PHYSIOLOGICAL ECOLOGY - ORIGINAL PAPER

Inter- and under-canopy soil water, leaf-level and whole-plant gas exchange dynamics of a semi-arid perennial C_4 grass

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Abstract It is not clear if tree canopies in savanna ecosystems exert positive or negative effects on soil moisture, and how these might affect understory plant carbon balance. To address this, we quantified rooting-zone volumetric soil moisture ($\theta_{25\ cm}$), plant size, leaf-level and whole-plant gas exchange of the bunchgrass, bush muhly (*Muhlenbergia porteri*), growing under and between mesquite (*Prosopis velutina*) in a southwestern US savanna. Across two contrasting monsoon seasons, bare soil $\theta_{25\ cm}$ was 1.0–2.5% lower in understory than in the intercanopy, and was consistently higher than in soils under grasses, where $\theta_{25\ cm}$ was similar between locations. Understory plants had smaller canopy areas and volumes with larger basal diameters than intercanopy plants. During an above-average monsoon, intercanopy and understory plants had similar seasonal light-saturated leaf-level photosynthesis ($A_{net-sat}$), stomatal conductance (g_{s-sat}), and whole-plant aboveground respiration (R_{auto}), but with higher whole-plant photosynthesis (GEP_{plant}) and transpiration (T_{plant}) in intercanopy plants. During a below-average monsoon, intercanopy plants had higher diurnally integrated GEP_{plant}, R_{auto}, and T_{plant}. These findings showed little evidence of strong, direct positive canopy effects to soil moisture and attendant plant performance. Rather, it seems understory conditions foster competitive dominance by drought-tolerant species, and that positive and negative canopy effects on soil moisture and community and ecosystem processes depends on a suite of interacting biotic and abiotic factors.

Keywords *Muhlenbergia porteri* · Photosynthesis · Respiration · Transpiration · Volumetric soil water

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Introduction

Soil water is the primary driver of aridland ecological processes (Noy-Meir 1973), and aridland vegetation structure frequently displays a stable shifting mosaic of intercanopy and understory microenvironments (Walker et al. 1981; Scholes and Archer 1997; D'Odorico et al. 2007). Critical to these dynamics is the effect plants themselves have on soil processes. Long-lived perennial plants serve as accumulation points for limiting nutrients (Titus et al. 2002), and canopy shading reduces temperature and soil evaporation, providing a favorable microenvironment for the establishment of many plant species (Turner et al. 1966; Franco and Nobel 1989; Evanari et al. 1982; McAuliffe 1986; Suzan et al. 1996; Brittingham and Walker 2000; Tielbörger and Kadmon 2000). Also, plant structural features can facilitate higher infiltration, resulting in higher sub-canopy soil moisture compared to exposed intercanopy soils (Greene et al. 1994; Breshears et al. 1997; Devitt and Smith 2002; Bhark and Small 2003).

These findings have led some to suggest direct positive feedbacks between vegetation and soil moisture are the dominant feature in shaping ecological patterns and processes in aridland systems (Lejeune et al. 2002; D'Odorico et al. 2007; Scanlon et al. 2007). However, canopy interception can reduce the effectiveness of individual precipitation events and limit plant available water (Scholes and Archer 1997; Carlyle-Moses 2004), and extensive sub-canopy water use by the canopy dominant may lower understory soil water availability below intercanopy levels (Cable 1977; Yoder and Nowak 1999). In addition, extreme "drought tolerators", such as cacti and other succulents, and extreme "drought avoiders" like desert annuals, most consistently occur in understory locations, suggesting favorable soil water is transient and limited to shallow depths (Turner et al. 1966; Evanari et al. 1982; Franco and Nobel 1989; Suzan et al. 1996; Brittingham and Walker 2000; Tielbörger and Kadmon 2000; Holzapfel et al. 2006). Field studies and physical process-based modeling also indicate there may be distinct thresholds between positive and negative canopy effects on soil moisture (Caylor et al. 2003, 2005; Caylor and Rodriguez-Iturbe 2004), and species-specific positive and negative understory plant performance (Pugnaire et al. 2004). Thus, generalizations on the ecological importance of strong positive canopy soil moisture interactions in aridland systems may be premature.

A critical need to resolve this is to link intercanopy and understory soil moisture to plant carbon uptake dynamics. Past research examining plant/soil interactions in arid and semi-arid systems has largely drawn on cover, stem density, biomass, and other growth-based metrics (Caylor et al. 2003; Hochstrasser and Peters 2004; Simmons et al. 2008; Garduño et al. 2009), and while these reflect integrated physiological processes, they do not provide insight into the seasonal variation in underlying physiological mechanisms of photosynthesis and respiration, which differ in their sensitivity to soil moisture (Potts et al. 2006). While ecophysiological studies have shown improved water relations and photosynthetic performance of some understory aridland plants (Pugnaire et al. 2004; Prider and Facelli 2004), such leaf-level studies can miss whole-plant respiratory responses that can strongly determine whole-plant and ecosystem-level carbon balance (Huxman et al. 2004; Potts et al. 2006; Jenerette et al. 2008).

Here, we address differences in soil moisture and associated whole-plant and leaf-level ecophysiological performance in open intercanopy and understory micro-habitats in a semiarid savanna. We tracked the seasonal and diurnal performance of the long-lived perennial warm-season bunchgrass, bush muhly (*Muhlenbergia porteri*), at a mesquite (*Prosopis velutina*) savanna site on the Santa Rita Experimental Range (SRER) in southern Arizona,

USA. SRER provides an ideal venue for addressing inter- and understory plant/soil dynamics. Average annual long-term precipitation and tree density at SRER is comparable to sites in other savanna systems where positive feedbacks to soil moisture have been reported (Caylor et al. 2003; D'Odorico et al. 2007; Scanlon et al. 2007). The consistently greater cover and density of bush muhly under trees and shrubs (McClaran and Bartolome 1989; Livingstone et al. 1997) have been attributed to enhanced understory soil moisture (Livingstone et al. 1997). However, more recently, Tiedemann and Klemmedson (2004) showed bush muhly productivity can increase with canopy removal, and McClaran and Angell (2007) suggested smaller plants sizes and higher densities of bush muhly under mesquite indicated limited soil moisture, as observed in other arid systems (Hamerlynck et al. 2002), and postulated that bush muhly's dominance in these locations reflected a high degree of drought tolerance. We specifically tested McClaran and Angel's hypothesis, and expected that if it were true:

1. Volumetric soil moisture (θ) would be lower in the understory.
2. Individual understory plants would be smaller than intercanopy plants.
3. Concurrent with lower θ, light-saturated leaf-level stomatal conductance ($g_{s\text{-}sat}$) and photosynthesis ($A_{net\text{-}sat}$) would be lower in the understory, since chronic water stress has been found to reduce maximum A_{net} and g_s in aridland plants (Smith et al. 1997).
4. Consistent with leaf-level responses, understory whole-plant transpiration (T_{plant}) and whole-plant photosynthesis (GEP_{plant}) would be lower than in intercanopy plants.
5. Autotrophic aboveground respiration (R_{auto}), which is sensitive to soil water availability in grasses (Flanagan and Johnson 2005), would be lower in understory plants.

