

Antecedent moisture and seasonal precipitation influence the response of canopy-scale carbon and water exchange to rainfall pulses in a semi-arid grassland

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Summary

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- The influences of prior monsoon-season drought (PMSD) and the seasonal timing of episodic rainfall ('pulses') on carbon and water exchange in water-limited ecosystems are poorly quantified.
- In the present study, we estimated net ecosystem exchange of CO₂ (NEE) and evapotranspiration (ET) before, and for 15 d following, experimental irrigation in a semi-arid grassland during June and August 2003. Rainout shelters near Tucson, Arizona, USA, were positioned on contrasting soils (clay and sand) and planted with native (*Heteropogon contortus*) or non-native invasive (*Eragrostis lehmanniana*) C4 bunchgrasses. Plots received increased ('wet') or decreased ('dry') monsoon-season (July–September) rainfall during 2002 and 2003.
- Following a June 2003 39-mm pulse, species treatments had similar NEE and ET dynamics including 15-d integrated NEE (NEE_{pulse}). Contrary to predictions, PMSD increased net C uptake during June in plots of both species. Greater flux rates after an August 2003 39-mm pulse reflected biotic activity associated with the North American Monsoon. Furthermore, August NEE_{pulse} and ecosystem pulse-use efficiency (PUE_e = NEE_{pulse}/ET_{pulse}) was greatest in *Heteropogon* plots.
- PMSD and rainfall seasonal timing may interact with bunchgrass invasions to alter NEE and ET dynamics with consequences for PUE_e in water-limited ecosystems.

Key words: evapotranspiration, net ecosystem CO₂ exchange, photosynthesis, respiration, Santa Rita Experimental Range, soil moisture storage.

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Introduction

In arid and semi-arid ecosystems, annual net primary production typically correlates with total annual precipitation (Gutierrez & Whitford, 1987; Huxman *et al.*, 2004a). However, precipitation in arid-land ecosystems occurs in discrete, episodic events ('pulses') separated by periods of low water availability (Noy-Meir, 1973). This suggests that biophysical investigations of production processes should focus on the mechanistic effects of these pulses (Weltzin & Tissue, 2002). The temporally and

spatially variable nature of precipitation and resource pulses, coupled with the nonlinear responses of biota, constrains ecosystem processes such as net primary productivity (BassiriRad *et al.*, 1999; Knapp *et al.*, 2001, 2002; Schwinning & Ehleringer, 2001; Weltzin *et al.*, 2003; Huxman *et al.*, 2004b).

Net ecosystem exchange of CO₂ (NEE) and evapotranspiration (ET) are fundamental ecosystem variables affected by above- and below-ground biophysical activity. Representing the balance of ecosystem photosynthesis and respiration, NEE integrates the carbon metabolism of all biota. Similarly,

ET encompasses the evaporative loss of water from plant tissues, intercepted water in the canopy and water from the soil surface. Plant and soil microbes may differ in their metabolic responses to a precipitation pulse (Huxman *et al.*, 2004b). Variations in phenology and morphology (Reynolds *et al.*, 2004), as well as growth responses (Snyder *et al.*, 2004), are possible means by which plants may vary in response to precipitation pulses. Temperature, soil nutrient requirements and wetting/drying cycles may constrain the responses of soil microbes to precipitation pulses (Birch, 1958; Austin *et al.*, 2004; Saetre & Stark, 2005). Interactions between autotrophic and heterotrophic communities may further affect responses through changes in soil nitrogen and organic matter, and the production and utilization of root exudates.

Understanding the responses of semi-arid grasslands to episodic precipitation is important because they cover a large area of North America, provide valuable goods and services, and have the potential to sequester atmospheric carbon in their soils (Knapp *et al.*, 1998). In southern Arizona, semi-arid grasslands are undergoing widespread vegetation transitions in the form of mesquite (*Prosopis velutina*) encroachment and invasions by several non-native bunchgrass species, including Lehmann lovegrass (*Eragrostis lehmanniana*) (McPherson, 1997). How such vegetation changes interact with precipitation variability to affect fluxes of semi-arid ecosystem carbon and water is not well understood (Huxman *et al.*, 2005). Through changes in leaf area and stomatal behavior, bunchgrasses may directly influence the transpiration of water. Indirectly, plant architecture and litter depth may influence soil evaporative losses by altering soil surface microclimate and may affect interception losses by changes in canopy display and litter deposition (Dunkerley, 2000). Furthermore, lag effects in productivity, associated with previous growing-season climate, may additionally constrain the ability of the grasslands to respond to precipitation pulses (Hanson *et al.*, 1982; Knapp & Smith, 2001; Wiegand *et al.*, 2004).

Our primary research objective was to assess the interactive effects of prior monsoon-season drought (PMSD), bunchgrass species type and soil physical characteristics on the response of semi-arid ecosystems to episodic rainfall events. To address this objective, we tracked soil moisture storage and ecosystem carbon and water fluxes before, and for 15 d after, simulated precipitation pulses in a semi-arid grassland ecosystem. Our experimental design included plots of native and non-native bunchgrass species, planted in monoculture on both coarse- and fine-textured soils, in a rainfall manipulation experiment (Huxman *et al.*, 2004c; English *et al.*, 2005; Potts *et al.*, 2006). We predicted that PMSD, induced by a 50% reduction in previous-year monsoon-season precipitation, would limit photosynthetic responses to the first large precipitation pulse of the following growing season. Furthermore, we predicted that the non-native bunchgrass, *Eragrostis*, would respond more rapidly to rainfall events (Huxman *et al.*, 2004c) than the native bunchgrass, *Heteropogon*, because it maintains

physiologically active tillers throughout extended dry periods and has high potential relative growth rates (Fernandez & Reynolds, 2000). Thus, the non-native grass would be better poised than the native grass to translate an early monsoon-season precipitation pulse into assimilated carbon at the ecosystem scale, regardless of the monsoon-season precipitation regime.

The seasonal timing of pulses may be as important as their magnitude in controlling ecosystem fluxes of carbon and water (Epstein *et al.*, 1999; Weltzin & Tissue, 2002; Schwinning *et al.*, 2004). For example, high evaporative demand, coupled with limited plant canopy development during the early growing season, could constrain transpiration and CO₂ assimilation. Thus, our secondary research objective was to assess how the seasonal timing of pulses may interact with PMSD, bunchgrass species type and soil physical characteristics to affect the temporal dynamics of soil moisture storage and ecosystem carbon and water fluxes. We predicted that during the early growing season (i.e. a very dry period of warm temperatures), pulses of precipitation would result in large soil microbe-mediated CO₂ efflux followed only by brief periods of plant-mediated photosynthetic activity. During monsoon-season precipitation pulses, when rain is preceded by moist soil conditions and when plant canopies and root systems are fully developed and active, the proportional activity of canopy photosynthesis should be enhanced and result in a higher net CO₂ uptake at the ecosystem level than with early growing-season pulses.

Materials and Methods

Experimental design

This experiment was conducted at the Santa Rita Experimental Range (SRER) rainfall manipulation experiment site (Huxman *et al.*, 2004c; English *et al.*, 2005; Yopez *et al.*, 2005; Potts *et al.*, 2006; N 31.78°, W 110.88°). Briefly, rainfall exclusion shelters were constructed at approx. 1100 m elevation on a gentle (2%) slope on two adjacent geomorphic surfaces. Three large shelters were located on a coarse-textured, loamy-sand soil developed on a Holocene-aged alluvium ('sand') and three on a clay soil developed on a Pleistocene-aged surface. The fine-textured, clay-rich Pleistocene soil ('clay') was characterized by a well-developed argillic horizon approx. 30 cm below the soil surface (McAuliffe, 1995).

