

Leaf gas exchange and water status responses of a native and non-native grass to precipitation across contrasting soil surfaces in the Sonoran Desert

Danielle D. Ignace · Travis E. Huxman ·
Jake F. Weltzin · David G. Williams

Received: 17 April 2006 / Accepted: 23 January 2007 / Published online: 2 March 2007
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Abstract Arid and semi-arid ecosystems of the southwestern US are undergoing changes in vegetation composition and are predicted to experience shifts in climate. To understand implications of these current and predicted changes, we conducted a precipitation manipulation experiment on the Santa Rita Experimental Range in southeastern Arizona. The objectives of our study were to determine how soil surface and seasonal timing of rainfall events mediate the dynamics of leaf-level photosynthesis and plant water status of a native and non-native grass species in response to precipitation pulse events. We followed a simulated precipitation event (pulse) that occurred prior to the onset of the North American monsoon (in June) and at the peak of the monsoon (in August) for 2002 and 2003. We measured responses of pre-dawn water potential, photosynthetic rate, and stomatal conductance of native (*Heteropogon contortus*) and non-native (*Eragrostis lehmanniana*) C₄ bunchgrasses on sandy and clay-rich soil surfaces. Soil surface did not always amplify differences in plant response to a pulse event. A June pulse event led to an increase in plant water status and photosynthesis. Whereas the August pulse did not lead to an increase in

plant water status and photosynthesis, due to favorable soil moisture conditions facilitating high plant performance during this period. *E. lehmanniana* did not demonstrate heightened photosynthetic performance over the native species in response to pulses across both soil surfaces. Overall accumulated leaf-level CO₂ response to a pulse event was dependent on antecedent soil moisture during the August pulse event, but not during the June pulse event. This work highlights the need to understand how desert species respond to pulse events across contrasting soil surfaces in water-limited systems that are predicted to experience changes in climate.

Keywords Invasive grass species · Photosynthesis · Stomatal conductance · Precipitation manipulation · Santa Rita Experimental Range

Introduction

Arid and semi-arid regions of the southwestern US are faced with two major global change factors that have implications for ecosystem structure and function. First, changes in climate are predicted to affect these ecosystems, with most regional climate models predicting an increase in variability of the timing, frequency, and the magnitude of rainfall events (Easterling et al. 2000). In particular, the American Southwest is predicted to experience an increase in the frequency of extreme hot events, longer heat waves, and an increase in the contribution of extreme precipitation events (Diffenbaugh et al. 2005). Second, invasions of non-native plant species are changing plant community structure and composition (Esque and Schwalbe 2002). It is currently unknown how these two changes will interact to influence leaf to ecosystem level processes in arid and

Communicated by Alan Knapp.

D. D. Ignace (✉) · T. E. Huxman
Ecology and Evolutionary Biology, University of Arizona,
1041 E. Lowell St, Tucson, AZ 85721-0088, USA
e-mail: ddignace@email.arizona.edu

J. F. Weltzin
Ecology and Evolutionary Biology,
University of Tennessee, Knoxville, USA

D. G. Williams
Renewable Resources and Botany,
University of Wyoming, Laramie, USA

semi-arid systems. In recent years there has been a heightened awareness that soil surface characteristics will strongly influence ecosystem structure and function, but current understanding of how the plant–soil–climate interaction will control ecosystem function is particularly lacking (Kerkhoff et al. 2004).

Understanding the implications of climate change for arid and semi-arid ecosystems is important since these systems are commonly water limited, with extended periods between rainfall events. Water becomes available in these systems through discrete inputs of rainfall, or “pulses” (Noy-Meir 1973). Most research across different ecosystems has focused on the effects of annual variability in precipitation on ecosystem production (Knapp and Smith 2001; Knapp et al. 2002; Fay et al. 2003; Zavaleta et al. 2003; Huxman et al. 2004a). Rainfall variability will also interact with antecedent soil moisture to influence seasonal variability in water recharge and plant growth (Reynolds et al. 2004). For example, early versus late growing season rainfall may have differential effects on physiological processes in plants due to variation in vegetative phenology among dominant species (Ogle and Reynolds 2004). Therefore, a mechanistic understanding of how individual pulses within a season affect plant-to-ecosystem level processes is required to adequately understand ecosystem response to global change (Weltzin et al. 2003; Weltzin and Tissue 2003; Huxman et al. 2004b).

Vegetation change associated with the introduction of non-native plants has large ramifications for community structure and ecosystem processes (D’Antonio and Vitousek 1992; Mack et al. 2000). Encroachment of native woody plants, such as *Prosopis glandulosa* (honey mesquite) and *Larrea tridentata* (creosote bush) together with the invasion of non-native grasses into historic grasslands represent the most prominent vegetation shifts in the American Southwest (Grover and Musick 1990; Schlesinger et al. 1990; Archer 1995; Boutton et al. 1998; Kieft et al. 1998; Bahre 1991, 1993; Weltzin and McPherson 2000; Williams and Baruch 2000). These altered grasslands are also affected by changes in precipitation, enhanced N deposition, disturbance and habitat fragmentation (Dukes and Mooney 1999). Invaders displacing native biota may alter rates and patterns of nutrient cycling (Vitousek and Walker 1989; D’Antonio and Vitousek 1992) and the flux of energy and materials through ecosystems (Walker and Smith 1997; Mooney and Hobbs 2000; Huxman et al. 2004c).

In southeastern Arizona, much of the native grassland community has been invaded by the non-native grass *Eragrostis lehmanniana* (McClaran and Van Devender 1995). This aggressive C₄ bunchgrass from southern Africa was introduced in southern Arizona during the 1930s (Anable et al. 1992). The success of this non-native species

is hypothetically due to its water-use characteristics; *E. lehmanniana* initiates growth several weeks before most native grasses and extracts soil water when most native grasses are dormant (Frasier and Cox 1994). *E. lehmanniana* also maintains significant leaf area during dry, inter-pulse periods, potentially making it quite responsive physiologically to episodic rainfall as compared to native species. However, only recently have studies shown how invasion of this grass alters CO₂ and water exchange of grassland ecosystems (Huxman et al. 2004c; Potts et al. 2006).

We still lack the development of a fundamental quantitative theory of atmosphere–soil–vegetation dynamics for water-limited systems undergoing climate change, which may partly be due to poor integration and ecological application of these issues in experimentation (Kerkhoff et al. 2004). Soil characteristics influence the availability of water for plant use by controlling the infiltration and percolation of water (McAuliffe 2003). For example, coarse-textured (sandy) soils allow for rapid and deep movement of water following a rainfall event (Walter 1979; Noy-Meir 1973; Sala et al. 1996; McAuliffe 1994, 2003). However, fine-textured (clay-rich) soils have higher water holding capacity in shallow layers but tend to restrict deep percolation (McAuliffe 1994, 2003). The deep percolation and storage of moisture in coarse-textured soils will provide a source of soil moisture for plants that is more persistent through time than the source of soil moisture that is found on fine-textured soil (McAuliffe 2003). Thus, coarse-textured soils may dampen seasonal variability in soil moisture by allowing deep percolation, while fine-textured soils may amplify seasonal variability by restricting deep infiltration (Noy-Meir 1973; Burgess 1995; McAuliffe 1994, 1999b). The characteristics of these two contrasting soil types are important for plant C and water exchange (Smith et al. 1995; Hamerlynck et al. 2000, 2002, 2004) and ultimately ecosystem processes (Huxman et al. 2004b, c). Due to the pulsed nature of precipitation inputs (Noy-Meir 1973), it is important to include how the water becomes available through the soil to understand plant- and ecosystem-level responses to changes in antecedent soil moisture in conjunction with changes in precipitation.

