

# Growing season ecosystem and leaf-level gas exchange of an exotic and native semiarid bunchgrass

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Received: 24 February 2009 / Accepted: 24 December 2009 / Published online: 10 January 2010  
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**Abstract** The South African grass, Lehmann lovegrass (*Eragrostis lehmanniana*), may alter ecosystem processes across extensive semiarid grasslands and savannahs of western North America. We compared volumetric soil moisture ( $\theta$ ), total and green tissue leaf area index (LAI), ecosystem (i.e. whole-plant and soil), and leaf-level gas exchange of Lehmann lovegrass and the native bush muhly (*Muhlenbergia porteri*) over the 2008 monsoon season in a semiarid savanna in southern Arizona, USA, to see if these were consistent with high productivity associated with lovegrass invasive success.  $\theta$  across 0–5 and 0–25 cm was higher while evapotranspiration (ET) was similar between lovegrass and bush muhly plots, except shortly after rainfall, when ET was 32–81% higher in lovegrass plots. Lehmann lovegrass had lower, quickly developing LAI with greater leaf proportions than bush muhly. When early season  $\theta$  was high, net ecosystem CO<sub>2</sub> exchange (NEE) was similar, but as storm frequency and  $\theta$  declined, NEE was more negative in lovegrass (–0.69 to –3.00  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) than bush muhly (+1.75 to –1.55  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ). Ecosystem respiration ( $R_{\text{eco}}$ ) responded quickly to monsoon onset and late-season rains, and was lower in lovegrass (2.44–3.74

$\mu\text{mol m}^{-2} \text{s}^{-1}$ ) than bush muhly (3.60–5.3  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) across the season. Gross ecosystem photosynthesis (GEP) was greater in Lehmann lovegrass, concurrent with higher leaf-level photosynthesis and stomatal conductance. We conclude that canopy structure facilitates higher  $\theta$  under Lehmann lovegrass, reducing phenological constraints and stomatal limitations to whole-plant carbon uptake through the short summer monsoon growing season.

**Keywords** Desert grassland · Ecosystem respiration · Evapotranspiration · Leaf area index · Net ecosystem exchange

## Introduction

Arid and semiarid ecosystems across the western US have repeatedly experienced exotic grasses invasions that frequently result in new ecological steady states that require novel land-use practices and considerable outlay of resources to manage or restore ecosystems to former conditions (Dukes and Mooney 2004; Bestelmeyer et al. 2006). Understanding basic functional ecology of invasive terrestrial plants is a critical tool for developing effective management, reclamation, and restoration policies, especially in highly variable, water-limited systems (Dukes and Mooney 2004). Moreover, the pressures exerted by non-native grasses on water-limited ecosystems of North America are expected to increase with climate change (Ryan et al. 2008).

Since its introduction for erosion control and rangeland reclamation in the 1930s, the South African C<sub>4</sub> bunchgrass, Lehmann lovegrass (*Eragrostis lehmanniana* Nees.), has spread across the semiarid grasslands of southwestern United States (Cox et al. 1990; Anable et al. 1992; McClaran

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Communicated by Marilyn Ball.

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and Anable 1992; Geiger and McPherson 2005). Lovegrass invasion dramatically reduces floral and faunal diversity (Bock et al. 1986). Since Lehmann lovegrass seems insensitive to grazing and is capable of higher annual productivity (McClaran and Anable 1992), lovegrass dominance may accelerate fire frequency (Anable et al. 1992; but see Geiger and McPherson 2005). Unusual for a C<sub>4</sub> warm-season grass, Lehmann lovegrass has been reported to maintain green leaves year round, and may utilize cool-season precipitation not generally exploited by most native grasses which rely largely on summer precipitation (Cable 1975; Frasier and Cox 1994). Maintaining foliar biomass might also permit rapid recovery from drought (Cox et al. 1990; Cox and Ruyle 1996; Geiger and McPherson 2005), sustaining Lehmann lovegrass spread and dominance over these drought-prone grasslands.

Higher net annual primary productivity in Lehmann lovegrass suggests it alters desert grassland ecosystem processes. Aridland productivity is highly “pulsed”, with the temporal distribution of individual rainfall events having as great, if not a greater, impact on annual productivity than total annual rainfall (Loik et al. 2004). It could be expected that higher productivity in Lehmann lovegrass reflects greater C-sequestration integrated across pulses (i.e., higher pulse use efficiency); however, field experiments show lovegrass-dominated ecosystems are less effective at utilizing precipitation pulses than native species, due to higher ecosystem respiratory fluxes ( $R_{\text{eco}}$ ) and more rapid declines in net ecosystem CO<sub>2</sub> exchange (NEE) following precipitation pulses (Huxman et al. 2004; Potts et al. 2006).

Lower C-sequestration and pulse-use efficiency needs to be reconciled with reports of two- to fourfold higher annual productivity in lovegrass-dominated grasslands (Cox et al. 1990; Anable et al. 1992), especially since seasonally integrated NEE and annual aboveground biomass in desert grasslands are usually in close agreement, with both closely tracking precipitation (Cable 1975; Mielnick et al. 2005). NEE reflects the balance between  $R_{\text{eco}}$  and gross ecosystem photosynthesis (GEP), and the mechanisms controlling these fluxes differ in sensitivity to soil moisture and temperature (Flanagan et al. 2002; Mission et al. 2006; Potts et al. 2006). Thus, comparing seasonal NEE and its components in Lehmann lovegrass and native species might give better insights on how higher productivity by this invasive exotic is attained.

Plant structure may also affect seasonal whole-plant gas exchange. Pulse studies suggest that differences in canopy structure influence precipitation interception and soil infiltration, increasing  $E$  and leading to drier soils under Lehmann lovegrass (Huxman et al. 2004; Potts et al. 2006). Reduced soil moisture could affect autotrophic belowground respiration, a major component of grassland  $R_{\text{eco}}$  (Knapp et al. 1998; Huxman et al. 2004; Flanagan and

Johnson 2005), as well as GEP by altering leaf-level gas exchange dynamics (Anderson and Toft 1993). However, few differences in leaf-level gas exchange between Lehmann lovegrass and native grasses have been found (Fernandez and Reynolds 2000; Huxman et al. 2004; Ignace et al. 2007). Indeed, Fernandez and Reynolds (2000) found allocation to aboveground and belowground growth more strongly affected soil water content than leaf-level gas exchange, and better explained accumulated plant biomass in desert grassland species.