Four plots, measuring 1.5 m × 1.8 m, were positioned under each of the three rainout shelters at each site. To isolate plots from horizontal transfer of subsurface soil water and to facilitate installation of time-domain reflectometry probes (Risler *et al.*, 1996), we excavated 75-cm-deep trenches around each plot. Trench faces were lined with 4 ml of (poly vinyl chloride) (PVC) film, secured to a wood frame, before being backfilled. In addition to securing the lining plastic, the wood frame delineated the plots clearly and prevented overland

flow. English *et al.* (2005) provide a complete description of site characteristics, rainout shelter design and construction. Beneath the rainout shelters there was a reduction of *c.* 24% in the maximum photosynthetic photon fluence rate at solar noon, and the night-time minimum and daytime maximum air temperatures were 1–2°C higher than in the surrounding environment (English *et al.*, 2005).

Plots in each shelter block were randomly assigned a planting treatment with a native (*H. contortus* L.) C_4 bunchgrass or a non-native (*E. lehmanniana* Nees) C_4 bunchgrass. Experimental plots were planted in monoculture with greenhouse-grown seedlings during June and July of 2001, with seedling densities typical of that observed in natural stands of these species on the SRER (21 plants per m^2). By June 2003, plant densities in experimental plots included in this study had declined to 16 ± 2 and 17 ± 1 plants per plot for *H. contortus* and *E. lehmanniana*, respectively (Yepez *et al.*, 2005). Furthermore, Yepez *et al.* (2005) reported that before the June 2003 experimental irrigation, green leaf area index (LAI) was greater in plots of *E. lehmanniana* than in those of *H. contortus* ($0.66 \pm 0.20 m^2 m^{-2}$ and $0.37 \pm 0.05 m^2 m^{-2}$, respectively); however, standing dead biomass was much greater in plots of *H. contortus* than in those of *E. lehmanniana*. As a result of this difference in standing dead biomass, *E. lehmanniana* canopies tended to be more diffuse than those of *H. contortus* and to have less dense plant litter, allowing greater incoming radiation on the soil surface (J. F. Weltzin, unpublished).

From July 2001 until June 2002, treatments received identical irrigation regimes that simulated long-term (1970–2000) rainfall patterns in nearby (≈ 15 km) Tumacacori, Arizona. Beginning in July 2002 and continuing through September 2002 (hereafter referred to as the ‘monsoon-season’), plots received either a 50% increase in individual precipitation event magnitude (wet treatment) or a 50% decrease in precipitation event magnitude (dry treatment; Fig. 1). During the period October 2002 to June 2003, plots again received identical precipitation regimes that mimicked the long-term rainfall pattern. During July 2003 to September 2003, differential summer precipitation regimes were again applied to wet and dry treatments. Annual rainfall in wet treatment plots was equivalent to 569 mm, whereas dry plots received

356 mm rainfall. At both sites, three rainout shelters each contained plots of two bunchgrass species grown under wet and dry monsoon-season precipitation regimes (24 plots in total).

A prolonged early summer dry period, and the onset of early July rainfall, are two climatic features consistent with the North American Monsoon, the dominant climate feature of southern Arizona. We focused intensive sampling on a period in mid-June 2003, when we applied a 39-mm watering to all plots after nearly 90 d without simulated precipitation (Fig. 1). Plots were not irrigated again for 21 d, when differential monsoon-season watering was initiated.

During a second intensive field campaign in August 2003, near the midpoint of the North American Monsoon, we conducted ecosystem measurements before and after pulses of differential magnitude (Fig. 1). Wet treatments were given another 39-mm irrigation pulse, and dry treatments received a 12-mm irrigation pulse.

Field measurements

We measured midday soil water content and diurnal time-course measurements (00:00, 08:00, 12:00 and 16:00 h) of ecosystem gas exchange for each plot 1 d before, and 1, 3, 7 and 15 d after, experimental irrigation during each field campaign. We measured changes in volumetric soil water content (θ) using time domain reflectometry (TDR) probes inserted at 15, 35 and 55 cm depth. We integrated measurements of θ to estimate soil profile moisture storage (S) to 75 cm depth using a geometric integration. This integration assumed that θ changed linearly between probes with increasing depth, that the soil surface (defined as 0 cm depth) had a constant θ equal to 0, and that θ_{75} cm equaled θ_{55} cm. Finally, this method yielded appropriate units (mm) of moisture storage within each plot’s soil profile.

We measured the time course of whole-plot CO_2 and H_2O exchange using a closed static chamber (1.5 m wide, 1.5 m tall, 1.8 m long), seated over each plot, using an open-path infrared gas exchange analyzer (LI-7500; Li-Cor Inc., Lincoln, NE, USA) fitted inside (Arnone & Obrist, 2003; Huxman *et al.*, 2004c). The infrared gas-exchange analyzer was mounted on a tripod fitted with two 15-cm-diameter electric fans to

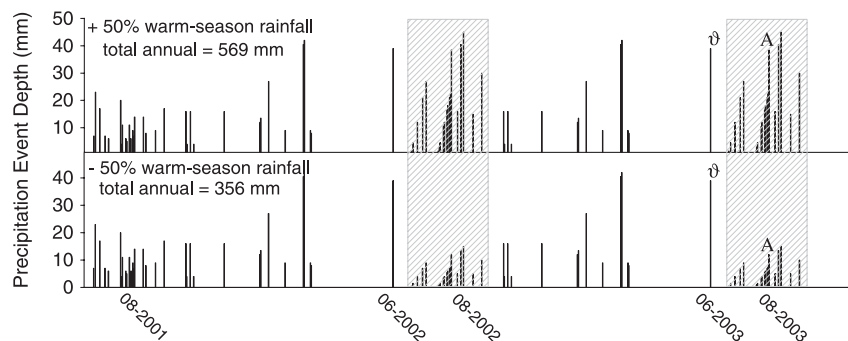


Fig. 1 Precipitation schedule for the period 2001 to 2003. The hatched portions of the figure indicate the period of differential monsoon-season watering. June and August pulses described in the present study are marked with θ and A, respectively.

promote atmospheric mixing within the chamber. The chamber consisted of a 3.2-cm-diameter PVC pipe frame covered by a tightly sewn polyethylene sheet (Shelter Systems, Santa Cruz, CA, USA) and was designed to fit around the wood frame surrounding each plot. The material used for chamber construction allowed 92% of photosynthetically active radiation to pass into the plots, while allowing infrared (IR) radiation to escape the chambers.

Chambers contained an appropriate vent to prevent the development of soil–atmosphere pressure gradients in the enclosed atmosphere of static chambers, which may reduce trace gas fluxes, particularly soil respiration of CO₂ (Saleska *et al.*, 1999; Bremer & Ham, 2005). Each type of chamber design has strengths and weaknesses (Davidson *et al.*, 2002; Pumpanen *et al.*, 2004). Our chamber was designed to emphasize ruggedness, portability and simplicity, in order to collect flux data rapidly under difficult field conditions and to capture effectively relative differences in flux between treatments within the context of a randomized and replicated experimental design.

After the chamber was seated and before any concentration data were collected, 20 s elapsed during which the chamber atmosphere was thoroughly mixed by the tripod-mounted fans. Carbon dioxide and water vapor concentrations were allowed to build up or decline, while a computer recorded the transient changes in the chamber atmosphere. Consistently linear changes in CO₂ and water vapor concentrations during the 90-s measurement period indicate that changes in concentrations of water vapor (upper limit of range above ambient of 1.0 mmol mol⁻¹) or CO₂ (upper limit of range above or below ambient of 15 μmol mol⁻¹) were insufficient to alter significantly plant stomatal conductance, canopy photosynthesis or soil CO₂ efflux (Huxman *et al.*, 2004c). Canopy temperature during an average measurement period increased by < 0.2°C (Huxman *et al.*, 2004c). By convention, positive NEE values indicate net loss of carbon by the ecosystem, while negative NEE values indicate net gain of carbon by the ecosystem.