The main question guiding our research activities is: how will global change in arid land ecosystems affect CO₂ exchange with the atmosphere? In this paper we focus on how photosynthetic gas exchange at the leaf-level responds to rainfall pulses. In the context of this overarching question our research focuses on answering two specific questions: (1) how do species (a native vs. non-native grass) differ in their response to precipitation pulses throughout the summer growing season, and (2) how do soil surface characteristics influence leaf-level CO₂ exchange for a

native and non-native grass species? We experimentally manipulated precipitation across two different geomorphologic soil surfaces (sandy = Holocene-aged alluvium soil, clay = Pleistocene-aged alluvium soil) within the Santa Rita Experimental Range (SRER) in southeastern Arizona for 2 consecutive years. We predicted that the timing of a precipitation pulse within the summer season would elicit a large physiological pre-monsoon response and a small peak monsoon response. Second, we predicted that *E. lehmanniana* would have a larger photosynthetic and water status response to precipitation events than the native grass species across sites because of its water-use characteristics. Finally, we predicted that following a pulse, there would be larger functional responses by plants on the sandy surface than on the clay surface due to the differences in water infiltration, percolation, and antecedent soil moisture conditions.

Materials and methods

Study site description

The precipitation manipulation experiment was conducted at the SRER, located 40 km south of Tucson, Arizona (McClaran and Van Devender 1995). Elevation ranges from 900 to 1,300 m and annual rainfall ranges from 250 to 500 mm (McClaran and Van Devender 1995). Plots were established beneath rainout manipulation shelters that were constructed on two different soil surfaces during the summer of 2001. Three shelters (161 m² covered area) were built on a Pleistocene-aged and a Holocene-aged alluvial surface. The Pleistocene surface is characterized by a well-developed argillic horizon at about 10–30 cm below the soil surface (McAuliffe 1995), while the Holocene surface is characterized by a poorly developed and texturally homogeneous soil (McAuliffe 1995). The sandy soil surface is the Holocene-aged alluvium soil and the clay-rich soil surface is a Pleistocene-aged alluvium soil. The soils on the Pleistocene surface contain 50% clay and 30% sand, whereas the Holocene surface soils contain 6% clay and 84% sand (gravimetric determination of 25–100 cm depths) (Huxman et al. 2004c; English et al. 2005). Across each soil surface, shelters were arranged in three replicated blocks.

Each precipitation treatment was assigned randomly to one of 12 plots within each shelter using a randomized complete block design. Each of the three shelters within a site covered 12 plots, where 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 to depths of 15, 35 and 55 cm from the soil surface. Huxman et al. (2004c) describes plot construction, plant densities and protocol for measuring

leaf area index in these experimental plots. Each plot was planted with greenhouse-grown transplants of either *H. contortus* or *E. lehmanniana* in the spring of 2001. A total of six plots of *H. contortus* and six plots *E. lehmanniana* were sampled at each site with $n = 3$ for each species and water treatment combination.

Precipitation manipulation

All 12 plots under each of the three shelters were prevented from receiving any natural precipitation. This allowed us to accurately control the amount of precipitation each plot received throughout the entire year. Therefore, natural precipitation occurring outside the shelters did not affect our comparisons of plant response to different precipitation treatments. Plot irrigation was conducted to mimic the natural bi-seasonal rainfall pattern typical of southeastern Arizona. Starting in July 2001 we added water in parallel with the naturally occurring North American monsoon affecting nearby Tumacacori, Arizona. Little to no rain occurs during the 3-month period before the onset of the summer monsoon (Adams and Comrie 1997). All plots received identical amounts of water from July 2001 until June 2002. On 10 June 2002, all plots received a 39-mm irrigation pulse event. The June pulse event marks the initiation of the summer growing season (a pre-monsoon effect). Immediately following this pulse, we implemented a water treatment throughout the summer season. The wet summer treatment received 50% more precipitation than the annual mean (hereafter “wet”). The dry summer treatment received 50% less precipitation (hereafter “dry”). On 16 August 2002, wet plots received a 39-mm pulse and dry plots received a 12-mm pulse event. The August pulse event has a peak monsoon and peak growing season effect. The same watering regime was applied throughout the remainder of the year and the same watering treatments and pulse events were applied on 10 June 2003 and 16 August 2003. We followed the dynamics of plant water relations and leaf-level H₂O and CO₂ exchange on one plant within each plot on the day before the pulse event and on 1, 3, 7, and 15 days following the pulse for plots of *H. contortus* and *E. lehmanniana* ($n = 3$) within the wet and dry water treatment.

Plant measurements

We randomly selected a recently fully expanded vegetative grass tiller within each plot and measured pre-dawn water potential (Ψ_{pd}) over the 15-day pulse period using a Scholander-type pressure chamber. On the day following pre-dawn water potential measurements, we selected a different individual with a recently fully expanded leaf from each plot and measured leaf-level net assimilation

rate (A_{net}) and stomatal conductance (g_s) with a portable photosynthesis system (LI-6400; Li-Cor, Lincoln, Neb.). We randomly selected different individuals for the June and August pulse events in order to measure Ψ_{pd} , A_{net} , and g_s . Mid-morning values of A_{net} and g_s were collected between 0900 and 1100 hours. For the June and August pulse in 2003, we additionally made diurnal measurements of A_{net} and g_s at the time periods of 0200–0400, 0900–1100, 1100–1300 and 1300–1500 hours for all plant, soil surface, and water treatment combinations. The light source on the Li-6400 leaf cuvette was set at a light intensity of $1,500 \mu\text{mol m}^{-2} \text{s}^{-1}$. Vapor pressure deficit, air temperature, and CO_2 concentration of the cuvette were set to values close to ambient environmental conditions, and maintained constant for all measurements across the plots in both sites during that measurement period.

