

SENSITIVITY OF MESQUITE SHRUBLAND CO₂ EXCHANGE TO PRECIPITATION IN CONTRASTING LANDSCAPE SETTINGS

DANIEL L. POTTS,^{1,5} RUSSELL L. SCOTT,² JESSICA M. CABLE,^{1,3} TRAVIS E. HUXMAN,¹ AND DAVID G. WILLIAMS^{3,4}

¹University of Arizona, Ecology and Evolutionary Biology, Tucson, Arizona 85721 USA

²Southwest Watershed Research Center, USDA-ARS, 2000 East Allen Road, Tucson, Arizona 85719 USA

³University of Wyoming, Department of Botany, Laramie, Wyoming 82071 USA

⁴University of Wyoming, Department of Renewable Resources, Laramie, Wyoming 82071 USA

Abstract. In semiarid ecosystems, physiography (landscape setting) may interact with woody-plant and soil microbe communities to constrain seasonal exchanges of material and energy at the ecosystem scale. In an upland and riparian shrubland, we examined the seasonally dynamic linkage between ecosystem CO₂ exchange, woody-plant water status and photosynthesis, and soil respiration responses to summer rainfall. At each site, we compared tower-based measurements of net ecosystem CO₂ exchange (NEE) with ecophysiological measurements among velvet mesquite (*Prosopis velutina* Woot.) in three size classes and soil respiration in sub-canopy and inter-canopy micro-sites. Monsoonal rainfall influenced a greater shift in the magnitude of ecosystem CO₂ assimilation in the upland shrubland than in the riparian shrubland. Mesquite water status and photosynthetic gas exchange were closely linked to the onset of the North American monsoon in the upland shrubland. In contrast, the presence of shallow alluvial groundwater in the riparian shrubland caused larger size classes of mesquite to be physiologically insensitive to monsoonal rains. In both shrublands, soil respiration was greatest beneath mesquite canopies and was coupled to shallow soil moisture abundance. Physiography, through its constraint on the physiological sensitivity of deeply rooted woody plants, may interact with plant-mediated rates of soil respiration to affect the sensitivity of semiarid-ecosystem carbon exchange in response to episodic rainfall.

Key words: eddy covariance; flux duration analysis; net ecosystem CO₂ exchange; photosynthesis; plant–water relations; *Prosopis velutina*; respiration.

INTRODUCTION

Hydrologists and ecologists, working in collaboration, have generated a number of conceptual models to address complex plant–soil–water interactions in semiarid ecosystems undergoing woody-plant encroachment (Wilcox and Breshears 1995, Ludwig and Tongway 2000, Reynolds et al. 2004, Huxman et al. 2005, Ludwig et al. 2005). In one such model, Huxman et al. (2005) recognized that physiography (landscape setting) constrains woody-plant effects on local and regional hydrologic budgets by influencing the availability of groundwater accessible to plants. Despite these recent developments in the understanding of the impacts of woody plants on water cycling, the effects of woody plants on carbon cycling, and on ecosystem CO₂ exchange in particular, remains poorly understood (Scott et al. 2006b).

In arid and semiarid ecosystems, net primary productivity is limited by the availability of water (Noy-Meir 1973, Webb et al. 1978, Sala et al. 1988, Huxman et al.

2004b). In such systems, long periods of dry conditions are interrupted by unpredictable and episodic precipitation events (Noy-Meir 1973, Reynolds et al. 2004). The sudden presence of water may trigger a complex cascade of physical, chemical, and biological processes (Sala and Lauenroth 1982, Huxman et al. 2004a, Ludwig et al. 2005, Potts et al. 2006a, b, Scott et al. 2006a). Investigations into the effects of episodic rainfall on organisms reveal a complex interplay between rainfall-event characteristics, such as magnitude and seasonal timing, and organismal natural history (BassiriRad et al. 1999, Schwinning and Ehleringer 2001, Fierer and Schimel 2003, Cable and Huxman 2004, Fravolini et al. 2005, Potts et al. 2006a).

The biological impacts of episodic rainfall span spatial and temporal scales (Schwinning and Sala 2004) that range from small storms affecting microbial activity over a few hours to a few days (Lange 2001, Fierer and Schimel 2003, Cable and Huxman 2004) to decadal trends in annual rainfall influenced by El Niño–Southern Oscillation affecting regional fire frequencies (Swetnam and Betancourt 1998). At an intermediate time scale, high-intensity, localized convective storms associated with the North American monsoon during July–September (Adams and Comrie 1997) trigger seasonal plant and soil microbial activity with implications for ecosystem carbon and water exchange. Future variabil-

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⁵ Present address: Buffalo State College, Biology Department, 1300 Elmwood Ave., Buffalo, New York 14222 USA. E-mail: pottsd@buffalostate.edu

ity in the intensity and duration of the North American monsoon will likely interact with human-mediated changes in vegetation cover to affect annual net primary productivity, nutrient cycling, and carbon storage in these ecosystems (Weltzin et al. 2003).

The physiological sensitivity of plants to episodic rainfall varies between plant functional types (Ogle and Reynolds 2004, Scott et al. 2006b) and is potentially mediated by ontogeny (deSoyza et al. 1996, Potts et al. 2006c), phenology (Snyder et al. 2004), and site characteristics such as soil texture and antecedent moisture conditions (Noy-Meir 1973, Huxman et al. 2004, Potts et al. 2006a). Physiography, through its effects on water and nutrient availability, may also impact plant performance (Knapp et al. 1993, Singh et al. 1998). For example, photosynthesis may be decoupled from rainfall in riparian settings where groundwater is available to plants (Potts and Williams 2004, Scott et al. 2006b).