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 ASL) on the Santa Rita Experimental Range (SRER), 45 km south of Tucson, AZ, USA (Scott et al. 2009). Mean precipitation is 377 mm (1937–2007), with most of the growing season coinciding with the North American monsoon starting late June to early July and continuing through September, with the sporadic, but often intense, rainfall through October associated with tropical

disturbances (Adams and Comrie 1997). The site is representative of semi-desert grassland conversion to savanna following ca. 100 years of velvet mesquite expansion (McClaran 2003). Vegetation consists of a mesquite overstory of ca. 35% cover, and a ground-layer of native C_4 grasses and the introduced Lehmann lovegrass (*Eragrostis lehmanniana*), with scattered sub-shrubs and succulents. Soils are Combate series; well-drained coarse-loamy, mixed, non-acid Ustic Torrifluvents, with poor soil-horizon development (Breckenfeld and Robinett 2003). The site is in SRER Pasture 2 N which was grazed year-round from 1957 to 2005 at about 0.028 cattle ha^{-1} year^{-1} (Ruyle 2003); since 2007, the site has been protected from grazing.

Precipitation and soil moisture

Rainfall was measured with a tipping bucket rain gauge at a eddy-covariance tower located 40 m NW of the study site. To establish the historical context of the two monsoon seasons, we calculated the standardized precipitation index (SPI) for the 1937–2009 period using continuous monthly rain totals recorded at a long-term rain gauge (SR#45 gauge) located about 0.5 km from the site. SPI provides a strong comparative context to studies in other systems with widely differing seasonal precipitation patterns; for any given time period, an SPI of −0.99 to +0.99 indicates near normal rainfall, with SPI of +1.0 to 1.49 and −1.0 to −1.49 indicating moderately wet and moderately dry conditions, respectively, SPI of +1.5 to +1.99 and −1.5 to −1.99 very wet and severely dry conditions, respectively, and values equaling or exceeding +2.0 and −2.0 indicating extremely wet or dry conditions compared to all other similar time periods in the dataset (McKee et al. 1993). We used the September 3-month SPI to compare all monsoon season periods (1 July to 30 September) across the entire 72-year dataset. Volumetric soil moisture from 0 to 25 cm ($\theta_{25\,cm}$) was measured using time domain reflectometry (TDR) probes (TDR-100; Campbell Scientific, Logan, UT, USA). TDR waveguides (30 cm length) were deployed May 2008 by inserting 60–70° from horizontal into soil underneath a single grass bunch within four individual 0.75 × 0.75 m² plots containing 1–2 bush muhly plants. All TDR cables running from the data logger were run through conduit, and buried in 15- to 20-cm-deep trenches, and no roots were observed in these trenches near any of the emplaced waveguides. Plots were selected from typical open intercanopy and mesquite understory locations, and in bare soil plots in close proximity (ca. 1–1.5 m) to vegetated plots in both locations, with 4 plots for each treatment. Plot-size matched dimensions of the ecosystem gas-exchange chamber (described below). Waveforms were generated every 30 min and converted to volumetric water content (cm³ cm^{-3}). Annual plants were removed regularly to insure clear bush

muhly or bare soil signals. To compare inter- and under-canopy bare soil and bush muhly $\theta_{25\,cm}$, probability distribution functions were generated by binning the 30 min data into 1% bins over the total range of soil moisture values for the 2008 and 2009 monsoon seasons (DOY 154–274), with frequency calculated as $f_{bin} = N_{bin}/N_{total.}$

To insure that differences in volumetric soil moisture were important to plant functioning, we related gravimetric soil water content (θ_{grav}) to soil water potential (ψ_{soil}) in soil samples spanning 10–20 cm depths under intercanopy and understory bush muhly plants. Samples were weighed, oven-dried for 24 h at 80°C; after cooling, the soils ($n = 4$ for each treatment) were measured for ψ_{soil} using a temperature-controlled dew point water potential meter (WP4t; Decagon Devices, Pullman, WA, USA), then re-wetted with ca. 1.5–2.2 g distilled water, periodically re-weighed and measured for ψ_{soil}. θ_{grav} was calculated for each observation and converted to volumetric θ assuming a bulk density of 1.4 Mg m^{-3} for sandy loam soil (Chan 2006). Non-linear regression (SigmaPlot v10.0) was used to relate volumetric θ to ψ_{soil}, and these relationships were used to see if differences in the probability distribution functions of $\theta_{25\,cm}$ resulted in substantial differences in basic ψ_{soil} between inter- and under-canopy locations within and between the two monsoon seasons.

Plant measurements

Plant size

Major and minor basal and canopy diameters (D) and plant height (H) of 90 plants in each microhabitat were measured at the end of the monsoon growing season to calculate elliptical canopy area (area cm² $= \pi ab$; with a and b ½ of the major and minor diameters, respectively) and eccentricity ($\varepsilon = \sqrt{(a^2 - b^2)/b^2}$). Canopy volume ($V$ in m³) estimations accounted for age-dependent differences in canopy height/diameter relationships. Young plants were modeled as prolate spheroids ($V = [4/3]\pi(H/2)(D/2)^2$). Adult bush muhly plants are spherical ($V = [1/6]\,3\,\pi D^3$), becoming hemispherical (for $H > D$, $V = [1/3]\pi H^2[3(D/2) - H]$; for $H < D$, $V = [1/6]\pi H[3(D/2)^2 + H^2]$; Hamerlynck et al. 2002). One-way ANOVA (Statistix v 8.0; Analytical Software, Tallahassee, FL, USA) was used to test for differences in basal diameter, canopy height, area, ε and volume; volume data were log$_{10}$-transformed to meet ANOVA data distribution assumptions (Zar 1974).

Seasonal gas exchange

Mid-morning (8:00 to 10:00 MST) whole-plant-and-soil (i.e. "ecosystem") water vapor and carbon-dioxide fluxes