Here, we compared the sensitivity of soil moisture, whole-plant (i.e., ecosystem-level) and leaf-level gas exchange of Lehmann lovegrass and the native grass, bush muhly (*Muhlenbergia porteri* Scribn. ex Beal), to precipitation through the 2008 summer monsoon season. These species have distinctly different canopy structures: Lehmann lovegrass is a semi-erect bunchgrass, while bush muhly forms a low, shrub-like crown from a single base (Kearney and Peebles 1951; Harvey 1975). These species provide a solid comparison between a native and non-native invader because both are considered drought-tolerant warm-season active arid grassland species (Cox and Ruyle 1996; McClaran and Angell 2007), and maintain cool-season active tissue (Welsh and Beck 1976; Frasier and Cox 1994), which will likely minimize the effect of antecedent conditions (Potts et al. 2006). Based on previous growth-chamber and field rainfall pulse experiments (Fernandez and Reynolds 2000; Huxman et al. 2004; Potts et al. 2006; Ignace et al. 2007), we hypothesized:

1. Seasonal ET to be higher and volumetric soil moisture ( $\theta$ ) to be lower under lovegrass, as found in short-term pulse experiments (Huxman et al. 2004; Potts et al. 2006).
2. More negative seasonal NEE in Lehmann lovegrass, supporting findings of higher annual net productivity in lovegrass-dominated grasslands (Cox et al. 1990; Anable et al. 1992). If soils are drier under lovegrass,  $R_{\text{eco}}$  could be more inhibited than photosynthesis (Flanagan et al. 2002; Potts et al. 2006), and NEE may be maintained at stronger sink levels over the season.
3. Leaf-level gas exchange would be similar between lovegrass and bush muhly (Fernandez and Reynolds 2000; Ignace et al. 2007).

## Materials and methods

### Site description

Field work was conducted at the USDA-ARS Southwest Watershed Research Center (SWRC) Santa Rita mesquite savanna site (31.8214°N, 110.8661°W, elevation 1,116 m)

on the Santa Rita Experimental Range (SRER), 45 km south of Tucson, AZ, USA. Mean annual precipitation is 377 mm (1937–2007; USDA-ARS rain gauge #45, <http://ag.arizona.edu/SRER/index.html>). Winters (December through March) are cool with occasional nighttime frosts, and slow-moving frontal storms that account for ca. 30% of the annual rainfall. From April through mid-June, conditions grow hotter and drier, with daytime temperatures often exceeding 35°C. In late June to early July and continuing through September, lower daytime and higher nighttime temperatures follow higher humidity and rainfall associated with the North American Monsoon (Adams and Comrie 1997) which generates thunderstorms that account for ca. 50% of annual rainfall. Monsoon rains typically end mid-September, with October and November generally dry.

The savanna site is representative of the increasing Lehmann lovegrass cover and conversion of intact semiarid desert grassland to savanna following velvet mesquite (*Prosopis velutina* Woot.) expansion across the SRER (McClaran 2003). Vegetation at the site consists of a mesquite overstory of ca. 35% cover, and ground-layer plant canopy cover of ca. 22% dominated by a mix of native  $C_4$  grasses and Lehmann lovegrass. Soils are Combate series, classified as well-drained coarse-loamy, mixed, non-acid Ustic Torrifluvents, with poor soil-horizon development, 5–15% surface gravel, a ca. 5-cm brown loamy-sand A-horizon and a brown coarse sandy-loam to sandy-loam A-C horizon from 5 to 150 cm (Breckenfeld and Robinett 2003). The site is in SRER Pasture 2N, and was grazed year-round from 1957 to 2005, and was ungrazed in 2007 then fenced in August 2008.

#### Soil water and precipitation

Four individual  $0.75 \times 0.75$  m lovegrass, bush muhly, and bare soil plots were established 24–27 May 2008 (total  $n = 12$ ). Grass plots contained 1–2 individual grass bunches; plot size matched dimensions of the ecosystem gas exchange chamber (described below). Volumetric soil moisture ( $\theta$ ) from 0 to 25 cm soil ( $\theta_{25\text{cm}}$ ) was measured every 30 min with a Campbell TDR-100 time domain reflectometer (TDR) system controlled by a CR-1000 datalogger (Campbell Scientific, Logan UT). To cover 25-cm profiles, 30-cm TDR waveguides were inserted at 60–70° from horizontal into the soil under a single grass, or into bare soil. Annual plants were removed regularly to insure clear plant or bare soil signals. Individual rainfall event totals were measured with a tipping bucket rain gauge, with data recorded on a CR-10X data logger (Campbell Scientific) at an eddy-covariance tower located 40 m NW of the soil moisture monitoring site.

To determine if soil drying rates were different between plots, e-folding times (in days) were estimated for  $\theta_{25\text{cm}}$

following four individual storm events followed by inter-storm periods of at least 8 days. To do this, daily values of  $\theta_{25\text{cm}}$  for each interstorm period were first normalized by dividing the maximum daily value occurring on the first day following the storm. Non-linear regressions of exponential decay ( $y = a \times e^{-b \times x}$ ; SigmaPlot v10.0; SPSS, Chicago, IL) were generated for  $\theta_{25\text{cm}}$  pooled for all four sampling plots for each storm. E-folding times were calculated as  $1/b$ , and show how long it took  $\theta_{25\text{cm}}$  to reduce ca. 33% of the maximum starting values.

Soil samples spanning 10–20 cm depths were gathered from under Lehmann lovegrass and bush muhly plants, weighed, and oven dried for 24 h at 80°C. After cooling, the soils were measured for matric potential ( $\psi_{\text{matric}}$ ) using a temperature-controlled dew point water potential meter (WP4t; Decagon Devices, Pullman, WA), then re-wetted with ca. 1.5–2.2 g distilled water, and periodically re-weighed and measured for  $\psi_{\text{matric}}$ . Gravimetric water content ( $\theta_{\text{grav}}$ ) was calculated for each observation, then converted to  $\theta$  assuming a bulk density of  $1.4 \text{ Mg m}^{-3}$  for sandy loam soil (Chan 2006). Non-linear regression (SigmaPlot v10.0) was used to relate estimated  $\theta$  to  $\psi_{\text{matric}}$ .

$\theta_{5\text{cm}}$  measurements were made during ecosystem- and leaf-level gas-exchange runs (see below) using a hand-held TDR (Theta Probe; Delta-T Devices, Kings Lynn, UK) inserted vertically into the soil within the area bounded by the ecosystem-flux chamber. Three  $\theta_{5\text{cm}}$  measurements were averaged for each plot for statistical analysis.

