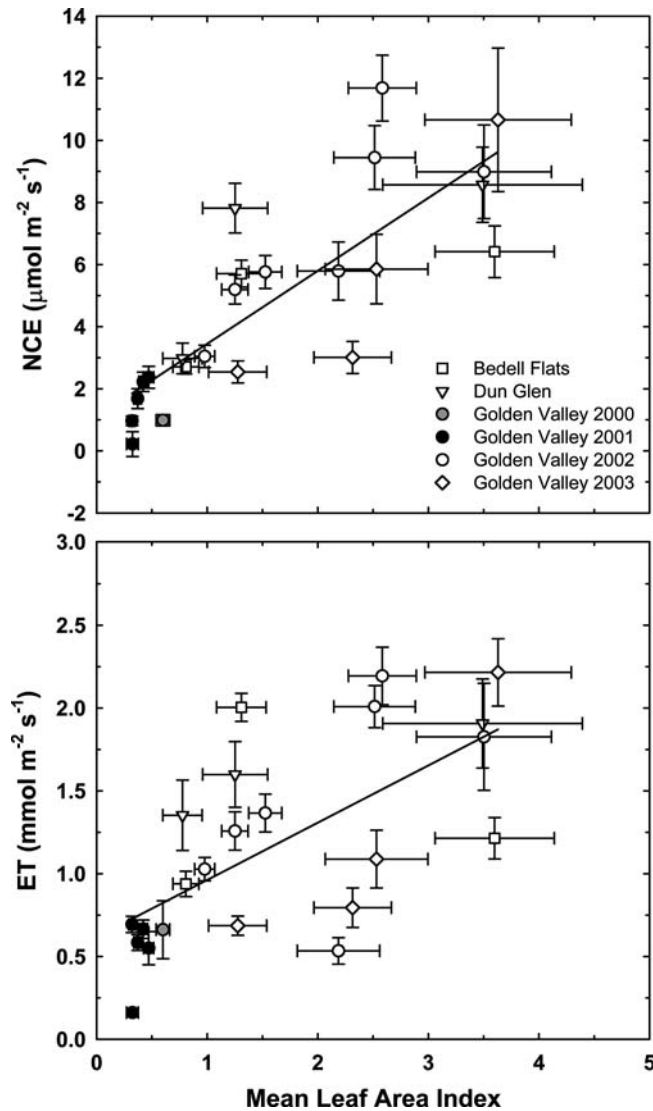
**Fig. 5** Relationship between shrub leaf area index (LAI) and instantaneous morning NCE of shrub plots at the Golden Valley (*circles*, *grey* 2000, *solid* 2001, *open* 2002, *diamonds* 2003), Bedell Flats (*squares*) and Dun Glen (*triangles*) sites. Points are means ± SE ($n = 10$ for Golden Valley and $n = 7$ for other sites). NCE regression line: $y = 2.3\ x + 1.1$, $r^2 = 0.67$, $P < 0.01$. ET regression line: $y = 0.3\ x + 0.6$, $r^2 = 0.43$, $P < 0.01$

**Fig. 6** Relationship between the percentage cover of postfire plots and instantaneous morning NCE at the Golden Valley (*circles*, *grey* 2000, *solid* 2001, *open* 2002, *diamonds* 2003), Bedell Flats (*squares*) and Dun Glen (*triangles*) sites. Points are means ± SE ($n = 10$ for Golden Valley and $n = 7$ for other sites). NCE regression line for Golden Valley site only: $y = 0.2x - 0.3$, $r^2 = 0.65$, $P < 0.01$