Statistical analysis

We used a split–split-plot ANOVA statistical analysis (JMP IN statistical software, version 4.0.4; SAS Institute) to determine the effects of soil surface (Holocene and Pleistocene), species (*H. contortus* and *E. lehmanniana*), water treatment (wet and dry), time (day of pulse period) and their interactions, on the response of plant function parameters of Ψ_{pd} , A_{net} , and g_s (from 1 day before the pulse up to day 15 post-pulse). Whole-plot factors included soil surface and time; split-plot factors included plant species, water treatment and their interaction with soil surface and; split–split-plot factors included all other interactions. The same model structure was completed for every pulse event, except during the June 2002 pulse, where the plots had not yet been exposed to a wet and dry summer water treatment. Ψ_{pd} , A_{net} , and g_s were log-transformed in June 2002 to meet the assumptions of normality, and all other sample periods met the assumptions of normality. We used ANOVA statistical analysis to test for differences in cumulative leaf-level net assimilation of C (over the entire 15-day pulse period). A simple regression was used (JMP IN statistical software, version 4.0.4) to analyze the relationship between g_s and A_{net} .

Results

June 2002

In June 2002 Ψ_{pd} differed between species and was affected by a soil surface and time interaction (Table 1; Fig. 1a, b). Across both surfaces, Ψ_{pd} became less negative after the pulse application, and slowly returned to more negative values by day 15. Both *H. contortus* and

Table 1 *df* and *F*-statistics from a split–split-plot ANOVA for the response of pre-dawn water potential (Ψ_{pd}), photosynthetic rate (A_{net}), and stomatal conductance (g_s)

Factors	Variable			
	<i>df</i>	Ψ_{pd}	A_{net}	g_s
<i>June 2002</i>				
Species	1,2	11.81 ^a	21.16*	18.99*
Time	1,2	n.s.	99.07**	n.s.
Species × Time	1,2	n.s.	n.s.	13.64 ^a
Surface × Time	1,2	7.67 ^a	n.s.	n.s.
<i>August 2002</i>				
Surface	1,2	n.s.	24.33*	20.85*
Time	1,2	86.95**	30.03*	18.72*
Water treatment	1,2	17.74*	19.46*	23.63*
Surface × Water treatment	1,2	n.s.	18.43*	n.s.
Surface × Species	1,2		9.92 ^a	n.s.
Species × Time	1,2	8.60 ^a	n.s.	n.s.
Surface × Water treatment × Species	1,2	n.s.	n.s.	10.88 ^a
<i>June 2003</i>				
Surface	1,2	46.70*	n.s.	n.s.
Species	1,2	n.s.	30.12*	n.s.
Time	1,2	n.s.	12.44 ^a	n.s.
Surface × Species	1,2	n.s.	7.80 ^a	n.s.
Surface × Water treatment × Species	1,2	n.s.	10.66 ^a	n.s.
<i>August 2003</i>				
Species	1,2	94.79*	7.66 ^a	n.s.
Time	1,2	75.71**	515.3***	95.2*
Water treatment	1,2	34.52*	41.61*	31.67*
Water treatment × Time	1,2	8.87 ^a	n.s.	n.s.

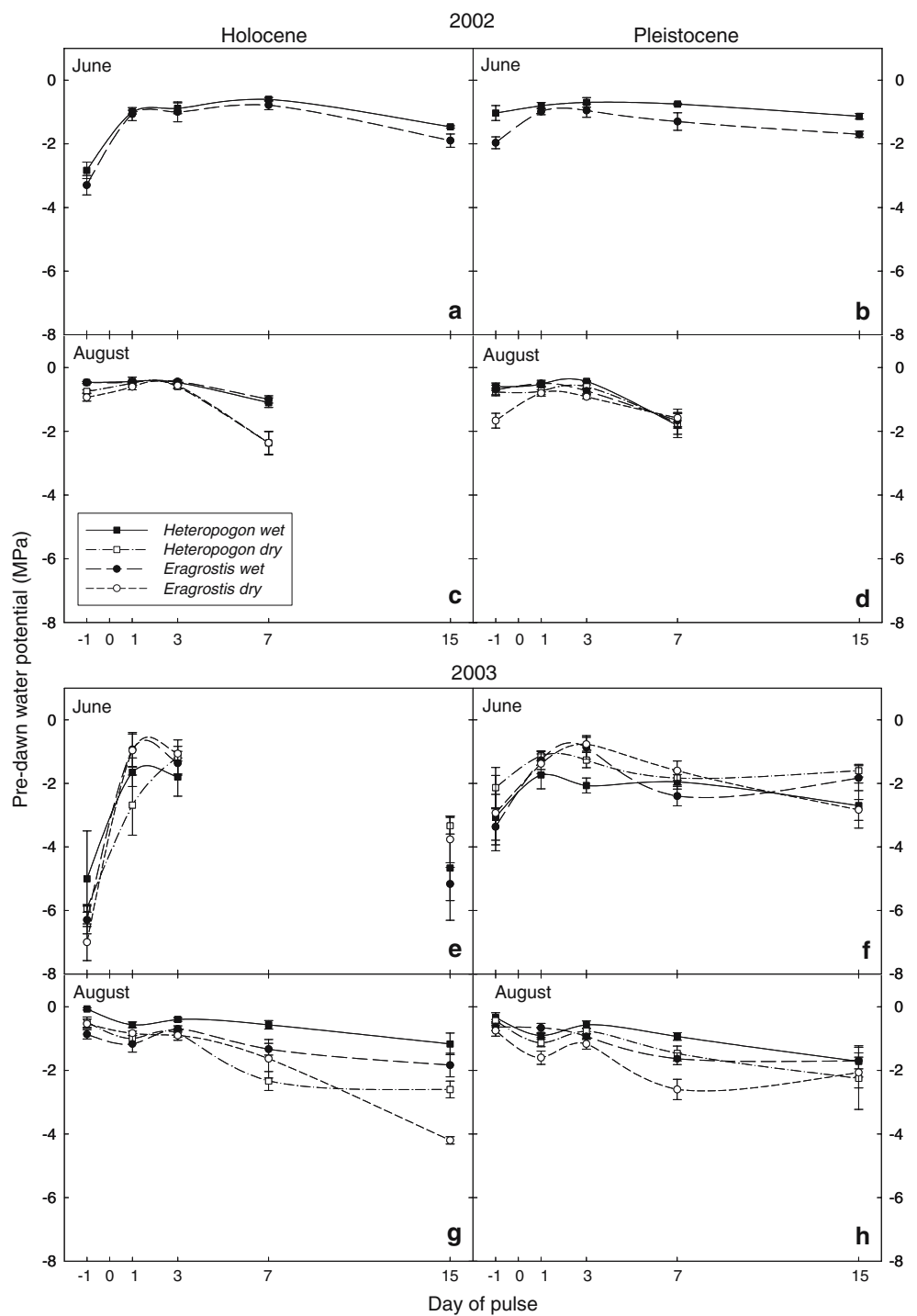
* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, n.s. not significant (factors that were not significant for any variable were not reported)

^a $P < 0.10$

E. lehmanniana initially had more negative Ψ_{pd} on the sandy soil surface than the clay surface. *H. contortus* on the clay surface maintained the least negative Ψ_{pd} throughout the pulse period.