In addition to direct effects on ecosystem CO₂ exchange via photosynthesis, plants may alter the horizontal and vertical distribution of soil carbon, nitrogen, and moisture, thereby influencing respiration rates of soil microbes (e.g., Huxman et al. 2004). At the soil surface, plant litter may alter soil properties to favor increased infiltration capacity (Bhark and Small 2003) and increased soil organic matter (Kelly and Burke 1997) with the effect of increasing soil microbial respiration. Deeper in the soil profile, patterns of root uptake, exudation, and turnover influence resource availability to microbial communities with corresponding effects on respiration rates (Reynolds et al. 1999). Furthermore, shrub canopies may interact with rainfall-event magnitude to increase or decrease sub-canopy soil moisture through rainfall inception or shading the soil surface (Dunkerley 2000) and thereby differentially influence the relative contribution of microbes to ecosystem CO₂ exchange (Huxman et al. 2004, Loik et al. 2004, Jarvis et al. 2007).

Tower-based micrometeorological techniques such as eddy covariance provide a means to integrate plant- and soil-microbe-mediated processes to assess ecosystem responses to rainfall at the inter- and intra-annual time scale (Goulden et al. 1996, Baldocchi 2003). Net ecosystem exchange of CO₂ (NEE) measured using eddy covariance integrates carbon exchange responses of all organisms within the ecosystem and physical and chemical processes triggered by sudden moisture availability (Xu et al. 2004, Scott et al. 2006b). Combined with measurements of component processes (e.g., soil and leaf level CO₂ exchanges), NEE measurements can be a powerful way to evaluate factors constraining whole ecosystem function (Huxman et al. 2003, Potts et al. 2006c). To date, few studies have examined the interplay between physiography and woody plants in constraining semiarid ecosystem energy and matter transformations. A more complete understanding of the influence of physiography on ecosystem CO₂

exchange may improve regional predictions of the impact of climate variability and ongoing woody-plant encroachment on carbon cycling while enhancing our understanding of the balance between plant- and soil-microbe-mediated processes in relation to rainfall in water-limited ecosystems.

In the present study, we hypothesized that physiography, through its impact on plant-accessible groundwater, would interact with rainfall to influence seasonal dynamics of photosynthesis and respiration at the ecosystem scale. We addressed this hypothesis by contrasting upland and riparian shrublands dominated by velvet mesquite (*Prosopis velutina* Woot.). We predicted that changes in ecosystem CO₂ exchange resulting from the onset of monsoonal rainfall would be greatest in the upland setting. Furthermore, we predicted that increased sensitivity of ecosystem CO₂ exchange in the upland shrubland would be derived in part from the greater physiological sensitivity of mesquite to shallow soil wetting than in the riparian shrubland, where shallow groundwater was accessible to mesquite. In contrast, we predicted that sensitivity of soil respiration to the onset of monsoonal rains would be greatest in micro-sites beneath mesquite canopies in the riparian shrubland owing to the greater carbon and nutrient accumulation in these soils from mesquite litter and overall increased primary production in the riparian shrubland.

MATERIALS AND METHODS

Site description

We selected the riparian and upland shrubland sites used in this study because of their suitability for tower-based measurements of ecosystem CO₂ exchange, similarities in elevation and soil texture, similarities in the abundance and size-distribution of mesquite, and the presence of C₄ bunchgrasses. The upland shrubland was located mid-slope on a broad, alluvial fan ~40 km south of Tucson, Arizona, USA on the Santa Rita Experimental Range (31°49' N, 110°51' W, elevation 1120 m above sea level). Vegetation consisted of mesquite growing in a matrix of native and nonnative perennial C₄ bunchgrasses (*Digitaria californica* (Benth.) Henr. and *Eragrostis lehmanniana* Nees, respectively), sub-shrubs (most commonly *Isocoma tenuisecta* Greene), and scattered *Opuntia* spp. Total canopy cover of perennial grasses, forbs, and sub-shrubs was ~22%. Mesquite cover was ~35%, and mean overstory mesquite plant area index (LI-2000; LI-COR, Lincoln, Nebraska, USA) ranged from 0.22 (without leaves) to 0.41 (fully leafed). Within 30 m of the tower, mesquite ranged in height from 0.25 to 6.5 m with a mean height of 2.5 m (SD = 1.6 m, *n* = 95 mesquite). Soils at the upland site were a coarse-textured sandy loam derived from Holocene-aged alluvium eroded from the nearby Santa Rita Mountains. Growing-season (April–September) precipitation at the upland site during 2005 was 256 mm, slightly above the historical mean of 229 mm at the

long-term rain gauge 0.5 km away (1936–2006 at Enclosure 45, Santa Rita Experimental Range, Arizona, USA, 31°49' N, 110°52' W, elevation 1138 m).

The riparian shrubland was located in the San Pedro Riparian National Conservation Area on a terrace adjacent to a perennial reach of the San Pedro River, ~12 km east of Sierra Vista, Arizona, USA (31°34' N, 110° 8' W, elevation 1237 m above sea level). Vegetation at this site consisted of mesquite growing in a matrix of big sacaton (*Sacaton wrightii* Munro ex Scribn.), a perennial C₄ bunchgrass commonly found on floodplain terraces in southern Arizona. Total canopy cover of perennial grasses, forbs, and sub-shrubs was ~25%. Mesquite cover was ~55%, and mean overstory plant area index of the mesquite overstory ranged from 0.25 (without leaves) to 0.71 (fully leafed). Within 30 m of the tower, mesquite ranged in height from 0.2 to 7 m tall, with a mean height of 3.5 m (SD = 1.28 m, $n = 90$ mesquite). Depth to groundwater measured by observation wells was 6.5 m. The alluvial soils were mainly sandy-loams interspersed with gravel and clay layers. Growing-season (April–September) precipitation at the riparian site during 2005 was 252.9 mm, slightly above the historical mean of 233.4 mm at the nearest long-term rain gauge (Tombstone, Arizona, USA, 31°43' N, 110°04' W, elevation 1384 m above sea level).

