

Consequences of wildfire on ecosystem CO₂ and water vapour fluxes in the Great Basin

DANIEL OBRIST*, EVAN H. DELUCIA† and JOHN A. ARNONE III*

*Division of Earth and Ecosystem Sciences, Desert Research Institute, 2215 Raggio Parkway, Reno, NV 89512, USA, †University of Illinois, Urbana, Champaign, Department of Plant Biology, 505 S. Goodwin Ave, Urbana, IL 61801, USA

Abstract

Increased fire frequency in the Great Basin of North America's intermountain West has led to large-scale conversion of native sagebrush (*Artemisia tridentata* Nutt.) communities to postfire successional communities dominated by native and non-native annual species during the last century. The consequences of this conversion for basic ecosystem functions, however, are poorly understood. We measured net ecosystem CO₂ exchange (NEE) and evapotranspiration (ET) during the first two dry years after wildfire using a 4-m diameter (16.4 m³) translucent static chamber (dome), and found that both NEE and ET were higher in a postfire successional ecosystem (−0.9–2.6 μmol CO₂ m^{−2} s^{−1} and 0.0–1.0 mmol H₂O m^{−2} s^{−2}, respectively) than in an adjacent intact sagebrush ecosystem (−1.2–2.3 μmol CO₂ m^{−2} s^{−1} and −0.1–0.8 mmol H₂O m^{−2} s^{−2}, respectively) during relatively moist periods. Higher NEE in the postfire ecosystem appears to be due to lower rates of above-ground plant respiration while higher ET appears to be caused by higher surface soil temperatures and increased soil water recharge after rains. These patterns disappeared or were reversed, however, when the conditions were drier. Daily net ecosystem productivity (NEP; g C m^{−2} d^{−1}), derived from multiple linear regressions of measured fluxes with continuously measured climate variables, was very small (close to zero) throughout most of the year. The wintertime was an exception in the intact sagebrush ecosystem with C losses exceeding C gains leading to negative NEP while C balance of the postfire ecosystem remained near zero. Taken together, our results indicate that wildfire-induced conversion of native sagebrush steppe to ecosystems dominated by herbaceous annual species may have little effect on C balance during relatively dry years (except in winter months) but may stimulate water loss immediately following fires.

Keywords: evapotranspiration (ET), net ecosystem CO₂ exchange (NEE), net ecosystem productivity (NEP), postfire plant succession, sagebrush

Received 10 May 2002; revised version received and accepted 23 August 2002

Introduction

Fire frequency in the native sagebrush (*Artemisia tridentata* Nutt.) steppe has dramatically increased in the Great Basin of North America's intermountain west (from every 40–100 years to less than every 10 years) during the last century (review by D'Antonio & Vitousek, 1992), and has resulted in widespread conversion of sagebrush-dominated plant communities to postfire communities dominated by herbaceous annual species (Billings, 1990;

Whisenant, 1990). One of the reasons for this transition has been the invasion of cheatgrass (*Bromus tectorum*), a Eurasian winter annual that was introduced to the Great Basin in the late 1800s and has since been promoted by overgrazing, intentional seeding, human-caused fires, and acceleration of the natural fire cycle (Mack, 1981; Yensen, 1981; Mack, 1986; Young & Allen, 1997). A recent study in the Mojave Desert indicates that rising atmospheric CO₂ levels may stimulate further conversion of arid shrublands to alien grass-dominated ecosystems because biomass and plant density of invasive annual grass species may respond more strongly to elevated CO₂ than that of native plant species (Smith *et al.*, 2000).

Although elimination of sagebrush and other native shrub species from the Great Basin landscape as a result

Correspondence: Daniel Obrist, Division of Earth and Ecosystem Sciences, Desert Research Institute, 2215 Raggio Parkway, Reno, NV 89512, USA, tel. (775) 673 7394, fax (775) 673 7485, e-mail: dobrist@dri.edu

of more frequent wildfires has had a detrimental effect on biotic diversity and habitat (Billings, 1990), little experimental data are available on the potential consequences of wildfire and postfire plant community alteration on other key ecosystem functions such as CO₂ and water balance (fluxes and stocks). Aside from massive losses of ecosystem C and nutrient stocks from sagebrush ecosystems during incineration (up to 980 g biomass m⁻² during prescribed fires; Sapsis & Kauffman, 1991), further postfire changes in ecosystem CO₂ fluxes (net ecosystem CO₂ exchange [NEE]) and evapotranspiration (ET) likely will affect plant succession and the ability of the ecosystem to return to its native state. Changes in NEE and ET after wildfires also may impact regional hydrology and arid shrubland C cycling. Although arid and semiarid ecosystems account for about one-third of the world's land area (Wickens, 1998) and are rapidly expanding as a result of human activities (Dregne, 1991), little baseline data on NEE and ET are available (e.g. Angell & Svejcar, 1999; Angell *et al.*, 2001). Moreover, no data are available on the effects of wildfire-induced alteration in plant community structure and postfire plant succession on NEE and ET.

The objectives of this study were to (1) quantify how wildfire-induced shifts in plant community structure in the Great Basin (from shrub-dominated steppe to postfire plant communities dominated by annual and perennial herbaceous species) affect the diel and seasonal dynamics of NEE and ET, (2) quantify the relationships of NEE and ET to environmental factors that may regulate these fluxes at different times of the year, (3) use these relationships to model daily net ecosystem productivity (NEP) and daily ET, and (4) explore the extent to which differences in NEE are due to shifts in below-ground (i.e. root and soil heterotrophic respiration) and above-ground (i.e. net canopy photosynthesis or dark respiration) processes. We specifically hypothesized that NEE of postfire ecosystems would be much lower than that of intact sagebrush ecosystems primarily due to the very limited CO₂ uptake capacity of sparse, short-lived annual plant species relative to the perennial, long-lived sagebrush canopies with significantly higher leaf area indices (LAI). Similarly, we hypothesized that ET would be significantly lower in postfire ecosystems because of a reduction in transpiring surface area and limited access to deeper soil water of postfire plant communities that no longer contain deep-rooted shrubs.

