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## 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

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**Abstract** Physiological activity and structural dynamics in arid and semi-arid ecosystems are driven by discrete inputs or “pulses” of growing season precipitation. Here we describe the short-term dynamics of ecosystem physiology in experimental stands of native (*Heteropogon contortus*) and invasive (*Eragrostis lehmanniana*) grasses to an irrigation pulse across two geomorphic surfaces with distinctly different soils: a Pleistocene-aged surface with high clay content in a strongly horizonated soil, and a Holocene-aged surface with low clay content in homogeneously structured soils. We evaluated whole-ecosystem and leaf-level CO<sub>2</sub> and H<sub>2</sub>O exchange, soil CO<sub>2</sub> efflux, along with plant and soil water status to understand potential constraints on whole-ecosystem carbon exchange during the initiation of the summer monsoon season. Prior to the irrigation pulse, both invasive and native grasses had less negative pre-dawn water potentials ( $\Psi_{pd}$ ), greater leaf photosynthetic rates ( $A_{net}$ ) and stomatal conductance ( $g_s$ ), and greater rates of net ecosystem carbon exchange (NEE) on the Pleistocene surface than on the Holocene. Twenty-four hours following the experimental application of a 39 mm irrigation pulse, soil CO<sub>2</sub> efflux increased leading to all plots losing CO<sub>2</sub> to the atmosphere over the

course of a day. Invasive species stands had greater evapotranspiration rates (ET) immediately following the precipitation pulse than did native stands, while maximum instantaneous NEE increased for both species and surfaces at roughly the same rate. The differential ET patterns through time were correlated with an earlier decline in NEE in the invasive species as compared to the native species plots. Plots with invasive species accumulated between 5% and 33% of the carbon that plots with the native species accumulated over the 15-day pulse period. Taken together, these results indicate that system CO<sub>2</sub> efflux (both the physical displacement of soil CO<sub>2</sub> by water along with plant and microbial respiration) strongly controls whole-ecosystem carbon exchange during precipitation pulses. Since CO<sub>2</sub> and H<sub>2</sub>O loss to the atmosphere was partially driven by species effects on soil microclimate, understanding the mechanistic relationships between the soil characteristics, plant ecophysiological responses, and canopy structural dynamics will be important for understanding the effects of shifting precipitation and vegetation patterns in semi-arid environments.

**Keywords** Net ecosystem exchange · Invasive species · Evapotranspiration · Precipitation manipulation · Santa Rita Experimental Range

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### Introduction

In the arid southwestern United States, ecosystem structure and function is shaped by variation in the spatio-temporal patterns of water availability (Noy-Meir 1973; Ehleringer 1985; Neilson 1995; Smith et al. 1997; Knapp and Smith 2001; Weltzin and McPherson 2003). Variation in the total availability, predictability, and seasonality of water resources have been used to describe differences in vegetation between North American deserts based on differential adaptive physiological and functional strategies of their respective flora (Smith and Nobel 1986; Smith et al. 1997). Currently, these arid land ecosystems

are undergoing extensive vegetation change caused by the introduction of several non-native grass species (Esque and Schwalbe 2002). Introductions of non-native species have implications for the flux of material and energy in terrestrial ecosystems (Walker and Smith 1997; Mooney and Hobbs 2000). Despite the importance of species invasions to global change, the influence of species invasions on ecosystem properties and processes is not well understood (D'Antonio and Vitousek 1992; Dukes 2000). The nature of potential interactions between biological invasions, shifts in species composition and changes in climate variability on ecosystem processes is unknown.

In semi-arid and arid ecosystems, soils translate a precipitation event into potential biological activity. Variation in soil surface characteristics modify surface and sub-surface infiltration, depth of soil moisture storage, and the temporal duration of biologically available soil water (Noy-Meir 1973; McAuliffe 2003). For example, the dominant North American shrub, *Larrea tridentata*, is heavily influenced by soil characteristics (Shreve and Mallery 1933; Smith et al. 1995; Hamerlynck et al. 2000), such that the presence of cemented subsurface Calcic horizons and surface pavement development affect soil water balance, plant water-relations and productivity (Cunningham and Burke 1973; Hamerlynck et al. 2002). Thus, characteristics of soil surfaces can modify climate signals into differential biological activity, impacting the surrounding vegetation composition and performance (McAuliffe 1994, 1999; Parker 1995; Smith et al. 1995; Hamerlynck et al. 2002). The interaction between plants and soil characteristics are also of importance for hydrological processes, such as runoff, recharge and sediment transport (Wainwright et al. 2002). How surface and subsurface soil characteristics may modify the fluxes of carbon and water between the biosphere and the atmosphere is not well understood.

Variation in resource availability results in shifts in physiological and structural states that may be important in controlling ecological processes. For example, the speed and extent to which species respond to a precipitation pulse can explain the ability of an invasive species to outperform native species (such as in *Bromus tectorum* in the Great Basin, for example, Megloza et al. 1990). When invasive potential is coupled with the length of the growing season, it has implications for patterns of productivity in stands. Responses to variation in water availability in individual plants, within soil microbiota and across the integrated ecological system vary in such a manner that ecosystem respiration and photosynthesis may have differing control over productivity through time (Huxman et al., in preparation). This is a result of variation in the kinetics of up-regulation of physiological processes in individual organisms relative to patterns of growth (Comstock and Ehleringer 1986). At the ecosystem scale, this variation can be a function of changes in species composition, ontogenetic changes in performance, or abiotic features impacting the flux of material and energy (Huxman et al., in preparation).

In this experiment we evaluated the patterns of plant, soil and whole-ecosystem exchange of CO<sub>2</sub> and H<sub>2</sub>O in stands of invasive (*Eragrostis lehmanniana*) and native (*Heteropogon contortus*) grass species across two geomorphic surfaces exposed to a precipitation pulse. This semi-arid ecosystem is characterized by infrequent large woody species (mesquite; *Prosopis*) with an understory of grasses. Recently, the non-native species *E. lehmanniana* has expanded to produce near-monocultures over a substantial portion of semi-arid grasslands (Anable et al. 1992). We evaluated whole-ecosystem fluxes on this system following the application of a pre-monsoon irrigation pulse. In the southwestern United States, rainfall occurs in a bimodal pattern, with nearly even distributions of summer and winter rain. The distinct characteristic of this region, however, is the occurrence of little to no rainfall during the 3 months preceding the onset of the summer monsoon.