In addition to reporting values of instantaneous midday maximum net ecosystem exchange of CO₂ (NEE_{max}), we also reported instantaneous night-time measurements of NEE as an estimate of ecosystem respiration (R_c). We calculated diurnal values of NEE (NEE_{diurnal}) and ET (ET_{diurnal}) for each plot using the spline-fit and integration function in SIGMAPLOT v7.0 (SPSS Inc., Chicago, IL, USA) to estimate total carbon and water exchange during the 15-d observation period after the precipitation pulses (NEE_{pulse} and ET_{pulse}, respectively). In addition, we calculated ecosystem pulse-use efficiency (PUE_c), as follows: PUE_c = [NEE_{pulse} (mmoles CO₂ m⁻²)/ET_{pulse} (moles H₂O m⁻²)].

Statistical analyses

A four-factor split-plot repeated-measures analysis of variance (ANOVA) (SPSS 7.5.1.; SPSS Inc.) was used to test for the

significance of soil type (main plot treatment), precipitation regime and bunchgrass species (subplot treatments), and time following the pulse and their interactions for each sample period for night-time R_c, maximum daylight instantaneous NEE (NEE_{max}), maximum daylight instantaneous ET (ET_{max}) and S. The differential effects of 39-mm precipitation pulses, during June and August, on ecosystem responses were quantified among wet treatments using a similar ANOVA framework, with season substituting for precipitation regime. To quantify differences in NEE_{pulse} and ET_{pulse}, a three-factor ANOVA was used to test for the effects and interactions of precipitation regime, soil type and bunchgrass species during each field campaign. To examine differences between June and August 39-mm pulses on NEE_{pulse} and ET_{pulse}, a repeated-measures ANOVA was used to test for the effects and interactions of season, soil type and bunchgrass species.

Results

Soil moisture storage

Throughout the June measurement period, S was consistently higher in clay plots than in the sand plots (Table 1, soil; Fig. 2). The immediate effect of the June pulse on S was most dramatic in clay plots and was followed by a decline in S throughout the remaining measurement periods (Fig. 2, left panels). Fifteen days following the June pulse, S returned to prepulse conditions.

During August, wet treatments had greater initial S than dry treatments (Fig. 2, right panels). The 12-mm pulse applied to dry treatments during August had little effect on S, while the response of S to the larger, 39-mm pulse in wet treatments was to increase rapidly and then decline during the 15-d measurement period (Table 2, precipitation × days). Similarly to the pattern observed in June, among all species and soil treatments, S returned to prepulse values within 15 d. Among wet treatments, high initial values of S during August contributed to seasonal differences in S associated with early and monsoon-season 39-mm pulses (Table 3, season). Higher initial values of S during August reflect precipitation inputs in the days before the August field campaign.

Evapotranspiration

The ET_{max} increased immediately following the June pulse in all of the treatments (Fig. 3). This initial peak in ET_{max} was followed by a gradual decline in plots of *Heteropogon* and a rapid decline in plots of *Eragrostis* (Table 1, species × days). Furthermore, following the June pulse, the initial peak in ET_{max} was greater in plots of *Eragrostis* than in those of *Heteropogon* (posthoc Student's *t*-test, *t* = 5.28, *df* = 22; *P* < 0.001).

PMSD did not influence ET_{max} after the June pulse. However, during August, wet plots had higher values of ET_{max}, both before and after the precipitation pulses (Table 2, precipitation).

Table 1 Degrees of freedom and *F*-statistics from the statistical analysis of soil moisture storage and ecosystem gas-exchange variables in response to a 39-mm precipitation pulse during June, 2003 in a semi-arid grassland manipulation in southern Arizona

Factors	df	S	ET _{max}	NEE _{max}	R _e
Ppt	1,2	0.04	0.10	0.29	1.85
Spp	1,2	1.40	411.25**	0.52	2.21
Soil	1,2	46.23**	6.49	20.82**	0.0002
Days	4,8	5.14**	83.83**	18.25**	138.21**
Ppt × Spp	1,2	0.61	0.18	1.60	2.91
Ppt × Soil	1,2	0.27	5.52	6.71	0.47
Ppt × Days	4,8	0.22	0.33	0.15	2.75*
Spp × Soil	1,2	0.01	3.97	6.92	2.25
Spp × Days	4,8	0.44	21.45**	6.21**	0.69
Soil × Days	4,8	3.09*	3.94	1.20	2.32
Ppt × Spp × Soil	1,2	5.14	1.44	0.009	0.007
Ppt × Spp × Days	4,8	2.32	0.48	0.15	1.67
Ppt × Soil × Days	4,8	1.56	0.27	0.24	0.25
Spp × Soil × Days	4,8	0.62	1.39	1.56	4.51**
Ppt × Spp × Soil × Days	4,8	4.65**	0.69	0.84	0.80

df, degrees of freedom; ET_{max}, maximum midday evapotranspiration; NEE_{max}, maximum midday net ecosystem exchange of CO₂; Ppt, precipitation (7, 9, 12); R_e, night-time ecosystem respiration; S, soil moisture storage; Spp, species (8, 10, 11, 13, 14).
*, *P* < 0.1; **, *P* < 0.05.

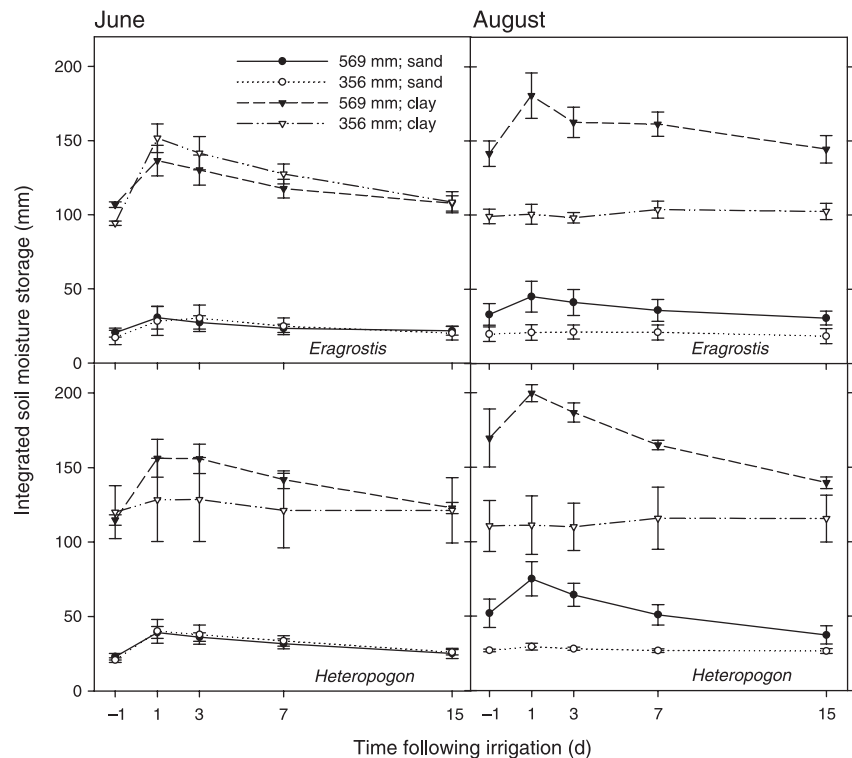


Fig. 2 Time course of mean \pm standard error (SE) soil moisture storage (S) during June and August 2003 (left and right panels, respectively). (Upper left) S in *Eragrostis* plots before and after a 39-mm pulse. (Upper right) S in *Eragrostis* plots before and after 39-mm and 12-mm pulses in 569-mm and 356-mm annual rainfall treatments, respectively. (Lower left) S in *Heteropogon* plots before and after a 39-mm pulse. (Lower right) S in *Heteropogon* plots before and after 39-mm and 12-mm pulses in 569-mm and 356-mm annual rainfall treatments, respectively.