Materials and methods

Study site

The study site is located in the western part of the Great Basin 10 km north of Reno, Nevada along a fire line

created by a 1999 wildfire (39°38'N, 119°48'W; elevation 1600 m a.s.l.). One side of the fire line is characterized as a native big sagebrush shrub steppe community composed of a mixture of native shrubs (*A. tridentata*, *Chrysothamnus viscidiflorus* Hook. Nutt., *Chrysothamnus nauseosus* Pallas Britt., *Ephedra viridis* Coville, *Prunus andersonii* Gray, *Purshia tridentata* Pursh DC.), native grasses (*Achnatherum hymenoides* Roemer & J.A. Schultes Barkworth, *Elymus elymoides* Raf. Swezey, *Agropyron* spp.), native perennial herbaceous species (*Astragalus* spp., *Eriogonum* spp.), annual forbs (*Eriastrum sparsiflorum* Eastw. Mason, *Mentzelia albicaulis* Dougl.), and the invasive annual cheatgrass. On the other side of the fire line, a wildfire completely incinerated all above-ground biomass in June 1999. The site was seeded (10 kg seeds ha⁻¹) in fall 1999 with a mixture of perennial shrubs (*P. tridentata*, *Atriplex canescens* Pursh Nutt.), forbs (*Sanguisorba* spp., *Medicago sativa* L.), and grasses (*Elymus lanceolatus* Scribn. & J.G. Sm. Gould, *Agropyron cristatum* L. Gaertn., *Leymus cinereus* Scribn. & Merr. A. Löve, *Agropyron* spp., *A. hymenoides*). None of the seeded plant species became established, however, and the few seedlings that did appear in 1999 disappeared by early summer of 2000. In July 2000, the first growing season following the fire, vegetation in the postfire area along the fire line consisted of a sparse covering of small native shrubs (*C. viscidiflorus*, *P. andersonii*, *E. viridis*), numerous native perennial forbs (*Stephanomeria spinosa* Nutt., *S. Tomb*, *Eriogonum* spp., *Astragalus* spp.) and grasses (*Distichlis spicata* L. Greene, *A. hymenoides*), as well as native annual forbs (*E. sparsiflorum*, *M. albicaulis*, *Gayphytum ramosissimum*), non-native annual forbs (*Erodium cicutarium* L. L'Hér., *Sisymbrium altissimum* L.) and the invasive cheatgrass. Soils are classified as a shallow stony sandy loam belonging to the Acrelane series developed in granodiorite bedrock (Baumer, 1983). Mean annual precipitation near the site is 308 mm, and mean annual temperature is 10 °C (15 years means, WRCC, 2002).

Measurement of NEE, ET, and soil CO₂ efflux

We established six blocks along 60 m of the fire line. In each block, we randomly established one 12.25 m² study plot in the intact sagebrush ecosystem and one plot in the postfire ecosystem 10 m from the fire line. In June 2000, all study plots were surrounded by 12-sided wooden base plates (4 cm thick × 30 cm wide × 150 cm long) embedded into the soil such that the top surface of the plates was flush with the surrounding soil surface. These base plates enabled rapid, airtight placement of a large, translucent, static chamber dome used for NEE and ET measurements.

Net ecosystem CO₂ exchange and ET were quantified on nine dates between July 2000 and November 2001

using the large static chamber method described in detail in Arnone & Obrist (2003). Briefly, ecosystem gas fluxes were measured using a 4-m diameter, 16.4 m³ translucent geodesic dome (ground area of 12.25 m²) by recording changes in CO₂ and water vapour inside the dome that was sealed to the wooden base-plates. The reinforced polyethylene dome skin had low attenuation of photosynthetic active radiation (>70% of photon flux density [PFD] transmitted) and high transmissivity to thermal radiation. Before sealing the dome onto the wooden base plates, we positioned two 100 W window fans on cinder blocks inside the plots to thoroughly mix the air and placed an open-path IRGA (Li7500, Licor, Lincoln, Nebraska, USA) inside the plot 50 cm from the perimeter to record changes in CO₂ and water vapour once the dome was in place. Complete sealing of the dome was achieved within 10 s. Measurements of NEE and ET were completed within 160 s after placing the dome over the plots during daytime and within 300 s at nighttime when fluxes were very low. We used a thermocouple attached to the open-path IRGA to record changes in dome air temperature during the measurements. We alternated measurements of intact sagebrush and postfire successional plots during each 24 h sampling period. This enabled four to five measurements of all 12 plots within a 24-h period, and it allowed us to construct diel time courses of NEE and ET. Since variability in measured fluxes between plots within each ecosystem was relatively small and because soil CO₂ efflux measurements required significant time, we reduced the number of plot replicates to four ($n=4$ per ecosystem) in 2001. Calibration and field testing of the dome method indicated that NEE as low as 0.1 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and ET of 0.1 $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ could be accurately detected. Flux estimates derived using static chambers generally agree well with other techniques (e.g. tower and aircraft measurement techniques; Oechel *et al.*, 1998; Angell *et al.*, 2001). The 30% reduction in PFD inside the dome may have only affected flux measurements immediately after sunrise and before sunset when PFD dropped below the ecosystem light saturation point (<1000 $\mu\text{mol m}^{-2} \text{ s}^{-1}$; see results). These periods represented only a small fraction of the photoperiod. Rates of air temperature increase inside the dome during the 160 s of flux measurements ranged from 0.1 °C min⁻¹ in the morning and evening hours to 0.8 °C min⁻¹ at mid-day. At no time, however, did leaf temperatures change during measurements, indicating that the dome also likely did not alter stomatal conductance. Wind speed in the dome averaged 0.8 ms⁻¹. This corresponded well with wind speed frequently occurring at the site (e.g. 40% of the time wind speed ranged between 0.5 and 1.5 ms⁻¹ in 2001).

We also measured soil CO₂ efflux in 2001 using small static chambers after whole ecosystem fluxes were

measured with the dome (at least 0.5 h but not more than 1 h after dome measurements). We installed two 40 × 25 × 5 cm PVC static chambers in each of the 12 experimental plots in June 2000 by pushing the frames halfway into the soil (2.5 cm of the frame in the soil, 2.5 cm above ground). In each of the intact sagebrush plots, one of the two respiration plots was placed under a shrub and one between shrubs. These plots were kept free of vegetation by clipping all plants that appeared inside the frames. Soil CO₂ efflux was quantified by placing the same open-path IRGA used for the dome measurements horizontally on the ground inside the respiration plot and recording CO₂ inside the capped static chamber for 2 min. A closed cell foam gasket attached to the chamber lid sealed the lid to the frame and allowed the cable of the open-path IRGA to pass between the chamber and the frame without creating any leaks. Due to the small volume of the respiration chamber and the observed linear increase of CO₂ inside the chamber, no air mixing was needed.

Measurement of environmental parameters

A 27 probe TDR system (ESI Inc., Vancouver, Canada) continuously monitored volumetric soil water contents (WC) in 24 locations in the two adjacent ecosystems starting in March 2001. Each of the 24, 100 cm long TDR probes included five 15 cm long segments which allowed measurement of soil WC in five consecutive 15 cm soil layers to a depth of 75 cm. Site disturbance was minimal since the probes were vertically inserted into the soil after creating a pilot hole using a rock drill with a 3.5-cm diameter drill bit. Each hole was back-filled with the same soil removed during the drilling. Eight probes were inserted directly under sagebrush canopies, eight in intercanopy locations in the sagebrush ecosystem, and eight in the adjacent postfire ecosystem. Each of the 24 probes was connected to a datalogger (Campbell Inc., Logan, Utah, USA) by a 20-m coaxial cable, which allowed placement of TDR probes in three of the postfire and three of the sagebrush ecosystem plots. Prior to installing the probes, we calibrated all TDR segments in the laboratory using air-dried soils from the study site in a manner described by Frueh & Hopmans (1987). The high spatial replication (24 locations) and frequent measurement at all locations (every 20 min) enabled detection of small differences in soil WC even under very dry soil conditions.