Invasive success is not often attributed to drought resistance (e.g., Williams and Black 1994), but may be related to resource exploitation in water-limited systems (e.g., Sala et al. 1996; Walker and Smith 1997). Thus we predicted that the non-native species *E. lehmanniana* will more rapidly utilize water resources for up-regulation of photosynthetic processes than the native species *H. contortus*. The rapid utilization of resources by the non-native species will result in greater carbon uptake into the ecosystem. The greater rate of carbon accumulation should accompany higher rates of evapotranspiration from the non-native species plots. Since the non-native species may more quickly utilize the water pulse, up-regulate photosynthesis and develop canopy leaf area, the duration of photosynthetic and transpiration activity following the precipitation pulse should be shorter in the non-native species plots than in the native species plots. Plant activity is an important component of ecosystem respiration (Franzluebbers et al. 2002), thus we expect that ecosystem respiration should increase in congruence with the development of photosynthetic activity in these grassland plots. This would suggest similar dynamics of ecosystem respiration and photosynthesis through time. Finally, because precipitation interacts with soil texture to regulate productivity in xeric biomes (e.g., the inverse texture hypothesis; Sala et al. 1988), we expect the relative carbon accumulation, with a pulse of precipitation, to be greater on a sandy, uniformly textured soil on a Holocene surface than on a finer-textured, well-developed, clay-rich soil on an older Pleistocene surface. This is primarily a function of the differences in infiltration rates, potential for water movement to lower soil levels, and soil water holding capacities of the different substrates.

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## Materials and methods

### Study site and precipitation manipulation

We evaluated the fluxes of CO<sub>2</sub> and H<sub>2</sub>O before and after a large pulse of precipitation in plots of native and non-

native species at the Santa Rita Experimental Range, located approximately 50 km south of Tucson, Arizona. Plots were established beneath rainout manipulation shelters that were constructed on two different soil surfaces during the summer of 2001. Three shelters (161-m<sup>2</sup> covered area) were built on an early Pleistocene surface, characterized by a well-developed argillic horizon at about 30 cm below the soil surface, and three shelters were built on a Holocene deposit characterized by poorly developed and texturally homogeneous soils (McAuliffe 1995). The soils on the Pleistocene surface contain 50% clay and 30% sand, while the Holocene surface soils contain 6% clay and 84% sand (gravimetric determination of 25- to 100-cm depths). Shelters were arranged in three replicated blocks on each soil surface.

Each of the three shelters within a site covered 12 plots containing stands of non-native grass, native grass, and bare plots. Each treatment was assigned randomly to one of 12 plots within each shelter using a randomized complete block design. Each plot (1.5 m × 1.8 m) was trenched to a depth of 1-m and time-domain reflectometry sensors were placed in each plot at 15-, 35- and 55-cm depths from the soil surface. Trench faces were lined with plastic to isolate soil columns from the surrounding soil environment. Plastic was attached to a wooden frame, lining the perimeter at the surface of each plot. The wooden frame provided a 5-cm barrier to prevent lateral movement of water and sediment into or out of the plot across the soil surface. During construction, we left the A horizon intact on all plots, but we removed all plant material from the plots before planting the grass.

In the spring of 2001, plots were planted with greenhouse-grown transplants of either a native grass (*H. contortus*) or an invasive grass (*E. lehmanniana*) at densities similar to that observed in adjacent natural stands (18.6 plants m<sup>-2</sup>). An equal mass of a 1:1 mix of *E. lehmanniana* and *H. contortus* litter was added to each plot in the fall of 2001. Plots were provided with the same irrigation regime at both soil surfaces throughout the course of the experiment, and they received ~149 mm of irrigation from 10 August 2001 to 1 April 2002. Plots received no irrigation from 1 April 2002 until 10 June 2002 (the date of the current pulse).

At each soil surface, plots of *H. contortus* had a greater leaf area index (LAI: m<sup>2</sup> leaf area m<sup>-2</sup> ground area) than *E. lehmanniana* (0.90 ± 0.23 vs 0.69 ± 0.19, Holocene surface; 1.05 ± 0.22 vs 0.59 ± 0.09, Pleistocene surface). There was a significant species effect in a two-way ANOVA,  $F=3.73$ ;  $df=1,8$ ;  $P<0.08$ . There was not a significant trend associated with the different soil surfaces. Plot LAI was estimated from measurements of individual plant size and plant density. Within each plot, all tillers on three randomly chosen bunchgrasses were counted and the length of ten randomly chosen tillers was determined. A regression, constructed from destructive harvests, was used to relate tiller length to tiller leaf area (m<sup>2</sup>) for each species. Thus, LAI was a multiplication of mean tiller leaf area, mean tiller number per individual, and plant density in a given plot.

On 10 June 2002, we applied a 39-mm pulse of irrigation to each plot on each soil surface. We followed the dynamics of transpiration and CO<sub>2</sub> exchange on individual plants and within the whole ecosystem for 15 days in response to the water pulse (for  $n=3$  plots in each treatment combination). Spot measurements of plant and soil gas exchange along with diurnal measurements of whole-system gas exchange were made prior to, and 1, 3, 7 and 15 days following the pulse event.

#### Plant- and soil-level measurements

We monitored mid-morning leaf photosynthetic gas exchange [net assimilation rate ( $A_{\text{net}}$ ) and stomatal conductance ( $g_s$ )] with a portable photosynthesis system (LI-6400, Li-Cor, Lincoln, Neb., USA) on two recently fully expanded leaves of different individuals per plot during the pulse experiment. Values of  $A_{\text{net}}$  and  $g_s$  collected between 0900 and 1100 hours are representative of the maximum rates for individuals at this time of year in this region (Naumburg et al. 2003). The red/blue light source on the LI-6400 was set at a light intensity of 1500  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . Vapor pressure deficit, air temperature, and CO<sub>2</sub> concentration of the cuvette were set to values close to ambient environmental conditions at mid-morning for any particular measurement period (3.0 kPa, 30 °C, and 370  $\mu\text{mol mol}^{-1}$ , respectively), and maintained constant for all measurements across the plots. We also measured the time-course of plant pre-dawn water potential ( $\Psi_{\text{pd}}$ ) with a Scholander-type pressure chamber during and following the application of precipitation on one individual plant per plot. Plot means of both  $A_{\text{net}}$ ,  $g_s$ , and  $\Psi_{\text{pd}}$  were used as statistical units.

We measured soil CO<sub>2</sub> efflux ( $R_s$ ) throughout the experiment in each of the treatment plots, using the standard soil chamber cuvette for the LI-6400 for two soil collars per plot. Soil collars were placed in each plot 2 weeks prior to the pulse of water. During the experiment, an average efflux of CO<sub>2</sub> from three “drawn-down” cycles on each collar was used to produce a plot mean. Soil temperature at 10 cm was measured along with soil flux rate for each measurement.

#### Plot-level measurements

We measured the time course of whole-plot CO<sub>2</sub> and H<sub>2</sub>O exchange with an open-path infrared gas exchange analyzer (LI-7500) located inside a static chamber (1.5 m wide × 1.8 m long × 1.8 m tall) placed and sealed upon the plots. This system is similar to that outlined in Arnone and Obrist (2003), which has been successfully used in a Great Basin shrubland to evaluate large-scale fluxes of CO<sub>2</sub> and water vapor (Obrist et al. 2003). The system consisted of the static chamber, constructed of a PVC pipe frame and polyethylene sheet, two fans, which mixed the air within the chamber, the LI-7500 and an attached laptop computer for data collection. Diurnal time-

courses (0, 0800, 1200, and 1600 hours) were determined on the following days; pre-pulse, day 1, day 3, day 7, and day 15 following the pulse application for each plot.