A_{net} increased following the June 2002 pulse event, but A_{net} differed between species and over time (Table 1; Fig. 2a, b). The two grasses had similar responses to the pulse on the sandy surface, while the clay surface amplified differences in physiological response of the two species. For example, species differences were observed with *H. contortus* increasing to higher maximum A_{net} than *E. lehmanniana*. *E. lehmanniana* on the clay surface responded to the pulse application with a change in approximately $5 \mu\text{mol m}^{-2} \text{s}^{-1}$ and maintained the same A_{net} rate from day 3 to day 15 of the pulse period.

Fig. 1a–h Pre-dawn water potential (MPa) over the pulse period, with measurements taken on days –1, 1, 3, 7, and 15. **a–d** Data taken in 2002, **e–h** data taken in 2003. **a, c, e, g** Results from the Holocene site (Holocene-aged alluvium soil; sandy soil); **b, d, f, h** results from the Pleistocene site (Pleistocene-aged alluvium soil; clay-rich soil). June data are given on **a, b, e, f**, and August data on **c, d, g, h**. *Square symbols* represent *Heteropogon contortus* and *circles* represent *Eragrostis lehmanniana*. *Solid symbols* demonstrate the wet treatment and *open symbols* represent the dry treatment. *Error bars* represent ± 1 SE of the mean of three samples. Note missing data for the dry treatment of June 2002, and day 7 of June 2003 on the Holocene site



Overall, both species responded to a pulse application by increasing g_s , and these values differed between species and were affected by a species by time interaction (Table 1; Fig. 3a, b). On the sandy soil surface, both species reached similar maximum g_s values by day 7 of the pulse period, and by day 15 decreased to g_s levels that were lower than those observed pre-pulse. However,

H. contortus on the clay surface took longer to reach maximum g_s values, but maintained much higher g_s rates than *E. lehmanniana* over the entire pulse period. Whereas *E. lehmanniana* on the clay surface reached an early maximum g_s by day 1 of the pulse period, these g_s values were short-lived and quickly declined to pre-pulse values by day 3 of the pulse period.

August 2002

Following an August 2002 pulse event, Ψ_{pd} differed between the wet and dry treatments, and the effects of water treatment were affected by time and a species by time interaction (Table 1; Fig. 1c, d). Generally, there was a lack of response to a pulse event. By day 3, all values across both surfaces became more negative (more water stressed) as soils began to dry. On the sandy surface, plants exposed to the wet treatment maintained less negative Ψ_{pd} than those exposed to the dry treatment by day 7. Whereas *E. lehmanniana* exposed to the dry treatment on the clay surface had the most negative Ψ_{pd} at the start of the experiment, they converged with the other treatments after the pulse application by day 7.

Following the August 2002 pulse event, A_{net} was affected by time, soil surface, water treatment, the interaction between soil surface and water treatment, and the interaction of soil surface and species (Table 1; Fig. 2c, d). On the sandy soil surface, initial A_{net} rates were between 10 and 15 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and A_{net} had decreased to rates lower than pre-pulse values by day 7 of the pulse period. Initial A_{net} rates on the clay soil surface were slightly lower than those found on the sandy soil surface, but A_{net} similarly decreased to rates lower than pre-pulse values by day 7 of the pulse period.

g_s values were significantly different across time, soil surface, water treatment, and the interaction between soil surface, water treatment, and species following an August 2002 pulse event (Table 1; Fig. 3c, d). Values of g_s were initially high and steadily decreased as the plots dried after the pulse was applied. Values of g_s on the sandy surface increased after the pulse application and all plants similarly decreased their g_s to lower than pre-pulse values by day 7 of the pulse period. On the clay surface, all treatment combinations showed an increase in g_s after the pulse application, except for *E. lehmanniana* exposed to the wet treatment. *E. lehmanniana* exposed to the dry treatment also maintained the lowest g_s values throughout the entire pulse period.

June 2003

Following the June 2003 pulse event, Ψ_{pd} only differed across soil surface (Table 1; Fig. 1e, f). Initial Ψ_{pd} was the most negative for plants on the sandy soil surface, but both plant species across surfaces had less negative Ψ_{pd} after the pulse application. By day 15 of the pulse period, both species returned to values near, although still less negative than, pre-pulse Ψ_{pd} values.

A_{net} differed between species, over time, across the soil surface and species interaction, and the soil surface, water treatment and species interaction during the June 2003

pulse period (Table 1; Fig. 2e, f). While A_{net} increased after the pulse application, each species achieved dissimilar maximum A_{net} on different days of the pulse period. For example, *E. lehmanniana*, under both water treatments, reached a lower maximum A_{net} rate than *H. contortus*. *E. lehmanniana* also reached its maximum A_{net} rate by day 3, whereas *H. contortus* reached its maximum A_{net} rate by day 7. Although *E. lehmanniana* reached maximum A_{net} rates quicker than *H. contortus*, both species decreased to similar A_{net} by day 15 of the pulse period as the plots dried out. *E. lehmanniana* exposed to a wet treatment also had lower A_{net} values throughout most of the pulse period than *E. lehmanniana* exposed to the dry treatment.

Results for g_s during the June 2003 pulse show no statistically significant differences across any factors or their interactions (Table 1; Fig. 3e, f). However, both species showed a decrease in g_s immediately following the June 2003 pulse event.