Soil temperature at a depth of 10 cm was recorded every 15 min in 12 locations (four in postfire plots, four in sagebrush plots underneath shrubs, four in sagebrush plots between shrubs) using Tidbit™ temperature loggers (Onset Computer, Bourne, Massachusetts, USA). We monitored precipitation, solar radiation, wind speed,

wind direction, temperature, and relative humidity throughout the experiment with a weather station (Model 012, Campbell Scientific Inc., Logan, Utah, USA) located on the fire line. We also used meteorological data from a weather station (WRCC, 2002) less than 2 km away to interpolate missing weather data. We determined LAI of annual and perennial vegetation in both plant communities in July 2000, June 2001, and July 2001 by using allometric relationships between branch basal area and leaf area for all shrub species and destructive harvest of herbaceous plant species outside the experimental plots.

To extrapolate soil WC, soil temperature, and soil CO₂ efflux data measured under shrubs and between shrubs in the sagebrush ecosystem to whole plot levels, we measured shrub cover in each of the six experimental plots and weighted shrub and intershrub measurements according to the representative shrub and intershrub areas in each plot.

Calculation of daily NEP and ET

To calculate daily NEP and ET, we performed multiple regressions between measured ecosystem fluxes and the continuously recorded environmental parameters PFD, soil temperature, and air temperature for each of the nine 24 h flux measurement periods. We applied linear models between ecosystem fluxes and environmental parameters, with the exception that we used rectangular hyperbola functions to describe the response of NEE to PFD (e.g. Stocker *et al.*, 1997). The correlations between ecosystem fluxes and environmental parameters (Fig. 3a, b; $r^2 \geq 0.85$) were used to calculate continuous fluxes for each 24 h measuring period.

Statistical analyses

The overall study was designed as a randomized complete block experiment with six blocks (four used in 2001). Blocks were arranged along a 60 m transect with one plot located in the postfire ecosystem and one plot in the intact sagebrush ecosystem. First, we performed paired Student *t*-tests for each date of flux measurements using the plot pairs to test for differences in fluxes during the entire 24 h flux measurement periods. Second, we analysed all flux measurements using repeated measures analysis of variance (ANOVA) with between-subject independent variables *Block* ($n = 6$ in 2000 and $n = 4$ in 2001) and *Treatment* ($n = 2$; intact sagebrush or postfire), and within-subject independent variables *Date* ($n = 9$ for NEE and ET; $n = 7$ for soil CO₂ efflux), *Time of day* ($n = 2$; daytime and nighttime), and interactions. Third, we performed separate repeated measures ANOVAs for daytime and nighttime NEE and ET using the same independent variables mentioned above excluding *Time of day*. The

block effect was never significant and was therefore removed from all statistical analyses.

All ANOVAs, paired Student *t*-tests, and multiple regression analyses were performed using Stata 6.0 (Stata Corporation, College Station, Texas, USA). Rectangular hyperbola functions for NEE were fitted using Delta Graph 5.0.1 (SPSS Inc., Chicago, Illinois, USA). Statistically significant effects were defined, as $P \leq 0.05$. All error estimates in the text are standard errors of the mean.

Results

NEE and water vapour fluxes

Net ecosystem CO₂ exchange (NEE) of the postfire ecosystem differed from NEE in the intact sagebrush ecosystem on four of the nine measurement dates ($P \leq 0.05$); however, no differences were observed on the five other dates (Fig. 1a). On three measurement dates, NEE in the postfire ecosystem was higher than that measured in the intact ecosystem (Fig. 1a; July 2000, March 2001, and November 2001). These three dates also corresponded to the wettest of the nine dates (see Fig. 2b for 2001 and text below for 2000). NEE measured in the postfire ecosystem was lower only in May 2001.

NEE in both ecosystems exhibited strong seasonal and diel fluctuations ($P < 0.01$; Table 1). NEE was relatively high in 2000 and spring 2001 but dropped dramatically in late spring and summer 2001. Highest NEE in the postfire ecosystem occurred in March 2001 ($2.63 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), while highest NEE in the sagebrush ecosystem occurred in April 2001 ($2.79 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). Lowest daytime NEE occurred in November 2001 (postfire: $0.30 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$; sagebrush: $0.61 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). Night-time NEE was always negative with highest ecosystem respiration observed in April 2001 (postfire: $-0.9 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$; sagebrush: $-1.3 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) when daytime NEE was among the highest. Across all nine flux measurement periods, nighttime NEE was significantly higher (i.e. more negative) in the sagebrush ecosystem than in the postfire ecosystem ($P = 0.05$, Table 2) but daytime NEE was not significantly different.

Analogous to NEE, ET measured in the postfire ecosystem exceeded that measured in the sagebrush ecosystem in July 2000, March 2001, and November 2001 (Fig. 1b) when soil WC was relatively high (Fig. 2b). These three dates contributed to the overall higher ET in the postfire ecosystem across all measurements (Table 1). Evapotranspiration (ET) in the postfire ecosystem, however, was lower than that measured in the sagebrush ecosystem on three dates (October 2000, May 2001, and September 2001) and not significantly different on the other three dates. Evapotranspiration (ET) varied strongly throughout the day ($P < 0.01$; Table 1) with the highest rates