with concurrent leaf-level gas exchange measurements were measured approximately every 2 weeks from 4 June to 22 October, 2008. Ecosystem fluxes were estimated by measuring changes in CO_2 and H_2O concentration with an open-path gas analyzer (Li-7500; LiCOR, Lincoln, NE, USA) following enclosure of the plot with a $0.75 \times 0.75 \times 0.75$ m (0.422 m^3) chamber of tightly sewn polyethylene (Shelter Systems, Santa Cruz, CA, USA) held taut within a tent frame of PVC pipe. Chamber material allowed 92% of photosynthetically active radiation to pass into the plots, while allowing infrared (IR) radiation to escape (Potts et al. 2006). A fan attached to the tripod holding the gas analyzer insured atmospheric mixing after enclosure and sealing the chamber base with a chain. Chamber air was mixed for 30 s prior to flux measurements, with concentrations logged every second for at least 90 s. The chamber was then removed, aerated for 0.5–1 min, re-placed over the plot, sealed, and shaded with a blanket to repeat measurements in the dark. Ambient-light fluxes allowed estimation of per unit ground area net ecosystem carbon exchange (NEE) and evapotranspiration (ET); dark measures gave ecosystem respiration (R_{eco}) and, by calculation, gross ecosystem photosynthesis [GEP $= -1 \times$ (NEE $+ R_{eco}$)]. As each plot contained 1–2 plants, we have expressed per unit ground area GEP as whole-plant photosynthesis (GEP$_{plant}$). Measurements on nearby bare soil plots were made to determine soil evaporation (E) and soil respiration (R_{soil}), used to partition R_{eco} into whole-plant autotrophic aboveground respiration ($R_{auto} = R_{eco} - R_{soil}$). Consistent with our treatment of GEP, ground area transpiration ($T = ET - E$) has been expressed as whole-plant T (T_{plant}). Potential sources of uncertainty are chamber leaks, dependence of photosynthetic rates to altered CO_2 partial pressures and build-up of temperature gradients; however, with our small chambers and rapid measurements, it is likely the same error was applied across all treatments, allowing valid inter-treatment comparisons (Saleska et al. 1999). To scale GEP$_{plant}$ to canopy integrated leaf-level photosynthesis (GEP$_{lai}$), green leaf area index (LAI$_{green}$; green leaf m^2 ground area m^{-2}) was estimated for intercanopy and understory plants using allometric relationships derived from off-plot harvests relating plant physical dimensions to LAI$_{green}$. Plant height, major and minor canopy diameter axes and basal diameter were measured; plants were harvested, and total silhouette area (SA, cm^2) of green and dead leaves and culms were measured (LiCOR 3000). Leaf SA were doubled to reflect both sides, culm surface area was converted to cylinder surface area (CSA) via linear regressions [Statistix v. 8.0; CSA in m$^2 = (-1.278 \pm 3.174*$culm SA$)/(10,000)$; $R^2 = 0.97$, $p \leq 0.001$]. LAI$_{green}$ was related physical plant dimensions via linear regressions (SigmaPlot v10.0, SPSS, Chicago, IL). From these, we estimated LAI$_{green}$ for all

plants measured for gas exchange, and estimated GEP$_{lai}$ as GEP$_{plant}$/LAI$_{green}$.

Leaf-level gas exchange was measured for leaves and green culms of each monitored plant with a portable photosynthesis system (LiCOR 6400). Tissue was enclosed in a cuvette under saturating photosynthetic photon flux densities (PPFD, 1,500 μmol m^{-2} s^{-1}) from a high intensity red/blue LED array. Cuvette CO_2 concentration was maintained at 380 μmol mol^{-1} by mixing external air with CO_2 from a source attached to the unit. Block temperature of a Peltier cooler attached to the cuvette was set to 25°C, giving leaf temperatures of 24–38°C and leaf to atmosphere vapor pressure deficits of 1.0–4.0 kPa, within 5–10% of ambient conditions measured with an open, shaded cuvette. Tissue equilibrated for 60 s, and then light-saturated net photosynthetic assimilation ($A_{net-sat}$) and stomatal conductance to water vapor (g_{s-sat}) were measured five times and averaged for statistical analysis.

A split-plot, repeated-measures analysis of variance (RM-ANOVA; Statistix v. 8.0) was used to test for seasonal differences in leaf-level and whole plant-level gas exchange of intercanopy and understory bush muhly. The between-treatment (whole-plot) effect was location (inter- and understory), using the type-by-replicate interaction as the whole-plot error term to test for differences pooled across all dates for both, with an associated α of 0.05. Within-treatment (sub-plot) effects were sampling date ($n = 11$), and type-by-time interaction, using the type-by-time-by-replicate interaction as the error term.

2009 diurnal whole plant gas-exchange

Predawn plant water potentials (ψ_{pd}) were measured at 03:00 MST with a Scholander pressure chamber (PMS, Corvallis, OR, USA) on 1, 16 and 31 July, 2009, with the latter two samplings followed by whole-plant gas exchange measured every 3 h from 3:00 to 21:00 MDT. The 1 July ψ_{pd} was made ca. 2 days prior to the first major rain of the 2009 season (21.1 mm; 3 July) and provided a baseline ψ_{pd} at the height of pre-monsoon water stress, being made 40 days after a rain (18.0 mm; 21 May), and 2 days after a minor event (5.5 mm; 29 June). Dates selected for diurnal measurements differed principally in θ, with the 16 July sampling made 2 days after an 11.3 mm rainfall, which had followed two other large storms (3 July and 14.2 mm on 8 July). The 31 July sampling was made 12 days after the last substantial storm of the monsoon season (18.2 mm, 19 July), with no rainfall in between. Data from a nearby eddy covariance station showed few differences in the diurnal course of air temperature, light, and humidity between these dates (Scott et al. 2009). Whole-plant gas exchange was measured as described above. The 24-h diurnal integration was determined using SigmaPlot v10.0

area transformation for each diurnal curve. Midnight respiratory and transpiration rates were estimated by taking average of 3:00 and 21:00 MST measures; these values were in agreement with other studies showing little or no change in ET or respiratory fluxes between these two periods (Huxman et al. 2004). A split-plot RM-ANOVA was used to test for differences in ψ_{pd}, and integrated whole-plant gas exchange of intercanopy and understory bush muhly between the sampling dates. Whole-plot effects were location (inter- and understory), using the type-by-replicate interaction as the whole-plot error term. Within-treatment (sub-plot) effects were sampling date (Wet, 16 July and Dry, 31 July), and location-by-time interaction, using the location-by-time-by-replicate inter-action as the error term. Of specific interest was the type-by-time interaction, which would indicate microsite-specific responses between dates. Linear regressions were used to determine cost/benefit relationships by regressing integrated GEP_{plant} against R_{auto}. We compared slopes and intercepts regression lines of intercanopy and understory plants to determine if these plants expressed different cost:benefit relationships, as well as deviation from 1:1 relationships to see if net carbon uptake (GEP_{plant}/R_{auto}) was constant across these moisture conditions and microhabitats.

Results

Hydrological context

The 2008 monsoon season precipitation totaled 262 mm, commencing DOY 178 (32.5 mm; Fig. 1), followed by near daily precipitation until DOY 194, and a second stormy period from DOY 200 to 208 (Fig. 1). This was followed by a dry period punctuated by a large storm on DOY 216 (34.3 mm; Fig. 1) that ended in a late-season rainy period (DOY 236–245), with the final major storms of the season on DOY 254–255 (12.7 and 20.8 mm, respectively; Fig. 1). Total 2009 monsoon season precipitation was 116 mm, 65% of which fell by 31 July (75.3 mm), within long-term average July accumulations (85.4 ± 45.15 mm SD for 1937–2009); however, of the remaining 35%, none of the seven events exceeded 10 mm (Fig. 1). The 2008 July through September rainfall accumulations were above normal (SPI = +1.16), while conditions in 2009 were moderately dry (SPI = −1.13), and both represented the 9th wettest and driest 1 Jul to 30 September periods in the 72-year record.