#### Plant measurements

Mid-morning (0800–1000 hours MST) ecosystem fluxes of  $\text{CO}_2$  and  $\text{H}_2\text{O}$  were measured using protocols adapted from Huxman et al. (2004) and Potts et al. (2006), with concurrent measurements of leaf-level gas exchange, from 4 June to 22 October 2008, ca. every 2 weeks, on the plants monitored for  $\theta_{25\text{cm}}$ .  $\text{CO}_2$  and water-vapor fluxes were estimated by measuring changes in  $\text{CO}_2$  and  $\text{H}_2\text{O}$  concentration with an open-path IRGA (LI-7500; LiCOR Instruments, Lincoln, NE) following enclosure of the plot with a  $0.75 \times 0.75 \times 0.75$  m ( $0.422 \text{ m}^3$ ) chamber of tightly sewn polyethylene (Shelter Systems, Santa Cruz, CA) held taut within a frame of PVC pipe. Chamber material allowed 92% of photosynthetically active radiation to pass into the plots, while allowing infrared (IR) radiation to escape, with chamber air temperatures remaining within 1–2°C of external conditions (Huxman et al. 2004; Potts et al. 2006). A fan attached to the tripod holding the IRGA insured atmospheric mixing after enclosure and sealing the chamber base with a chain, which also reduces the effects of leaks, which are minor given the relatively large volume of air (Huxman et al. 2004). Chamber air was mixed for at least 30 s prior to flux measurements, which lasted ca. 90 s, with

the chamber on plot usually 2–3 min. The chamber was removed, aerated for 0.5–1 min, then re-placed over the plot, sealed, and shaded with a blanket to repeat measurements in the dark. Tags driven into the soil at each corner of the chamber frame insured exact repositioning. Ambient-light fluxes allowed estimation of net ecosystem carbon exchange (NEE) and evapotranspiration (ET); dark measurements gave ecosystem respiration ( $R_{\text{eco}}$ ) and, by calculation, gross ecosystem photosynthesis [GEP;  $\text{GEP} = -1 \times (\text{NEE} - R_{\text{eco}})$ ]. Such mid-morning measurements have been found to be fair to excellent predictors of daily integrated measurements across a range of soil moisture conditions ( $\text{NEE } R^2 = 0.31$ ,  $p = 0.025$ ;  $R_{\text{eco}} R^2 = 0.62$ ,  $p = 0.0003$ ;  $\text{GEP } R^2 = 0.88$ ,  $p < 0.0001$ ;  $\text{ET } R^2 = 0.72$ ,  $p < 0.0001$ ; Hamerlynck, unpublished data), and thus are adequate indicators for seasonal species comparisons. Measurements on bare soil plots (available only after 14 July) were made to estimate soil evaporation ( $E$ ) and soil respiration ( $R_{\text{soil}}$ ), and these were used to further partition ET and  $R_{\text{eco}}$  on the grass plots.

To quantify plant canopy structure, 3–5 Lehmann lovegrass and bush muhly plants were harvested early (29 June–1 July) and at peak mid-monsoon biomass (30 July 30–1 August; Cable 1975; Cox et al. 1990). Prior to harvesting, a Li-2000 (LiCOR Instruments) optically measured leaf area index (LAI), and the physical dimensions of height, major and minor canopy diameter and basal diameter were measured. After separating into green and dead leaves and culms, total silhouette area (SA in  $\text{cm}^2$ ) of each portion were measured (LiCOR 3000; LiCOR Instruments). Leaf areas were doubled to reflect both sides, culm cylinder surface area (CSA) was estimated via linear regression (Statistix v. 8.0; Analytical Software, Tallahassee, FL) relating culm SA to CSA ( $\text{CSA } \text{m}^2 = (-1.278 \pm 3.174 \times \text{SA}) / (10,000)$ ;  $R^2 = 0.97$   $p \leq 0.001$ ). Total LAI and green tissue LAI ( $\text{LAI}_{\text{green}}$ ) were estimated by dividing by the ecosystem exchange chamber area ( $0.5265 \text{ m}^2$ ). Two-way ANOVA (Statistix v.8.0) was used to test differences in LAI,  $\text{LAI}_{\text{green}}$ , and proportional contributions of green leaves and stems to total canopy area between species, times, and species-by-time interaction.  $\text{LAI}_{\text{green}}$  was used to scale plot-level GEP to leaf-level ( $\text{GEP}_{\text{lai}}$ ) using allometric regressions relating plant dimensions to  $\text{LAI}_{\text{green}}$ .

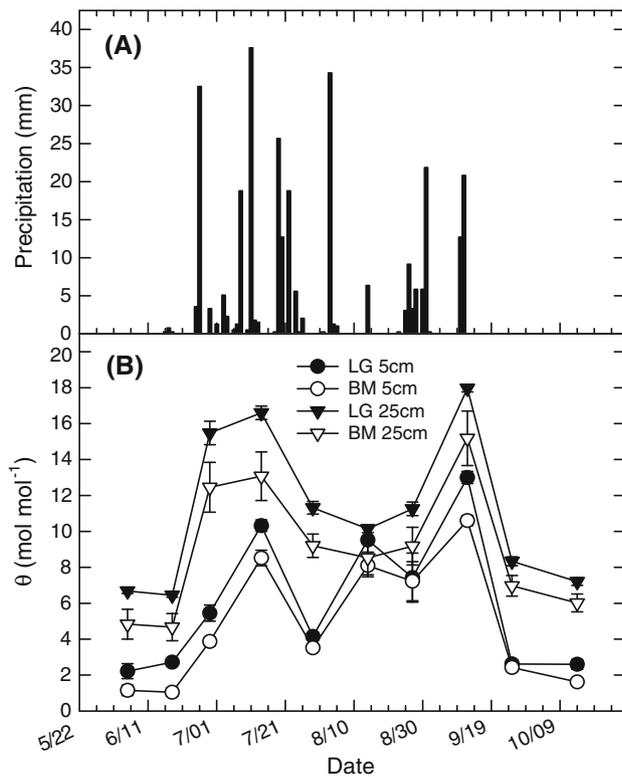
Leaf-level gas exchange was measured with a portable photosynthesis system (LiCOR 6400; LiCOR Instruments). Leaves from the second or third internodes (to insure against confounding age effects) were enclosed in a cuvette under saturating photosynthetic photon flux densities ( $1,500 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ) from the standard high intensity red/blue LED array. Cuvette  $\text{CO}_2$  was held at  $380 \mu\text{mol mol}^{-1}$  by mixing external air with  $\text{CO}_2$  from an attached source. The temperature of a Peltier cooler attached to the cuvette was set to  $25^\circ\text{C}$ , giving leaf temperatures of  $24$ – $30^\circ\text{C}$  and

leaf to atmosphere vapor pressure deficits of  $1.0$ – $4.0 \text{ kPa}$ , within 5–10% of ambient conditions measured with an open, shaded cuvette. Leaves equilibrated for 60 s, and then net photosynthetic assimilation ( $A_{\text{net}}$ ) and stomatal conductance to water vapor ( $g_s$ ) were measured five times and averaged for each sample. Since we intend this to be the start of a long-term study, we did not harvest enclosed leaves in order to calculate specific leaf mass.