To make a measurement, the IRGA and fans were placed in the center of a plot mounted to a tripod. Chambers were placed on plots, with a small padded sleeve pressed tightly on the plot's wooden frame by a heavy steel chain which produced a seal. CO<sub>2</sub> and H<sub>2</sub>O concentrations were allowed to build up or draw down over time, from which flux rates were determined from the time-course of the concentration [net ecosystem CO<sub>2</sub> exchange in the light (NEE), net loss of CO<sub>2</sub> in the dark ( $R_c$ ), or net loss of H<sub>2</sub>O to the atmosphere (ET)]. Whole-plot measurements took approximately 90 s, which results in insufficient water vapor build-up (upper limit of range above and below ambient of 1.0 mmol mol<sup>-1</sup>) or CO<sub>2</sub> draw-down (upper limit of range about ambient of 15 μmol mol<sup>-1</sup>) to significantly alter plant stomatal conductance, canopy photosynthesis or soil CO<sub>2</sub> efflux. For the first 20 s that the chambers were on a plot, we avoided data collection to allow for complete mixing within the chamber volume. The polyethylene sheeting used for chamber construction (Shelter Systems, Santa Cruz, Calif.) allows 92% of photosynthetically active radiation to pass into the plots, while allowing IR radiation to escape the chambers, resulting in only a small change in light environments or canopy temperature (less than 0.2°C during an average measurement period) (Arnone and Obrist 2003). The large volume-to-exchange surface relationship combined with the narrow range of gas density changes resulted in no significant change in chamber pressure that could lead to an inhibition of CO<sub>2</sub> efflux from soil (Livingston and Hutchinson 1995; Davidson et al. 2002).

From the spot measurements of carbon dioxide exchange throughout the day and night, an integrated daily measure of CO<sub>2</sub> flux (NEE<sub>daily</sub>) for each plot was constructed. Using the integrating function in SigmaPlot, v7.0, we evaluated the area under a spline-fit to the 24 h profile. In order to integrate CO<sub>2</sub> fluxes across night and day, we assumed that dawn and dusk represented periods of compensation (Saleska et al. 1999), unless net CO<sub>2</sub> efflux to the atmosphere was observed during daylight

hours. Under these conditions, dawn and dusk were set to the nighttime measured flux rate.

### Statistical analysis

A four-factor split-plot repeated measures ANOVA (SPSS, Chicago, Ill.) was used to test for the significance of geomorphic surface, species, time and their interactions for the extent of the precipitation pulse experiment, using  $A_{net}$ ,  $g_s$ ,  $\Psi_{pd}$ ,  $R_s$ , maximum instantaneous NEE, maximum ET, daily integrated NEE (NEE<sub>daily</sub>), gross ecosystem exchange (GEE), NEE/ET, and  $A_{net}/g_s$  as response variables. The surface×time×species×block error was used as the sub-plot *F*-test denominator, while the surface×block was used as the whole-plot *F*-test denominator. Data were transformed to meet ANOVA distribution assumptions and post-hocs were tested using LSD with  $\alpha=0.05$ . Soil water potential was analyzed with a five-factor split-plot repeated measures ANOVA, with a similar structure to that above, except that depth in each plot was included in the model.

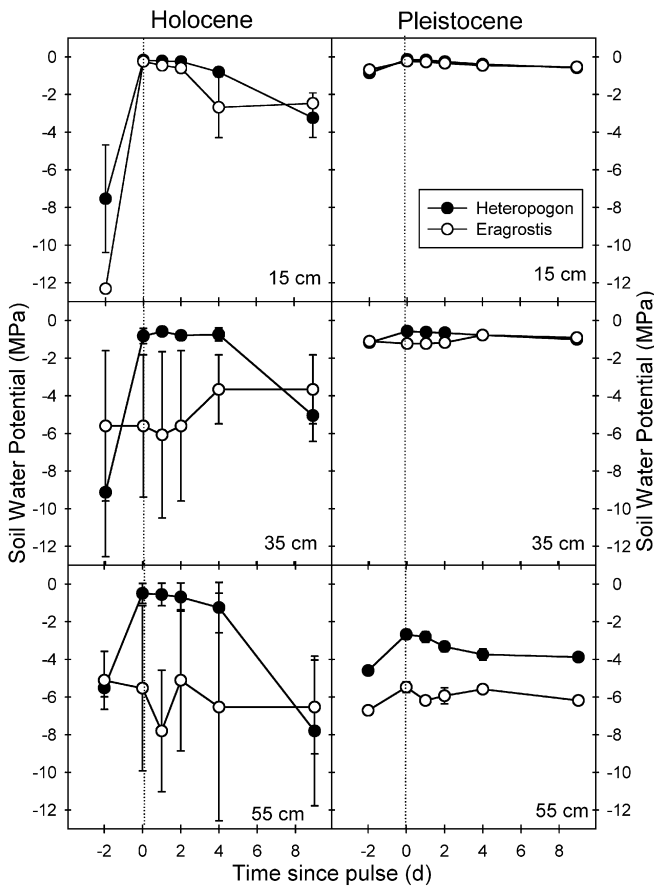
## Results

Initially, soil water potential in the upper soil layers was extremely negative (<-5 MPa) on the Holocene surface, but greater than -2 MPa on the Pleistocene surface, with functionally insignificant differences for native and non-native plots (Fig. 1). Upon irrigation, native stands of *Heteropogon* achieved less negative soil water potential than stands of the invasive *Eragrostis* for both the Pleistocene and Holocene sites at all depths (significant species×surface×depth×time interaction;  $P<0.05$ ). The pulse of water significantly altered soil water potential in shallow layers, but moisture declined after 9 days to near pre-pulse levels for all species, sites and depths. The pulse of water influenced the water potential of the deepest soil layer only in the *Heteropogon* plots, and altogether to the greatest proportional extent on the Holocene surface. The upper soil layers of the Pleistocene surface showed the smallest proportional response to the pulse and species composition.