Soil moisture measurements

We measured volumetric soil water content (θ) using water-content reflectometers (Model CS616-L; Campbell Scientific, Logan, Utah, USA) inserted at 5, 10, 20, 30, and 50 cm depths located in an inter-mesquite canopy position and beneath a large mesquite in the riparian and upland shrublands and were calibrated for the soils at each site. Measurements were recorded automatically every 30 minutes and stored on a data logger in the field (Model CR-10X; Campbell Scientific). We integrated daily mean θ measurements to estimate moisture storage to 50 cm depth (S_{50}) using a geometric integration. This integration assumed that θ changed linearly between probes with increasing depth and that the soil surface (defined as 0 cm depth) had a constant θ equal to 0. To assess relative changes in soil moisture during the growing season, we standardized daily S_{50} values to the maximum S_{50} value observed in each location. The resulting unitless metric facilitated qualitative, within-site comparisons of the seasonal responsiveness of soil moisture to monsoonal rainfall.

Tower-based collection and analysis of NEE

A three-dimensional sonic anemometer (Model CSAT-3; Campbell Scientific) and an open-path infrared gas analyzer (LI-7500; LI-COR) were mounted on 6-m towers to record wind speed and direction, temperature, and the concentrations of water vapor and carbon dioxide in the riparian and upland shrublands. Infrared gas analyzers were routinely zero- and span-calibrated using a CO₂/H₂O-free gas, a standard gas (CO₂) and a

dew point generator every one to two months, or whenever CO₂ or H₂O concentrations fell outside of reasonable boundaries. Both sites have fetches greater than the typical 50–200 m turbulent flux source areas (Schmid 1997). At the upland site the fetch is quite homogeneous and very extensive (more than several square kilometers), while the riparian tower stood in the middle of a less homogeneous patch ~500 m east–west by 500 m north–south.

Data were sampled at 10 Hz, averaged and calculated to 30-minute covariances, and recorded by a datalogger (CR5000; Campbell Scientific) following the methodology of Scott et al. (2006b). Thirty-minute data were screened for non-steady-state conditions by excluding fluxes measured when the variances of CO₂ or H₂O concentrations exceeded the 95% threshold of their distributions. By convention, positive NEE values indicate net carbon loss and negative NEE values indicate net carbon gain by the ecosystem. We examined only daylight NEE data collected from time periods when friction velocity was >0.15 m/s. Because we were interested in a probability distribution of flux, we did not gap-fill missing NEE values.

To examine seasonal changes, the dynamics of carbon exchange associated with the onset of monsoon precipitation, the growing season was divided into two approximately equal parts: a pre-monsoon period (day of year 130–199) and a monsoon period (day of year 200–270). This division of the growing season at day of year 199 is based on the beginning of monsoon circulation according to atmospheric conditions defined by the National Weather Service in Tucson, Arizona, USA during 2005. To address the prediction that the greater physiological sensitivity of upland mesquite would translate to greater sensitivity of NEE to monsoonal rainfall in the upland site than in the riparian site, we compared pre-monsoon and monsoon daylight NEE fluxes for the two portions of the growing season at each site using flux duration curves (Huxman et al. 2004, Potts et al. 2006c). Flux duration curves are the ecosystem flux analog of stream flow duration curves used commonly in hydrology (Huxman et al. 2004c, Potts et al. 2006c). Flux duration analysis ranks and assigns a frequency to time-series NEE values plotted as a function of the probability in time that a flux value will be equaled or exceeded. Flux duration analysis incorporates episodic periods of high activity associated with rainfall and extended periods of low activity associated with dry conditions into a single calculation. By yielding a probabilistic description of NEE for a given period of interest, flux duration analysis complements traditional time-series and cumulative approaches in the interpretation of tower-based measurements of NEE. Briefly, NEE data for the period of interest at each site was assigned a rank in order of descending magnitude, from positive to negative. An exceedence frequency (E) was calculated for each ranked value (r) according to the formula:

$$E = [r/(n + 1)] \times 100$$

where n is the number of ranked NEE values for the period of interest.

We used Kolmogorov-Smirnov (K-S) tests to compare pre-monsoon and monsoon flux duration curves to one another at each site and linear regression (JMP In 4.0; SAS Institute, Cary, North Carolina, USA) to correlate site-specific pre-monsoon and monsoon flux duration curves to one another. In effect, we used linear regression to quantify site-specific shifts in the shape of flux frequency distributions in relation to the onset of monsoon rains. If NEE were unresponsive to monsoon rains, then the slope of the regression would be equivalent to 1. Alternatively, if monsoon rains stimulated NEE, then the slope of the regression would be greater than 1. The slope of the linear correlation between pre-monsoon and monsoon flux duration curves therefore provides an easily quantified index of NEE sensitivity to the monsoon that may be compared between sites.

Plant physiological measurements

To characterize plant physiological sensitivity to monsoonal rainfall, we selected five mesquite in each of three size classes within the flux footprint of micrometeorological towers present in the upland and riparian shrubland sites for repeated measurements during 2005. Individual mesquite were selected because they appeared in a representative, healthy condition and they fit into one of the a priori size classes (Table 1). Canopy dimensions of each mesquite plant were estimated with a meter stick. Mean canopy diameter was calculated from measurements made on the cardinal compass directions.