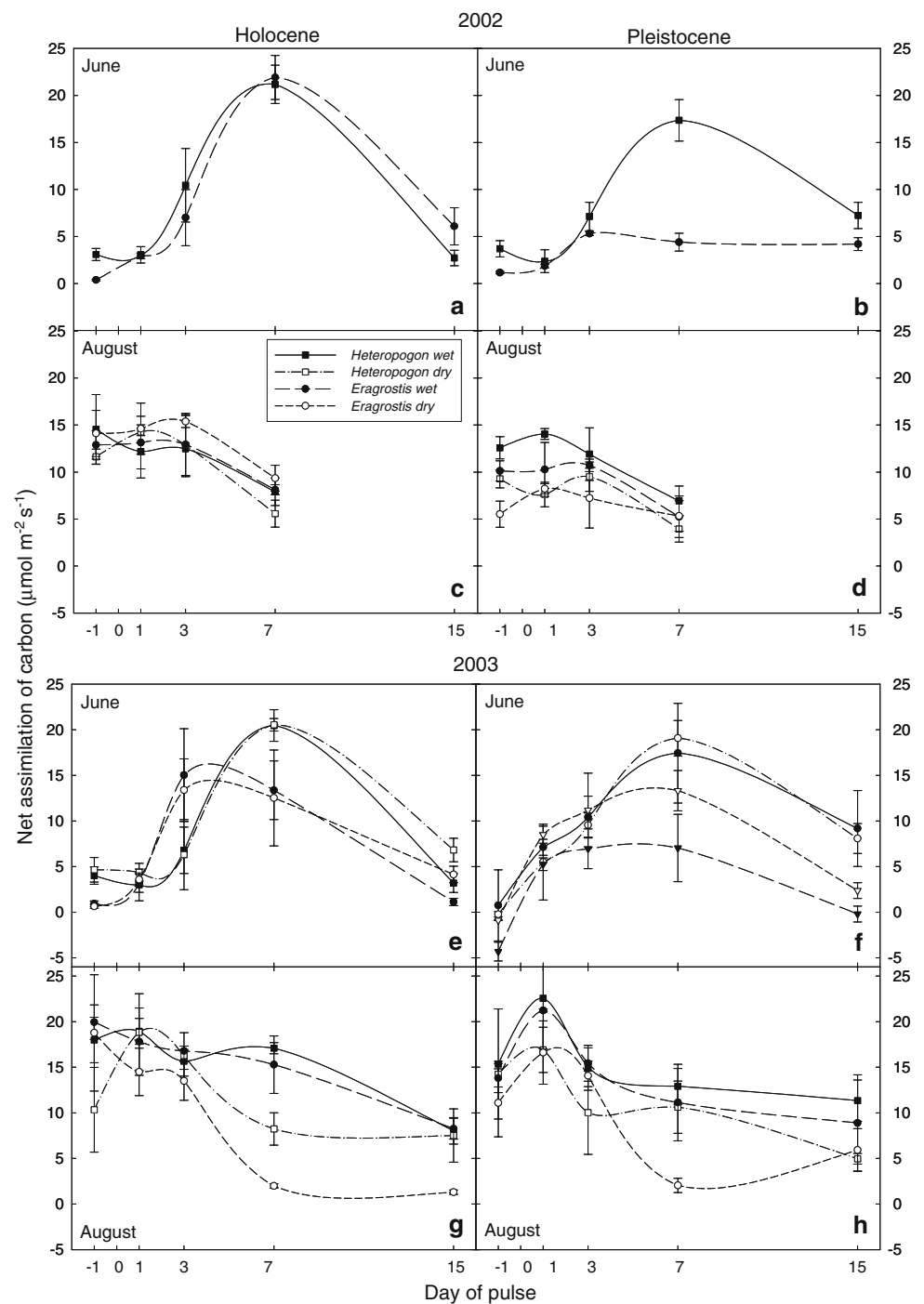
August 2003

There was a significant effect of time, species, water treatment, and the interaction between water treatment and time on Ψ_{pd} in response to a pulse event during the August 2003 pulse event (Table 1; Fig. 1g, h). The August pulse event occurs during the peak of the summer monsoon, thus all the species and water treatment combinations initially have little water stress across both soil surfaces. After the pulse event Ψ_{pd} gradually decrease as the plots dry across both soil surfaces. By day 15 of the pulse period, the sandy soil surface amplifies differences in Ψ_{pd} across all species and water treatment combinations compared to the clay soil surface.

A_{net} rates were different over time, between species and between water treatment in response to the pulse event (Table 1, Fig. 2g, h). All plants had relatively high A_{net} rates at the start of the pulse period, while not all species and water treatment combinations responded with an increase in A_{net} after the pulse event. By day 7 of the pulse period *E. lehmanniana* exposed to the dry water treatment had the lowest A_{net} rates. Grass species in both water treatments across soil surfaces decreased to A_{net} rates equal to or less than pre-pulse values by day 15 of the pulse period.

Following the August 2003 pulse event, there were significant differences in g_s between water treatments and over time (Table 1; Fig. 3g, h). Throughout most days of the pulse period, the wet treatments for both species had higher g_s rates than plants exposed to the dry treatment. Although not all plants responded with an increase in g_s after the pulse event, all plants gradually decreased their g_s rates to pre-pulse values by day 15 of the pulse period.

Fig. 2a–h Net assimilation of C ($\mu\text{mol m}^{-2} \text{s}^{-1}$) over the pulse period, with measurements taken on days -1, 1, 3, 7, and 15. Positive values indicate fixed CO_2 by the plants, and negative values indicate respired CO_2 . Note missing data for the dry treatment in June 2002 and day 15 of August 2002. See Fig. 1 for detailed descriptions of figure parts