$\theta_{25\ cm}$ were largely similar under intercanopy and understory bush muhly grasses; there was a distinct tendency for intercanopy bush muhly soils to achieve slightly lower $\theta_{25\ cm}$ at the end of drying periods from DOY

180–220 in 2008 (Fig. 1). However, following this, $\theta_{25\ cm}$ under intercanopy bush muhly were consistently higher, regardless of wetting or drying status (Fig. 1). Across both monsoon seasons, probability distributions of $\theta_{25\ cm}$ were similar in soils under intercanopy and understory bush muhly, and these soils had a distinct shift towards higher probabilities of being drier than soils in bare soil plots (Fig. 2). The soil release curves showed identical exponential relationships between θ and ψ_{soil} between locations, and all data was pooled to give $\psi_{soil} = -153.36 + 152.62 \times (1 - e^{(-1.3529 \times \theta)})$; $R^2 = 0.998$, $p < 0.0001$. This predicted the highest probability θ in 2008 (21% values at $\theta_{25\ cm} = 4.5\%$) were equivalent to soil ψ_{soil} of −1.09 MPa, while in 2009, 76–78% of $\theta_{25\ cm}$ were between 5.5 and 6.6%, equivalent to −0.83 and −0.76 MPa. Bare soil water potentials were predicted to range from −0.83 to −0.74 MPa across both years.

Plant size

Individual understory plants had significantly larger basal diameters compared to intercanopy bush muhly plants ($F_{1,178} = 8.35$; $p = 0.004$; Fig. 3), but had significantly lower canopy height ($F_{1,178} = 53.1$; $p \le 0.0001$), smaller individual plant canopy areas ($F_{1,178} = 7.67$; $p = 0.006$) and volumes ($F_{1,178} = 21.1$; $p \le 0.0001$; Fig. 3). Plant shape, indicated by eccentricity (ε), did not differ between understory (0.56 ± 0.023 SE) and intercanopy plants (0.58 ± 0.020 SE; $F_{1,178} = 0.50$; $p = 0.173$).

2008 monsoon season gas exchange responses

Seasonally pooled $A_{net-sat}$ and g_{s-sat} were the same in understory and intercanopy plants, with significant type-by-time interactions (Table 1), resulting from date-specific location differences on DOY 181, when intercanopy $A_{net-sat}$ and g_{s-sat} were higher, and on DOY 227, when understory rates exceeded those in the intercanopy (Fig. 4). After this, $A_{net-sat}$ and g_{s-sat} declined to similar levels in both locations, followed by a pronounced spike on DOY 269, after which $A_{net-sat}$ and g_{s-sat} were higher in intercanopy bush muhly (Fig. 4). Whole-plant photosynthesis (GEP_{plant}) was significantly higher in intercanopy bush muhly (3.85 ± 0.731 µmol m^{-2} s^{-1} SE) than in understory plants (2.18 ± 0.435 µmol m^{-2} s^{-1} SE) pooled across the season, with a significant type-by-time interaction (Table 1), due to similar GEP_{plant} during drier pre-monsoon and late-monsoon periods, and higher intercanopy GEP_{plant} in July compared to understory plants (Fig. 4). In contrast, GEP_{lai} did not differ between locations, with no type-by-time interaction (Table 1; Fig. 4). Whole-plant transpiration (T_{plant}) did not differ between locations, but did show a type-by-time interaction (Table 1), due to higher T_{plant} in

Fig. 1 2008 and 2009 monsoon-season precipitation and daily average rooting depth volumetric soil moisture ($\theta_{25\ cm}$) of soil under bush muhly (*Muhlenbergia porteri*) and bare soil in intercanopy and mesquite understory locations. Daily values are the average of 48 half-hour observations made in 4 individual plots for each cover type
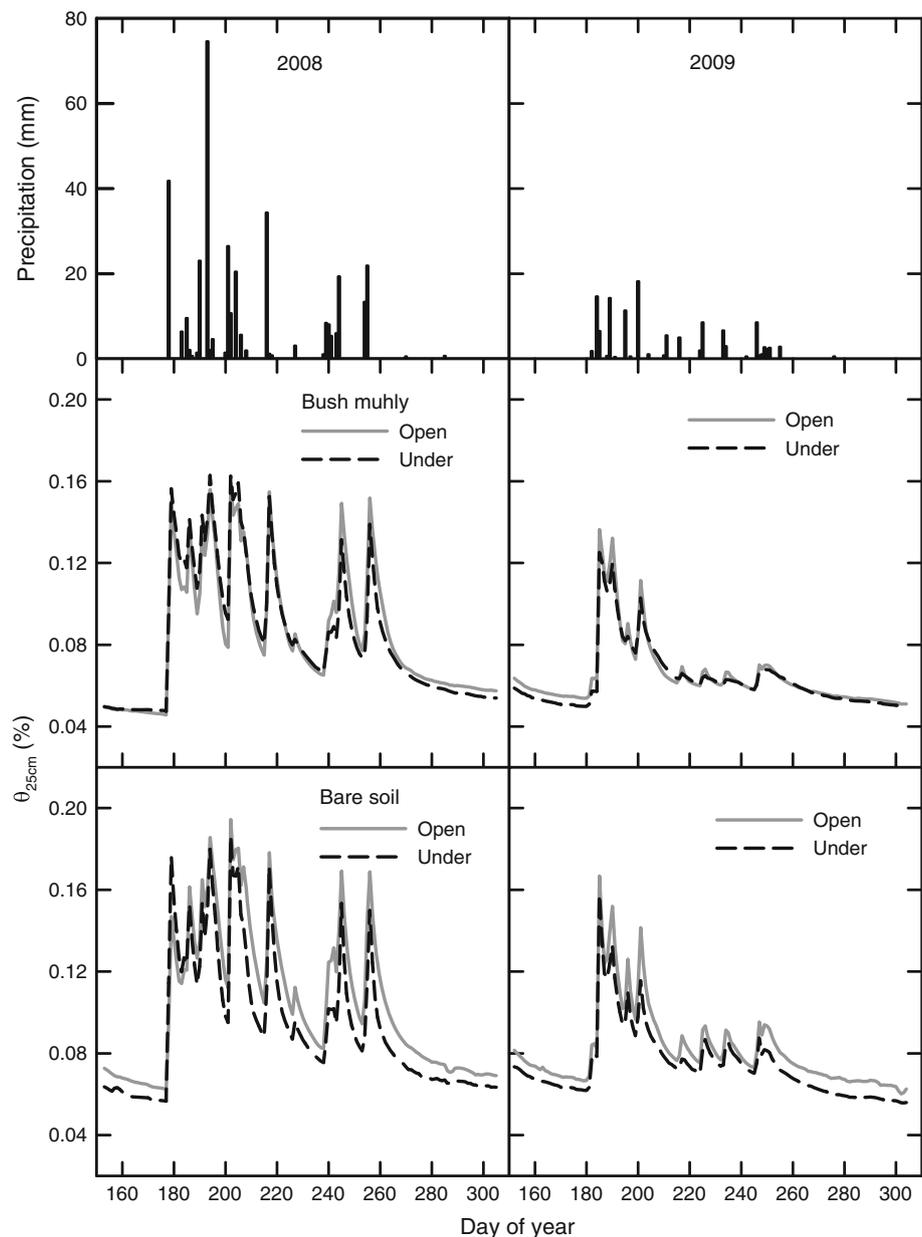
intercanopy plants on DOY 211, 269 and 288, and higher T_{plant} in understory plants on DOY 227; and similar T_{plant} across all other sampling dates (Fig. 4). R_{auto} did not significantly differ between locations with no type-by-time interaction (Table 1; Fig. 4), despite pooled understory R_{auto} (1.47 ± 0.254 µmol m^{-2} s^{-1} SE) being nearly half of rates in intercanopy plants (2.22 ± 0.300 µmol m^{-2} s^{-1} SE); indeed, at a lower α-value, these differences were significant ($p = 0.068$).