To assess seasonal patterns of plant-water status, we measured predawn leaf water (ψ_{pd}) using a Scholander-type pressure chamber (PMS Instruments, Corvallis, Oregon, USA). Measurements were made between 01:30 and 02:30 hours. Middle canopy height mesquite leaves were cut with a sharp blade, placed in a plastic bag, sealed, and stored in a plastic cooler before measurement with the pressure chamber. At the upland shrubland, measurements of ψ_{pd} were made prior to and after the onset of monsoon circulation on day of year 140, 155, 197, 230, and 273, at the riparian shrubland, ψ_{pd} was measured on day of year 131, 161, 191, 228, and 271.

To assess the physiological sensitivity of mesquite and their potential contribution to ecosystem-level patterns of CO₂ exchange, we measured seasonal patterns of maximum rates of net CO₂ assimilation (A_{net}) and stomatal conductance of H₂O (g_s). We conducted measurements of leaf gas exchange periodically throughout the growing season, between 09:00 and 11:00 hours, a period of diurnal behavior that is reflective of daily CO₂ exchange patterns (Naumburg et al. 2003). We used a portable photosynthesis system (LI-6400; LI-COR) on

TABLE 1. Canopy characteristics of mesquite by size class, expressed as mean \pm SD ($n = 5$ individuals per size class).

Canopy characteristic	Height (m)	Mean diameter (m)
Upland shrubland		
Small	0.72 \pm 0.09	1.31 \pm 0.31
Medium	1.78 \pm 0.26	2.15 \pm 0.42
Large	3.86 \pm 0.59	4.15 \pm 0.51
Riparian shrubland		
Small	0.95 \pm 0.15	0.97 \pm 0.13
Medium	2.34 \pm 0.21	2.72 \pm 0.14
Large	4.14 \pm 0.19	4.78 \pm 0.29

sunlit leaves positioned at middle canopy height of each mesquite. Within the LI-6400 leaf cuvette, the red/blue light source was set to 1500 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and CO₂ concentration was set to 370 $\mu\text{mol}/\text{mol}$. Vapor pressure deficit and air temperature were set to ambient conditions in the cuvette during each measurement period. Leaves were collected in the field after gas exchange measurements and their area were estimated using a desktop scanner and imaging software (Scion Image; Scion, Frederick, Maryland, USA). At the upland shrubland, midday leaf gas exchange was measured on day of year 140, 155, 197, 230, and 273, at the riparian shrubland, midday leaf gas exchange was measured on day of year 131, 161, 191, 228, and 271.

Plant physiological data were found to be normally distributed prior to statistical analysis (JMP In 4.0). We used repeated-measures ANOVA to examine the dependence of ψ_{pd} , g_s , and A_{net} on mesquite size class, time, and their interaction. The interaction of time and mesquite size class is reported as Wilks' lambda F values.

Soil respiration measurements

To measure soil respiration, we first installed chamber bases (PVC, 10.16 cm diameter) into the soil (5 cm deep) within a 20 m radius of the eddy covariance tower at each site. Bases were situated in open areas ("intercanopy," upland shrubland, $n = 2$; riparian shrubland, $n = 3$) and beneath the canopy of a large mesquite ("subcanopy," upland shrubland, $n = 2$, riparian shrubland, $n = 5$). We measured mid-morning (08:00–09:30 hours) soil respiration (R_s) during the pre-monsoon (day of year 172 and 175 in the riparian and upland shrublands, respectively) and monsoon (day of year 231 and 227 in the riparian and upland shrublands, respectively) periods. To make a measurement, we fit a tightly sealed, cylindrical PVC chamber (volume of 3 L) upon the chamber bases. This static chamber formed a closed loop system with a LI-820 infrared gas analyzer (LI-COR), where air was drawn from the chamber, through the gas analyzer and then returned with a pump (0.8 L/min flow rate). In addition, the chamber was fit with a 2.5 mm wide, 25 mm long capillary tubing vent (Davidson et al. 2002) and a 4.5-V microfan to promote