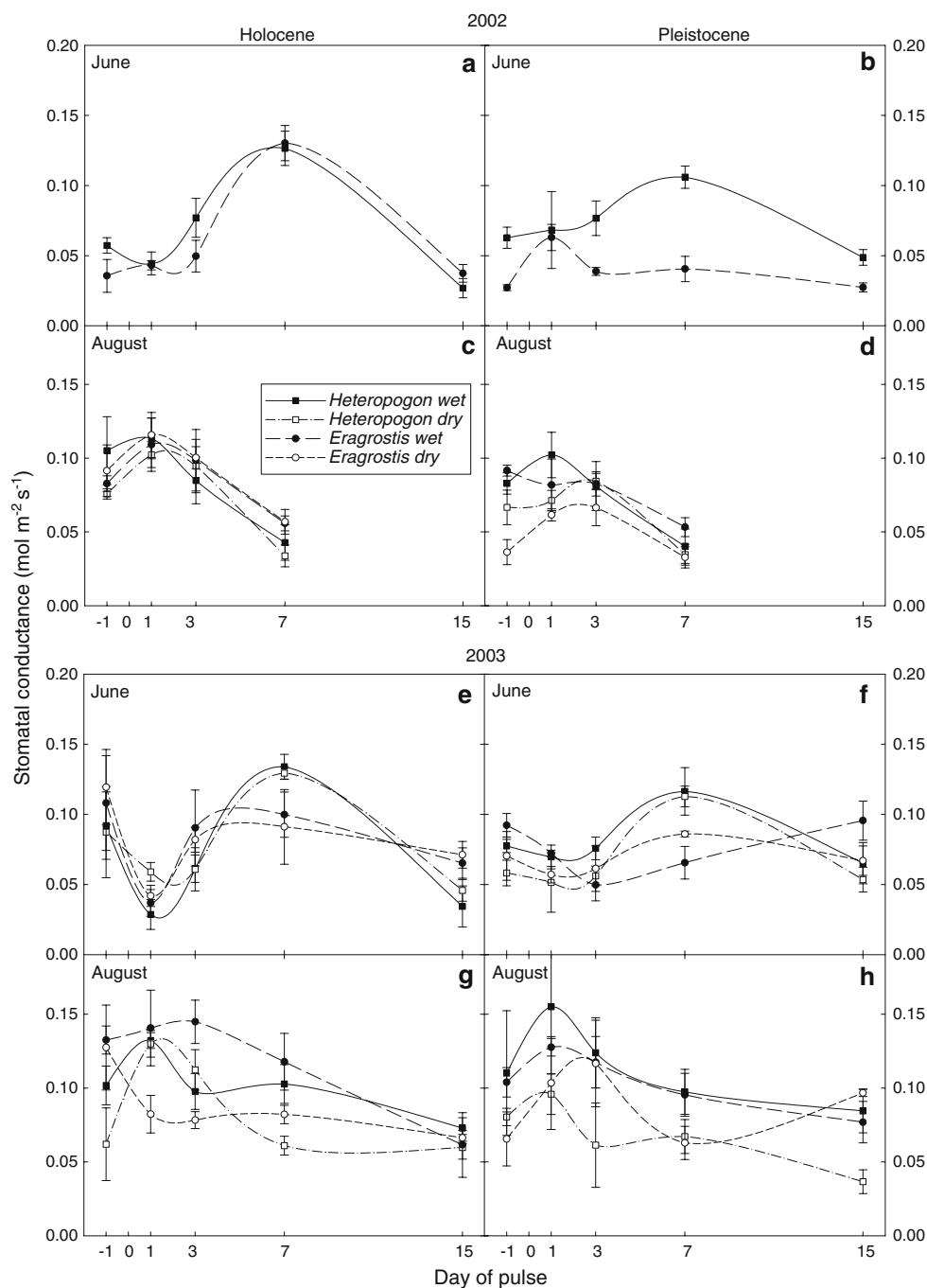


Relationship between A_{net} and g_s

There was no difference in the relationship between g_s and A_{net} for *H. contortus* and *E. lehmanniana* when data were pooled across all seasons, treatments and years (Table 1; Fig. 4a). However, a difference in the $A_{\text{net}}-g_s$ relationship was observed between watering treatments and species for data collected in June; the relationship between g_s and A_{net} for *E. lehmanniana* on the sandy surface exposed to the dry

treatment had a shallower slope than all surface, plant and treatment combinations in the grouped data set, and *E. lehmanniana* on the clay surface exposed to the wet treatment showed a negative relationship (Fig. 4b). *E. lehmanniana* in June did not up-regulate photosynthetic capacity in concert with increases in stomatal aperture during the June pulse event. No species, soil type or treatment effects were seen in the $A_{\text{net}}-g_s$ relationship in August in either year (Fig. 4c).

Fig. 3a–h Stomatal conductance ($\text{mol m}^{-2} \text{s}^{-1}$) over the pulse period, with measurements taken on days -1 , 1 , 3 , 7 , and 15 . Note missing data for the dry treatment for June of 2002 and day 15 of August 2002. See Fig. 1 for detailed descriptions of figure parts



Discussion

We applied large pulses of moisture to experimental monocultures of a native (*H. contortus*) and non-native (*E. lehmanniana*) grass on two contrasting soil surfaces (Holocene and Pleistocene) in June (pre-monsoon) and August (peak monsoon season). We sought to understand how pulse events occurring at different times during the summer growing season influence leaf-level CO_2 and H_2O exchange, and how responses are modified by soil

characteristics. Responses to these environmental drivers are important for predicting how ecosystem processes may be modified by future changes in precipitation.

The inverse texture hypothesis (Noy-Meir 1973) predicts that sandy soils should support higher productivity than fine-textured soils under low rainfall regimes owing to greater infiltration characteristics of coarse soils. We predicted that the sandy, Holocene-aged surface would allow for a relatively greater plant water status and photosynthetic response to precipitation than would the fine-textured

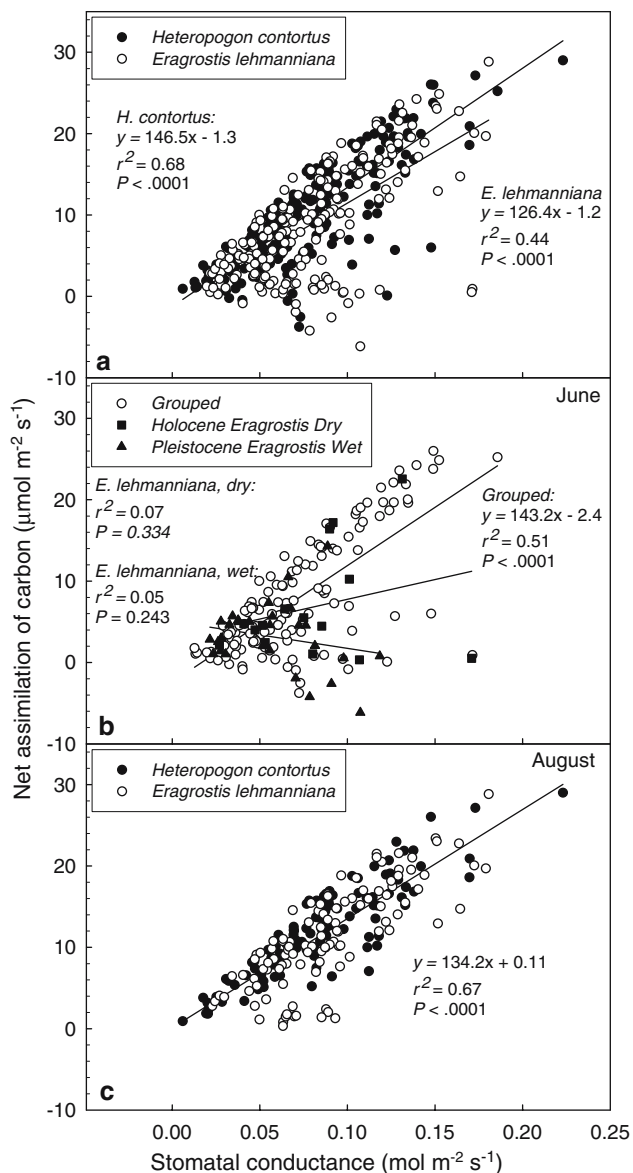


Fig. 4a–c Relationship between net assimilation of C ($\mu\text{mol m}^{-2} \text{s}^{-1}$) and stomatal conductance ($\text{mol m}^{-2} \text{s}^{-1}$). **a** Comparison between *H. contortus* (filled circle) and *E. lehmanniana* (open circle), where all data points from each month, year, site and water treatment are included for each species. **b** Relationship between stomatal conductance and net assimilation of C for *E. lehmanniana* on the Holocene site with the dry treatment (filled square) and *E. lehmanniana* on the Pleistocene site with the wet treatment (filled triangle) all other site, plant and treatment combinations (open circle), where the data points are from both years in June. **c** A single line represents the same relationship for *H. contortus* (filled circle) and *E. lehmanniana* (open circle), where data are from both years in August