2009 integrated diurnal whole plant responses

Predawn water potential (ψ_{pd}) did not differ between bush muhly in open or understory locations at the height

of pre-monsoon drought (−6.95 ± 2.53 and −7.97 ± 1.08 MPa SE for intercanopy and understory plants, respectively), or on 16 July when soils were moist (−0.65 ± 0.09 and −0.75 ± 0.06 MPa SE, for intercanopy and understory plants, respectively), or dry on 31 July (−2.75 ± 0.67 and −2.00 ± 0.12 MPa SE, respectively; $F_{1,6} = 0.04$; $p = 0.852$), with no location-by-time interaction ($F_{2,12} = 0.56$; $p = 0.584$). Diurnally integrated GEP_{plant}, GEP_{lai} and R_{auto}, showed similar responses in declining soil moisture; pooled across both days, all three variables were higher in intercanopy plants compared to understory levels (Fig. 5), significantly so for GEP_{plant} and R_{auto}, but not for GEP_{lai} (Table 1), with significant type-by-time interactions in all three (Table 1), due to significant

Fig. 2 Probability distribution function of rooting depth volumetric soil moisture ($\theta_{25\ cm}$) of bush muhly and bare soil plots at intercanopy and understory locations for the 2008 and 2009 monsoon seasons. $\theta_{25\ cm}$ are averages of 48 daily half-hour observations
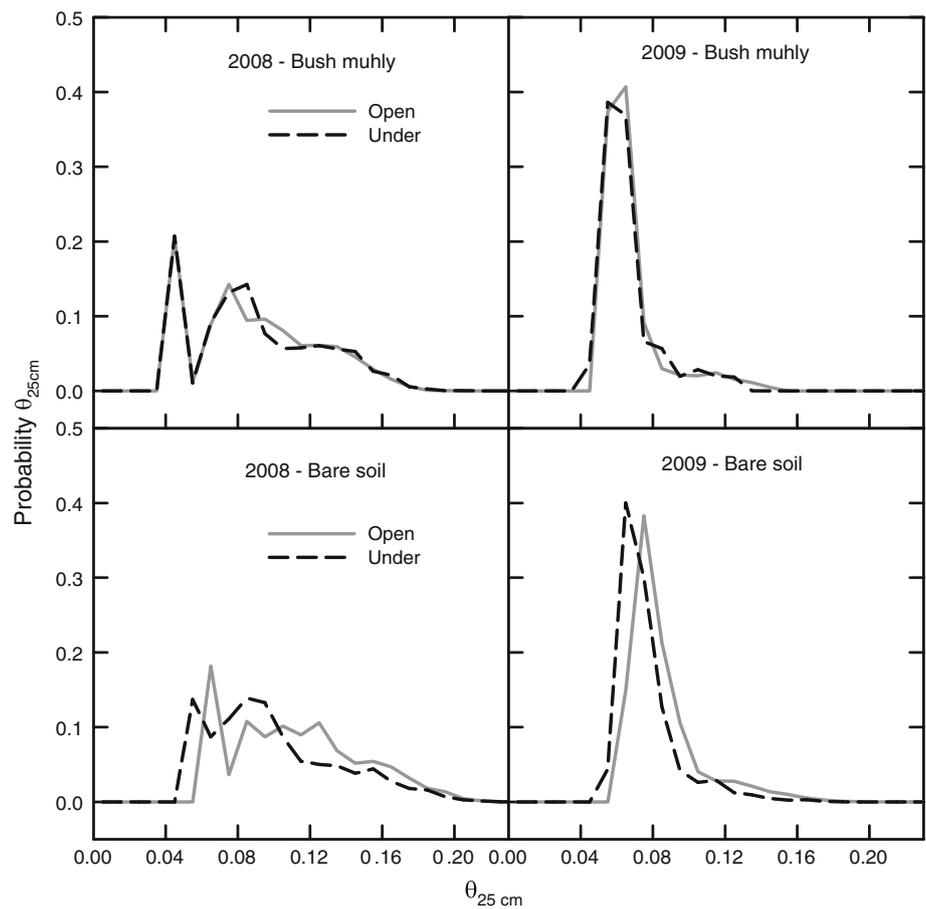

Fig. 3 Individual plant **a** basal diameters, **b** canopy heights, **c** canopy areas, and **d** canopy volumes of intercanopy and understory bush muhly. *Bars* are the mean of 90 measurements, *error bars* indicate ±1SE; *letters* differ at $p \leq 0.05$ (LSD, one-way ANOVA)
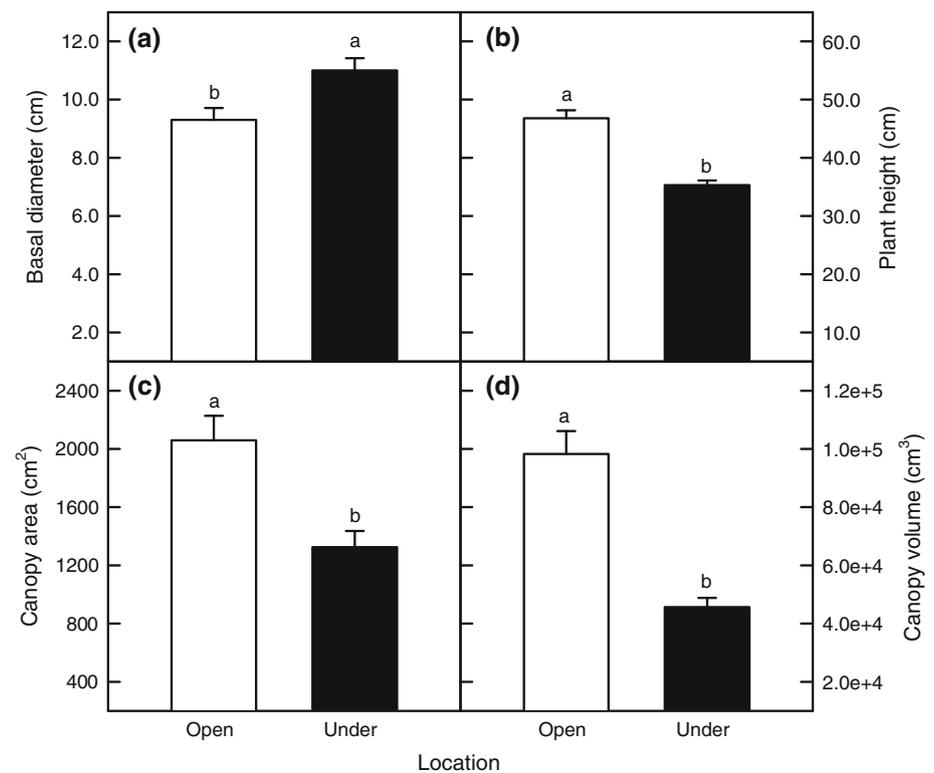
Table 1 Repeated-measures ANOVA F test results comparing intercanopy and understory bush muhly (*Muhlenbergia porteri*) mid-morning 2008 monsoon season light-saturated leaf-level net photosynthesis ($A_{net-sat}$) and stomatal conductance (g_{s-sat}) and per ground area whole-plant transpiration (2008-T_{plant}), whole-plant gross ecosystem photosynthesis (2008-GEP_{plant}) and green leaf-area corrected GEP (2008-GEP_{lai}), whole-plant aboveground respiration (2008-R_{auto}), and 2009 monsoon season daily integrated whole-plant gas exchange