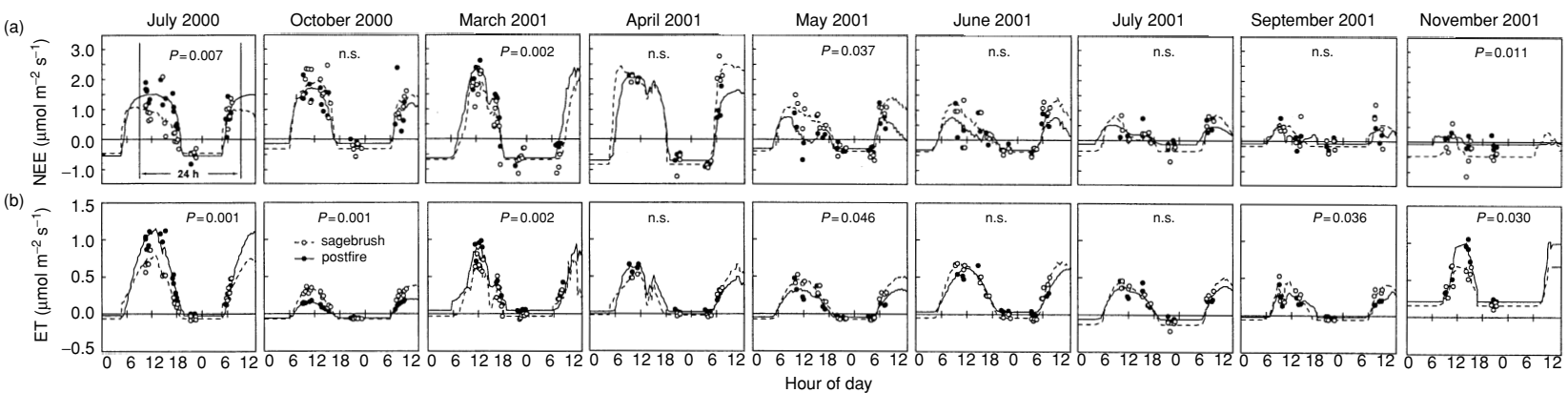


Fig. 1 (a) Diel time courses of measured net ecosystem CO₂ exchange (NEE) in adjacent intact sagebrush (open symbols) and postfire (filled symbols) ecosystems for nine measurement dates ($n = 6$ plots). Positive values represent CO₂ uptake by ecosystems from the atmosphere. (b) Diel time courses of water vapour fluxes (ET) in the two ecosystems. Positive values represent water loss from ecosystems to the atmosphere. Lines in both figures represent modelled diel time courses of NEE and ET for sagebrush (dashed lines) and postfire (solid lines) ecosystems constructed from multiple regressions of NEE or ET with continuously recorded PFD, soil temperature, and air temperature data. P -values are based on paired t -tests of the measured fluxes using plot pairs to test for differences between the two ecosystems for each 24 h measurement period. Six plots (replications) were measured in each ecosystem in 2000 ($n = 6$), and four plots were measured in 2001 ($n = 4$).

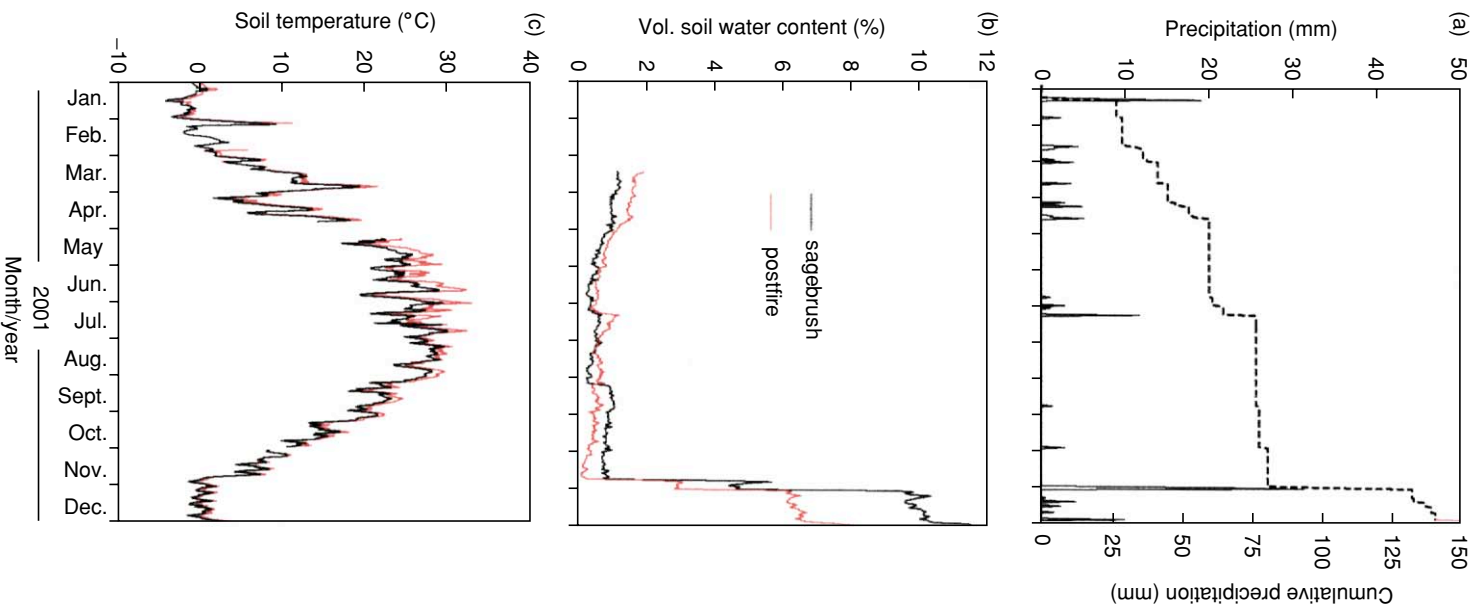


Fig. 2 (a) Daily precipitation (solid line) and cumulative daily precipitation (dashed line) in 2001 measured at a nearby (2 km distance) Western Regional Climate Center weather station (WRCC, 2002). (b) Time course of plot-level volumetric soil water contents in the upper 75 cm of sagebrush (black line) and postfire (red line) ecosystems. (c) Time course of plot-level daily mean soil temperatures at 10 cm depth.

always occurring at mid-day in both ecosystems. Evapotranspiration (ET) also exhibited seasonal patterns ($P < 0.01$; Table 1) with the highest rates observed in July 2000 and early spring 2001 (postfire: $1.12 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$; sagebrush: $0.86 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$) and lower rates seen with the onset of summer drought in 2001 (lowest daytime ET occurred in September 2001 — postfire: $0.42 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$; sagebrush: $0.53 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$; Fig. 1b). Evapotranspiration (ET) rebounded in November 2001 after the resumption of significant rain (Fig. 2a). Lowest ET always was observed at night with some water uptake by ecosystems (condensation of water on soil and plants) observed on several occasions.

Relationships between environmental factors and ecosystem fluxes, and modelled daily NEP and ET

All measured environmental parameters together (i.e. PFD, soil temperature, air temperature, soil WC, LAI) used in multiple regressions with NEE and ET explained 80% and 76% of all variation in measured NEE in postfire and sagebrush ecosystems, respectively, and 64% and 74% of the variation in measured ET fluxes in the two ecosystems, respectively. We were able to further refine these relationships by performing multiple regressions for each date separately even when only using PFD, air temperature, and soil temperature, the three continuously recorded environmental parameters (> 85% of the variation in NEE and ET; Fig. 3 a, b). It is noteworthy that a large amount of the variability in NEE and ET was explained by PFD alone (NEE: r^2 up to 0.97; Fig. 4a; ET: r^2 up to 0.95; Fig. 4b). These relationships, however, weakened later in 2001 as diel patterns of NEE and ET became less pronounced (Fig. 1a, b).

The good correlation between ecosystem fluxes and the three continuously recorded environmental variables (PFD, air temperature, and soil temperature) enabled us to predict fluxes for 24 h of each of the nine flux measurements (lines in Fig. 1a, b) and to calculate daily sums for NEE (i.e. daily NEP) and ET (Table 3). Daily NEP was remarkably close to zero for all but a few measurements in both ecosystems. Among the nine 24 h flux measurement periods, daily NEP was highest in April 2001 in both ecosystems and decreased steadily towards summer 2001. Lowest daily NEP was observed in November 2001 with both systems exhibiting net CO_2 losses. Daily NEP in July 2000 was similar to fluxes measured in spring 2001 and remained relatively high into October 2000. The largest differences in daily NEP between the two ecosystems were observed in November 2001 ($0.39 \text{ g C m}^{-2} \text{ d}^{-1}$) resulting in much higher C losses in intact sagebrush ecosystems compared to postfire ecosystems at this

point of the year. In general, daily ET followed precipitation patterns with highest daily ET observed shortly after rains (e.g. in November 2001) and decreasing ET as conditions became drier (e.g. in October 2000).