**Table 1** Degrees of freedom (*df*) and *F*-Statistics from the statistical analysis on individual plant, soil and whole plot variables through time in response to an irrigation pulse in a semi-arid grassland

Factors	Variable												
	<i>df</i>	$\Psi_{pd}$	$g_s$	$A_{net}$	ET	NEE	$R_s$	$R_c$	GEE	NEE <sub>int</sub>	NEE / ET	$A_{net} / g_s$	
Species	1,2	12.5**	762.0*	21.5*	0.001	1.38	0.09	0.68	0.40	12.5**	1.13	0.28	
Surface	1,2	7.6	1.14	9.99**	0.01	0.01	7.53	2.79	0.25	0.43	20.6	0.24	
Time	4,8	27.0*	21.6*	75.1*	70.8*	67.5*	298.0*	46.4*	32.6*	118.3*	30.3*	28.9*	
Species × Surface	1,2	1.36	15.7*	16.2*	1.37	0.02	0.01	0.5	0.09	28.5*	0.80	2.84	
Species × Time	4,8	4.3*	2.18	1.7	47.8*	11.6*	4.05*	5.1*	15.7*	7.98*	0.65	1.50	
Surface × Time	4,8	39.7*	8.64*	6.4*	23.4*	0.66	24.5*	1.14	1.00	5.22*	10.67*	1.03	
Species × Surface × Time	4,8	0.5	0.98	2.7**	1.28	1.09	2.36	3.29**	2.28	0.75	0.15	1.15	

manipulation in southern Arizona. *F*-statistics with a single asterisk indicate significance at  $P<0.10$ , whereas a double asterisk indicates  $P<0.05$

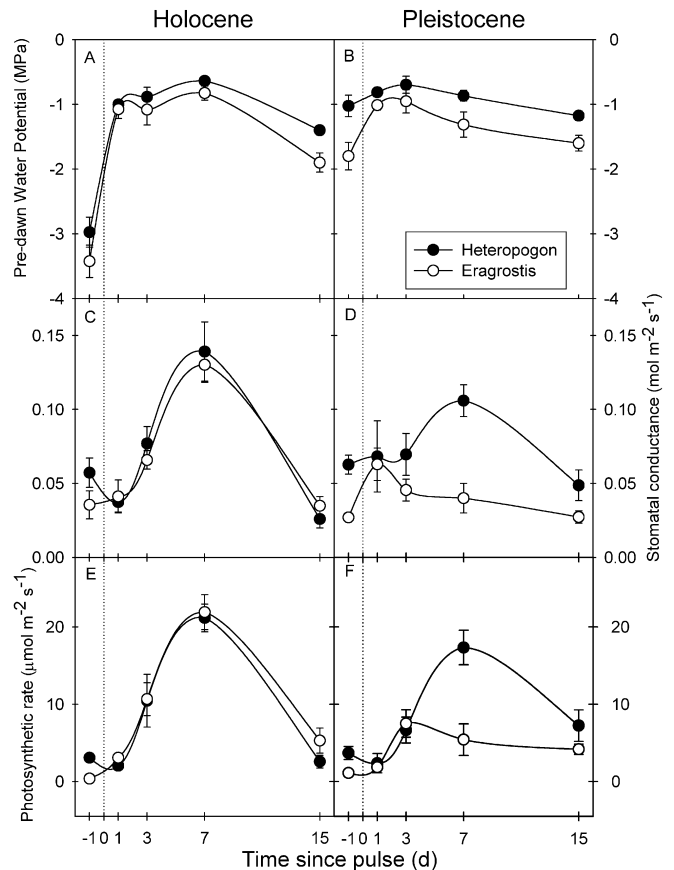


**Fig. 1** The dynamics of soil water potential (MPa) through time across two geomorphic surfaces (Holocene and Pleistocene) and a non-native (*Eragrostis*) and native (*Heteropogon*) community with respect to a 39-mm simulated pulse of precipitation. Data presented are means  $\pm$ 1SE, for 15-, 35-, and 55-cm depths. The dashed vertical line indicates the timing of the irrigation pulse

There were significant effects of species $\times$ time and geomorphic surface $\times$ time interactions in pre-dawn plant water potential ( $\Psi_{pd}$ ; Table 1), which resulted in a time course throughout the pulse that was similar to soil water potential at 15 cm. Prior to the irrigation pulse, there were large differences in  $\Psi_{pd}$  for the two sites, with the Holocene site having much more negative values (Fig. 2A, B). Following the irrigation pulse, both species on both surfaces showed less negative  $\Psi_{pd}$  than prior to the pulse.  $\Psi_{pd}$  increased dramatically following the application of water at the Holocene site, converging with values similar to the Pleistocene surface. The only obvious species differences occurred on the Pleistocene surface, where the native species had much less negative  $\Psi_{pd}$  than did the invasive species. Following a maximum at day 7, both species on both surfaces showed declines in  $\Psi_{pd}$ , however, the declines through time were larger at the Holocene site than at the Pleistocene site. On the Pleistocene surface the two species showed similar proportional  $\Psi_{pd}$  responses, but the invasive species always had more negative values. On the Holocene surface, a difference between the native and invasive

species developed through time, such that the invasive species had more negative  $\Psi_{pd}$  after 15 days.

Variation in stomatal conductance to water vapor ( $g_s$ ) in this experiment was a function of significant geomorphic surface $\times$ time and species $\times$ surface interactions (Table 1). Prior to the application of irrigation,  $g_s$  was greater in the native species *Heteropogon* than the invasive species *Eragrostis* at the Pleistocene and Holocene sites (Fig. 2C, D). Following a pulse of precipitation, both species on the Holocene surface showed substantial increases in  $g_s$ , up to values that were 3 $\times$  higher than pre-pulse values, with maximums occurring at day 7 and a similar pattern of decline following this maximum. Responses of  $g_s$  to a pulse of water for both species was different on the Pleistocene, rather than on the Holocene surface. The native species was more homeostatic across the precipitation pulse duration than was the invasive species at the Holocene site, and the invasive species showed a statistically insignificant response in  $g_s$  across time on the Pleistocene surface.  $g_s$  for all species, surfaces and plots, returned to pre-pulse levels 15 days after the pulse application.



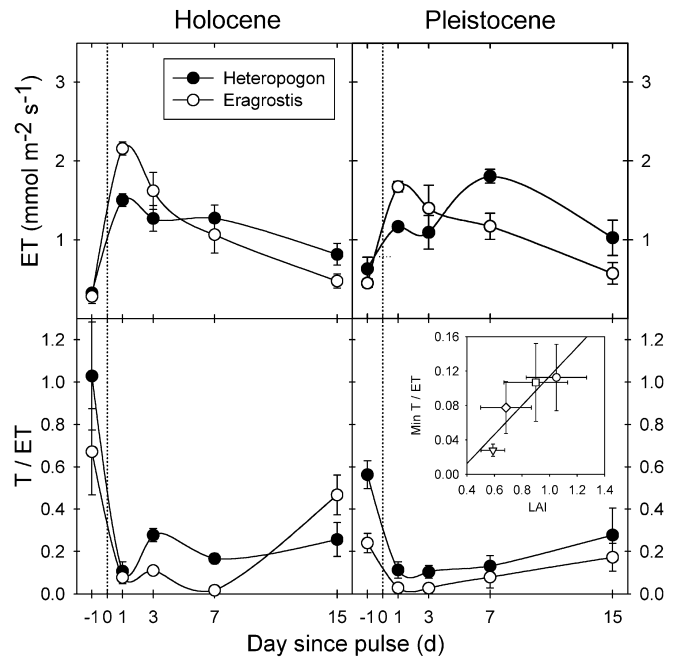
**Fig. 2** The time course of plant response to a 39-mm precipitation pulse across two geomorphic surfaces for pre-dawn water potential ( $\Psi_{pd}$ ) (panel A Holocene, panel B Pleistocene), stomatal conductance to water vapor ( $g_s$ ) (panel C Holocene, panel D Pleistocene), and net assimilation rate ( $A_{net}$ ) (panel E Holocene, panel F Pleistocene) for a non-native (*Eragrostis*) and native (*Heteropogon*) community. Data presented are means  $\pm$ 1SE. Leaf gas exchange was collected at mid-morning (0900–1100 hours)