with prevailing climate and the species composition of the postfire community. At the Golden Valley site, instantaneous NCE of the recently established annual mustard community was consistently lower than the native sagebrush community, although the differences were less in dry years (Fig. 1). While substantial reductions in NCE and et also were observed at the Dun Glen site where repeated fires have contributed to a strong dominance of cheatgrass, this was not the case for the postfire community composed primarily of crested wheatgrass, a non-native bunchgrass (Fig. 4). In this community, when soil moisture was abundant in early spring, NCE in the postfire community was greater than the native sagebrush community. Non-native plants are aggressively invading many sagebrush communities in
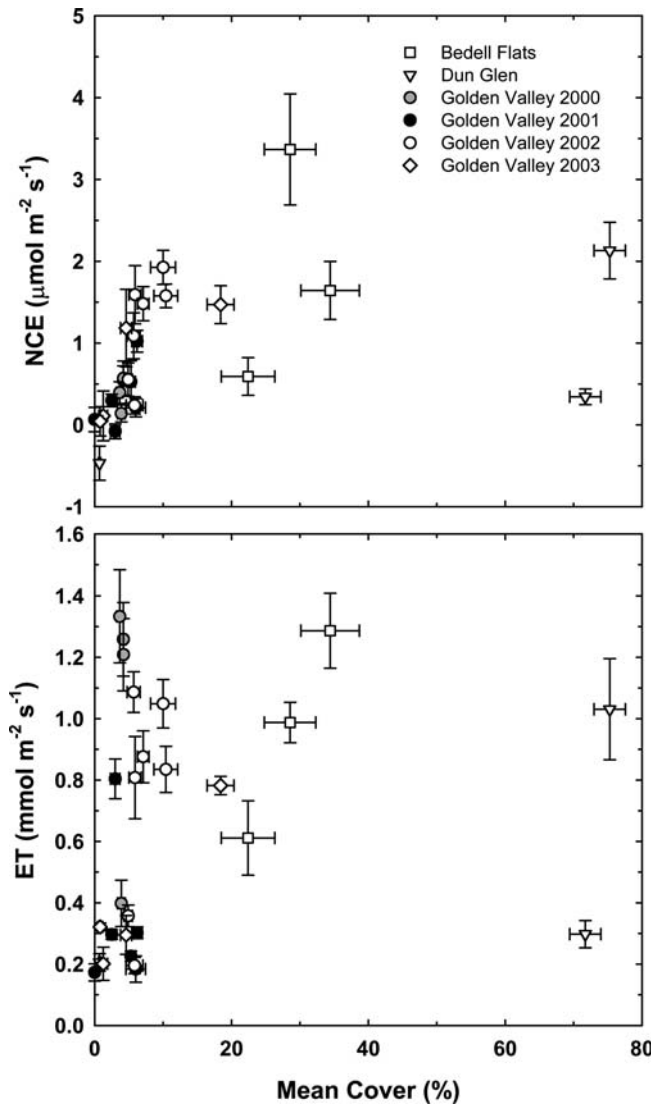
the Great Basin Desert, and at least where these species becomes dominant after fire, this invasion may reduce the carbon storage capacity and alter the hydrologic cycle in this ecosystem.

The static chamber provided an effective method to spatially resolve ecosystem C and water fluxes in this arid ecosystem. Estimates of daily integrated NCE and ET (Table 1) for the sagebrush communities in 2002 and 2003 were similar to those reported by Smith et al. (2003) and Obrist et al. (2003). The absolute rates of NCE for sagebrush reported by Angell et al. (2001) were greater than those measured in this study, but the sagebrush communities in Oregon and Idaho had greater cover of understory vegetation than any of the locations in this study. The rates of NCE and ET for the

postfire communities in this study were lower than native semi-arid grasslands (Dugas et al. 1996; Sims and Bradford 2001; LeCain et al. 2002), possibly attributable to lower leaf area in the non-native postfire communities than in native grasslands.

Abundant spring precipitation in most years contributed to relatively high rates of NCE and ET early in the growing season, and the depletion of soil moisture during the summer caused reductions in LAI, NCE and ET in sagebrush and postfire communities. Consistently greater NCE by shrubs resulted in greater rates of carbon assimilation early in the season in the sagebrush community compared to the postfire community. However, nighttime ecosystem respiration (above and belowground components; Fig. 3) also was greatest when soil moisture was abundant early in the growing season. While rates were considerably lower than in more mesic ecosystems where microbial and root activity is greater (e.g. Raich and Schlesinger 1992), nighttime respiration was similar to rates found in other semi-arid ecosystems (LeCain et al. 2000; Angell et al. 2001) where soil respiration is driven more by soil moisture than temperature (Bremer et al. 1998; LeCain et al. 2002). Despite these greater respiratory C losses, daytime C uptake was sufficiently large that integrated daily NCE was greater in the sagebrush community than the postfire community (Table 1). This difference in NCE between communities diminished as water became progressively more limiting.