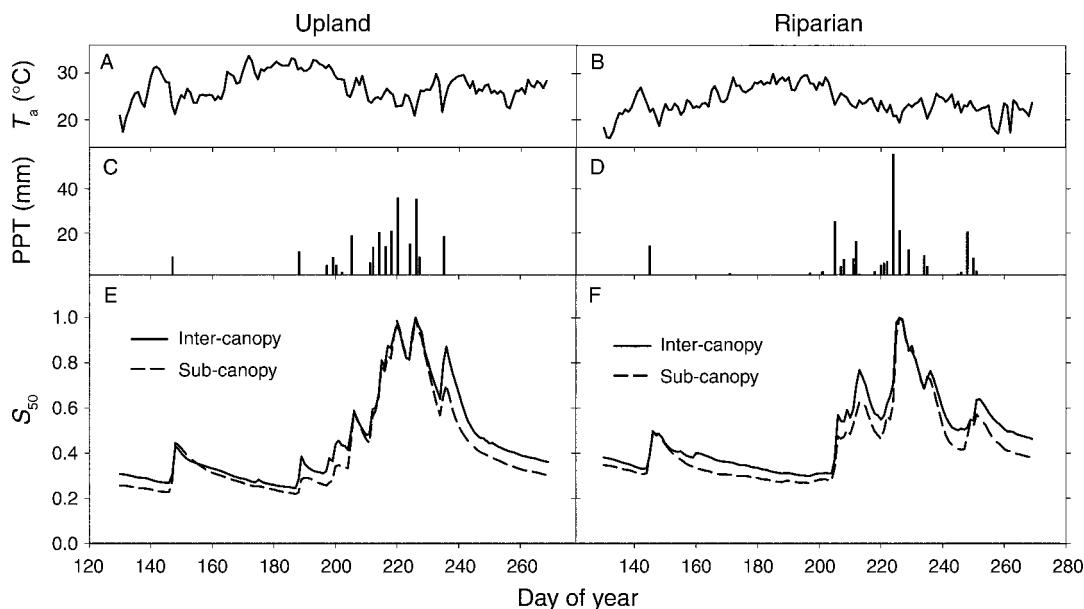


FIG. 1. (A–D) 2005 growing season mean daily temperature (T_a) and precipitation (PPT) by event in (A, C) an upland and (B, D) riparian mesquite shrubland in southern Arizona, USA. (E, F) Standardized daily 50-cm soil moisture storage (S_{50}) in an upland and riparian mesquite shrubland. Solid lines indicate inter-canopy soil moisture storage; dotted lines indicate soil moisture storage beneath a mesquite canopy.

chamber atmosphere mixing. Chamber CO_2 concentration was sampled at 1 Hz for 2 minutes and converted to flux density with volume/area corrections. We log-transformed R_s data to meet assumptions of normality and used ANOVA to test the factorial effects of physiography, season, and micro-site on soil respiration rates.

RESULTS

NEE sensitivity to monsoonal rains

Typical of southern Arizona, the pre-monsoon growing season (day of year 130–199) was characterized by prevailing hot, dry conditions at both sites (Fig. 1A–D). Throughout this period, soil-moisture storage (S_{50}) declined as water stored in the profile from cool-season precipitation was lost to evapotranspiration (Fig. 1E, F). Following the onset of monsoonal rains (~day of year 200), S_{50} increased and peaked during the middle of August (~day of year 230) at both sites. Overall patterns of growing-season S_{50} were similar between micro-sites, although inter-canopy micro-sites tended to have consistently greater S_{50} than sub-canopy micro-sites, particularly before and after the monsoon period.

During the winter and early spring of 2005, patterns of net exchange of CO_2 (NEE) were similar in the upland and riparian shrublands (Fig. 2). With the onset of warm, dry conditions associated with the pre-monsoon period of the growing season around day of year 130, NEE became more negative in the riparian shrubland while remaining near 0 in the upland shrubland. This divergence is consistent with the presence of plant-accessible groundwater in the riparian setting that

supports photosynthesis and low rates of soil CO_2 efflux in the absence of surface soil wetting from precipitation. In both shrublands, shallow soil wetting associated with monsoonal rains stimulated a period of increased ecosystem respiration (illustrated by an increase in NEE values toward more positive values, see Fig. 2). Later in the monsoon period, NEE fluxes became increasingly negative as autotrophic activity peaked around day of year 260 at both sites. By day of year 330, ecosystem carbon exchange returned to pre-monsoon levels in both systems.

Flux duration analysis of NEE for the two sites illustrates shifts in the frequency and magnitude of CO_2 exchange during the 2005 growing season (Fig. 3). In the upland shrubland, a flattened flux-duration curve shows that pre-monsoon daytime NEE was consistently near 0. The probability value where the flux duration curve of NEE crosses 0 indicates how frequently the ecosystem was a net assimilator of CO_2 . In this case, the upland shrubland had negative NEE just 29% of the time (Fig. 3A). Pre-monsoon daytime NEE fluxes in the riparian shrubland stand in sharp contrast to those in the upland. Here, flux duration analysis reveals that NEE remained negative 87% of the time, indicating consistent daytime assimilation CO_2 in the absence of significant rainfall (Fig. 3B).

In both the upland and riparian shrublands there was a significant shift in the flux-duration curve of NEE with the onset of the monsoon (K-S test, $D = 0.49$, $P < 0.001$ and $D = 0.33$, $P < 0.001$, respectively). In the upland shrubland, the onset of the monsoon caused negative NEE fluxes to increase in magnitude (indicated by a