Similar to the patterns seen in  $g_s$ ,  $A_{net}$  was influenced by significant species $\times$ surface and geomorphic surface $\times$ time interactions (Table 1). Moreover, for all of the response variables measured in the current study,  $A_{net}$  was one of two in which the three way interaction (species $\times$ surface $\times$ time) was potentially significant ( $P < 0.10$ ; Table 1). Prior to the irrigation, at both the Pleistocene and Holocene sites, leaf-level  $A_{net}$  was greater for the native than for the non-native species (Fig. 2 E, F). Following the precipitation pulse, both species on the Holocene surface showed substantial increases in  $A_{net}$ , up to values that are typical of a  $C_4$  plant during the active growing season. Following a maximum at day 7, both species showed a similar pattern of decline in  $CO_2$  uptake mid-morning.  $A_{net}$  behaved differently on the Pleistocene surface compared to the Holocene surface, where the pulse of precipitation resulted in species differences. In contrast to  $g_s$ , the native species showed similar photosynthetic responses to the pulse as compared to the Holocene site. Photosynthesis increased in the invasive species during the first few days of the pulse, but the response did not persist. Fifteen days after the pulse of precipitation, there was a new rank order of  $A_{net}$  across the different surfaces and species.

Whole-plot ET was governed by significant species $\times$ time and surface $\times$ time interactions (Table 1) that led to stands of *Eragrostis* on both the Pleistocene and Holocene surfaces having greater evapotranspiration rates during the initial phases of the pulse duration (Fig. 3). This resulted in an earlier “peak” of ET for the invasive species than for the native species, which showed a more gradual increases in ET. High ET rates were maintained over longer periods in the *Heteropogon* plots, than in the invasive grass plots across both soil surfaces, which is consistent with soil moisture data presented in Fig. 1.

Using the measured stomatal conductance for each species along with plot LAI, we estimated the canopy conductance for each treatment at mid-morning. We calculated canopy transpiration, using air temperature and vapor pressure, then compared this to the chamber-based estimates of evapotranspiration. The large increase in ET with a pulse of precipitation occurred mainly through increases in soil water evaporation ( $E$ ) rather than plant transpiration ( $T$ ).  $T/ET$  showed species specific and soil specific patterns through time (Fig. 3). Prior to the pulse,  $T/ET$  was greater on the Holocene surface than on the Pleistocene, which is consistent with the soil water potential patterns for 15 cm (e.g., there was little to no available water in the soil surface of the Holocene site). Immediately following the application of water,  $T/ET$  was strongly correlated with LAI, regardless of species or soil (inset Fig. 3).  $T/ET$  increased through time for all species and soil combinations, to the greatest extent for the Holocene *Eragrostis* plots, which also showed the greatest reductions in surface soil water potential through time.

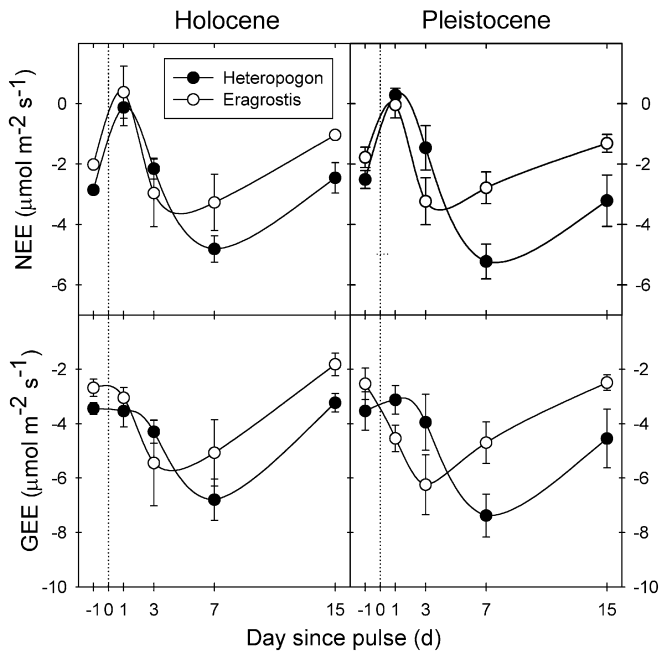
The mid-day maximum net exchange of  $CO_2$  (NEE) between whole-plots and the atmosphere was influenced by a species $\times$ time interaction (Table 1). NEE was influenced by the pulse of precipitation such that immediately following the pulse, the ecosystem was a



**Fig. 3** The time course of whole-plot evapotranspiration (ET) and the ratio of transpiration ( $T$ ) to ET relative to the application of 39 mm of precipitation across two geomorphic surfaces (Holocene and Pleistocene) and a non-native (*Eragrostis*) and native (*Heteropogon*) community. Transpiration from the canopy was determined for each plot by using leaf-level estimates of stomatal conductance and plot estimates of LAI. Air temperature and vapor pressure were used to determine water flux from the canopy of each plot, and then related to chamber-based estimates of whole-plot water flux (ET). The inset figure is the relationship between minimum recorded  $T/ET$  on day 1 following the irrigation and plot LAI for the different treatment combinations (symbols: *Eragrostis*, Holocene  $\circ$ ; *Eragrostis*, Pleistocene  $\nabla$ ; *Heteropogon*, Holocene  $\square$ ; *Heteropogon*, Pleistocene  $\circ$ ). Data are means  $\pm$ 1SE

net source of  $CO_2$  to the atmosphere (Fig. 4). Across both surfaces, the invasive *Eragrostis* appeared to show proportionally greater increases in NEE through time, up to day 4, which was the peak value for all surfaces and species. Following day 4, *Eragrostis*, on both surfaces, showed reductions in NEE as compared to the native species which maintained NEE longer following the irrigation. The pattern of change in GEE was very similar to NEE, but did not contain the large reduction during day 1. Additionally, the GEE pattern followed the change in leaf photosynthesis during the pulse (Fig. 2).