The seasonality of ET at Golden Valley differed between the sagebrush and postfire communities. Instantaneous ET for the sagebrush community was greater than postfire ET early in the season (Fig. 2), but the decrease in leaf area and soil evaporation caused ET from the sagebrush community to decrease as soil moisture declined during the season. In contrast, the postfire mustard community maintained similar ET rates through most of the growing season. High transpiration rates by mustards in the middle of the summer may have compensated for low rates of soil evaporation, contributing to greater ET from the postfire community than from the sagebrush community at this time. As the mustards senesced and postfire cover decreased (in late summer and during the drought conditions of 2001), surface soil moisture and ET became similar between these two communities. Differences in the timing of maximum ET during the year and the relative contribution of transpiration to ET may alter ecosystem water balance and interactions with local climate.

Inter-annual variation in precipitation during the growing season affects carbon fluxes in sagebrush ecosystems (Gilmanov et al. 2003), as well as the differences in surface fluxes between the native sagebrush and postfire community at Golden Valley (Figs. 1, 2). In 2002 and 2003, years with above average spring rains, maximum NCE was considerably greater and peaked earlier in the summer in the sagebrush community compared to the postfire community. In contrast, extremely low winter and spring precipitation in 2001 greatly reduced the rates of surface carbon and water fluxes, and the magnitude and seasonal variation in these fluxes was similar in both community types. Using a larger static chamber (Arnone and Obrist 2003) at this same site, Obrist et al. (2003) determined that lower respiratory losses and greater soil evaporation contributed to greater C uptake and ET in the postfire community than the adjacent sagebrush community during the extreme drought of 2000–2001. While C and water fluxes may be slightly greater in postfire communities exposed to extreme drought (Obrist et al. 2003), the sagebrush community supports substantially great fluxes in years when soil moisture is more readily available.

The decrease in NCE by sagebrush during the growing season was related to changes in leaf morphology and a reduction of leaf area caused by decreasing soil moisture (Fig. 5). In early spring, sagebrush produces large ephemeral leaves that maximize carbon gain when soil moisture is abundant (DePuit and Caldwell 1973). These leaves had higher photosynthetic rates than leaves produced later in the summer, and the combination of high tissue-specific photosynthetic rates greater leaf area index contributed to high NCE for sagebrush in May and June (Fig. 1). As soils dried, these large leaves were replaced with smaller leaves (Miller and Shultz 1987) that had lower photosynthetic rates; the 75% reduction in leaf area associated with changing leaf morphology and lower tissue-specific rates of photosynthesis contributed low NCE in the sagebrush community during the summer. Similar seasonal declines in leaf area (Black and Mack 1986; Kolb and Sperry 1999) and carbon uptake (Wylie et al. 2003) have been observed in other sagebrush ecosystems. The plasticity in leaf morphology and total leaf area allows sagebrush to maximize C gain early in the season but also maintain positive carbon and water balance during unfavorable seasonal conditions (Cunningham and Strain 1969).

The phenology of the dominant vegetation contributed to the seasonal patterns of NCE and ET in the three postfire communities, but the relationship between surface fluxes, phenology and soil moisture appeared to vary among sites (Fig. 6). The decline in NCE and ET during the summer was pronounced in the cheatgrass community at Dun Glen, where rapid senescence of cheatgrass caused a complete loss of C uptake and a 60% decline in late season ET by July. The other postfire communities maintained greater plant cover and surface fluxes than the cheatgrass community late in the summer. The cheatgrass community was the only one where significant differences in surface soil moisture and temperature were detected. With no active vegetation and low ET, late season decreases in soil moisture and increased soil temperature may result in further changes in surface energy balance, including increases in sensible heat (Bremer and Ham 1999).