Among wet treatments, ET_{max} was greater after the August 39-mm pulse than the June 39-mm pulse (Table 3, season).

Net ecosystem exchange

Before the June pulse, all plots had a slightly negative NEE_{max}, indicating a low level of carbon assimilation by the ecosystem (Fig. 4). Immediately following the pulse, NEE_{max} values

became less negative, consistent with rapid up-regulation of soil microbes and the physical displacement of soil CO₂ by infiltrating water (Huxman *et al.*, 2004c). Three days following experimental irrigation, NEE_{max} was more negative in *Eragrostis* plots than *Heteropogon* plots, suggesting either a greater decline in respiration or a greater increase in the contribution of photosynthesis to daytime carbon flux (Table 1, species \times days).

Factors	df	S	ET _{max}	NEE _{max}	R _e
Ppt	1,2	20.27**	123.14**	22.70**	76.96**
Spp	1,2	13.09*	3.50	4.37	2.08
Soil	1,2	43.26**	0.57	2.88	0.07
Days	4,8	13.51**	1.94	2.25	33.77**
Ppt × Spp	1,2	0.18	0.58	13.96*	63.11**
Ppt × Soil	1,2	18.17**	1.99	0.04	0.05
Ppt × Days	4,8	11.49**	2.23	1.57	1.56
Spp × Soil	1,2	0.001	0.51	0.93	0.15
Spp × Days	4,8	0.99	2.79*	1.58	0.40
Soil × Days	4,8	0.62	1.22	1.14	3.09
Ppt × Spp × Soil	1,2	0.17	1.15	0.01	0.68
Ppt × Spp × Days	4,8	1.11	0.16	0.43	1.38
Ppt × Soil × Days	4,8	1.51	1.04	1.30	0.39
Spp × Soil × Days	4,8	1.02	0.17	0.15	0.20
Ppt × Spp × Soil × Days	4,8	0.28	2.30	0.37	0.33

df, degrees of freedom; ET_{max}, maximum midday evapotranspiration; NEE_{max}, maximum midday net ecosystem exchange of CO₂; Ppt, precipitation (7, 9, 12); R_e, night-time ecosystem respiration; S, soil moisture storage; Spp, species (8, 10, 11, 13, 14).

P* < 0.1; *P* < 0.05.

Factors	df	S	ET _{max}	NEE _{max}	R _e
Season	1,2	88.50**	143.76**	77.50**	52.61**
Spp	1,2	10.59*	0.039	13.76*	0.20
Soil	1,2	79.42**	0.168	0.74	0.05
Days	4,8	31.07**	1.78	2.13	193.66**
Season × Spp	1,2	0.29	5.28	15.63*	16.50*
Season × Soil	1,2	7.59	4.36	0.02	0.03
Season × Days	4,8	0.94	1.17	1.63	84.99**
Spp × Soil	1,2	0.05	0.445	0.15	0.05
Spp × Days	4,8	0.82	1.63	0.70	1.50
Soil × Days	4,8	2.51	0.99	1.11	3.98**
Season × Spp × Soil	1,2	1.68	1.05	0.07	0.13
Season × Spp × Days	4,8	1.00	1.63	1.57	0.38
Season × Soil × Days	4,8	0.12	0.30	1.09	2.29
Spp × Soil × Days	4,8	0.21	1.69	2.56	0.58
Season × Spp × Soil × Days	4,8	0.40	1.33	1.10	0.65

df, degrees of freedom; ET_{max}, maximum midday evapotranspiration; NEE_{max}, maximum midday net ecosystem exchange of CO₂; R_e, night-time ecosystem respiration; S, soil moisture storage; Spp, species (8, 10, 11, 13, 14).

P* < 0.1; *P* < 0.05.

During August, wet treatments had more negative NEE_{max} than dry treatments, reflecting a combination of differential pulse magnitude during August (39 mm vs 12 mm) and the effects of differential watering throughout the current and previous monsoon-seasons (Table 2, precipitation). Among wet treatments, NEE_{max} was more negative after the August 39-mm pulse than the June 39-mm pulse (Table 3, season).

Night-time carbon efflux

Before the June pulse, R_e values reflected low levels of metabolic activity, consistent with a biotic community undergoing severe water limitation (Fig. 5). Among all treatments during

June, R_e peaked immediately after the pulse and declined steadily thereafter, returning to near prepulse levels 15 d after irrigation.

Before the August pulses, R_e was highest among wet plots and comparable to peak rates observed on the first day following the June pulse (Fig. 5; Table 2, precipitation). Among dry treatments during August, species did not influence R_e. However, among wet treatments, *Heteropogon* plots had a greater R_e than *Eragrostis* plots (Table 3, precipitation × season; posthoc Student's *t*-test, *t* = 2.66, df = 56; *P* < 0.01).

Among wet treatments there were overall higher rates of R_e throughout the August observation period than during June (Table 3, season). Furthermore, among wet treatments, R_e increased only slightly after the August pulse before declining

Table 2 Degrees of freedom and *F*-statistics from the statistical analysis on soil moisture storage and ecosystem gas-exchange variables in response to precipitation pulses during August, 2003 in a semi-arid grassland manipulation in southern Arizona

Table 3 Degrees of freedom and *F*-statistics from the statistical analysis on soil moisture storage and ecosystem gas-exchange variables in response to a 39-mm precipitation pulse during June and August, 2003 in a semi-arid grassland manipulation in southern Arizona

Fig. 3 Time course of mean \pm standard error (SE) midday maximum evapotranspiration (ET_{max}) during June and August 2003 (left and right panels, respectively). (Upper left panel) ET_{max} in *Eragrostis* plots before and after a 39-mm pulse. (Upper right panel) ET_{max} in *Eragrostis* plots before and after 39-mm and 12-mm pulses in 569-mm and 356-mm annual rainfall treatments, respectively. (Lower left panel) ET_{max} in *Heteropogon* plots before and after a 39-mm pulse. (Lower right panel) ET_{max} in *Heteropogon* plots before and after 39-mm and 12-mm pulses in 569-mm and 356-mm annual rainfall treatments, respectively.