The application of a 39-mm irrigation pulse resulted in significant increases in soil  $CO_2$  efflux through time, and was influenced by significant species $\times$ time and geomorphic surface $\times$ time interactions (Table 1). Peak soil  $CO_2$  efflux was measured on day 1, when the integrated layers were still presumably at their maximum soil  $H_2O$  content, and soil efflux rates diminished to low levels by day 7 (Fig. 5). Soil  $CO_2$  efflux rates across species plots were similar on the Holocene site, but soil  $CO_2$  efflux from *Eragrostis* plots were significantly greater than the *Heteropogon* plots during the first few days of the treatment on the Pleistocene site. That trend was reversed toward the end of the pulse-use period ( $P < 0.05$ ). This

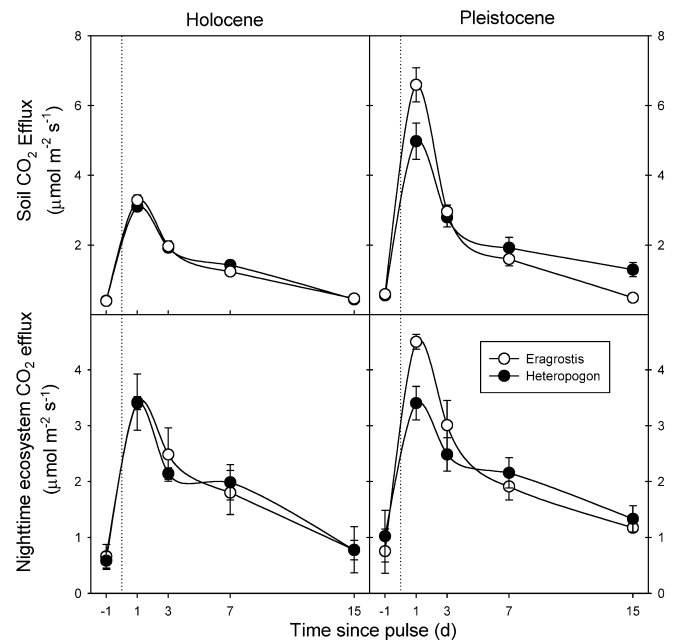


**Fig. 4** The time course of net ecosystem exchange of  $\text{CO}_2$  and gross ecosystem exchange of  $\text{CO}_2$  relative to the application of 39 mm of precipitation across two geomorphic surfaces (Holocene and Pleistocene) and a non-native (*Eragrostis*) and native (*Heteropogon*) community. Positive values represent  $\text{CO}_2$  efflux to the atmosphere. Data are means  $\pm 1\text{SE}$

pattern matches the differences in water content in the 15- and 35-cm soil layers across the sites, which suggests that the efflux of  $\text{CO}_2$  was to some extent driven by the physical displacement of  $\text{CO}_2$  in the soil rather than solely microbial and plant respiration. A pattern that matched shallow soil layer  $\text{H}_2\text{O}$  content may have indicated a stronger influence of microbial activity.

Ecosystem respiration ( $R_e$ ) was influenced by the three-way interaction between species, geomorphic surface and time ( $P < 0.10$ ; Table 1). Dynamics of soil respiration were similar to the  $\text{CO}_2$  efflux measured at midnight on the whole plots (Fig. 5). On the Pleistocene surface, the invasive *Eragrostis* plots had higher respiratory rates following the pulse application, but diminished through time to values similar to *Heteropogon* (a significant species $\times$ time interaction; Table 1). At the Holocene site, there were no differences between species in ecosystem respiration trends. All species, across both surfaces, had returned to similar, low values of  $\text{CO}_2$  efflux in the dark by day 15 post-precipitation pulse.

Comparisons of ecosystem and leaf-level water use-efficiency consisted of two different data states; NEE-to-ET and  $A_{\text{net-to-}g_s}$  differed dramatically from prior to the pulse to day 1 in all plots (Fig. 6). Following the pulse of precipitation, ecosystem water-use efficiency and leaf water-use efficiency showed a similar positive relationship for all treatment combinations. This biphasic trend in carbon accumulation with water loss at the two different scales (plant and ecosystem) is most likely a result of the strong relationship between ET and  $R$  at the ecosystem scale. In general,  $R_e$  had a more consistent relationship



**Fig. 5** The time course of soil and whole-ecosystem respiration relative to the application of 39 mm of precipitation across two geomorphic surfaces (Holocene and Pleistocene) and a non-native (*Eragrostis*) and native (*Heteropogon*) community. Positive values represent  $\text{CO}_2$  efflux to the atmosphere. Data are means  $\pm 1\text{SE}$

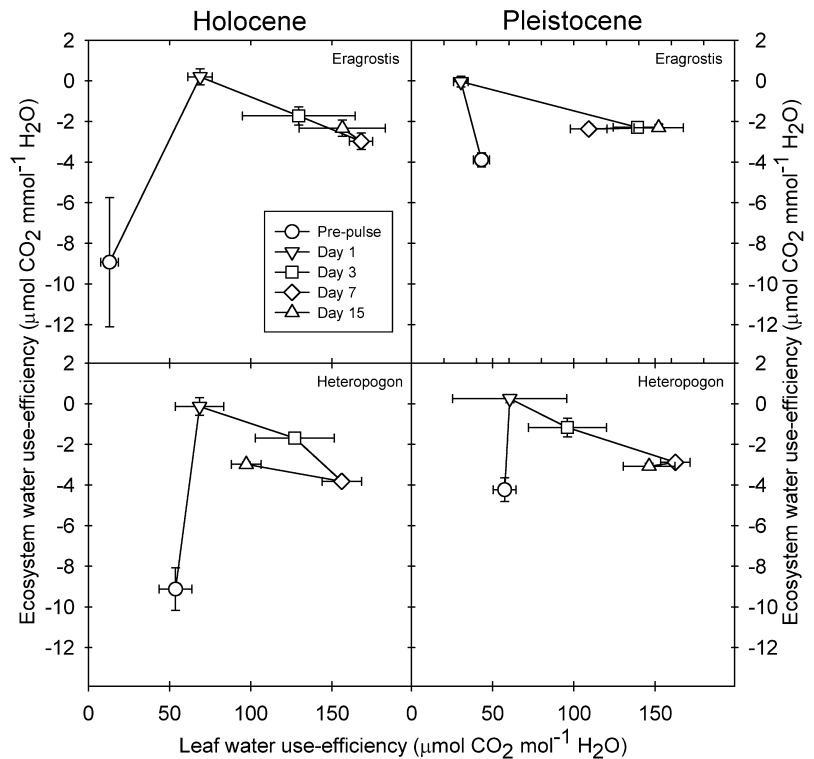
with ET as compared to the variable relationship between ET and GEE for each treatment combination (Fig. 7).

When integrated from diurnal measurements, both species systems across both soil surfaces became sources of  $\text{CO}_2$  to the atmosphere following the application of a pulse of water (Fig. 8). By day 3, each system had become sinks for  $\text{CO}_2$  from the atmosphere, but the Pleistocene surface had greater  $\text{CO}_2$  accumulation than the Holocene. On both surfaces, by day 7 following the pulse, the native stands of grass were greater carbon sinks than that of the invasive species. By day 15, *Eragrostis* plots on the Pleistocene surface had reached a compensatory daily  $\text{CO}_2$  exchange with the atmosphere. Using the diurnal responses ( $\text{NEE}_{\text{daily}}$ ) and integrating across the entire 15-day period (with the same method described for  $\text{NEE}_{\text{daily}}$  in the materials and methods), the native species plots fixed more total carbon than the non-native species plots (Table 2). The Holocene site was slightly less productive than the Pleistocene sites, but the species responded differently across the two surfaces.