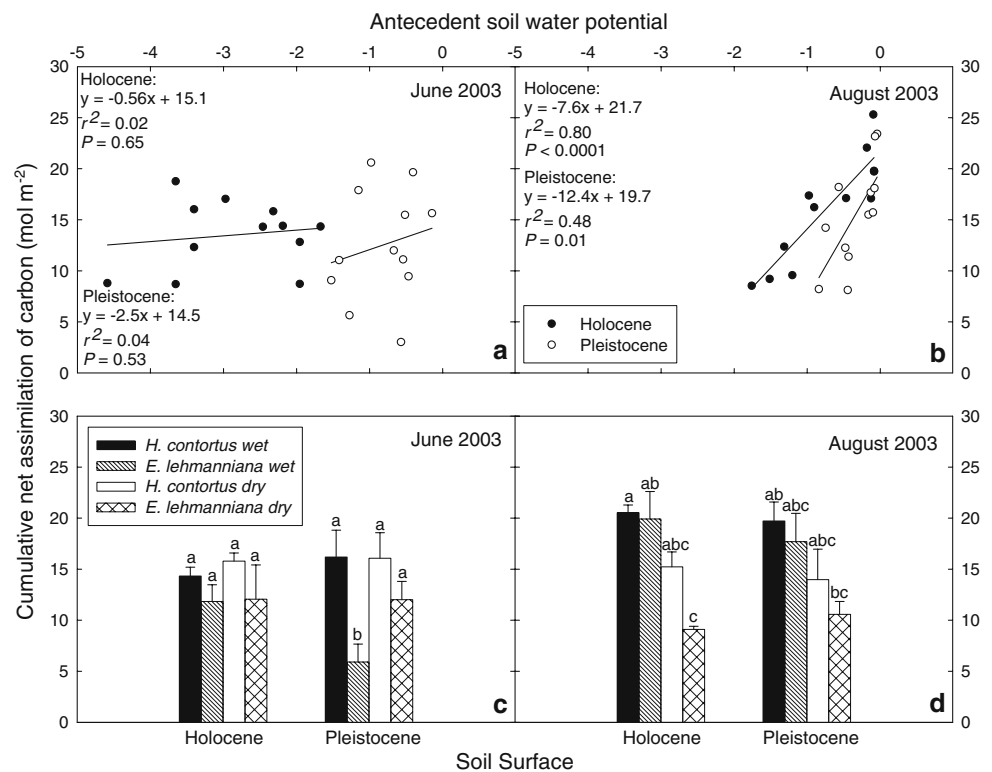
clay soils developed on the Pleistocene-aged alluvium. Ψ_{pd} only differed between soil surfaces during the June pulse events, where initial Ψ_{pd} values were more negative for plants on the sandy soil surface, while g_s only differed during the August 2002 pulse event. The August 2003

pulse event was the only pulse period that did not demonstrate any soil surface differences in all plant function parameters. There were no differences in A_{net} rates between soil surfaces during the June 2002 or August 2003 pulse event. When we integrate the photosynthetic responses across the entire 15-day pulse period for each pulse event, our results clearly did not follow the prediction. There were generally no differences between soil surfaces in response to a June or August pulse event when comparing the leaf-level accumulated CO_2 across the entire 15-day pulse period (Fig. 5c, d), which contradicts our original prediction. Plant Ψ_{pd} responses to the pulse application on the sandy surface may be mostly due to initial soil moisture conditions, rather than soil water content following the pulse application. Indeed, the clay soil surface has higher soil moisture storage initially than the sandy surface, regardless of watering treatments (Potts et al. 2006), likely resulting in greater plant water stress on the sandy surface prior to the pulse.

The greater ability of the coarse soil on the sandy surface to release water promoted high rates of water uptake and leaf gas exchange during periods of high water content following rain, greatly exceeding the rates observed on fine-textured soil, despite lower absolute soil moisture storage. Soil texture has been shown to strongly influence vegetation distribution (McAuliffe 2003), as well as plant performance (McAuliffe 1994, 1999; Parker 1995; Smith et al. 1995; Hamerlynck et al. 2002, 2004). Antecedent soil moisture can predict plant photosynthetic response across the sandy and clay soil surface (as cumulative net assimilation of CO_2 over the 15-day pulse period) during the August pulse event, when initial soil moisture conditions are more favorable compared to June (Fig. 5b). Whereas, during the June pulse event, after a prolonged period of drought, there is no relationship between antecedent soil moisture and leaf-level accumulated CO_2 across any soil surface (Fig. 5a). Our data suggest it is important to consider initial soil moisture conditions and changes in soil water content following rainfall events in order to understand plant responses to precipitation pulses (Reynolds et al. 2004; Ogle and Reynolds 2004).

Because *E. lehmanniana* initiates growth earlier in the growing season than most native grasses and reduces soil water to very low values, thereby competitively excluding native species (Frasier and Cox 1994), we predicted that this non-native grass would show a greater response to rain pulses than *H. contortus*. This prediction generally did not always hold for Ψ_{pd} and stomatal response to the precipitation events in June and August. Ψ_{pd} did not differ between species during the June 2003 pulse event and g_s differed between species only during June 2002. Although A_{net} differed between species in specific interactions, this prediction does not always hold when we consider the

Fig. 5a–d Leaf-level cumulative CO₂ (mol m⁻²) for each soil surface over the 15-day pulse period across antecedent soil moisture (water potential, MPa). **a, b** Each regression is for all species and water treatments during June 2003 and August 2003 across the Holocene surface (filled circle) and the Pleistocene surface (open circle). **c, d** Cumulative CO₂ for each species (*H. contortus* and *E. lehmanniana*) and water treatment (wet and dry) combinations within the Holocene and Pleistocene soil surfaces during June 2003 and August 2003. June 2002 had the same values of cumulative CO₂, but is not plotted here since there was no dry water treatment during this pulse period. Day 15 data was missing for August 2002, thus was not included in this analysis. All cumulative CO₂ values are an average ± 1 SE (*n* = 3)



cumulative net assimilation pulse period response. During the June 2003 pulse event, there were no species differences in leaf-level response of accumulated CO₂ over the entire 15-day pulse period, except for *E. lehmanniana* exposed to the wet water treatment (Fig. 5c). During this pulse period, *E. lehmanniana* exposed to the wet treatment had significantly lower cumulative net assimilation of CO₂ than all other species and water treatment combinations ($F_{1,16} = 13.32$, $P = 0.002$). During the August pulse event, there were generally no species differences in response to the pulse event. However, *E. lehmanniana* exposed to the dry water treatment had the lowest leaf-level accumulated CO₂ (Fig. 5d). *E. lehmanniana* exposed to the wet treatment on the Pleistocene, during the June 2003 pulse event, showed no relationship between g_s and A_{net} (Fig. 4). Thus, *E. lehmanniana* was unable to up-regulate photosynthesis after the June pulse application. This unexpected result may be due to differences in leaf area. *E. lehmanniana* (0.66 ± 0.20 m² m⁻²) exposed to a wet treatment has higher green leaf area index than *H. contortus* (0.37 ± 0.05 m² m⁻²) (Yepez et al. 2005). Even though all plots receive the same sized pulse event, *E. lehmanniana* exposed to the wet treatment has less water available per unit leaf area.