A split-plot, repeated-measures analysis of variance (RM-ANOVA; Statistix v. 8.0) tested for differences in  $\theta$ , ecosystem- and leaf-level gas exchange of Lehmann lovegrass and bush muhly. The between-treatment (whole-plot) effect was species (lovegrass vs bush muhly), using the type-by-replicate interaction as the whole-plot error term, with an associated  $\alpha$  of 0.05. Within-treatment (sub-plot) effects were sampling date (11 from June to October), and species-by-time interaction, using the species-by-time-by-replicate interaction as the error term. For  $\theta_{25\text{cm}}$ , the plot mean of all 48 daily measurements was used; all  $\theta$  data were arcsine transformed (Zar 1974). Linear regression (Statistix v8.0) was used to compare slopes and slope elevations of  $A_{\text{net}}$  versus  $g_s$  and  $\theta_{25\text{cm}}$  in bush muhly and lovegrass to see if regulation of leaf-level gas exchange and soil moisture underlay differences in ecosystem exchange.

## Results

The 2008 monsoon precipitation totaled 262 mm, and started 26 June (32.5 mm; Fig. 1), followed by a distinct ramp-up period with nearly daily precipitation until 13 July, followed by a stormy period from 19 July to 24 July. The late monsoon was more heterogeneous: following a large storm on 3 August (34.29 mm; Fig. 1), there was a pronounced dry period from 4 to 24 August, with little activity until 10 and 11 September (12.7 and 20.82 mm, respectively; Fig. 1). Seasonally pooled  $\theta_{5\text{cm}}$  was significantly higher in lovegrass ( $6.00 \pm 0.606\% \text{ SE}$ ) than bush muhly plots ( $4.80 \pm 0.545\% \text{ SE}$ ; Table 1). During inter-storm periods,  $\theta_{5\text{cm}}$  converged (Fig. 1), but higher  $\theta_{5\text{cm}}$  in lovegrass plots in the 4 and 18 June pre-monsoon period, and shortly after larger storms (14 July, 14 August, 12 September, and 14 October) offset these, and no significant species-by-time interaction was apparent (Table 1).  $\theta_{25\text{cm}}$  was higher under lovegrass than bush muhly (Fig. 1), though this difference was significant at a lower probability level ( $F_{1,6} = 4.92$ ;  $p = 0.0683$ ) than the species-by-time interaction (Table 1), which reflects within-species differences between sampling dates. In lovegrass,  $\theta_{25\text{cm}}$  increased significantly from 29 June to 14 July, and was lower than preceding and following sampling dates on 14 August; these were not significantly different in bush muhly plots (Fig. 1).



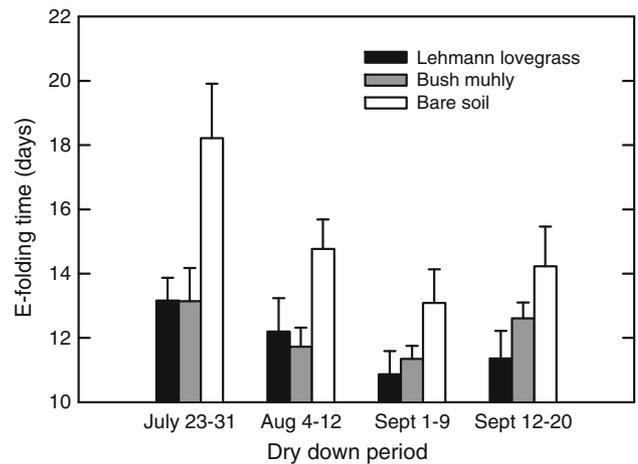
**Fig. 1** a 2008 monsoon season rainfall and volumetric soil moisture across b 0–5 cm (circles) and 0–25 cm (triangles) soil profiles under Lehmann lovegrass and bush muhly. Each symbol is the mean of four measurements, error bars  $\pm 1$  SE

**Table 1** Repeated measures analysis of variance (RM-ANOVA) mean square error (MSE) results comparing seasonal 5- and 25-cm volumetric soil moisture and evapotranspiration of Lehmann lovegrass (*Eragrostis lehmanniana*) and bush muhly (*Muhlenbergia porteri*) plots

Effect <sub>(df)</sub>	$\theta_{5cm}$	$\theta_{25cm}$	ET
Spp <sub>(1)</sub>	<b>28.800</b>	91.036	0.336
Error <sub>a(6)</sub>	0.820	18.485	0.233
Time <sub>(9)</sub>	<b>106.996</b>	<b>122.230</b>	<b>5.733</b>
S x T <sub>(9)</sub>	1.052	<b>1.140</b>	<b>0.249</b>
Error <sub>b(52)</sub>	1.070	0.471	0.106

Significant effects ( $p \leq 0.05$ ) are highlighted in bold, degrees of freedom are presented in parentheses

Since  $\theta$  and  $\psi_{\text{matric}}$  relationships were identical between Lehmann lovegrass or bush muhly soils, we pooled data from all samples to get the exponential relationship  $\psi_{\text{matric}} = -153.36 + 152.62 \times (1 - e^{(-1.3529 \times \theta)})$  ( $R^2 = 0.998$ ,  $p < 0.0001$ ). This predicted that  $\psi_{\text{matric}}$  across the 25-cm volumes did not differ between species, and ranged between  $-0.72$  and  $-0.99$  MPa for both species. Shallow soils were more dynamic, and were below  $-2.0$  MPa four times under Lehmann lovegrass ( $-8.3$  and  $-4.6$  MPa on 5 June and 18



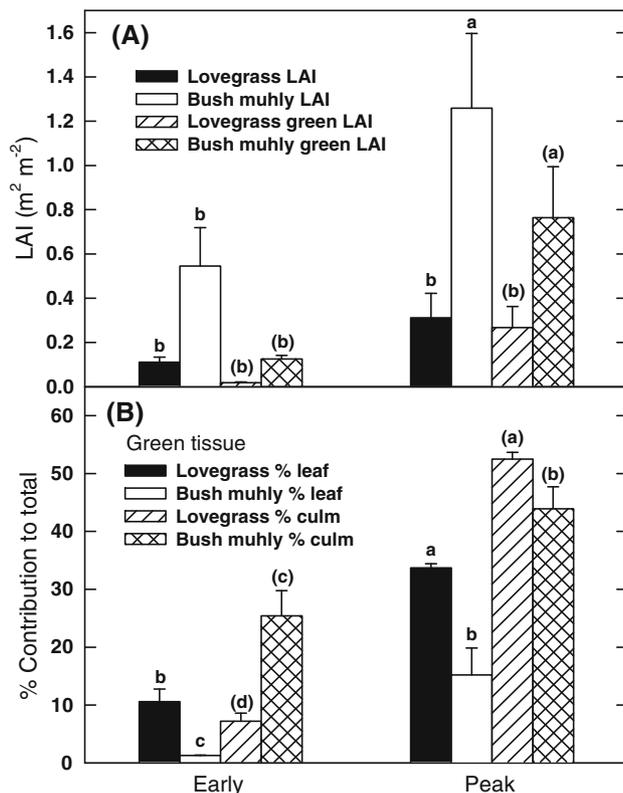
**Fig. 2** E-folding coefficients of maximum-normalized  $\theta_{25cm}$  of Lehmann lovegrass, bush muhly, and bare soil plots. Error bars  $\pm 1$  SE from non-linear, exponential decay regressions fit to daily  $\theta_{25cm}$  derived from continuously monitored  $\theta_{25cm}$