**Table 2** Irrigation pulse effects on ecosystem  $\text{CO}_2$  accumulation ( $\text{mmol m}^{-2}$ ) over the course of the study period (15 days). Data are integrations of the spline fit on daily net ecosystem exchange through time for the four different treatments

Species	Surface	
	Pleistocene	Holocene
<i>Heteropogon contortus</i>	921	663
<i>Eragrostis lehmanniana</i>	46	222

**Fig. 6** The relationship between water use-efficiency at two scales for the treatment combinations in the current experiment. Ecosystem water use-efficiency is determined as maximum NEE over maximum ET for a given plot for a given day. Leaf water use-efficiency is estimated from the relationship of net assimilation to stomatal conductance. The time course for each treatment combination is plotted with different symbols in individual panels for each day of the pulse experiment

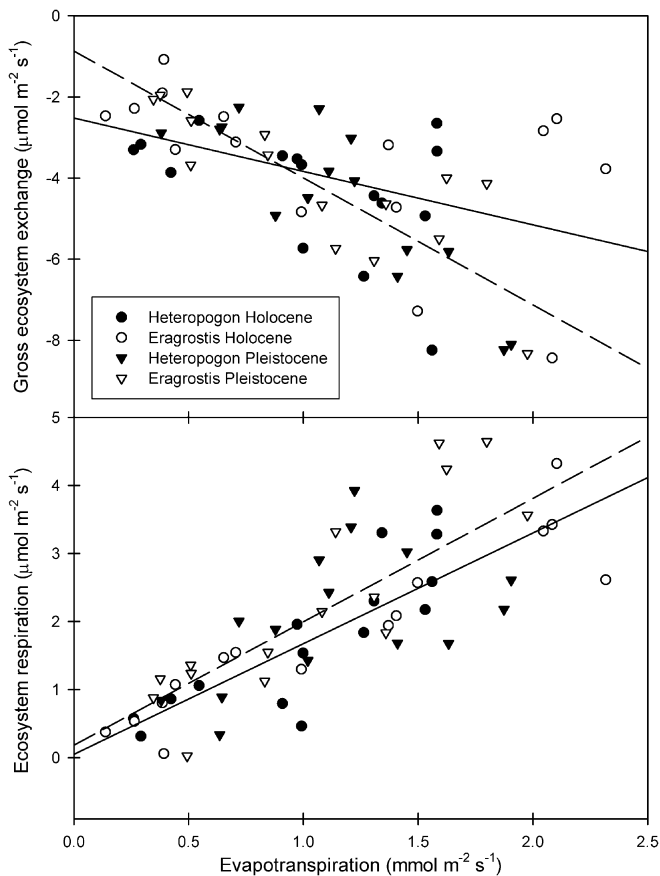


## Discussion

In this experiment we evaluated  $\text{CO}_2$  and  $\text{H}_2\text{O}$  exchange for plants, soils and whole stands of an invasive and native species across two soil surfaces prior to, and following the application of a pre-monsoon pulse of rainfall. We predicted that the non-native bunchgrass *E. lehmanniana* would more rapidly utilize the water resource and up-regulate photosynthetic processes, resulting in greater carbon accumulation in the ecosystem than the native *H. contortus*. We found that whole-plot water loss to the atmosphere matched this prediction (Fig. 3), but greater water use did not translate into greater (or faster) whole-plot  $\text{CO}_2$  accumulation for the invasive species (Fig. 4). Additionally, the greater plot-level water use for the non-native species as compared to the native species was most likely a function of greater soil evaporation, rather than plant transpiration (Fig. 3).  $\text{CO}_2$  efflux from the plots drove the patterns of ecosystem carbon exchange (Figs. 4, 5, 7). Differences in the ecosystem  $\text{CO}_2$  efflux between the species and soils (Fig. 5), along with a lack of complete up-regulation of canopy photosynthesis in the non-native species on the Pleistocene soils (Fig. 2) partially accounted for variation in ecosystem carbon balance. Additionally, contrary to the prediction that the irrigation pulse would have a greater effect on carbon exchange dynamics in the relatively uniform textured Holocene soils than in the well-developed, clay-rich Pleistocene soils (e.g., inverse texture hypothesis; Sala et al. 1988), we found that the carbon accumulation characteristics were species-specific across the two geomorphic surfaces (Table 2). The native species ecosystem showed greater carbon accumulation through time on the Pleistocene soils, and the invasive

species ecosystem showed greater carbon accumulation on Holocene soils.

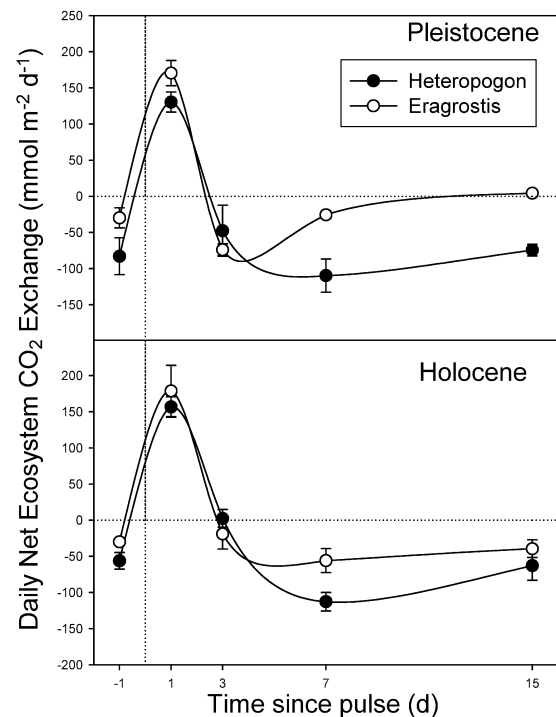
The invasive success of several non-native grass species has been attributed to the rapid utilization of resources for growth and reproduction, prior to the potential up-regulation of activity in native species (Melgoza et al. 1990). The current study illustrates that these species-specific ecophysiological attributes may only partially be driving processes at large scales, such as evapotranspiration and net ecosystem carbon exchange. For example, *Eragrostis* appeared to exploit the pulse of water resources at a greater rate than *Heteropogon*, but the data showed that greater ET in *Eragrostis* plots occurred primarily through greater soil evaporation than native plots. In a number of systems, a relationship between LAI and the fractional ecosystem water loss as *E* has been demonstrated (Law et al. 2002). Lower LAI may promote higher soil temperatures in *Eragrostis* plots, which favors the evaporation of soil water rather than infiltration following rain events (Scott et al. 2000). The lack of increase in soil moisture with water application on the Pleistocene soils in *Eragrostis* plots, compared to that on the Holocene surface (Fig. 1) provides additional evidence for this. The lack of significant infiltration of water and higher rates of ET in the few days following the pulse contributed to a limitation of NEE later in the pulse time course for *Eragrostis* plots. Considering that the increased water use was not related to greater carbon accumulation on the plots, the invasive success of this species may be partially related to plant-induced changes in the soil microclimate that results in greater soil evaporation, precluding use by other species. According to this view, we should not have



**Fig. 7** The relationship between gross ecosystem exchange of CO<sub>2</sub> (NEE-R) and evapotranspiration (*top panel*) and ecosystem respiration and evapotranspiration (*bottom panel*) for all data collected from the simulated rainfall event across both geomorphic surfaces (Holocene and Pleistocene: ● and ▲, respectively). Non-native (*Eragrostis*) and native (*Heteropogon*) communities are represented by *solid* and *open* symbols, respectively. The regression lines are drawn for each geomorphic surface inclusive of both species (*solid line* Holocene, *dashed line* Pleistocene)

expected to see a more rapid up-regulation of photosynthesis in this invasive species.