Establishment of non-native species alters the seasonality of carbon and water fluxes in other ecosystems,

including grasslands (Ham and Knapp 1998) and shrub-invaded semi-arid grasslands (Huenneke et al. 2002). One consequence of the change in seasonality of water fluxes is altered availability and spatial distribution of soil water in arid systems. For example, with early senescence, invasive annuals in California and Arizona grasslands do not utilize summer precipitation, leading to increased soil moisture (Frasier and Cox 1994; Holmes and Rice 1996). In the Great Basin Desert where summer precipitation is infrequent, a decrease in cover associated with the establishment of non-native species contributed to greater soil temperature and lower surface soil moisture (this study, Obrist et al. 2004). Sagebrush utilizes moisture in deeper soil layers (Campbell and Harris 1977) and replacement of these shrubs by postfire communities may decrease surface soil moisture but increases its storage below the effective rooting zone of the postfire plants (Link et al. 1990). Furthermore, increased snow deposition around shrubs (data not shown) may cause greater recharge in intact sagebrush compared to postfire communities. Obrist et al. (2004) found significantly lower soil water content (< 75 cm) in postfire soils throughout the spring growing season in Golden Valley. Changes in the spatial and temporal distribution of soil moisture may reduce the capacity of native vegetation to colonize postfire communities.

The amount and type of plant cover has a strong influence on carbon and water balance of ecosystems, and replacing the dominant plant functional type in a community changes many ecosystem processes (Hooper and Vitousek 1997; Tilman et al. 1997; e.g. Chapin et al. 2000). Our results indicated that conversion of native sagebrush to postfire communities alters the magnitude and the seasonal patterns of carbon and water exchange, particularly during times when moisture is available. Additionally, changes in soil moisture and temperature as a result of vegetation and inter-annual climate variability will further alter carbon and water fluxes in these non-native communities. As the extent of postfire cheatgrass communities increases, decreases in NCE and ET are likely to become more pronounced and have a greater impact on ecosystem function. The capacity of Great Basin Desert ecosystems to store carbon and the regional water balance may be severely affected by this landscape transformation.

## References

Anderson EW (1986) A guide for estimating cover. Rangelands 8:236–238

Angell R, Svejcar T (1999) A chamber design for measuring net $CO_2$ exchange on rangeland. J Range Manag 52:27–31

Angell RF, Svejcar T, Bates J, Saliendra NZ, Johnson DA (2001) Bowen ratio and closed chamber carbon dioxide flux measurements over sagebrush steppe vegetation. Agric For Meteorol 108:153–161

Arnone JA, Obrist D (2003) A large daylight geodesic dome for quantification of whole-ecosystem $CO_2$ and water vapour fluxes in arid shrublands. J Arid Environ 55:629–643

Black RA, Mack RN (1986) Mount St. Helens ash: recreating its effects on the steppe environment and ecophysiology. Ecology 67:1289–1302

Blank RR, Allen F, Young JA (1994) Extractable anions in soils following wildfire in a sagebrush–grass community. Soil Sci Soc Am J 58:564–570

Bonan GB (1999) Frost Followed the Plow: Impacts of Deforestation on the Climate of the United States. Ecol Appl 9:1305–1315

Bremer DJ, Ham JM (1999) Effect of spring burning on the surface energy balance in a tallgrass prairie. Agric For Meteorol 97:43–54

Bremer DJ, Ham JM, Owensby CE, Knapp AK (1998) Responses of soil respiration to clipping and grazing in a tallgrass prairie. J Environ Qual 27:1539–1548

Busch DE, Smith SD (1995) Mechanisms associated with decline of woody species in riparian ecosystems of the southwestern U.S. Ecol Monogr 65:347–370

Campbell GS, Harris GA (1977) Water relations and water use patterns for *Artemisia tridentata* Nutt. in wet and dry years. Ecology 58:652–659

Chapin FS (2003) Effects of plant traits on ecosystem and regional processes: a conceptual framework for predicting the consequences of global change. Ann Botany 91:455–463

Chapin FS, Walker BH, Hobbs RJ, Hooper DU, Lawton JH, Sala O, Tilman D (1997) Biotic control over the functioning of ecosystems. Science 277:500–504