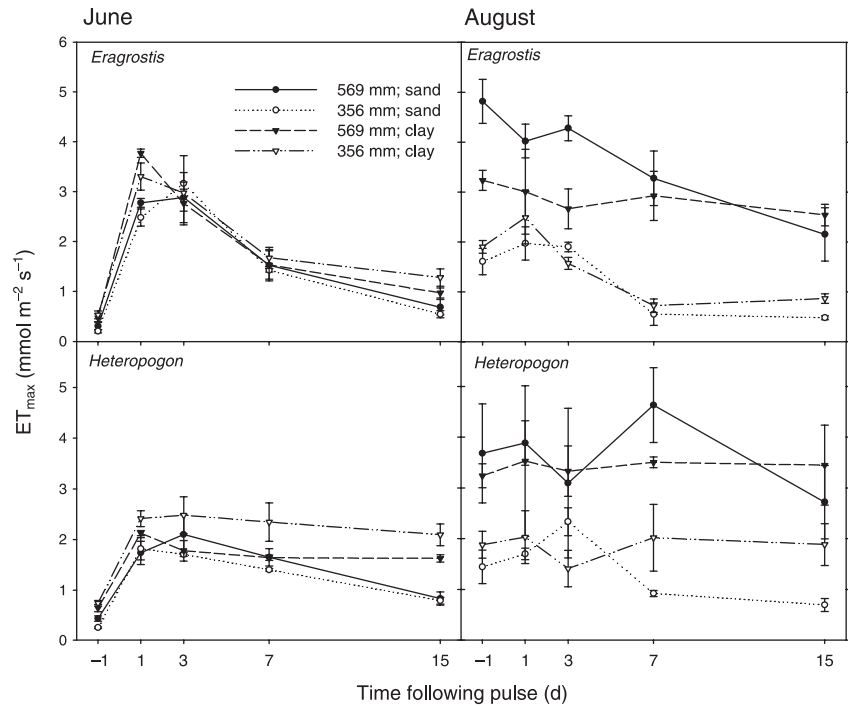
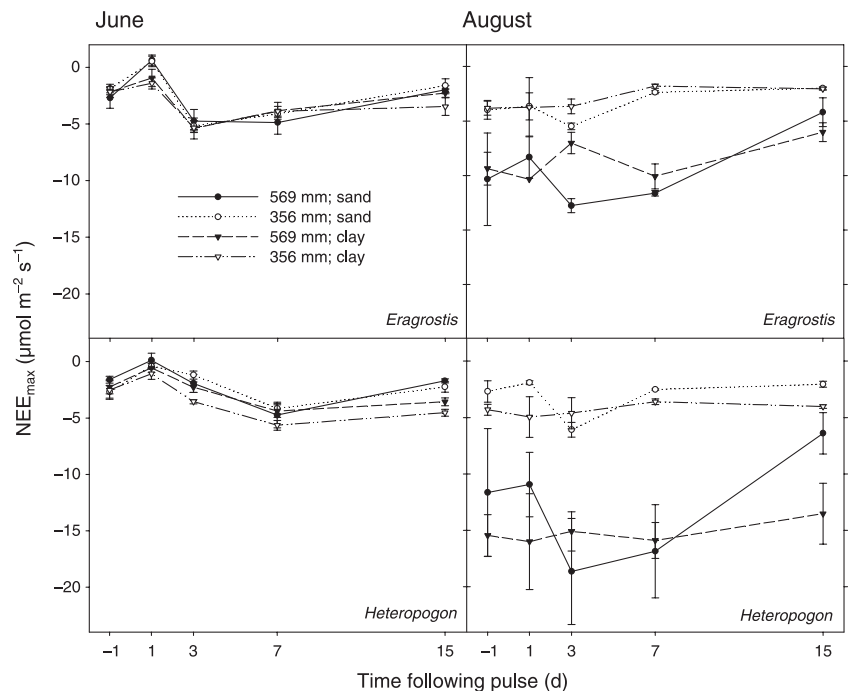


Fig. 4 Time course of mean \pm standard error (SE) midday maximum net ecosystem exchange (NEE_{max}) during June and August 2003 (left and right panels, respectively). By convention, positive values indicate net loss of carbon by the ecosystem, while negative values indicate net gain of carbon by the ecosystem. (Upper left panel) NEE_{max} in *Eragrostis* plots before and after a 39-mm pulse. (Upper right panel) NEE_{max} in *Eragrostis* plots before and after 39-mm and 12-mm pulses in 569-mm and 356-mm annual rainfall treatments, respectively. (Lower left panel) NEE_{max} in *Heteropogon* plots before and after a 39-mm pulse. (Lower right panel) NEE_{max} in *Heteropogon* plots before and after 39-mm and 12-mm pulses in 569-mm and 356-mm annual rainfall treatments, respectively. (Bars represent the SE.)



gradually throughout the remainder of the observation period (Table 3, season \times days).

Integrated carbon and water exchange

During June, PMSD increased the net ecosystem C uptake (indicated by larger, negative values of NEE_{pulse} ; Table 4,

precipitation; Fig. 6, left panels; posthoc Student's t -test, $t = 1.98$, $df = 22$; $P = 0.06$). Among *Heteropogon* treatments during June, NEE_{pulse} values were more negative in clay plots than in sand plots (Table 4, species \times soil; posthoc Student's t -test, $t = 3.08$, $df = 10$; $P = 0.01$). During August, the NEE_{pulse} value was more negative among wet treatments of *Heteropogon* than those of *Eragrostis* (Table 4, species \times precipitation;

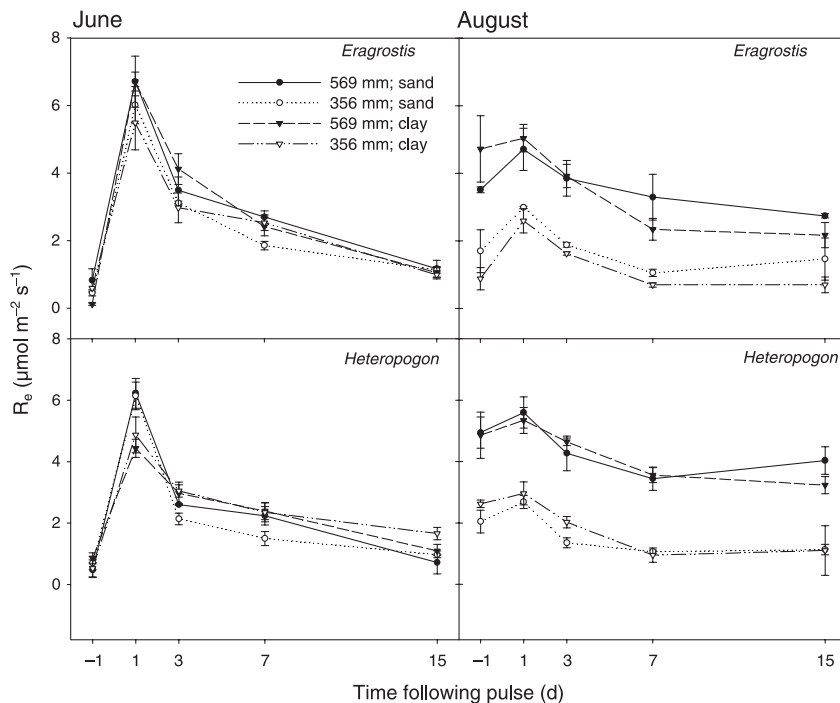


Fig. 5 Time course of mean \pm standard error (SE) night-time ecosystem exchange of CO_2 (R_e) during June and August 2003 (left and right panels, respectively). (Upper left panel) R_e in *Eragrostis* plots before and after a 39-mm pulse. (Upper right panel) R_e in *Eragrostis* plots before and after 569-mm and 12-mm pulses in 569-mm and 356-mm annual rainfall treatments, respectively. (Lower left panel) R_e in *Heteropogon* plots before and after a 39-mm pulse. (Lower right panel) R_e in *Heteropogon* plots before and after 39-mm and 12-mm pulses in 569-mm and 356-mm annual rainfall treatments, respectively. (Bars represent the SE.)

Table 4 Degrees of freedom and *F*-statistics from the statistical analysis of 15-d postpulse integrated NEE and ET and ecosystem pulse-use efficiency in response to precipitation pulses during June and August, 2003 in a semi-arid grassland manipulation in southern Arizona

Factors	df	NEE _{pulse}		ET _{pulse}		PUE _e	
		June	August	June	August	June	August
Spp	1,1	0.001	6.04**	1.00	2.28	0.17	5.83**
Soil	1,1	3.83*	0.11	2.52	1.78	1.73	0.04
Ppt	1,1	3.30*	28.73**	0.08	114.38**	5.574**	10.21**
Spp \times Soil	1,1	3.62*	0.01	2.91*	0.48	4.53**	0.03
Spp \times Ppt	1,1	0.01	5.16**	0.85	0.83	0.89	3.61*
Soil \times Ppt	1,1	0.94	0.08	1.90	7.22**	0.79	0.64
Spp \times Soil \times Ppt	1,1	0.16	0.06	0.71	1.53	0.06	0.07

df, degrees of freedom; ET_{pulse}, 15-d postpulse integrated evapotranspiration; NEE, net ecosystem exchange of CO_2 ; NEE_{pulse}, 15-d postpulse integrated NEE; Ppt, precipitation (7, 9, 12); PUE_e, ecosystem pulse-use efficiency; Spp, species (8, 10, 11, 13, 14).
*, $P < 0.1$; **, $P < 0.05$.

posthoc Student's *t*-test, $t = 2.70$, $df = 10$; $P = 0.02$). Among wet treatments, the NEE_{pulse} value was more negative during August than during June after a precipitation pulse of the same magnitude (Table 5, season).