June,  $-5.1$  and  $-5.2$  MPa on 9 September and 14 October) a mid-monsoon season low of  $-1.28$ . Drier  $\theta_{5cm}$  in bush muhly resulted in  $-32.9$  to  $-37.6$  MPa in June, and  $-6.5$  and  $-17.8$  MPa in late September and October, and mid-monsoon season lows of  $-1.53$  and  $-2.0$  MPa.

Soil moisture declined at similar rates under lovegrass and bush muhly, as indicated by markedly lower e-folding times in these compared to bare soil (Fig. 2). Bare soil plots dried out much slower during the first interterm period in July (e-folding times of  $18.2 \pm 1.69$  SE) and more rapidly toward the end of the monsoon (ca. 14 days), while both types of grass plots had similar e-folding times across the monsoon (10–13 days; Fig. 2).

Lehmann lovegrass plots had significantly lower total LAI ( $0.21 \text{ m}^2 \text{ m}^{-2}$ ) and green LAI ( $0.14 \text{ m}^2 \text{ m}^{-2}$ ) compared to bush muhly plots ( $0.90 \text{ m}^2 \text{ m}^{-2}$  and  $0.78 \text{ m}^2 \text{ m}^{-2}$  and for total and green LAI, respectively;  $F_{1,11} = 18.42$ ,  $p = 0.0013$ ). Total LAI and LAI<sub>green</sub> increased by 139.5 and 620.6%, respectively, from early to peak periods ( $F_{1,11} = 8.08$ ,  $p = 0.016$ ; and  $F_{1,11} = 18.12$ ,  $p = 0.0014$ , respectively), with no significant species-by-time interaction (Fig. 3). Lehmann lovegrass canopies had higher proportions of green leaves (22.2%) compared to bush muhly (7.7%;  $F_{1,11} = 36.12$ ,  $p = 0.0001$ ). Species differences in the proportion of green culms depended on seasonal period ( $F_{1,11} = 27.62$ ,  $p = 0.0003$ ). In the early season, bush muhly had greater proportions of green culms compared to Lehmann lovegrass, but later in the season, the invasive grass had significantly higher green culm contributions (Fig. 3).

Net ecosystem  $\text{CO}_2$  exchange (NEE) also did not differ between lovegrass and bush muhly plots pooled across the monsoon season ( $-1.95 \pm 0.370 \mu\text{mol m}^{-2} \text{ s}^{-1}$  and  $-1.23 \pm 0.555 \mu\text{mol m}^{-2} \text{ s}^{-1}$  SE, respectively) with a significant



**Fig. 3** **a** Early (30 June to 1 July) and peak monsoon season (30 July to 1 August) leaf area index on a whole-plant (LAI) and photosynthetically active (green leaves and culms) tissue basis (LAI<sub>green</sub>), and **b** percent contributions of green leaves and culms to total canopy area of Lehmann lovegrass and bush muhly plants. Letters indicate significant post-hoc means tests (LSD;  $p < 0.05$ ); error bars  $\pm 1$  SE

species-by-time interaction (Table 2). Following very low and similar NEE in lovegrass and bush muhly during the dry season ( $-0.23$  to  $-0.40 \mu\text{mol m}^{-2} \text{s}^{-1}$ ), NEE rapidly rose and was more positive in bush muhly ( $2.83 \pm 0.439 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) compared to lovegrass ( $1.71 \pm 0.274 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) following the first storm (Fig. 4a). After this, NEE in Lehmann lovegrass and bush muhly closely tracked each other through July, a period of marked mid-morning sink activity, ranging from  $-5.03$  to  $-5.27 \mu\text{mol m}^{-2} \text{s}^{-1}$  for lovegrass and  $-6.65$  to  $-7.80 \mu\text{mol m}^{-2} \text{s}^{-1}$  for bush muhly (Fig. 4a). Both species showed a trend toward more positive NEE during the mid-monsoon dry period (Fig. 4a), with bush muhly plots having NEE at or exceeding compensation ( $-1.03 \pm 1.300 \mu\text{mol m}^{-2} \text{s}^{-1}$  and  $1.75 \pm 0.415 \mu\text{mol m}^{-2} \text{s}^{-1}$ ), while lovegrass plots were negative NEE ( $-2.66 \pm 0.600 \mu\text{mol m}^{-2} \text{s}^{-1}$  and  $-0.69 \pm 0.381 \mu\text{mol m}^{-2} \text{s}^{-1}$  SE; Fig. 4). Following this, bush muhly plot NEE reduced and converged with lovegrass NEE, and both remained at similar levels following the last storm of the season and until the end of sampling (Fig. 4a).

**Table 2** Repeated measures analysis of variance (RM-ANOVA) mean-square error (MSE) results comparing ecosystem- and leaf-level gas exchange of Lehmann lovegrass (*Eragrostis lehmanniana*) and bush muhly (*Muhlenbergia porteri*)

Effect <sub>(df)</sub>	NEE	$R_{\text{eco}}$	GEP <sub>plot</sub>	GEP <sub>lai</sub>	$A_{\text{net}}$	$g_s$
Spp <sub>(1)</sub>	4.055	<b>9.123</b>	1.013	166.716	<b>828.001</b>	<b>0.063</b>
Error <sub>a(6)</sub>	3.626	1.385	6.710	41.147	14.772	0.002
Time <sub>(9)</sub>	<b>49.821</b>	<b>19.972</b>	<b>95.455</b>	<b>301.258</b>	<b>440.896</b>	<b>0.021</b>
$S \times T$ <sub>(9)</sub>	<b>4.816</b>	<b>1.372</b>	<b>7.125</b>	<b>147.392</b>	<b>47.273</b>	<b>0.004</b>
Error <sub>b(52)</sub>	1.781	0.514	2.323	14.236	15.809	0.001