Chapin FS, Zavaleta ES, Eviner VT, Naylor RL, Vitousek PM, Reynolds HL, Hooper DU, Lavorel S, Sala OE, Hobbie SE, Mack MC, Diaz S (2000) Consequences of changing biodiversity. Nature 405:234–242

Charley JL, West NE (1975) Plant-induced soil chemical patterns in some shrub-dominated semi-desert ecosystems of Utah. J Ecol 63:945–963

Cunningham GL, Strain BR (1969) An ecological significance of seasonal leaf variability in a desert shrub. Ecology 50:100–408

D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annu Rev Ecol Syst 23:63–87

DePuit EJ, Caldwell MM (1973) Seasonal pattern of net photosynthesis of *Artemisia tridentata*. Am J Bot 60:426–435

Dugas WA, Hicks RA, Gibbens RP (1996) Structure and function of C-3 and C-4 Chihuahuan Desert plant communities. Energy balance components. J Arid Environ 34:63–79

Eastman JL, Coughenour MB, Pielke SRA (2001) The regional effects of $CO_2$ and landscape change using a coupled plant and meteorological model. Global Change Biol 7:797–815

Frasier GW, Cox JR (1994) Water balance in pure stand of Lehmann lovegrass. J Range Manag 47:373–378

Gilmanov TG, Johnson DA, Saliendra NZ (2003) Growing season $CO_2$ fluxes in a sagebrush-steppe ecosystem in Idaho: bowen ration/energy balance measurements and modeling. Basic Appl Ecol 4:167–183

Halvorson JJ, Bolton H, Smith JL (1997) The pattern of soil variables related to *Artemisia tridentata* in a burned shrub-steppe site. Soil Sci Soc Am J 61:287–294

Ham JM, Knapp AK (1998) Fluxes of $CO_2$, water vapor, and energy from a prairie ecosystem during the seasonal transition from carbon sink to carbon source. Agric For Meteorol 89:1–14

Harris GA (1967) Some competitive relationships between *Agropyron spicatum* and *Bromus tectorum*. Ecol Monogr 37:89–111

Holmes TH, Rice KJ (1996) Patterns of Growth and Soil-water utilization in some exotic annuals and native perennial bunchgrasses of California. Ann Botany 78:233–243

Hooper DU, Vitousek PM (1997) The effects of plant composition and diversity on ecosystem processes. Science 277:1302–1305

Hooper DU, Cardon ZG, Chapin III FS, Durant M (2002) Corrected calculations for soil and ecosystem measurements of $CO_2$ flux using the LI-COR 6200 portable photosynthesis system. Oecologia, pp 1–18

Houghton RA (1999) The annual net flux of carbon to the atmosphere from changes in land use 1850–1990. Tellus 51B:298–313

Huenneke LF, Anderson JP, Remmenga M, Schlesinger H (2002) Desertification alters patterns of aboveground net primary production in Chihuahuan ecosystems. Global Change Biol 8:247–264

Kolb KJ, Sperry JS (1999) Differences in drought adaptation between subspecies of sagebrush (*Artemisia tridentata*). Ecology 80:2373–2384

Lacey JR, Olson BE (1991) Environmental and economic impacts of noxious range weeds. In: James LF, Evans JO, Ralphs MH, Child RD (eds) noxious range weeds. Westview, San Francisco, pp 5–16

Law BE, Falge E, Gu L, Baldocchi DD, Bakwin P, Berbigier P, Davis K, Hollinger D, Janssens IA, Jarvis P, Jensen NO, Katul G, Mahli Y, Matteucci G, Meyers T, Monson R, Munger W, Oechel W, Olson RA, Pilegaard K, Paw U KT, Thorgeirsson H, Valentini R, Verma S, Vesala T, Wilson K, Wofsy S (2002) Environmental controls over carbon dioxide and water vapor exchange of terrestrial vegetation. Agric For Meteorol 113:97–120

LeCain DR, Morgan JA, Schuman GE, Reeder JD, Hart RH (2000) Carbon exchange rates in grazed and ungrazed pastures of Wyoming. J Range Manag 53:199–206