Soil CO_2 efflux

Across all measurements performed in 2001 (seven measurement dates), soil CO_2 efflux extrapolated to the dome plot level was not significantly different in the postfire ecosystem than in the intact sagebrush ecosystem (Table 1). On three of the seven dates (April, June, and November 2001), however, CO_2 efflux rates were higher in the postfire ecosystem (paired *t*-test between plot pairs; Fig. 5). Lower rates of soil respiration in sagebrush ecosystems on these three dates were due to especially low rates occurring in intershrub spaces which were 36% lower than rates measured under shrubs (intershrub: $0.18 \pm 0.01 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$; shrub: $0.28 \pm 0.03 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$; $P < 0.01$). Rates of soil CO_2 efflux in both ecosystems generally decreased with decreasing soil WC ($P < 0.01$) and increasing soil temperature ($P < 0.01$). Still, these two environmental factors together only explained 15% of the overall variability in measured soil CO_2 efflux (multiple regression analysis), and no relationships were observed between these two factors and CO_2 efflux when analysed on individual dates. Comparison of plot-level nighttime NEE (ecosystem dark respiration) and extrapolated plot-level nighttime soil CO_2 efflux (small static chamber subplots extrapolated to whole plot level) showed that soil CO_2 fluxes exceeded ecosystem fluxes measured using the dome 25% of the time. This result precluded us from partitioning whole-ecosystem fluxes into above-ground plant and below-ground root plus heterotrophic respiration (Objective 4; see Discussion). Nonetheless, direct comparisons of soil CO_2 fluxes between the two ecosystems that were measured at the level of the small static chamber are valid.

Precipitation, soil WC, and microclimatic conditions

The year 2001 was one of the driest years on record with a total of only 150 mm of precipitation (< 50% of long-term average precipitation; Fig. 2a). Up to the end of September 2001, the site received only 33% of the precipitation it usually receives by that time of the year. The year 2000 also was relatively dry and experienced below-average precipitation (202 mm; 66% of long-term average precipitation). Very low rainfall in 2001 resulted in corresponding low soil WC throughout most of the year (Fig. 2b). At the beginning of the growing season in March 2001, soil WC in the upper 75 cm of the soil was higher ($P < 0.01$) in the postfire ecosystem ($1.9 \pm 0.1\%$) than in the sagebrush ecosystem ($1.2 \pm 0.1\%$). By May

Table 1 Summary of statistical analyses (P -values from repeated measures ANOVAs) evaluating the effects of wildfire-induced conversion of native sagebrush steppe ecosystem to postfire successional ecosystem (Treatment), time of day (Time of day; first repeated measure variable), time of year (Date; second repeated measure variable) on NEE, ET, and soil CO₂ efflux (df: degrees of freedom; MS: mean squares; $n = 6$ in 2000, and $n = 4$ in 2001)

Source of Error	Dependent variable								
	NEE			ET			Soil CO ₂ efflux		
	df	MS	P	df	MS	P	df	MS	P
<i>Between-subject variable</i>									
Treatment	1	0.012	0.626	1	0.037	0.005**	1	0.010	0.527
Error	10	0.047		10	0.003		10	0.023	
<i>Within-subject variable</i>									
Date	8	1.004	< 0.001**	8	0.188	< 0.001**	6	0.216	< 0.001**
Time of day	1	55.044	< 0.001**	1	6.052	< 0.001**	1	0.212	< 0.001**
Treatment × Date	8	0.164	0.099(*)	8	0.020	0.012 *	6	0.021	0.151
Treatment × Time of day	1	0.419	0.006**	1	0.014	0.020*	1	0.037	0.045*
Treatment × Date × Time of day	16	1.287	< 0.001**	16	0.029	< 0.001**	12	0.030	< 0.001**
Error	120	0.053			0.002				

(*) $P < 0.1$; * $P < 0.05$; ** $P < 0.01$.

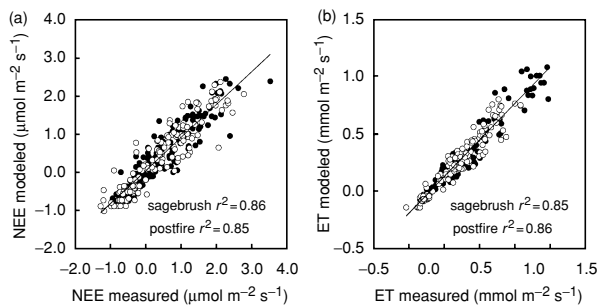


Fig. 3 (a) Regression between measured and modelled NEE in sagebrush (open symbols) and postfire (filled symbols) ecosystems. (b) Regression between measured and modelled ET in the two ecosystems (P -values for all four regressions < 0.01).

2001, soil WC in the top 75 cm dropped below 1% in both ecosystems and remained extremely low until snow fell in November 2001, one week before the last flux measurement was performed. Soil WC measured on two occasions in 2000 in the top 15 cm indicated higher WC in July 2000 (postfire: $6.9 \pm 0.2\%$; sagebrush: $7.8 \pm 0.2\%$) and October 2000 (postfire: $1.0 \pm 0.1\%$; sagebrush: $1.4 \pm 0.1\%$) compared to the same months in 2001.

Patterns of change in soil WC in 2001 differed between the two ecosystems (Fig. 2b). Soil WC was higher in the postfire ecosystem early in the year (March 2001) compared to WC in the sagebrush ecosystem ($P < 0.01$); but by the end of the dry season in November 2001 before substantial recharge occurred, soil WC was lower in the postfire ecosystem ($P = 0.02$). Additionally, soil water recharge following rains was greater in the postfire plant ecosystem (e.g. July 13, 2001; $P = 0.01$). In

contrast, snowfalls generally led to lower soil water recharge in the postfire ecosystem (e.g. November 26, 2001; $P = 0.02$).

Mean daily soil temperature at 5 cm depth remained consistently higher in the postfire ecosystem than in the sagebrush ecosystem ($P < 0.01$; Fig. 2c). In 2001, mean annual soil temperature in the postfire ecosystem averaged $15.2 \pm 0.6^\circ\text{C}$ compared to $13.3 \pm 0.6^\circ\text{C}$ in the intact sagebrush ecosystem.