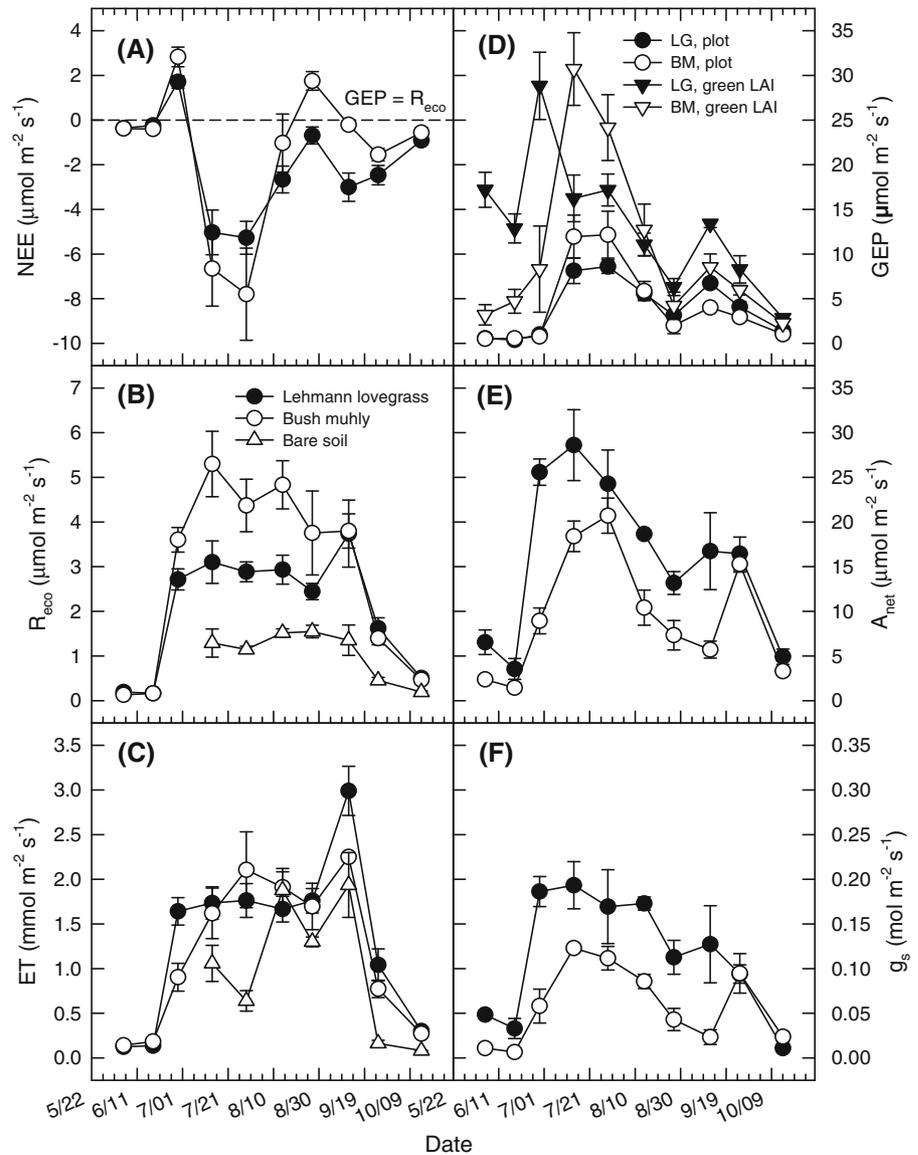
Significant effects ( $p \leq 0.05$ ) are highlighted in bold, degrees of freedom are presented in parentheses

Pooled across the season, bush muhly  $R_{\text{eco}}$  ( $2.62 \pm 0.341 \mu\text{mol m}^{-2} \text{s}^{-1}$  SE) was significantly greater than in lovegrass ( $1.98 \pm 0.227 \mu\text{mol m}^{-2} \text{s}^{-1}$  SE; Table 2). The species-by-time interaction in  $R_{\text{eco}}$  (Table 2) was due to similar, low  $R_{\text{eco}}$  in lovegrass and bush muhly plots preceding the monsoon, followed by a rapid rise to seasonal maximum values in lovegrass plots ( $2.72 \pm 0.235 \mu\text{mol m}^{-2} \text{s}^{-1}$  on 29 June to  $3.10 \pm 0.475 \mu\text{mol m}^{-2} \text{s}^{-1}$  on 14 July) and a more sustained rise to higher  $R_{\text{eco}}$  in bush muhly following the onset of the monsoon ( $3.60 \pm 0.274 \mu\text{mol m}^{-2} \text{s}^{-1}$  on 29 June to  $5.30 \pm 0.731 \mu\text{mol m}^{-2} \text{s}^{-1}$  by 14 July). In addition, there was a sharp rise in lovegrass  $R_{\text{eco}}$  following the last monsoon season storm that did not occur in bush muhly plots (Fig. 4b). Following this,  $R_{\text{eco}}$  in both were identical and declined to the end of the season (Fig. 4b).

Seasonally pooled evapotranspiration did not differ between lovegrass ( $1.31 \pm 0.148 \text{mmol m}^{-2} \text{s}^{-1}$  SE) and bush muhly plots ( $1.17 \pm 0.145 \text{mmol m}^{-2} \text{s}^{-1}$  SE), but there was a significant species-by-time interaction (Table 1). We have found diurnally integrated ET to not differ between these plots across moist and dry soil conditions (Hamerlynck, unpublished data). Thus, these measures suggest that seasonally integrated ET did not differ between these species. ET dramatically increased in lovegrass plots following the first monsoon storm (from  $0.137 \pm 0.006 \text{mmol m}^{-2} \text{s}^{-1}$  SE to  $1.64 \pm 0.153 \text{mmol m}^{-2} \text{s}^{-1}$  SE). Bush muhly ET increased less rapidly following this first major rain (from  $0.183 \pm 0.010 \text{mmol m}^{-2} \text{s}^{-1}$  SE to  $0.904 \pm 0.155 \text{mmol m}^{-2} \text{s}^{-1}$  SE), and did not attain levels similar to lovegrass until 1 month after monsoon onset (29 July,  $ET = 2.11 \pm 0.425 \text{mmol m}^{-2} \text{s}^{-1}$  SE; Fig. 4c). Once established, mid-morning ET did not differ between lovegrass and bush muhly plots; however, following the last summer storms, lovegrass ET rose and was higher than in bush muhly (Fig. 4c).