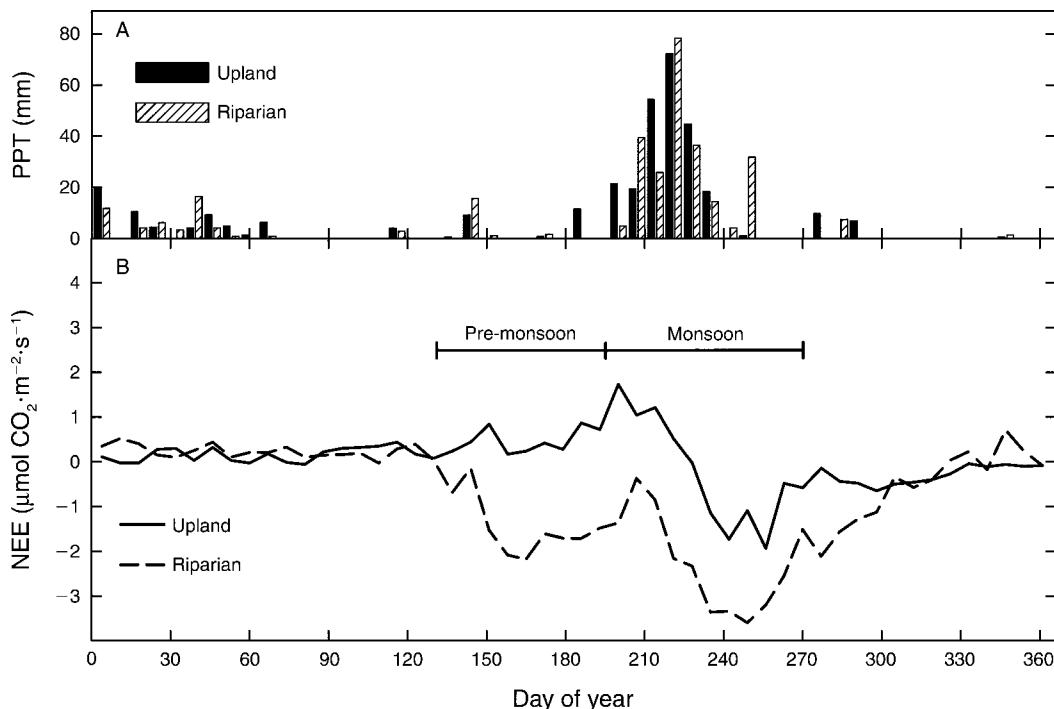


FIG. 2. (A) Weekly total precipitation (PPT) by event in an upland and riparian mesquite shrubland (solid and hatched bars, respectively). (B) Weekly mean net ecosystem exchange of CO₂ in an upland (solid line) and a riparian mesquite shrubland (dotted line) in southern Arizona, USA, during 2005. Negative net ecosystem exchange (NEE) values indicate increasing ecosystem carbon assimilation.

downward shift in the flux duration curve) and to become more frequent (indicated by a rightward shift in the point where the flux duration curve crosses the 0 value of NEE). In the riparian shrubland, the onset of the monsoon triggered an increase in the magnitude of negative NEE fluxes but had little effect on the frequency with which negative NEE occurred. Shallow soil wetting during the monsoon altered the frequency but not the magnitude of daytime positive NEE values in the upland shrubland. In the riparian shrubland however, monsoonal rainfall increased the magnitude of positive daytime NEE fluxes while having little impact on their frequency.

To quantify and compare shifts in frequency and magnitude of NEE fluxes to the onset of the monsoon, we used least-squares linear regression to compare flux-duration curves of NEE prior to and after the onset of the monsoon (Fig. 4). We interpret the magnitude of the linear regression slope as a quantification of NEE sensitivity to the onset of the monsoon. The regression slope in the upland shrubland (mean = 3.26, 95% CI = 2.94–3.54, $n = 99$) was distinct from that of the riparian shrubland (mean = 1.71, 95% CI = 1.67–1.74, $n = 99$), and both were greater than the null hypothesis value of 1. A greater regression slope in the upland shrubland suggests that ecosystem carbon metabolism was more sensitive to monsoonal rainfall in the upland than in the riparian shrubland.

Plant physiological and soil respiration sensitivity to monsoonal rains

We predicted that the physiological sensitivity of mesquite to the onset of monsoonal rainfall would be dependent on the accessibility of alluvial groundwater during the pre-monsoon period. In the upland shrubland where no alluvial groundwater was present, pre-dawn plant-water potential (ψ_{pd}) declined during the pre-monsoon period (day of year 141–197) among all mesquite size classes, consistent with declining soil moisture availability and increasing transpiration demand from rising daytime temperatures, high vapor-pressure deficits and full development of the canopy (Fig. 5A). However, values of ψ_{pd} of the largest mesquite were distinctly less negative on day of year 197 than those of the smaller size classes (post-hoc Student's t test, $t = 6.05$, $df = 13$, $P < 0.001$). Among the smaller size classes of riparian mesquite, ψ_{pd} declined during the pre-monsoon period (day of year 131–191), while ψ_{pd} remained constant among the largest mesquite (Table 2; size class \times time, $P = 0.02$).

All size classes of mesquite responded strongly to the onset of monsoon circulation in mid-July (day of year 199) in the upland shrubland and among smaller size classes in the riparian shrubland. The last ψ_{pd} measurements of the 2005 growing season in late September revealed declining soil moisture availability among upland mesquite. By the end of September, ψ_{pd} of the

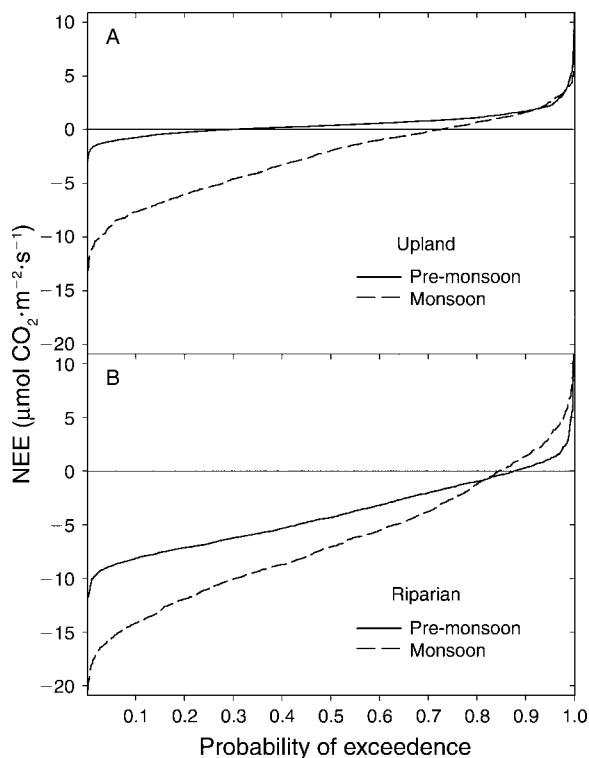


FIG. 3. Flux duration curves of daytime 30-minute averaged NEE in (A) an upland and (B) a riparian mesquite shrubland during the pre-monsoon (day of year 130–199) and monsoon (day of year 200–270) portions of the growing season (solid and dotted lines, respectively). Negative NEE values indicate increasing ecosystem carbon assimilation.

smallest upland mesquite were distinctly more negative than those of the larger mesquite (post-hoc Student's *t* test, $t = 4.97$, $df = 13$, $P = 0.003$).