	Location	Date	Date x Location
$A_{net-sat}$	$1.24_{(1,6)}$	$49.11_{(9,51)}$**	$2.84_{(9,51)}$**
g_{s-sat}	$0.00_{(1,6)}$	$30.03_{(9,51)}$**	$4.95_{(9,51)}$**
2008-T_{plant}	$0.33_{(1,6)}$	$6.46_{(6,28)}$**	$2.45_{(6,28)}$*
2008-GEP_{plant}	$7.23_{(1,6)}$*	$22.55_{(9,47)}$**	$2.79_{(9,47)}$*
2008-GEP_{lai}	$0.57_{(1,6)}$	$15.29_{(9,47)}$**	$0.50_{(9,47)}$
2008-R_{auto}	$4.94_{(1,6)}$	$7.76_{(6,31)}$**	$1.10_{(6,31)}$
Daily-T_{plant}	$16.39_{(1,6)}$**	$6.13_{(1,6)}$*	$0.34_{(1,6)}$
Daily-GEP_{plant}	$20.33_{(1,6)}$**	$38.58_{(1,6)}$**	$19.85_{(1,6)}$**
Daily-GEP_{lai}	$4.77_{(1,6)}$	$19.57_{(1,6)}$**	$13.33_{(1,6)}$**
Daily-R_{auto}	$35.50_{(1,6)}$**	$36.88_{(1,6)}$**	$17.55_{(1,6)}$**

Degrees of freedom are presented parenthetically, sub-plot effect (Date and Date × Location) *df* vary with differing number of sampling dates

* $p < 0.05$

** $p < 0.01$

declines only in intercanopy plants (Fig. 5). Intercanopy plant transpiration (T_{plant}) was significantly higher compared to understory plants (Table 1), the modest reductions at each location (Fig. 5) resulted in significantly lower T_{plant} from wet to dry periods with no significant interaction (Table 1).

Linear regressions showed mid-morning and daily integrated values to be strongly correlated, with mid-morning GEP_{plant} and R_{auto} explaining 89 and 80% of the variation in diurnally integrated values (Daily $GEP_{plant} = 0.0053 + 0.0324$*AM GEP_{plant}; $p \leq 0.001$ and Daily $R_{auto} = -0.0116 + 0.0510$*AM R_{auto}). In both cases, the slopes and intercepts of these relationships did not differ between intercanopy and understory plots. Applying these relationships to the 2008 data, daily integrated GEP_{plant} and R_{auto} summed across DOY 196–288 were predicted to be 72 and 74% higher in intercanopy plants, respectively, with GEP_{plant} in both locations exceeding integrated R_{auto} by 78–81% across this period. Cost/benefit regressions showed integrated R_{auto} to be significantly and positively correlated to integrated GEP_{plant} ($GEP_{plant} = 0.004 + 1.56$*$R_{auto}$, $F_{1,14} = 174.19$; $p \leq 0.001$; Fig. 6); the slopes and intercepts of the individual lines fit to intercanopy and understory plots did not differ in slope ($F_{1,12} = 0.35$; $p = 0.56$) or intercept ($F_{1,13} = 0.22$; $p = 0.65$). Moreover, the R_{auto} versus GEP_{plant} relationship was significantly steeper in slope ($F_{1,28} = 21.6$; $p = 0.0001$) and was

significantly elevated ($F_{1,29} = 27.56$; $p \leq 0.0001$) compared to the 1:1 line (Fig. 6), indicating bush muhly had positive integrated carbon gain across these soil moisture conditions.

Discussion

We did not find mesquite canopies to have a strong, positive effect on soil moisture, even during a year with higher than average monsoon rainfall (2008 SPI = +1.16; Fig. 1) when such effects are considered likely (Bhark and Small 2003; Scanlon et al. 2007), and in contrast to results from other savanna systems showing consistently greater soil moisture under canopy dominants (D'Odorico et al. 2007). Early in the 2008 monsoon (DOY 180–220), soils did dry down to slightly lower $\theta_{25\,cm}$ under intercanopy bush muhly compared to understory levels (Fig. 4). In some cases, this may have been due to higher intercanopy plant T_{plant}, though this was not always the case (Fig. 4). Bush muhly can extend lateral roots into bare soil across its rooting zone (Gibbens and Lenz 2001). Thus, the greater differences between bush muhly and bare soil plots in the open and limited differences between these in the understory (Figs. 1 and 2), suggest this bunchgrass has access to more soil moisture in surrounding soils in the intercanopy (Casper et al. 2003), and that canopy interception and extraction of soil moisture even in bare soil areas in the under-canopy (Cable 1975; Belsky et al. 1989; Scott et al. 2008) limits soil moisture in the understory. These soil water differences likely underlay differences in individual plant growth (Fig. 3). Bunchgrass architecture varies to focus limiting resources to the rooting zone (Caldwell et al. 1983; Anderson and Toft 1993; Smith et al. 1997). Decreasing canopy area per unit basal area in understory grasses may reflect a more open canopy structure, allowing precipitation to more readily infiltrate, which may be important if tree canopy interception reduces rainfall reaching the plant.