One of the most striking results from this experiment is the large efflux of CO<sub>2</sub> from whole plots that occurred during the night and day following the precipitation pulse (Fig. 5). This loss of CO<sub>2</sub> most likely was a result of substantial physical displacement of soil CO<sub>2</sub> by water and the up-regulation of respiration rates of plant and microbial systems in soils (Fig. 4). Differences between species and surfaces in soil efflux rate followed the pattern of CO<sub>2</sub> accumulation over the time-course following the precipitation event (Table 2). We measured greater CO<sub>2</sub> efflux for all plots in clay-rich Pleistocene soils (Fig. 5), where the physical displacement of CO<sub>2</sub> by infiltrating water may be large as compared to sandy Holocene soils with similar increases in soil water content. Clay-rich soils have low porosity and air filled space, which depending upon macropore structure may result in enhancements in soil gas fluxes (Glinski and Stepniowski 1985). As a result, the fluxes we measured on day 1 are most likely a



**Fig. 8** The time course of whole-plot, daily-integrated net ecosystem exchange of CO<sub>2</sub> relative to the application of 39 mm of precipitation across two geomorphic surfaces (Holocene and Pleistocene) and a non-native (*Eragrostis*) and native (*Heteropogon*) community. Positive values represent CO<sub>2</sub> efflux to the atmosphere. Data are means  $\pm$ 1SE

result of a physical process, not biological, but of a magnitude that influences ecosystem carbon balance.

Soil respiration has been identified as a dominant component of whole-ecosystem respiratory flux in the tall grass prairie when there is a minimal potential for plant growth (Franzluebbers et al. 2002). In this semi-arid grassland we would expect that as the season develops and the potential for plant growth increases, soils would become a smaller component of the overall efflux. However, our highest soil respiration values were from plots with the invasive grass *E. lehmanniana*, which maintains activity during portions of the year when other species are dormant (Frasier and Cox 1994). We would have expected soil efflux to be a smaller component of the overall efflux for the invasive species, as vascular plant activity would already be occurring at a relatively high rate. These data highlight the importance of evaluating the components of carbon balance during periods of transition, where slight differences in the factors driving ecosystem photosynthesis and respiration may scale up to large impacts on carbon accumulation.

The sensitivity of both respiration and photosynthesis to precipitation may be pronounced in semi-arid grasslands, where these processes are governed by the transient nature of resource availability (Noy-Meir 1973). In grassland ecosystems, nonlinear responses of ecosystem respiration and photosynthesis, driven by potentially different climate drivers, combine to influence ecosystem carbon balance

(Flanagan et al. 2002), resulting in an ecosystem type that has the largest interannual variation in aboveground productivity (Knapp and Smith 2001). The data from this current study suggest that an understanding of dynamics of ecosystem carbon balance requires evaluation of the individual time courses of both ecosystem photosynthesis and respiration in response to a pulse of resources, each of which may be differentially driven by climate and ecological factors (Goulden et al. 1997; Valentini et al. 2000; Meyers 2001; Monson et al. 2002) or driven by similar factors but at different rates (e.g., Fig. 7). In addition, our data suggest that predictions based on interannual or cross-ecosystem comparisons may not necessarily predict the responses of ecosystem CO<sub>2</sub> exchange during a single precipitation event or season, requiring a much finer evaluation of CO<sub>2</sub> dynamics along with their biotic and abiotic drivers (Ham and Knapp 1998; Meyers 2001; Flanagan et al. 2002; Huxman et al. 2003).

The important role of whole-system CO<sub>2</sub> efflux during single precipitation pulse events to whole-ecosystem CO<sub>2</sub> flux is similar to the pattern that has been found for forests in Europe across entire seasons where the dynamics of respiration strongly influences net ecosystem exchange of CO<sub>2</sub> (Valentini et al. 2000). In subalpine coniferous forests, the temperature response of ecosystem respiration, not necessarily photosynthesis, controls overall carbon balance dynamics within a season (Huxman et al. 2003). Taken together, these data from different spatial and temporal scales highlight the fact that soil physical factors and soil microbial respiration must be evaluated relative to autotrophic activity throughout a season (Franzluebbers et al. 2002; Monson et al. 2002; Huxman et al. 2003). A strong conceptual framework for understanding variation in respiration must be developed (Enquist et al. 2003) in order to generate a better understanding of whole-ecosystem carbon balance. Additional respect should also be given to both the physical and biological factors that underlie these ecosystem efflux processes.

Following the transient response of  $R_e$  to a pulse event, canopy photosynthetic characteristics are important in controlling net ecosystem exchange of CO<sub>2</sub>. This occurs partially as a result of the differential dynamics of up-regulation of respiration as compared to that of photosynthesis (Fig. 2) and the construction of canopy leaf area. Several studies have identified the constraint on net ecosystem exchange by the development of leaf area within a canopy (e.g., Flanagan et al. 2002), but the disparity in the timing of the up-regulation of photosynthesis and respiration primarily led to the large differences in total carbon accumulation in the current investigation. Similar to how the development of canopy leaf display relative to photosynthetic capacity constrains individual plant growth in arid ecosystems (e.g., Comstock and Ehleringer 1986), the timing of physiological (respiratory and photosynthetic capacities) and morphological (canopy development) processes constrain whole-ecosystem carbon balance during a pulse of resources, illustrating the “surface limitation” of this water-limited ecosystem (Smith et al. 1997).

The differences between the species in their pulse use characteristics were amplified on the Pleistocene as compared to the Holocene surface. Plant photosynthetic characteristics and soil CO<sub>2</sub> efflux differed between the species on this surface, which in part added to the differences in net ecosystem CO<sub>2</sub> exchange between non-native and native species plots beyond the influence of LAI. The cumulative response of carbon sequestration over the pulse event was a function of soil surface and species composition. The non-native species fixed less total carbon over the period following the application of rain than the native species. In light of the current interest in understanding the factors that control carbon accumulation and water use in terrestrial ecosystems, the results from the current research indicate that we must consider the complexities of species novel to environments, species-specific controls, and interactions with soil surface. The interactions between species composition and soil surface suggest that changes in species composition may alter the manner in which pulses of precipitation in the southwestern United States are translated into biological activity. Considering the potential for changes in the frequency and intensity of precipitation inputs into the southwest (Giorgi et al. 1998; NAST 2000), we need to develop a mechanistic understanding of the drivers of ecosystem respiration and photosynthesis, especially their time-course as it relates to precipitation variation.

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