In the upland shrubland, mesquite in all three size classes had similar, low levels of conductance (g_s) during the pre-monsoon (Fig. 5C). In contrast, the pre-monsoon in the riparian shrubland was marked by size-class divergence in g_s : larger mesquite increased g_s slightly while the smallest mesquite maintained low values (Fig. 5D). After the onset of the monsoon (day of year 200), g_s increased among all classes of upland mesquite and among the smallest riparian mesquite. Following the end of monsoonal rains, g_s declined sharply among upland mesquite consistent with increasing vapor pressure deficits and drying surface soils following the end of monsoonal precipitation in late August.

Prior to monsoon circulation, upland mesquite maintained low levels of photosynthesis (A_{net}) while in the riparian shrubland, larger mesquite had comparatively high A_{net} (Fig. 5E, F). Following the onset of monsoonal precipitation, A_{net} of upland mesquite increased dramatically and as did A_{net} of the smallest riparian mesquite. In the upland shrubland where mesquite shrubs were dependent on shallow soil moisture, A_{net} peaked around day of year 230, declining again by late September.

Overall patterns of soil respiration (R_s) were similar in the upland and riparian shrublands (Fig. 6A, B). During the pre-monsoon, low R_s values reflect prevailing hot and dry shallow soil conditions. While overall R_s was greater in the riparian shrubland (Table 3, R_s , site; $P = 0.0019$), in contrast with our prediction, R_s was similarly sensitive to the onset of monsoonal rains at both sites (Table 3, site \times season; $P = 0.16$). During the monsoon, R_s increased in sub-canopy micro-sites to a greater extent than those in inter-canopy locations in both shrublands (Table 3, micro-site \times season; $P = 0.0016$).

DISCUSSION

In the present study, we hypothesized that physiography, through the presence of groundwater accessible to plants, would influence the sensitivity of net ecosystem CO_2 exchange to monsoonal rains through limits on the physiological sensitivity of woody plants and the responsiveness of soil respiration to rainfall. We found that patterns of seasonal plant-water status and rates of leaf gas exchange of upland mesquite was coupled to the onset of monsoonal rains and that this physiological sensitivity was expressed as increased sensitivity of NEE at the ecosystem scale. In contrast, apparent access to shallow groundwater by the larger size classes of mesquite in the riparian shrubland, along with increased rates of soil respiration contributed to a partial decoupling of NEE in response to monsoonal rains.

We used flux-duration analysis of tower-based NEE data to quantify and compare the sensitivity of two semiarid shrubland ecosystems to monsoonal rainfall. While the application of duration analysis to hydrological time-series data is long established (Searcy 1959), the application of these tools to terrestrial ecological

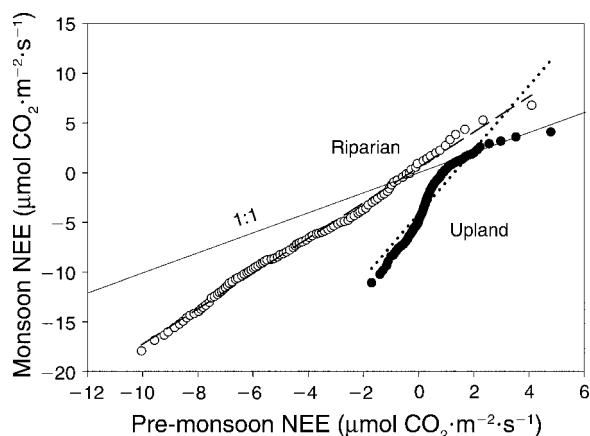


FIG. 4. Linear correlation of daytime, 30-minute averaged NEE flux-duration curves prior to (day of year 130–199) and during the monsoon (day of year 200–270) in an upland shrubland (solid circles, dotted line) and a riparian shrubland (open circles, dashed line) during 2005. The solid line is the 1:1 line. Slope magnitude is interpreted as an index of NEE sensitivity to monsoonal rains.