June ET_{pulse} values among *Heteropogon* treatments in sand plots were lower than in any other treatment (Fig. 6, right panels; Table 4, species \times soil). Predictably, given the differential pulse magnitudes simulated during August in wet and dry treatments, the ET_{pulse} was greater in wet plots (Table 4, precipitation). While the August ET_{pulse} values did not differ among soils in wet treatments, in dry treatments clay plots had greater ET_{pulse} values than sand plots (Table 4, soil \times precipitation; posthoc Student's *t*-test, $t = 2.98$, $df = 10$; $P =$

0.013). Among wet treatments, the ET_{pulse} value was greater during August than during June after a precipitation pulse of the same magnitude (Fig. 6, right panels; Table 5, season).

PMSD increased the June PUE_e (Fig. 7; Table 4, precipitation). This relationship appears to be driven by precipitation regime contrasts on the clay soil, particularly among plots of *Eragrostis* (Fig. 7; Table 4, species \times soil). In contrast, wet treatments had more negative PUE_e than dry treatments during August (Table 4, precipitation). Furthermore, during August, plots of *Heteropogon* had more negative PUE_e than those of *Eragrostis* (Fig. 7; Table 4, species). Among wet treatments, August PUE_e was more negative among *Heteropogon* treatments than those of *Eragrostis* (Fig. 7, lower panel; Table 5,

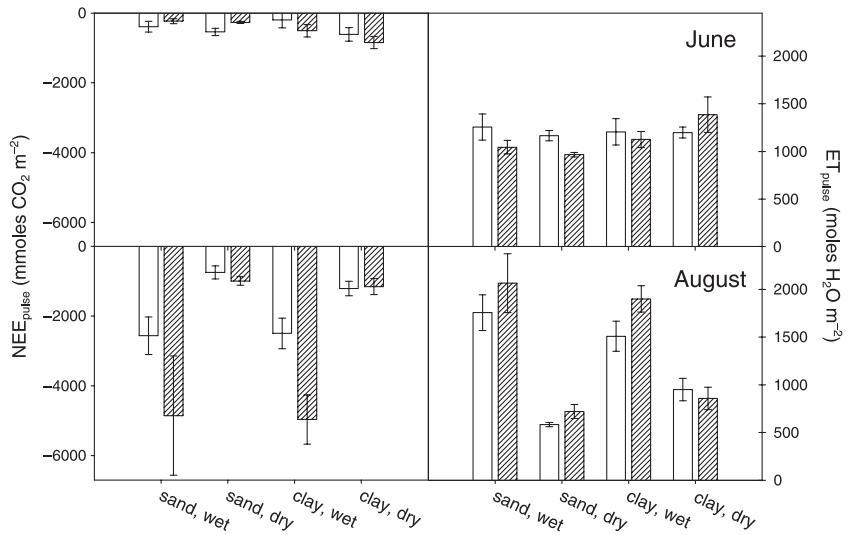


Fig. 6 Mean \pm standard error (SE) 15-d integrated values of net ecosystem exchange (NEE_{pulse}) and evapotranspiration (ET_{pulse}) after pulses in plots of non-native *Eragrostis* (open bars) and in plots of native *Heteropogon* (hatched bars). Upper panels represent June measurements; lower panels represent August measurements. (Left panels) NEE_{pulse} ; by convention, negative values indicate a net gain of carbon by the ecosystem. (Right panels) ET_{pulse} ; positive values reflect water loss by the ecosystem.

Table 5 Degrees of freedom and *F*-statistics from the statistical analysis of 15-d postpulse integrated NEE and ET (NEE_{pulse} and ET_{pulse} , respectively) and ecosystem pulse-use efficiency (PUE_e) among wet treatments in response to June and August 39 mm precipitation pulses in a semi-arid grassland manipulation in southern Arizona

Factors	df	NEE_{pulse}	ET_{pulse}	PUE_e
Spp	1,9	5.93**	0.48	6.18**
Soil	1,9	0.004	0.43	0.70
Season	1,9	58.83**	104.5**	123.3**
Spp \times Season	1,9	6.78**	15.14**	6.24**
Soil \times Season	1,9	0.005	3.08	0.73

df, degrees of freedom; ET_{pulse} , 15-d postpulse integrated evapotranspiration; NEE, net ecosystem exchange of CO₂; NEE_{pulse} , 15-d postpulse integrated NEE; PUE_e , ecosystem pulse-use efficiency; Spp, species (8, 10, 11, 13, 14). ***, $P < 0.05$.

species; posthoc Student's *t*-test, $t = 2.41$, $df = 10$; $P = 0.036$). Despite a smaller August pulse, dry treatments had more negative PUE_e during August than June (Fig. 7; Table 5, season; $t = 7.95$, $df = 22$; $P < 0.0001$).

Discussion

The role of the precipitation regime

We predicted that PMSD would constrain an ecosystem's ability to accumulate carbon in response to a large, early growing season precipitation pulse. In contrast to this prediction, PMSD enhanced ecosystem carbon accumulation and the PUE_e in response to the June pulse. From a grass production perspective, a previous season's drought acts to constrain production in a subsequent year (Hanson *et al.*, 1982; Knapp *et al.*, 2001; Wiegand *et al.*, 2004). From

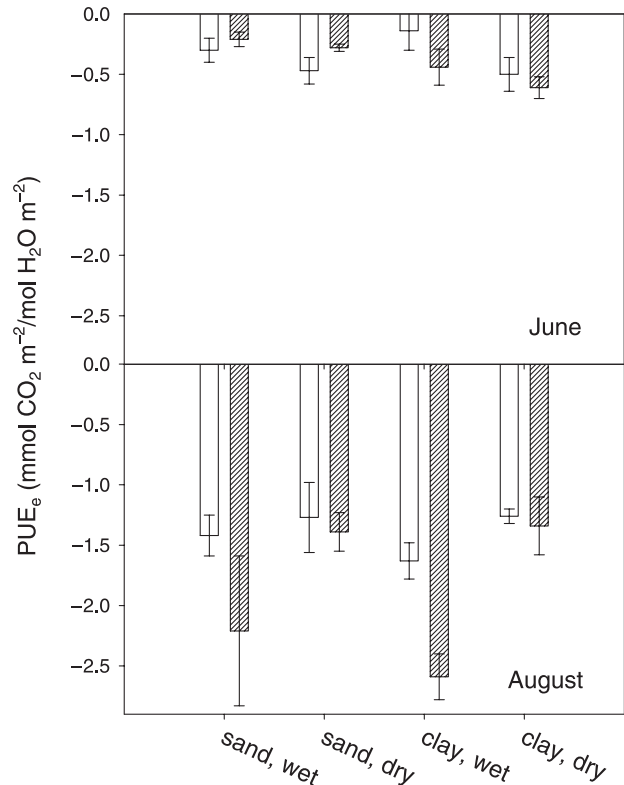


Fig. 7 Mean \pm standard error (SE) ecosystem pulse-use efficiency (PUE_e) for the 15-d period among plots of *Eragrostis* (open bars) and *Heteropogon* (hatched bars) pulses. Upper panels represent June measurements; lower panels represent August measurements. Larger negative values of PUE_e reflect increased efficiency.

an ecosystem production perspective, this does not appear to hold true – greater decreases in R_c compensate for reductions in NEE_{max} , such that greater C accumulation occurs in response to a precipitation event. For example, PMSD may

have limited substrate availability for soil microbes after the June pulse (Austin *et al.*, 2004). Likewise, PMSD may have reduced the pool of soil nitrogen available for mineralization upon rewetting, imposing a stoichiometric limitation on soil microbes, thereby constraining ecosystem respiration (Austin *et al.*, 2004).