LeCain DR, Morgan JA, Schuman GE, Reeder JD, Hart RH (2002) Carbon exchange and species composition of grazed pastures and exclosures in thes hortgrass steppe of Colorado. Agric, Ecosyst Environ 93:421–435

Link SO, Gee GW, Thiede ME, Beedlow PA (1990) Response of a shrub-steppe ecosystem to fire: Soil water and vegetational change. Arid Soil Res Rehabil 4:163–172

Mack RN (1981) Invasion of *Bromus tectorum* L. into western North America: An ecological chronicle. Agro-Ecosyst 7:145–165

Melgoza G, Nowak RS, Tausch RJ (1990) Soil water exploitation after fire: competition between *Bromus tectorum* (cheatgrass) and two native species. Oecologia 83:7–13

Miller RF, Shultz LM (1987) Development and longevity of ephemeral and perennial leaves on *Artemisia tridentata* Nutt. ssp. *wyomingensis*. Great Basin Nat 47:227–230

Obrist D, DeLucia EH, Arnone III JA (2003) Consequences of wildfire on ecosystem $CO_2$ and water vapour fluxes in the Great Basin. Global Change Biol 9:563–574

Obrist D, Yakir D, Arnone III JA (2004) Temporal and spatial patterns of soil water following wildfire-induced changes in plant communities in the Great Basin in Nevada, USA. Plant Soil 262:1–12

Pellant M (1994) History and Applications of the Intermountain Greenstripping Program. In: proceedings-ecology and management of annual rangelands, General Technical Report INT-GTR-313 edn. USDA Forest Service, Intermountain Research Station

Raich JW, Schlesinger WH (1992) The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. Tellus 44B:81–99

Sala A, Smith SD, Devitt DA (1996) Water use by *Tamarix ramosissima* and associated phreatophytes in a Mojave desert floodplain. Ecol Appl 6:888–898

Schlesinger WH, Reynolds JF, Cunningham GL, Huenneke LF, Jarrell WM, Virginia RA, Whitford WG (1990) Biological feedbacks in global desertification. Science 247:1043–1048

Schlesinger WH, Raikes JA, Hartley AE, Cross AF (1996) On the spatial pattern of soil nutrients in desert ecosystems. Ecology 77:364–374

Shukla J, Nobre C, Sellers P (1990) Amazon deforestation and climate change. Science 247:1322–1325

Sims PL, Bradford JA (2001) Carbon dioxide fluxes in a southern plains prairie. Agric For Meteorol 109:117–134

Smith WK, Kelly RD, Welker JM, Fahnestock JT, Reiners WA, Hunt ER (2003) Leaf-to-aircraft measurements of net $CO_2$ exchange in sagebrush steppe ecosystem. J Geophys Res 108:4122–4155

Tilman D, Knops J, Wedin D, Reich P, Ritchie M, Siemann E (1997) The influence of functional diversity and composition on ecosystem processes. Science 277:1300–1302

Vitousek PM, Walker LR (1989) Biological invasion by *myrica faya* in hawai'i: plant demography, nitrogen fixation, ecosystem effects. Ecol Monogr 59:247–265

Vourlitis GL, Oechel WC, Hastings SJ, Jenkins MA (1993) A system for measuring *in situ* $CO_2$ and $CH_4$ flux in unmanaged ecosystems: an arctic example. Funct Ecol 7:369–379

Wylie BK, Johnson DA, Laca E, Saliendra NZ, Gilmanov TG, Reed BC, Tieszen LL, Worstell BB (2003) Calibration of remotely sensed, coarse resolution NDVI to $CO_2$ fluxes in a sagebrush-steppe ecosystem. Remote Sens Environ 85:243–255

Young JA, Evans RA (1978) Population dynamics after wildfires in sagebrush grasslands. J Range Manag 31:283–289

Young JA, Evans RA, Major J (1972) Alien plants in the Great Basin. J Range Manag 25:194–201

Young JA, Evans RA, Eckert RE Jr, Kay BL (1987) Cheatgrass Rangelands 9:266–270