Such canopy-level adjustment likely explains why GEP_{plant} were higher and GEP_{lai} were similar throughout the 2008 monsoon season (Fig. 4). Lower understory plant canopy area and volumes (Fig. 3) likely results in lower total leaf area per plant, reducing understory GEP_{plant}, but maintaining similar GEP_{lai} despite considerable variation in $A_{net-sat}$ and g_{s-sat} through the season (Fig. 4). This is similar to dynamics observed in desert shrubs growing in contrasting soils that differ in infiltration depth and persistence of seasonal rainfall (Hamerlynck et al. 2002). Such changes may also explain the higher intercanopy R_{auto} frequently observed across 2008; however, the large degree of within-location variation (Fig. 4) did not result in strong enough statistical support to our hypothesis that R_{auto}

Fig. 4 Intercanopy and understory bush muhly seasonal leaf-level light saturated **a** stomatal conductance ($g_{s\text{-}sat}$) and **b** photosynthesis ($A_{net\text{-}sat}$), **c** per-ground area whole-plant transpiration (T_{plant}), **d** aboveground autotrophic respiration (R_{auto}), and **e** whole-plant photosynthesis (GEP_{plant}) and **f** GEP on a green leaf area index basis (GEP_{lai}). Each *symbol* is the mean of 4 independent measures, *error bars* indicate ±1SE
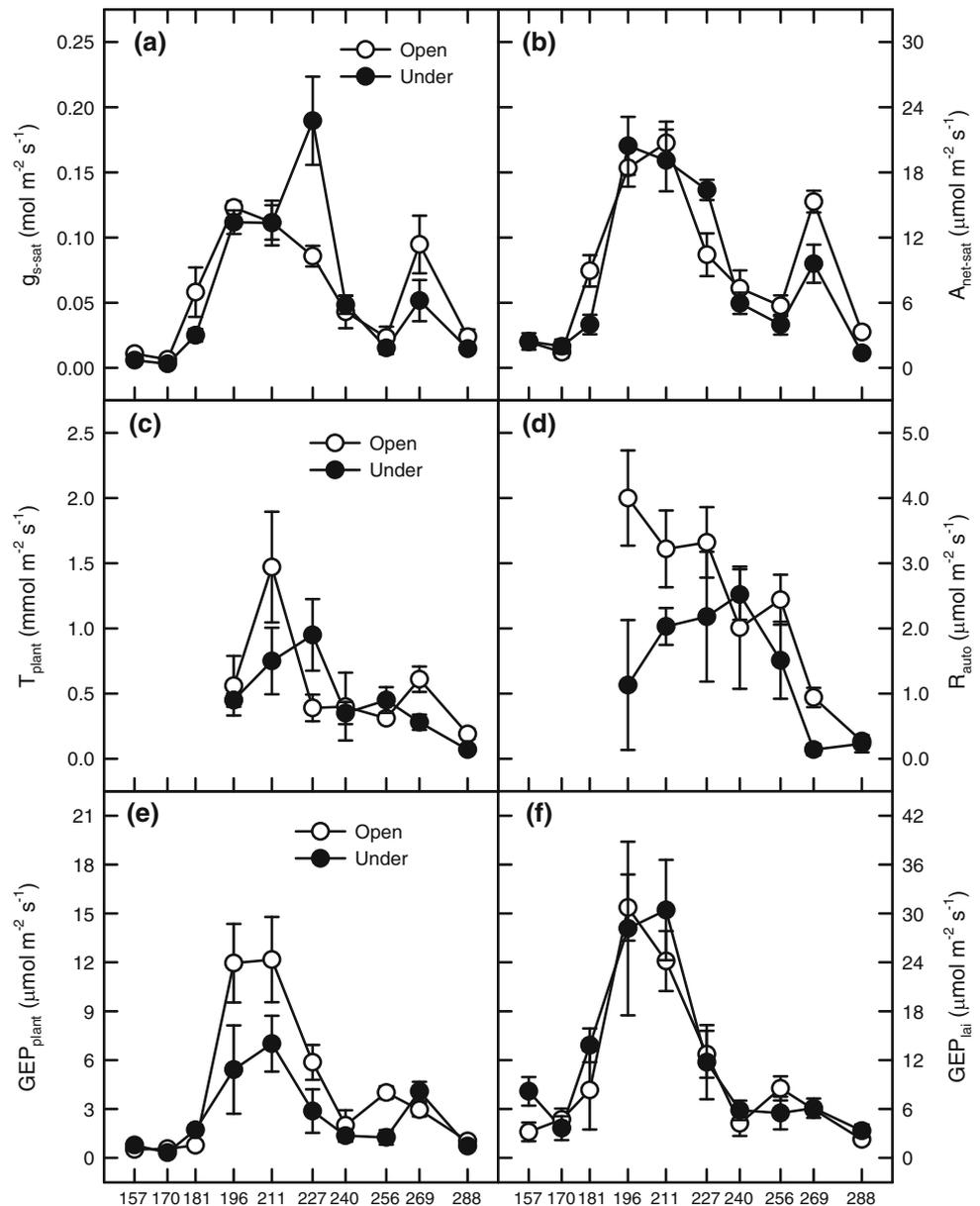
should be lower in understory plants (Table 1). In addition, similar ambient-light GEP_{lai} suggest lower GEP_{plant} in the understory was not due to light limitation (Smith et al. 1997); indeed, GEP_{lai} were similar to light-saturated leaf-level A_{net} (Fig. 4). The higher $g_{s\text{-}sat}$ and $A_{net\text{-}sat}$, in intercanopy bush muhly later in the 2008 season (DOY 240–280; Fig. 4) also suggest these plants have sufficient soil moisture to prolong late season activity. Similar GEP_{plant} during this period probably reflect both adjustments in leaf-level gas exchange and active canopy leaf area; the spike in understory $A_{net\text{-}sat}$ and GEP_{plant} on DOY 269 (Fig. 4) reflects contributions of a short-lived leaf cohort initiated in understory plants following the last rain of the 2008 season (DOY 254–255; Fig. 1). Intercanopy

bush muhly at this time did not initiate new leaves, and increased $A_{net\text{-}sat}$ and GEP_{plant} on DOY 256–269 likely reflect rapid up-regulation of leaf-level photosynthesis in response to this late-season rain (Fig. 4), suggesting intercanopy plants were better able to utilize late-season rains compared to understory plants. Overall, these results showed that leaf-level gas exchange, which were sometimes higher in undercanopy plants, did not necessarily translate to higher whole-plant performance (Fig. 4), a feature likely missed in previous leaf-level studies comparing intercanopy and undercanopy plant performance (Prider and Facelli 2004; Pugnaire et al. 2004).