Vegetation and leaf area

Leaf area indices (LAI) in the two ecosystems was similar relatively early in the growing seasons before the onset of summer droughts (e.g. in July 2000 — postfire: 0.22 ± 0.02 ; sagebrush: 0.23 ± 0.03 ; June 2001 — postfire: 0.18 ± 0.05 ; sagebrush: 0.17 ± 0.03). Leaf area indices (LAI) in both plant communities decreased significantly in the dry summers of both years, with LAI in the postfire plant community dominated by annual species experiencing a much stronger decline than that observed in the sagebrush plant community (e.g. July 2001 — postfire: 0.03 ± 0.01 ; sagebrush: 0.10 ± 0.02). In the postfire ecosystem, annual species accounted for most of the LAI. The two forbs, *S. altissimum* and *G. ramosissimum*, as well as cheatgrass dominated the postfire ecosystem in 2000. In 2001, cheatgrass was essentially absent in the postfire ecosystem. The contribution of perennial plant species to LAI in the postfire ecosystem remained very low throughout 2000 and 2001, with *C. viscidiflorus* and *E. viridis* accounting for most of this. In the intact sagebrush ecosystem,

Table 2 Summary of statistical analyses (*P*-values from repeated measures ANOVAs) evaluating the effects of wildfire-induced conversion of native sagebrush steppe ecosystem to postfire successional ecosystem (Treatment) and time of year (Date: repeated measure variable) on daytime NEE, nighttime NEE, daytime ET, and nighttime NEE (df: degrees of freedom; MS: mean squares; *n* = 6 in 2000, and *n* = 4 in 2001)

Source of error	Dependent variable											
	Daytime NEE			Nighttime NEE			Daytime ET			Nighttime ET		
	df	MS	<i>P</i>	df	MS	<i>P</i>	df	MS	<i>P</i>	df	MS	<i>P</i>
<i>Between-subject variable</i>												
Treatment	1	0.0684	0.323	1	0.1844	0.054*	1	0.0070	0.211	1	0.0334	< 0.001**
Error	10	0.0633		10	0.0388		10	0.0039		10	0.0011	
<i>Within-subject variable</i>												
Date	8	2.9364	0.001**	8	0.4208	0.005**	8	0.1836	< 0.001**	8	0.0529	< 0.001**
Treatment × Date	8	0.3260	0.082(*)	8	0.0411	0.246	8	0.0344	0.026*	8	0.0011	0.164
Error	56	0.0794		54	0.0255		56	0.0043		54	0.0247	

(*)*P* < 0.1; **P* < 0.05; ***P* < 0.01.

Table 3 Modelled daily NEP (i.e. sum of NEE) and ET, and sums of daytime and nighttime NEE for sagebrush and postfire ecosystems using multiple regressions of measured NEE and ET with continuously recorded environmental variables

Year	Month	NEP (g C m ⁻² day ⁻¹)						ET (mm H ₂ O day ⁻¹)	
		Sagebrush			Postfire			Sagebrush daily	Postfire daily
		Daytime	+ nighttime	= daily	Daytime	+ nighttime	= daily		
2000	June	0.44	-0.18	0.26	0.72	-0.22	0.50	0.40	0.62
	October	0.66	-0.18	0.48	0.54	-0.08	0.46	0.08	0.02
2001	March	0.38	-0.34	0.04	0.62	-0.31	0.31	0.25	0.41
	April	0.96	-0.36	0.59	0.85	-0.31	0.55	0.25	0.36
	May	0.45	-0.14	0.31	0.17	-0.11	0.06	0.23	0.16
	June	0.36	-0.15	0.21	0.19	-0.12	0.07	0.38	0.39
	July	0.14	-0.14	0.01	0.16	-0.05	0.11	0.14	0.17
	September	0.12	-0.09	0.03	0.08	-0.05	0.03	0.13	0.13
	November	-0.11	-0.29	-0.39	0.03	-0.05	-0.01	0.44	0.60

sagebrush consistently accounted for more than 95% of the LAI. In 2000, cheatgrass growing under sagebrush canopies contributed most to the remaining, mainly annual leaf area, while in 2001 little cheatgrass was present and annuals were dominated by *E. sparsiflorum* and *M. albicaulis*.

Discussion

Effects of postfire plant succession on NEE and daily NEP

Use of the large static chamber dome (Arnore & Obrist, 2002) allowed the detection of very small ecosystem fluxes on adjacent sites in close proximity while simultaneously covering all major elements (e.g. shrubs and intershrub areas) of the landscape in both ecosystems.

The results showing an increase of NEE in the postfire ecosystem on three different dates, the absence of detectable differences on five other dates, and a decrease in NEE on one date (Fig. 1a) led us to reject our first hypothesis that lower LAI in a postfire ecosystem would decrease NEE relative to that occurring in an intact sagebrush ecosystem. The occurrence of lower LAI in the postfire ecosystem for most of the year indicated that observed higher NEE in this ecosystem on some dates was either due to lower ecosystem respiration relative to rates occurring in the sagebrush ecosystem, or to higher leaf-level photosynthetic activity in the postfire ecosystem. Lower nighttime ecosystem respiration observed in the postfire ecosystem supports the first theory. We have not measured leaf-level gas exchange in this study, however, and therefore cannot assess the role

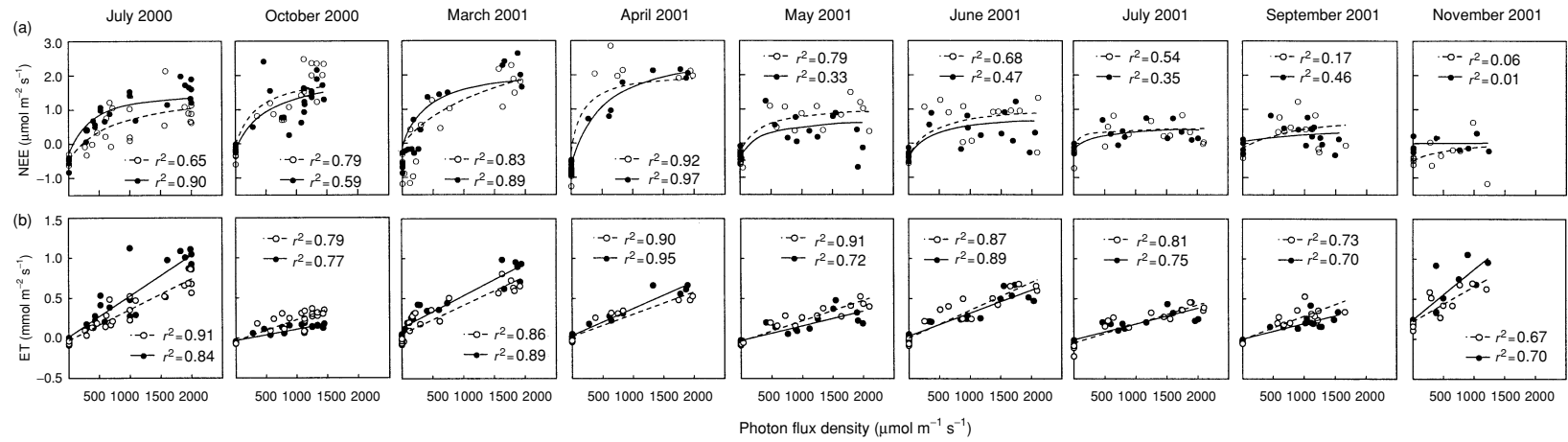


Fig. 4 (a) Regressions between measured NEE and PFD using rectangular hyperbola functions in sagebrush (open symbols, dashed lines) and postfire (filled symbols, solid lines) ecosystems for each measurement date, (b) Linear regressions between measured ET and PFD for both ecosystems (all P -values ≤ 0.05).