The constraining effect of PMSD, and its differential effect on native and non-native bunchgrasses, became evident during August when soil moisture was abundant. These findings suggest that periods of abundant rainfall may be as important as those of drought in understanding the biogeochemical consequences of non-native grasses such as *Eragrostis*. Other studies have noted that precipitation may mediate the influence of other global change factors in semi-arid ecosystems. For example, Naumberg *et al.* (2003) found that among perennial shrubs grown under free-air CO₂ enrichment in the Mojave Desert, CO₂ fertilization enhanced productivity the greatest during years of abundant precipitation.

Soil microbes in arid-land ecosystems are metabolically responsive to ephemeral soil moisture (Cable & Huxman, 2004; Huxman *et al.*, 2004b). The duration and magnitude of soil microbe metabolic response appears to be closely linked with the duration of shallow soil moisture availability, which is a function of evaporative and transpirational demand, not pulse magnitude. Consistent with the theoretical predictions of Huxman *et al.* (2004b), an increase in pulse magnitude from 12 mm to 39 mm did not elicit a larger or longer-lasting R_c response during August (Table 2, precipitation × days). Thus, shifts in the seasonal timing or frequency of rainfall may have a larger impact on R_c than shifts in the event-size distribution of precipitation.

The role of bunchgrass species and soil type

Based on the work of Huxman *et al.* (2004c), we predicted that regardless of prior monsoon-season precipitation, plots of the non-native bunchgrass, *Eragrostis*, would accumulate more carbon than those of the native *Heteropogon* in response to the June pulse. Time-course data of ecosystem carbon exchange parameters do not support this prediction, nor do estimates of NEE_{pulse}. We observed species treatment differences in ET during June, consistent with the observation of Huxman *et al.* (2004c) that the open canopy of *Eragrostis* stands facilitates rapid evaporation from the soil surface (Fig. 3). Furthermore, our estimates of PUE_c suggest the potential for system-level shifts in carbon assimilation efficiency, associated with the seasonal timing of precipitation and with the replacement of native bunchgrasses by monotypic stands of *Eragrostis* (Fig. 7). Precipitation regime and soil texture interact to influence net primary production (Noy-Meir, 1973; Sala *et al.*, 1988), soil moisture storage (Dodd & Lauenroth, 1997), nitrogen mineralization (Austin *et al.*, 2004) and decomposition (Epstein *et al.*, 2002) in grasslands. NEE_{pulse}, an analogue of NPP, was not influenced by the interaction of monsoon-

season precipitation regime and soil type during June or August. Among *Heteropogon* treatments, the June NEE_{pulse} was more negative in clay plots than in sand plots. Among *Eragrostis* treatments, no such soil-mediated differences in NEE_{pulse} were observed. These results demonstrate, as Sala *et al.* (1988) noted, that site characteristics and species-specific traits may obscure the relationship among soil texture, plant productivity and precipitation.

Early vs middle-growing season pulses

A common pattern of ecosystem gas-exchange emerged from all treatment combinations after the June pulse. Immediately after wetting, R_c briefly increased, thus reducing NEE_{max}. Consistent with our prediction, this pattern is probably the result of rapid up-regulation of soil microbe activity (Fierer & Schimel, 2003; Austin *et al.*, 2004) and the physical displacement of CO₂ from soil pores following shallow soil wetting (Jassal *et al.*, 2005). After the June pulse, variation in soil moisture storage and carbon and water fluxes among species, soil type and precipitation regime treatments were minor compared with the variation observed for these factors in ecosystem fluxes following the August precipitation pulses.

Throughout the August measurement period, treatments that received increased monsoon-season precipitation had higher R_c and NEE_{max} values, indicating greater metabolic activity in both above- and below-ground portions of the ecosystem. The importance of seasonality in constraining canopy gas exchange in response to precipitation events is illustrated by comparisons among plots that received 39-mm pulses during both June and August (wet treatments). These results suggest that biotic factors, such as phenological limitation, and abiotic factors, such as atmospheric vapor pressure deficit, may interact to influence the sensitivity of ecosystem carbon metabolism to rainfall pulses.

Comparisons of PUE_c during June and August highlight the strong effect that pulse seasonal timing has on the translation of pulses into ecosystem carbon accumulation (Fig. 7). Lower efficiencies during June (illustrated by smaller negative numbers) suggest that a large fraction of the pulse evaporated quickly from the soil surface or was intercepted by the canopy and hence never available for plant transpiration. Values of ET_{pulse} following the June pulse substantially underestimated the 39-mm pulse (*c.* 2260 mole equivalent), supporting the idea that a fraction of the applied water did not infiltrate the soil and was lost quickly to the atmosphere in the form of evaporation from canopy, litter and soil surfaces before our first measurements of instantaneous ET, several hours after the precipitation pulse was applied. Soil moisture storage data (Fig. 1) does not support an alternative explanation, that 15 d was an insufficient time for ET to remove the 39-mm pulse. Greater August efficiencies reflect high levels of photosynthesis during the peak growing season. Among dry

plots, PUE_c increased during August, despite the fact that these plots received much smaller pulses during August than June (12 mm vs 39 mm, respectively).

Conclusions

These experimental results have implications for the representation of rainfall pulses in production models of semi-arid ecosystems. For example, this research demonstrates that the ability of semi-arid grassland ecosystems to translate soil moisture into assimilated carbon varies widely during the growing season and may be influenced not only by site characteristics, such as bunchgrass species and soil type, but also by antecedent precipitation. The positive effect of PMSD on ecosystem carbon accumulation in response to rainfall pulses suggests that plant and soil microbes differ in their response to precipitation variability. Furthermore, the potential for precipitation-mediated lag effects in ecosystem carbon metabolism may complicate the interpretation of short-term studies on rain use. Finally, this study contributes to a growing body of evidence which suggests that a more complete conceptual model of aridland pulse dynamics should incorporate the above- and below-ground responses of ecosystem components to episodic resource availability.