Under drier conditions in 2009, diurnally integrated gas exchange indicated understory conditions were more
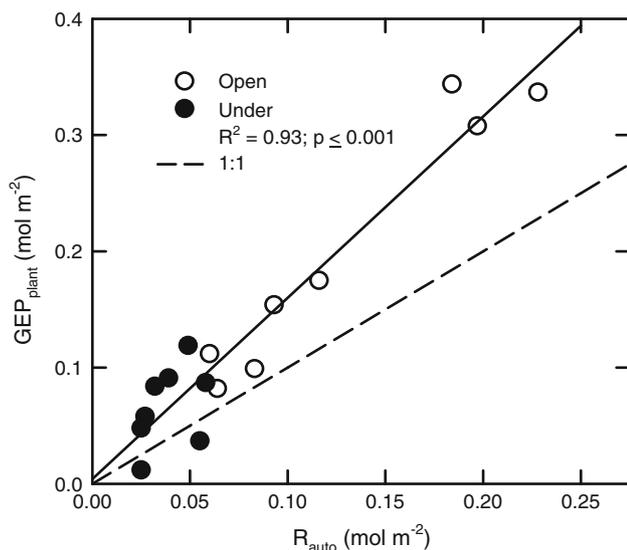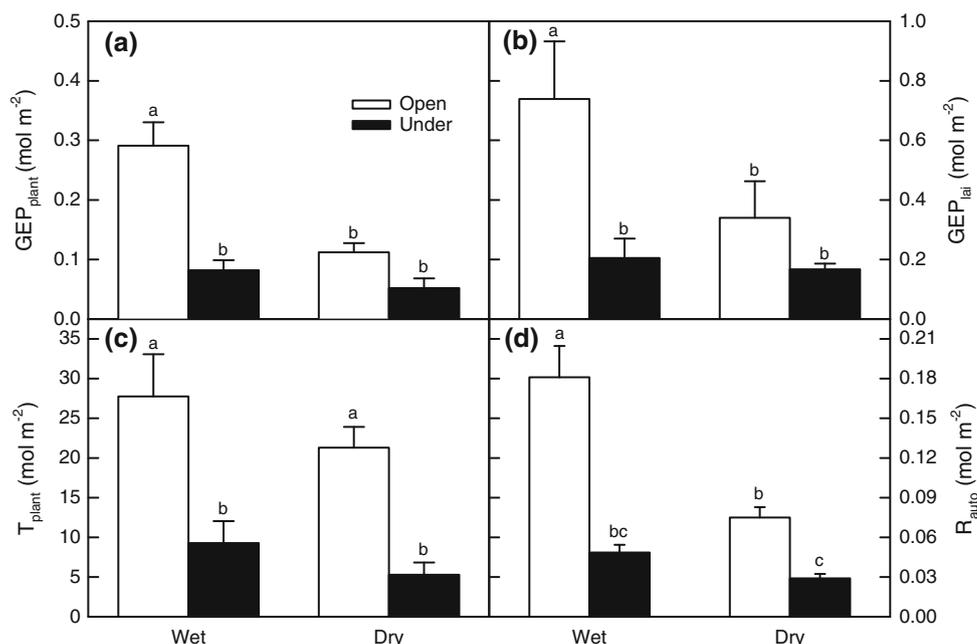
Fig. 6 Unforced linear regression of diurnally integrated per ground
area whole-plant photosynthesis (GEP_plant) and autotrophic above-
ground respiration (R_auto) of intercanopy and understory bush muhly
from the 2009 growing season. *Dashed 1:1 line* indicates carbon
break even (GEP_plant = R_auto)

and understory plants not apparent in 2008 (Fig. 4). Also, in
2009, understory plants may not have initiated as much leaf
growth compared to intercanopy plants, and relied more on
photosynthetically active stems which have markedly lower
photosynthetic and respiratory rates compared to leaves
(Smith et al. 1997; E.P.H., unpublished data). Previous
researchers have shown within a species, aridland under-
story plants can be more drought sensitive than intercanopy
conspecifics (Prider and Facelli 2004). Linear regressions of
GEP_plant with R_auto show that understory plants overlapped
and extended this relationship from intercanopy plants, and
R_auto/GEP_plant exceeds a 1:1 relationship, suggesting C-gain
could occur across all locations, even during a very dry
monsoon season. Thus, the low understory GEP_plant and
R_auto (Fig. 5) indicates understory plants sustain low carbon
returns at less risk, a typical drought-tolerant strategy
(Smith et al. 1997). However, our data only reflect a single
drying trend, and respiratory processes show distinct hys-
teresis in response to soil re-wetting (Sponseller 2007;
Jenerette et al. 2008). We had planned to quantify this, but
the limited precipitation after 31 July was likely insufficient
to induce grass activity (Emmerich and Verdugo 2008).
Even though the relationships derived from our 2009 diur-
nal measurements span a limited range of conditions, it
seems likely the 2008 mid-morning measurements reflect
daily integrated dynamics of higher sustained carbon gain in
intercanopy plants (see above). Bush muhly preferentially
allocates to aboveground biomass (Fernandez and Reynolds
2000). Thus, it seems likely photosynthesis in both loca-
tions was enough to offset aboveground and belowground
respiratory carbon loss across the range of inter- and intra-
annual soil moisture apparent here (Fig. 1).

limiting than in the intercanopy. GEP_plant, GEP_lai, T_plant and
R_auto were significantly higher in intercanopy plants and
changed to a greater degree than in understory plants, which
showed similar levels between the sampling periods
(Fig. 5). A critical threshold of 23 mm is needed to sustain
carbon uptake in these systems (Emmerich and Verdugo
2008), and it may be mesquite water use and canopy
interception early in the 2009 monsoon were enough to
induce differences in GEP_lai and R_auto between intercanopy

In conclusion, our findings do not readily support assertions that direct, positive soil hydrological effects enhance understory plant performance and are primary determinants to aridland community and ecosystem processes (Livingstone et al. 1997; Bhark and Small 2003; Devitt and Smith 2002; Lejeune et al. 2002; Prider and Facelli 2004; Caylor et al. 2004, 2005; D'Odorico et al. 2007). It may be that exceptional rainfall years (i.e. SPI exceeding +2.0) could lead to higher seasonal subcanopy soil moisture, but the lasting effects of these infrequent events have yet to be demonstrated. Thus, it seems direct, positive plant canopy effects are amelioration of light and temperature stress (Turner et al. 1966; Franco and Nobel 1989), improved nutrient availability (Titus et al. 2002), and refuge from herbivory (McAuliffe 1986), especially in establishing plants. Our findings show the sub-canopy is a hydrologically challenging environment, and that drought-tolerant bunchgrasses such as bush muhly that alter canopy structure (Fig. 3) in order to optimize carbon gain (Figs. 4, 6) can effectively utilize understory soil water, and possibly exclude other species, including the canopy dominant (Belsky et al. 1989; Anderson and Toft 1993; McClaran and Angell 2007; Simmons et al. 2008; Riginos 2009). Additionally, intra-species competition may also inhibit understory grass performance (Fernandez et al. 2002). Future research using a whole-plant approach across a coordinated multi-site, multi-species study, much as along the Kalahari rainfall gradient (Caylor et al. 2003; D'Odorico et al. 2007) would show if our initial findings reflect a general trend in savanna systems. Indeed, along the Kalahari rainfall gradient, where strong positive plant/soil moisture feedbacks have been demonstrated (D'Odorico et al. 2007), understory woody stem densities increased with decreasing mean annual rainfall, reaching maximum levels at a site with mean annual rainfall very similar (ca. 365 mm) to our SRER site, with declines at drier sites attributed to competitive exclusion (Caylor et al. 2003). Our study suggests the balance between positive and negative canopy effects on soil moisture depends on features other than mean annual rainfall. In addition to plant–plant interactions, cumulative long-term effects of repeated plant occupancy and biotic modification of soil structure (McAuliffe and McDonald 2006; McAuliffe et al. 2007), variation in canopy-dominant architecture (Belsky et al. 1989; Carlyle-Moses 2004) and variation in the distribution, intensity and duration of individual storms (Loik et al. 2004) may also play a highly important role in determining the nature of the critical hydrological and ecological linkages in these water-limited systems.

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