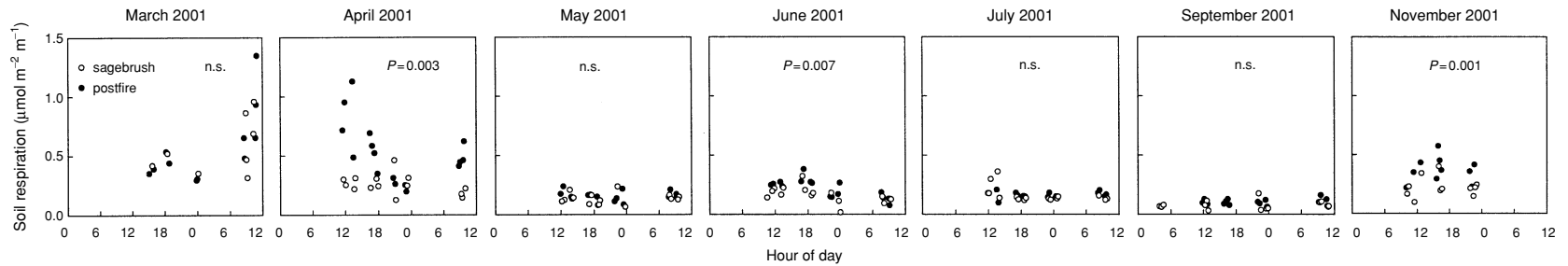


Fig. 5 Plot-level soil CO_2 efflux in sagebrush (○) and postfire (●) ecosystems measured in 2001. P -values are based on paired t -tests using plot pairs to test for differences in CO_2 efflux for each 24 h measurement period.

that leaf physiology (e.g., species differences or seasonal changes) may play in explaining patterns observed at the ecosystem level. Although we were unable to partition ecosystem fluxes into below-ground and above-ground contributions since nighttime soil CO₂ efflux exceeded whole-ecosystem nighttime respiration on a number of occasions, the presence of comparable plot-level soil respiration rates in the postfire and sagebrush ecosystems (Fig. 5) indicates that differences in whole-ecosystem respiration must have been caused by higher respiration of above-ground biomass in the sagebrush ecosystem. This inference agrees well with observations that as much as 80% of above-ground respiration in sagebrush ecosystems originated from above-ground shrub respiration (measured with a 1-m³ static chamber; M. Prater, personal communication). The reasons for the apparent discrepancies between nighttime ecosystem respiration and extrapolated nighttime soil respiration are unclear but may be due to the use of different methodologies to measure fluxes (large dome versus small respiration chamber) or to errors in extrapolating subplot fluxes to whole-plot fluxes. The only other study that measured NEE in intact sagebrush ecosystems in Oregon and Idaho (Angell *et al.*, 2001) reported daytime maximum values (7–10 μmol CO₂ m⁻² s⁻¹) up to three times higher than peak rates measured in the sagebrush ecosystem in our study (3 μmol CO₂ m⁻² s⁻¹). One possible explanation for the difference is considerably higher precipitation at Angell *et al.*'s sites, which may have led to greater LAI.

The remarkably low predicted (modelled using multiple regressions) daily NEP for both ecosystems during most of the year (i.e. near zero; Table 3) indicates that ecosystem respiration balances ecosystem CO₂ uptake. In other words, when CO₂ uptake is high, CO₂ release is also high (Fig. 1; Table 3). The small differences in NEP observed between the two ecosystems, however, could still result in shifts in ecosystem C balance in the long term. For example, higher ecosystem respiration observed during November in the sagebrush ecosystem could lead to an amplification of differences between the two ecosystems if the difference persisted throughout the winter. In fact, modelling fluxes for the entire year of 2001 indicated that annual NEP in the postfire ecosystem remained positive (+34 g C m⁻² yr⁻¹) but that NEP in the intact sagebrush ecosystem dropped below zero (–20 g C m⁻² yr⁻¹) driven by higher wintertime respiration.

Effects of postfire plant succession on ET at various time scales

The occurrence of higher measured ET in the postfire ecosystem when soil water was relatively abundant (Fig. 1b) led us to also reject our second major hypothesis,

that lower leaf areas and limited access to deep soil water would decrease ET in the postfire ecosystem. Consistently higher soil temperatures observed in the postfire ecosystem (Fig. 2c) as well as greater soil water recharge after rains (Fig. 2b; possibly due to lower interception of sparse postfire vegetation) could have led to increased soil evaporation in the postfire ecosystem when soil water was relatively abundant and explain a lack of such an effect when the top soil layers were very dry. Similar fire effects on soil temperature have been observed in grasslands (Whisenant *et al.*, 1984) and can be inferred from lower temperatures measured under perennial canopies compared to intercanopy areas (Breshears *et al.*, 1997). Evapotranspiration (ET) of the intact sagebrush ecosystem only exceeded ET measured in the postfire ecosystem when soil WC was very low (Figs 1b and 2b). This may have been due to the ability of deep-rooted sagebrush shrubs (e.g. Reynolds & Fraley, 1989) to access deep soil water stores in the dry summers and possibly to the occurrence of hydraulic lift by sagebrush (Caldwell & Richards, 1989), compared to the inability of shallow-rooted annual plant species in postfire communities to do the same. Such declines in rooting depth have been reported to occur in sagebrush ecosystems after fires (Cline *et al.*, 1977). Some of the differences in ET and daily ET (e.g. March 2001) also may be explained by the presence of higher soil WC in the postfire ecosystem in the spring of 2001 after a relatively warm winter when most precipitation fell as rain and when higher interception by sagebrush communities may have occurred (Young & Evans, 1987). The patterns of soil water recharge, and potentially ET, could be opposite if winter precipitation were to fall predominately in the form of snow, as it did in November and December 2001 when greater snow accumulation under sagebrush canopies (M. Prater, pers. communication) appeared to result in higher soil water recharge in the intact sagebrush ecosystem (Fig. 2b).

Our results showing higher ET in the postfire ecosystem across all nine measurements contrast with results from other studies in sagebrush steppe ecosystems (Cline *et al.*, 1977; Link *et al.*, 1990). The differences between our results and those in the other studies may be due to much higher plant cover on the other study sites and consequently cooler soil surface temperatures in the postfire ecosystems as well as to lower air temperatures.