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References

- Arnone JA, 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* 55: 629–643.
- Austin AT, Yahdjian L, Stark JM, Belnap J, Porporato A, Norton U, Ravetta DA, Schaeffer SM. 2004. Water pulses and biogeochemical cycles in arid and semi-arid ecosystems. *Oecologia* 141: 221–225.
- BassiriRad H, Tremmel DC, Virginia RA, Reynolds JF, de Souza AG, Brunell MH. 1999. Short term patterns in water and nitrogen acquisition by two desert shrubs following a simulated summer rain. *Plant Ecology* 145: 27–36.
- Birch HF. 1958. The effect of soil drying on humus decomposition and nitrogen availability. *Plant and Soil* 10: 9–31.
- Bremer DJ, Ham JM. 2005. Measurement and partitioning of *in situ* carbon dioxide fluxes in turfgrasses using a pressurized chamber. *Agronomy Journal* 97: 627–632.
- Cable JM, Huxman TE. 2004. Precipitation pulse size effect on Sonoran Desert soil microbial crusts. *Oecologia* 141: 317–324.
- Davidson EA, Savage K, Verchot LV, Navarro R. 2002. Minimizing artifacts and biases in chamber-based measurements of soil respiration. *Agricultural and Forest Meteorology* 113: 21–37.
- Dodd MB, Lauenroth WK. 1997. The influence of soil texture on the soil water dynamics and vegetation structure of a shortgrass steppe ecosystem. *Plant Ecology* 133: 13–28.
- Dunkerley D. 2000. Measuring interception loss and canopy storage in dryland vegetation: a brief review and evaluation of available research strategies. *Hydrological Processes* 14: 669–678.
- English NB, Weltzin JF, Fravolini A, Thomas L, Williams DG. 2005. The influence of soil texture and vegetation on soil moisture under rainout shelters in a semi-desert grassland. *Journal of Arid Environments* 63: 324–343.
- Epstein HE, Burke IC, Lauenroth WK. 1999. Response of the shortgrass steppe to changes in rainfall seasonality. *Ecosystems* 2: 139–150.
- Epstein HE, Burke IC, Lauenroth WK. 2002. Regional patterns of decomposition and primary production rates in the US Great Plains. *Ecology* 83: 320–327.
- Fernandez RJ, Reynolds JF. 2000. Potential growth and drought tolerance of eight desert grasses: lack of a trade-off? *Oecologia* 123: 90–98.
- Fierer N, Schimel JP. 2003. A proposed mechanism for the pulse in carbon dioxide production commonly observed following the rapid rewetting of a dry soil. *Soil Science Society of America Journal* 67: 798–805.
- Gutiérrez GR, Whitford WG. 1987. Chihuahuan desert annuals: importance of water and nitrogen. *Ecology* 68: 2032–2045.
- Hanson CJ, Wright JR, Smoliak S. 1982. Use of historic yield data to forecast range herbage production. *Journal of Range Management* 35: 614–616.
- Huxman TE, Smith MD, Fay PA, Knapp AK, Shaw MR, Loik ME, Smith SD, Tissue DT, Zak JC, Weltzin JF, Pockman WT, Sala OE, Haddad BM, Harte J, Koch GW, Schwinning S, Small EE, Williams DG. 2004a. Convergence across biomes to a common rain-use efficiency. *Nature* 429: 651–654.
- Huxman TE, Snyder K, Tissue D, Leffler AJ, Pockman W, Ogle K, Sandquist D, Potts DL, Schwinning S. 2004b. Precipitation pulses and carbon balance in semi-arid and arid ecosystems. *Oecologia* 141: 254–268.
- Huxman TE, Cable JM, Ignace DD, Eilts AJ, English NB, Weltzin J, Williams DG. 2004c. Response of net ecosystem gas exchange to a simulated precipitation pulse in a semi-arid grassland: the role of native versus non-native grasses and soil texture. *Oecologia* 141: 295–305.
- Huxman TE, Wilcox BP, Breshears DD, Scott RL, Snyder KA, Small EE, Hultine K, Pockman WT, Jackson RB. 2005. Ecohydrological implications of woody-plant encroachment. *Ecology* 86: 308–319.
- Jassal R, Black A, Novak M, Morgenster K, Nestic Z, Gaumont-Gray D. 2005. Relationship between soil CO₂ concentrations and forest-floor CO₂ effluxes. *Agricultural and Forest Meteorology* 130: 176–192.
- Knapp AK, Smith MD. 2001. Variation among biomes in temporal dynamics of aboveground primary production. *Science* 291: 481–484.
- Knapp AK, Briggs JM, Hartnett DC, Collins SL. 1998. *Grassland dynamics: long-term ecological research in tallgrass prairie*. New York, NY, USA: Oxford University Press.
- Knapp AK, Briggs JM, Koelliker JK. 2001. Frequency and extent of water limitation to primary production in a mesic temperate grassland. *Ecosystems* 4: 19–28.
- Knapp AK, Fay PA, Blair JM, Collins SL, Smith MD, Carlisle JD, Harper CW, Danner BT, Lett MS, McCarron JK. 2002. Rainfall variability, carbon cycling and plant species diversity in a mesic grassland. *Science* 298: 2202–2205.
- McAuliffe JR. 1995. Landscape evolution, soil formation and Arizona's desert grasslands. In: McClaran MP, Van Devender TR, eds. *The desert grassland*. Tucson, AZ, USA: University of Arizona Press, 100–129.
- McPherson GR. 1997. *Ecology and management of North American savannas*. Tucson, AZ, USA: University of Arizona Press.

- Naumberg E, Housman DC, Huxman TE, Charlet TC, Loik ME, Smith SD. 2003. Photosynthetic responses of Mojave Desert shrubs to free air CO₂ enrichment are greatest during wet years. *Global Change Biology* 9: 276–285.
- Noy-Meir I. 1973. Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics* 4: 25–51.
- Potts DL, Huxman TE, Enquist BJ, Weltzin JF, Williams DG. 2006. Resilience and resistance of ecosystem functional response to a precipitation pulse in a semi-arid grassland. *Journal of Ecology* 94: 23–30.
- Pumpanen J, Kolari P, Ilvesniemi H, Minkkinen K, Vesala T, Niinistö S, Lohila A, Larmola T, Morero M, Pihlatie M, Janssens I, Curiel Yuste J, Grünzweig JM, Reth S, Subke J, Savage K, Kutsch W, Østreng G, Ziegler W, Anthoni P, Lindroth A, Hari P. 2004. Comparison of different chamber techniques for measuring soil CO₂ efflux. *Agricultural and Forest Meteorology* 123: 159–176.
- Reynolds JF, Kemp PR, Ogle K, Fernandez RJ. 2004. Modifying the 'pulse-reserve' paradigm for deserts in North America: precipitation pulses, soil water, and plant responses. *Oecologia* 141: 194–210.
- Risler PD, Wraith JM, Gaber HM. 1996. Solute transport under transient flow conditions estimated using time domain reflectometry. *Soil Science Society of America Journal* 60: 1297–1305.
- Saetre P, Stark JM. 2005. Microbial dynamics and carbon and nitrogen cycling following rewetting of soils beneath two semi-arid plant species. *Oecologia* 142: 247–260.
- Sala OE, Parton WJ, Joyce LA, Lauenroth WK. 1988. Primary production of the central grassland region of the United States. *Ecology* 69: 40–44.
- Saleska SR, Harte J, Torn MS. 1999. The effect of experimental ecosystem warming on CO₂ fluxes in a montane meadow. *Global Change Biology* 5: 125–141.
- Schwinning S, Ehleringer JR. 2001. Water use trade-offs and optimal adaptations to pulse-driven arid ecosystems. *Journal of Ecology* 89: 464–480.
- Schwinning S, Sala OE, Loik ME, Ehleringer JR. 2004. Thresholds, memory and seasonality: understanding pulse dynamics in arid/semi-arid ecosystems. *Oecologia* 141: 191–193.
- Snyder KA, Donovan LA, James JJ, Tiller RL, Richards JH. 2004. Extensive summer water pulses do not necessarily lead to canopy growth of Great Basin and northern Mojave Desert shrubs. *Oecologia* 141: 325–334.
- Weltzin JF, Tissue DT. 2002. Resource pulses in arid environments – patterns of rain, patterns of life. *New Phytologist* 157: 171–173.
- Weltzin JF, Loik ME, Schwinning S, Williams DG, Fay PA, Haddad BM, Harte J, Huxman TE, Knapp AK, Lin GH, Pockman WT, Shaw MR, Small EE, Smith MD, Smith SD, Tissue DT, Zak JC. 2003. Assessing the response of terrestrial ecosystems to potential changes in precipitation. *Bioscience* 53: 941–952.
- Wiegand T, Snyman HA, Kellner K, Paruelo JM. 2004. Do grasslands have a memory: modeling phytomass production of a semi-arid south African grassland. *Ecosystems* 7: 243–258.
- Yepez EA, Huxman TE, Ignace DD, English NB, Weltzin JF, Castellanos AE, Williams DG. 2005. Dynamics of transpiration and evaporation following a moisture pulse in semi-arid grassland: a chamber-based isotope method for partitioning flux components. *Agricultural and Forest Meteorology* 132: 359–376.