Gross ecosystem exchange (GEP) was species-specific through the season, whether expressed on a whole-plot

**Fig. 4** Whole plant-level mid-morning **a** net ecosystem carbon exchange (NEE), **b** ecosystem respiration ( $R_{eco}$ ), **c** evapotranspiration (ET), **d** gross ecosystem photosynthesis (GEP) on plot- and green LAI-basis, and leaf-level **e** net photosynthetic carbon assimilation ( $A_{net}$ ) and **f** stomatal conductance to water vapor ( $g_s$ ) of Lehmann lovegrass and bush muhly; each *symbol* is the mean of four measurements, *error bars*  $\pm 1$  SE

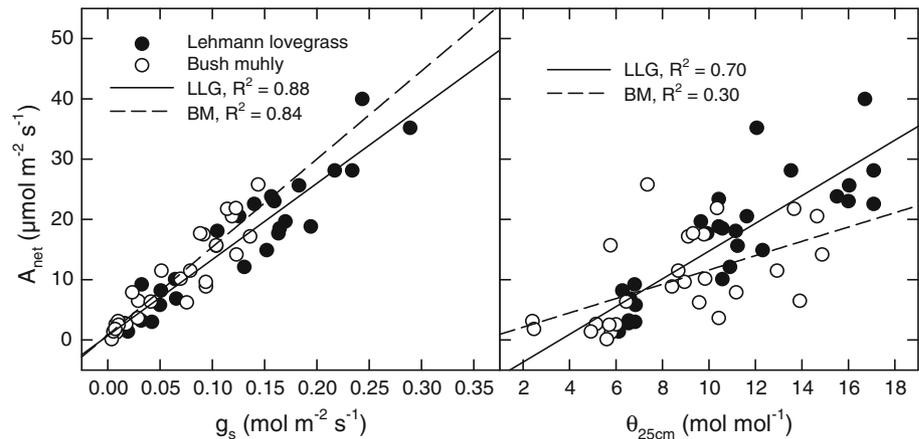


( $GEP_{plot}$ ) or green leaf area ( $GEP_{lai}$ ) basis, as indicated by two-way interactions in these variables (Table 2).  $GEP_{plot}$  was similar between species during pre-monsoon drought and through early monsoon peak periods (8 June–29 July; Fig. 5). Following the mid-monsoon dry period, lovegrass  $GEP_{lai}$  was higher than in bush muhly plots (Fig. 4d). Prior to the monsoon,  $GEP_{lai}$  was higher in lovegrass plots, and reached seasonal highs rapidly following the first rain (29 June). In contrast,  $GEP_{lai}$  developed later in bush muhly plots, and was less than the rates in lovegrass through both July sampling periods (Fig. 4d).

Leaf-level  $A_{net}$  was significantly higher in lovegrass ( $15.60 \pm 1.519 \mu\text{mol m}^{-2} \text{s}^{-1}$  SE) compared to bush muhly plants ( $9.40 \pm 1.118 \mu\text{mol m}^{-2} \text{s}^{-1}$  SE) pooled across the monsoon season, as was stomatal conductance ( $g_s$ ;  $0.113 \pm 0.0121 \text{ mol m}^{-2} \text{s}^{-1}$  SE and  $0.058 \pm 0.0074 \text{ mol m}^{-2} \text{s}^{-1}$  SE, for lovegrass and bush muhly, respectively) with a signifi-

cant two-way interaction in both (Table 2). This was due to slower development of  $A_{net}$  and  $g_s$  in bush muhly following monsoon onset, and similar  $A_{net}$  and  $g_s$  between species over the final two sampling periods (Fig. 4e, f). The late-season spike in bush muhly gas exchange was due to a second flush of leaves following the September rain (Fig. 1). In order to directly compare Lehmann lovegrass and bush muhly  $A_{net}$  responses to  $g_s$  and  $\theta_{25\text{cm}}$ , we omitted the last three sampling periods from our regression analysis (Fig. 5). Linear regressions showed  $g_s$  explained 83% of the variability in  $A_{net}$  ( $F_{1,52} = 258.62$ ,  $p < 0.0001$ ), with identical positive slopes ( $F_{1,50} = 1.96$ ,  $p = 0.17$ ) and intercepts ( $F_{1,51} = 0.58$ ,  $p = 0.45$ ) between the two species, and that bush muhly achieved markedly lower  $g_s$  and  $A_{net}$  maxima compared to lovegrass (Fig. 5). Concurrent  $\theta_{25\text{cm}}$  regression with  $A_{net}$  was also positive and significant ( $R^2 = 0.55$ ;  $F_{1,52} = 64.25$ ,  $p < 0.0001$ ), but with a significantly lower

**Fig. 5** Linear regression relationship between  $A_{\text{net}}$  and  $g_s$  and  $\theta_{25\text{cm}}$  of Lehmann lovegrass and bush muhly for individual samples of a common leaf cohort taken through the 2008 monsoon season ( $n = 27$  for both species)



slope in bush muhly ( $F_{1,50} = 5.61$ ,  $p = 0.022$ ) compared to lovegrass (Fig. 5).  $\theta_{25\text{cm}}$  explained a similar degree of variation in  $g_s$  ( $g_s = -0.0276 + 0.0124 \times \theta_{25\text{cm}}$ ,  $R^2 = 0.44$ ;  $F_{1,52} = 40.47$ ;  $p < 0.0001$ ), with bush muhly having a lower, but parallel slope ( $F_{1,51} = 6.48$ ,  $p = 0.014$ ) to Lehmann lovegrass (data not shown).

## Discussion

Contrary to our hypotheses and to findings from shorter duration pulse experiments (Huxman et al. 2004; Potts et al. 2006), soil moisture was consistently higher in lovegrass plots than under the native grass across 5- and 25-cm soil profiles (Fig. 1), while ET was largely similar between plot types (Fig. 4). Diurnal data from moist and dry soil conditions show that integrated ET did not differ between lovegrass and bush muhly plots; in addition, mid-morning ET was a strong predictor of integrated ET (see above). Thus, it seems likely that seasonally integrated ET would be similar between lovegrass- and bush muhly-dominated plots. The lower  $\theta$  under bush muhly may result from greater interception and lower precipitation transmission because of its denser canopy, as indicated by higher total LAI (Fig. 3), much as canopy structure affects soil moisture in other semiarid systems (Bhark and Small 2003; D’Odo-rico et al. 2007). Bush muhly is considered drought tolerant (McClaran and Angell 2007), and greater plant extraction and lowering of  $\theta$  can affect competitive interactions between aridland grasses varying in drought tolerance (Anderson and Toft 1993). However, Lehmann lovegrass and bush muhly had identical dry-down rates (Fig. 2), suggesting no differences in plant extraction. Bush muhly is a long-lived grass, and consistently occurs in one microsite over several generations (McClaran and Angell 2007), which is frequently associated with processes that alter  $\theta$  and  $\psi_{\text{matrix}}$  and plant water potentials (McAuliffe et al. 2007). However,  $\theta - \psi_{\text{matrix}}$  relationships were identical

between Lehmann lovegrass and bush muhly soils, indicating differences in  $\theta_{25\text{cm}}$  likely did not affect differences in plant water potential. Thus, the chronically low  $\theta$  in bush muhly soils is a consequence of canopy features that affect soil water volumetric dynamics, and these affect whole-plant and leaf-level performance (Figs. 4, 5).