Environmental factors controlling NEE and ET

Photon flux density (PFD), and solar radiation (not directly measured) were clearly the most important environmental factors modulating other environmental conditions (soil and air temperature) and affecting NEE and ET (Fig 4a, b). The importance (r^2) of PFD as a controlling factor for NEE and ET was surprisingly high

early in the season (accounted for up to 90% of variability in NEE and ET) but decreased through the summer and into the fall of 2001 as water availability in both ecosystems dropped. Although peak daytime NEE in both ecosystems was high when LAI and soil WC were high, calculated daily NEP was not correlated with LAI or soil WC in either ecosystem. This was because nighttime respiration also was relatively high when daytime NEE was high and low when daytime NEE was low. This dramatically reduced variability in daily NEP and negated relationships between daily NEP and environmental factors such as LAI and soil WC.

Taken together, the results of our study indicate that the conversion of native sagebrush steppe to ecosystems dominated by herbaceous annual species (1) may have little effect on C balance during relatively dry years except in winter months but may stimulate water loss immediately following fires; (2) may still affect ecosystem C storage in the long term; (3) may have different effects on NEE and ET in years with normal or above-normal precipitation since differences in NEE and ET between the two ecosystems mainly occurred when water was available.

Acknowledgements

We thank D. Schorran for assistance in instrumenting the field site and for help conducting the CO₂ and water vapour dome calibrations; K. Leavitt of the Carson City, Nevada Office of the Bureau of land management (BLM) for facilitating our use of the field site; C. Bowman, H. Weatherly, J. Boc, L. Sotoodeh, J. Rosta, L. Beers, J. Kuchsnicki, J. Mayer, J. Hunter, and M. Prater, for their help in setting up the field site and for round-the-clock help with field dome measurements; and R. Kreidberg, G. Royce, P. Verburg, and two anonymous reviewers for constructive comments on an earlier version of the manuscript. We are grateful to the International Arid Lands Consortium (grant awarded to: E. Delucia, J. Arnone, and D. Yakir), Nevada NSF EPSCoR, A.W. Mellon Foundation, the Nevada Medal Research Fellowship of the Desert Research Institute, and University of Nevada – Reno's Graduate Program in Hydrologic Sciences for financial support of this project.

References

- Angell RF, Svejcar T (1999) A chamber design for measuring net CO₂ exchange on rangeland. *Journal of Range Management*, **52**, 27–31.
- Angell RF, Svejcar T, Bates J *et al.* (2001) Bowen ratio and closed chamber dioxide flux measurements over sagebrush steppe vegetation. *Agricultural and Forest Meteorology*, **108**, 153–161.
- Arnone JA III, Obrist D (2003) A large daylight geodesic dome for quantification of whole-ecosystem CO₂ and water vapour fluxes in arid shrublands. *Journal of Arid Environments*.
- Baumer OW (1983) *Soil Survey of Washoe County, Nevada, South Part*, USDA Soil Conservation Service. US Government Printing Office, Washington DC, USA, p. 36.
- Billings WD (1990) *Bromus tectorum*, a biotic cause of ecosystem impoverishment in the Great Basin. In: *The Earth in Transition: Patterns and Processes of Biotic Impoverishment* (ed. Woodwell GM), pp. 301–322. Cambridge University Press, Cambridge, UK.
- Breshears DD, Rich PM, Barnes FJ *et al.* (1997) Overstory-imposed heterogeneity in solar radiation and soil moisture in a semiarid woodland. *Ecological Applications*, **7**, 1201–1215.
- Caldwell MM, Richards JH (1989) Hydraulic lift: water efflux from upper roots improves effectiveness of water uptake by deep roots. *Oecologia*, **79**, 1–5.
- Cline JF, Uresk DW, Rickard WH (1977) Comparison of soil water used by a sage-brush-bunchgrass and a cheatgrass community. *Journal of Range Management*, **30**, 199–201.
- D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics*, **23**, 63–87.
- Dregne HE (1991) Global status of desertification. *Annals of the Arid Zone*, **30**, 179–185.
- Frueth WT, Hopmans JW (1987) Soil moisture calibration of a TDR multilevel probe in gravelly soils. *Soil Science*, **162**, 554–565.
- Link SO, Gee GW, Thiede ME (1990) Response of a shrub ecosystem to fire: soil water and vegetation change. *Arid Soil Research and Rehabilitation*, **4**, 163–172.
- Mack RN (1981) Invasion of *Bromus tectorum* L. into western North America: an ecological chronicle. *Agro-Ecosystems*, **7**, 145–165.
- Mack RN (1986) Alien plant invasion into the Intermountain West: a case history. In: *Ecology of Biological Invasions of North America and Hawaii* (eds Mooney HA, Drake JA), pp. 191–213. Springer-Verlag, New York, USA.
- Oechel WC, Vourlitis GL, Brooks S *et al.* (1998) Intercomparison among chamber, tower, and aircraft net CO₂ and energy fluxes measured during the arctic system science land-atmosphere interactions (ARCSS-LAII) flux study. *Journal of Geophysical Research*, **103**, 28993–29003.
- Reynolds TD, Fraley L Jr. (1989) Root profiles of some native and exotic plant species in southeastern Idaho. *Environmental and Experimental Botany*, **29**, 241–248.
- Sapsis DB, Kauffman JB (1991) Fuel consumption and fire behavior associated with prescribed fires in sagebrush ecosystems. *Northwest Science*, **65**, 173–179.
- Smith SD, Huxman TE, Zitzer SF *et al.* (2000) Elevated CO₂ increases productivity and invasive species success in an arid ecosystem. *Nature*, **408**, 79–82.
- Stocker R, Leadley PW, Körner CH (1997) Carbon and water fluxes in a calcareous grassland under elevated CO₂. *Functional Ecology*, **11**, 222–230.
- Whisenant S (1990) Changing fire frequencies on Idaho's Snake River plains: ecological and management implications. In: *Proceedings of the Symposium on Cheatgrass Invasion, Shrub Die-off, Other Aspects of Shrub, Management*. USDA. Forest Service Intermountain Research Station GTR-276, Ogden, UT, USA, pp. 4–10.
- Whisenant SG, Scifres CJ, Ueckert DN (1984) Soil water and temperature response to prescribed burning. *Great Basin Naturalist*, **44**, 558–562.

- Wickens GE (1998) In: *Ecophysiology of Economic Plants in Arid and Semi-Arid Lands* (ed. Wickens GE), p. 5. Springer-Verlag, Heidelberg, Germany.
- WRCC (2002) Western Regional Climate Center. [<http://www.wrcc.dri.edu>. January 2002.]
- Yensen DL (1981) The 1900 invasion of alien plants into southern Idaho. *Great Basin Naturalist*, **41**, 176–183.
- Young JA, Allen FL (1997) Cheatgrass and range science: 1930–50. *Journal of Range Management*, **50**, 530–535.
- Young JA, Evans RA (1987) Stem flow on western juniper (*Juniperus occidentalis*) trees. In: *Proceedings of the Pinyon Juniper Conference*. USDA Forest Service Intermountain Research Station, GTR-215, Odgen, UT, USA, pp. 373–381.