The temporal shift in the time needed for plants to achieve maximum gas exchange may be explained by a combination of aboveground leaf area development and belowground root characteristics. For example, during the

June pulse event, photosynthetic up-regulation in *H. contortus* is lagged compared to *E. lehmanniana*, because *H. contortus* must grow new leaves after the pulse, while *E. lehmanniana* maintains leaf material readily active once water is applied. Flanagan et al. (2002) similarly observed that the magnitude of C fixation after a rainfall event was highly dependent on canopy leaf-area development. However, the magnitude of the photosynthetic response is also determined by drought duration prior to water availability relieving moisture stress (Yan et al. 2000; Schwinning et al. 2002). Since *E. lehmanniana* maintains green leaf tissue to take advantage of water when it becomes available after long periods of drought, it is able to up-regulate its photosynthesis quicker than *H. contortus*. The spatial distribution and the density of roots can also influence plant response to precipitation pulses (Cohen 1970), especially in our comparisons of leaf-level responses of *E. lehmanniana* and *H. contortus*. Although we did not rigorously test for differences in rooting patterns between these species, there is some evidence that suggests that *E. lehmanniana* has a higher density of its roots in shallow soil layers than *H. contortus* (A. Eilts, unpublished data). As previously mentioned above, *E. lehmanniana* had higher green leaf area index than *H. contortus* during the June 2003 pulse period. Thus, we suggest that a combination of above- and below-ground plant characteristics is driving the differences in the speed of photosynthetic plant response to the pulse event.

The amount and timing of rainfall events has a strong influence on the physiological response of plants to increases in water availability (Huxman et al. 2004b). We predicted that a pulse event applied at the beginning of the growing season, in June, would produce a larger proportional plant response than a similar event applied in August, at the peak of the growing season. Our results did not quite match this prediction. Although our observations of Ψ_{pd} , A_{net} , and g_s during the June pulse event produced an increase in plant functional response following the pulse event, plant function did not respond to an August pulse event and decreased over time since the pulse event. We hypothesize that this pattern occurs because favorable initial soil moisture conditions in August had maintained high plant function up to the August pulse event, and the post-pulse period represented a dry down. Thus, an August pulse event across all soil, species and water treatments, has higher accumulated CO_2 ($15.8 \pm 1.0 \text{ mol m}^{-2}$) than a June ($13.0 \pm 1.0 \text{ mol m}^{-2}$) pulse event (linear contrast, $F_{1,32} = 7.65$, $P = 0.009$). Such a pattern is similar to previous results of woody plants responding to pulses after a prolonged period of drought as compared to within growing season rainfall events (Williams and Ehleringer 2000; Snyder et al. 2004), where antecedent soil moisture is high. Our results demonstrate that during the June pulse event, when soil moisture conditions are less favorable, there is little change in leaf-level accumulated CO_2 over the 15-day pulse period across different antecedent soil moisture levels (Fig. 5a). However, during the August pulse event, when soil moisture conditions are favorable, high antecedent soil moisture corresponds with high leaf-level accumulated CO_2 (Fig. 5b). These observations coincide with those of Reynolds et al. (2004), who suggested that future studies of plant responses to pulse events should take into account how soil water recharge and soil water availability are affected by antecedent soil moisture conditions (Reynolds et al. 2004; Ogle and Reynolds 2004).

A decrease in stomatal conductance following the June 2003 pulse was an unexpected result, since the pulse led to less negative Ψ_{pd} compared to pre-pulse values. This result is not indicative of stomatal closure, but rather the initiation of the plants up-regulating photosynthetic activity. For example, the decrease in g_s rates after the pulse application was partially due to shifts in the time of maximum g_s over the diurnal period (Fig. 6). Maximum g_s rates on day -1 of the pulse period were observed between 0900–1100 hours. However, the day after the pulse, nearly all species and water treatment combinations across soil surface did not achieve maximum g_s until 1300–1500 hours. By day 3 of the pulse period, all plants on the Holocene surface had shifted their maximum g_s rates to either 1300–1500 hours. This type of stomatal response may involve active osmoregulation by guard cells (Buckley

2005). Arid land plants typically have maximal photosynthesis during the morning hours (Naumburg et al. 2003). However, our results show how the up-regulation of photosynthesis in response to changes in water status will not respond in such a predictable manner. Therefore, future studies will need to incorporate temporal shifts in maximum diurnal gas exchange rates in order to understand how plants and ecosystems respond to changes in climate.

Conclusions

The native *H. contortus* and non-native *E. lehmanniana* differed in their physiological response to a pulse of precipitation after an extended period of drought, but soil surface did not always amplify differences in plant function of these species throughout the summer growing seasons. Surprisingly *E. lehmanniana* did not have a higher pulse response in all water treatments. In fact, *E. lehmanniana* had the lowest cumulative 15-day photosynthetic response to a pulse event. After a prolonged period of drought, the June pulse event had unfavorable soil moisture conditions, which lead to a larger increase in plant function response. While, favorable antecedent soil moisture conditions late in the summer growing season lead to maintained plant function and a dampened response to a large pulse event. Our work highlights the need to incorporate soil surface characteristics and their influence on plant and ecosystem level CO_2 and H_2O exchange, as well as the need to understand plant response to single rainfall events. Including the sequences of individual rainfall events and their influence on soil moisture recharge is important for understanding within-season plant and ecosystem responses to rainfall variability (Reynolds et al. 2004).

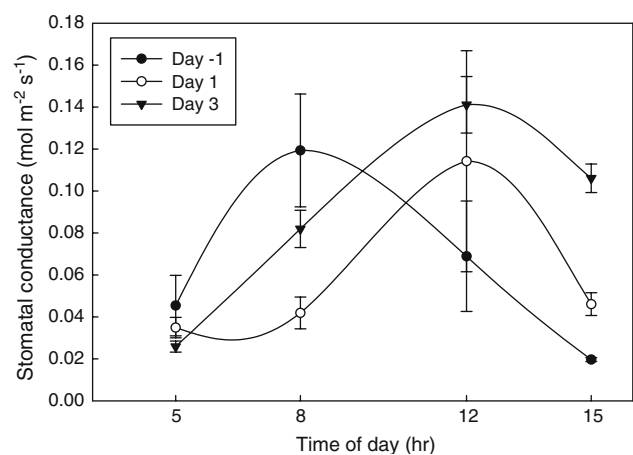


Fig. 6 A representative diurnal curve (for most of the site, plant and water treatment combinations) of g_s ($\text{mol m}^{-2} \text{ s}^{-1}$) plotted from 0500 to 1500 hours for days -1, 1, and 3 following the June 2003 pulse event. g_s at all times periods within the diurnal are means ($n = 3$) \pm 1

Acknowledgements The authors acknowledge the support of the USDA-CSREES (grant no. 00-35101-9308), the International Arid Lands Consortium, the University of Arizona, Sustainability of Semi-Arid Hydrology and Riparian Areas under the STC Program of the National Science Foundation, agreement no. EAR-9876800 and NSF awards DEB 041-5977, DEB 041-8363 and DEB 041-8134 to T. E. H., J. F. W., and D. G. W. D. D. I. was supported by the University of Arizona—Alfred P. Sloan Foundation Fellowship. J. Cable, D. Potts, A. Eilts, N. English, M. Mason, J. Chen and P. B. Allen assisted in the field.

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