Similar ET between Lehmann lovegrass and bush muhly for most sampling runs may be due to enough time elapsing for species differences to have converged following rainfall events. Indeed, the two times when ET was greater in lovegrass plots were shortly after large rains early in the monsoon (29 June) and the last rain (12 September; Fig. 4). In both cases, higher ET in lovegrass might be due to greater soil evaporation, as these were taken under conditions similar to experimental studies showing higher  $E$  in lovegrass-dominated plots (Huxman et al. 2004; Potts et al. 2006). Indeed, the 12 Sept measurement occurred 1 day after rain, and the June sample after 3 days, had much lower ET (Fig. 4), suggesting  $E$  was likely higher in lovegrass plots at these times. Scott et al. (2006) found that soil  $E$  dominates ET for 1–2 days following rain at another sandy loam site in southern Arizona. However, there were leaf-level responses that may have resulted in greater  $T$  contributions to ET, as stomatal conductance ( $g_s$ ) was markedly higher in Lehmann lovegrass on 29 June and 12 September (Fig. 4).

Bush muhly showed greater proportional canopy growth (Fig. 3), hence the arc trajectory in ET development early in the monsoon compared to the step response in lovegrass (Fig. 4). These canopy-level responses likely affected whole-plant carbon processes as well, since ecosystem respiration- ( $R_{\text{eco}}$ ; Fig. 4) and LAI<sub>green</sub>-corrected gross ecosystem exchange reached seasonal maxima later in bush muhly compared to lovegrass (Fig. 4). Thus, the ability of Lehmann lovegrass to rapidly establish full canopy display and to maintain higher proportions of green leaves (Fig. 3) indicate this exotic species has less phenological constraints to water utilization and carbon uptake than does the native bunchgrass (Huxman et al. 2004).

Species differences in net ecosystem exchange (NEE) varied through the season (Fig. 4). During the initial “wet-up”, NEE in both species reached similar maximum uptake (i.e., most negative). In contrast, during the latter portion of the monsoon, when rain frequency and accumulations reduced, lovegrass NEE was consistently more negative than bush muhly (Fig. 4). We have found mid-morning NEE to be significantly correlated with diurnally integrated NEE in these grasses (see above), and integrated GEP exceeds nighttime  $R_{\text{eco}}$  (Hamerlynck, unpublished data). Thus, the lower mid-morning NEE likely reflects greater seasonal carbon sink potential in Lehmann lovegrass-dominated plots, supporting findings of higher productivity that seem to contribute to its invasive success (Cox et al. 1990; Anable et al. 1992).

More negative NEE reflected lower  $R_{\text{eco}}$  in Lehmann lovegrass as hypothesized (Fig. 4), but not due to lower soil moisture (Fig. 1) as expected. Lower  $R_{\text{eco}}$  might be due to smaller root-to-shoot ratios for the exotic grass (Cox et al. 1990), giving rise to smaller root biomass and lower  $R_{\text{eco}}$  (Knapp et al. 1998; Johnson and Matchett 2001), or lower aboveground respiration (Flanagan and Johnson 2005). Indeed, many invasive herbaceous exotics have lower leaf C-construction costs compared to native species, which could result in lower aboveground growth and maintenance respiration rates (Nagel et al. 2004). Bush muhly is a long-lived grass (McClaran and Angell 2007), and higher  $R_{\text{eco}}$  may reflect long-term accumulation of organic material that could sustain larger active microbial populations (Sponseller 2007). Higher  $\theta$  under Lehmann lovegrass during drier periods likely sustained more physiologically active tissue (Fig. 3) and higher  $A_{\text{net}}$  than in bush muhly (Fig. 4), allowing higher  $\text{GEP}_{\text{lai}}$  (Fig. 4) to offset  $R_{\text{eco}}$  losses more effectively over dry periods (Mission et al. 2006). Rapid early season up-regulation and mid-season spike in  $R_{\text{eco}}$  in lovegrass is also suggestive of a “pulse-sensitive”  $R_{\text{eco}}$  (Jenerette et al. 2008), which, in addition to rapid canopy development (Fig. 3), may be important mechanisms in explaining why lovegrass productivity is more strongly affected by intra-annual rainfall variation than native grasses (Anable et al. 1992; Cox and Ruyle 1996; Geiger and McPherson 2005).

Contrary to our expectations, leaf-level  $A_{\text{net}}$  and  $g_s$  were higher in Lehmann lovegrass (Fig. 4). These findings contrast with those showing few differences in gas exchange between lovegrass and other native species (Fernandez and Reynolds 2000; Ignace et al. 2007). Thus, in addition to the differences in leaf area display alluded to above, lower stomatal limitations to photosynthesis also likely contributed to greater carbon sink activity and higher whole-plant carbon assimilation in lovegrass (Figs. 4, 5). Higher  $A_{\text{net}}$  in lovegrass was likely due to higher rooting zone  $\theta$  under lovegrass (Fig. 1), facilitating stomatal opening (Fig. 5).

The pronounced late-season spike in bush muhly NEE (Fig. 4a) and leaf-level  $A_{\text{net}}$  and  $g_s$  (Fig. 4e, f) reflect the full expansion of a second flush of leaves over 2 weeks after the last monsoon storm. Lower NEE preceding this late-season storm might reflect a greater contribution of culm photosynthesis, which have markedly lower  $A_{\text{net}}$  and  $g_s$  than in leaves, or may reflect photo-protective down-regulation that can persist for several days following prolonged soil drying (Smith et al. 1997). Though our findings suggest  $g_s$  as the primary limitation to  $A_{\text{net}}$  (Fig. 5), analysis of  $A_{\text{net}}/C_i$  curves is needed to fully determine seasonal stomatal and non-stomatal limitations (Smith et al. 1997).

In summary, we found the physical structure of Lehmann lovegrass likely fostered favorable soil water dynamics, reducing seasonal canopy- and leaf-level constraints to water uptake and whole-plant carbon assimilation. Also, lower and more dynamic  $R_{\text{eco}}$  enhanced carbon uptake, supporting findings that higher productivity is associated with the invasive success of Lehmann lovegrass in these water-limited systems (Cox et al. 1990; Anable et al. 1992). Though limited to a single “average” growing season, this study shows that short-term pulse studies (Huxman et al. 2004; Potts et al. 2006) may miss critical seasonal dynamics of desert grassland function.

**Acknowledgments** We thank Ashley Wiede, J.J. Dale, Evan Sommer, Maggie Heard and Donna King for their help in the field, and support from the Philecology Foundation to T. Huxman.

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