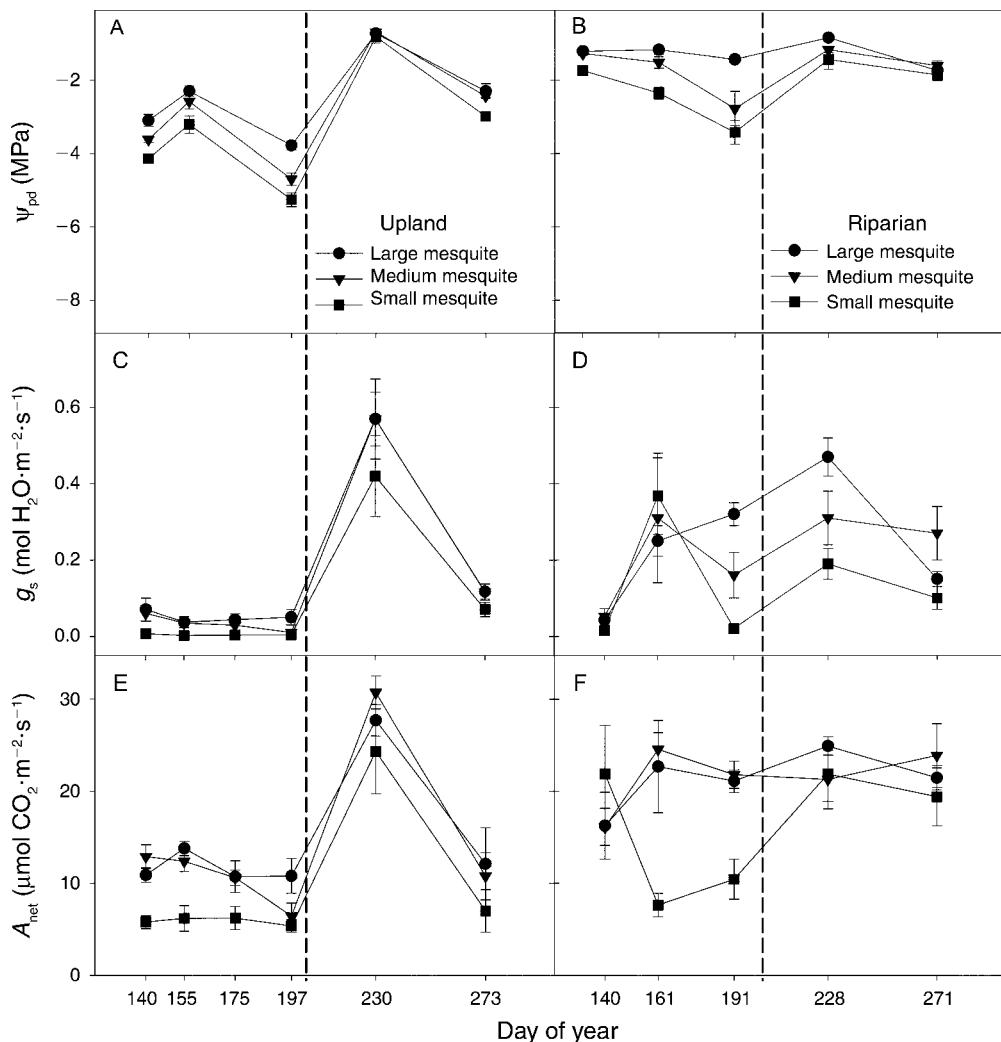


FIG. 5. Predawn leaf-water potential (ψ_{pd} , mean \pm SE) of mesquite in three size classes during 2005 in (A) an upland and (B) a riparian shrubland. Dashed lines indicate the onset of monsoon circulation on day of year 200. (C, D) Mid-morning stomatal conductance of water vapor (g_s , mean \pm SE) among mesquite in three size classes during 2005 in (C) an upland and (D) a riparian shrubland. (E, F) Mid-morning net assimilation of CO_2 by leaves (A_{net} , mean \pm SE) among mesquite in three size classes during 2005 in (E) an upland and (F) a riparian shrubland.

time-series data remains largely unexplored. Huxman et al. (2004c) used flux-duration analysis of tower-based NEE time-series to succinctly illustrate differences between a “pulse-driven” and “steady-state” ecosystem (a semiarid grassland and a conifer forest, respectively). Potts et al. (2006c) compared 2003 growing-season NEE fluxes in the present study’s riparian shrubland with those of a nearby riparian grassland to demonstrate increased sensitivity of grassland NEE to monsoonal rainfall. As longer duration NEE data sets become more widely available, a probabilistic perspective, such as provided by flux-duration analysis, may compliment traditional time-series analysis to better understand the ways in which terrestrial ecosystems respond to temporal environmental variability.

In both shrublands, we observed a seasonally dynamic influence of shrub size class on plant-water status. Late in the pre-monsoon period (DOY 197), large mesquite had less negative ψ_{pd} than smaller size classes in the upland shrubland (Fig. 1A, C, E). These data, along with patterns of g_s and A_{net} (Fig. 5C, E, respectively) suggest that the ability of large mesquite to exploit an increased volume and/or greater depth of soil, buffers them against the most extreme conditions of plant water stress and are consistent with the observation that larger mesquite are capable of hydraulic redistribution (Hultine et al. 2004).

In the riparian shrubland, larger mesquite exhibited limited physiological response to the onset of monsoonal rains, a pattern we attribute to the availability of shallow

TABLE 2. Mean square (MS), degrees of freedom (df), *F* statistic (*F*), and corresponding *P* values (*P*) from the repeated-measures ANOVA statistical analysis of predawn leaf-water potential (ψ_{pd}), net assimilation of CO₂ by the leaf (A_{net}), and leaf stomatal conductance of water vapor (g_s) during the 2005 growing season.

Factors	Upland shrubland				Riparian shrubland			
	MS	df	<i>F</i>	<i>P</i>	MS	df	<i>F</i>	<i>P</i>
ψ_{pd}								
Size class	2.51	2, 12	15.04	0.0005	4.69	2, 7	16.42	0.002
Size class \times time	0.07	8, 18	6.08	0.0007	0.03	8, 18	4.74	0.02
Time	485	4, 9	1091	0.0001	37.5	4, 4	35.7	0.002
g_s								
Size class	0.40	2, 12	2.42	0.13	0.57	2, 8	2.28	0.16
Size class \times time	0.35	8, 18	1.52	0.21	0.17	8, 10	1.75	0.19
Time	8.83	4, 9	19.87	0.0002	8.82	4, 5	11.02	0.01
A_{net}								
Size class	1.55	2, 12	9.31	0.003	0.96	2, 8	3.86	0.067
Size class \times time	0.30	8, 18	1.81	0.14	0.16	8, 10	1.83	0.18
Time	9.93	4, 9	22.35	0.0001	1.24	4, 5	1.56	0.312

Note: Size class refers to mesquite in different size classes.

groundwater during the pre-monsoon period at this site (Fig. 5D, F). However, we cannot rule out the possibility that larger shrubs supplement groundwater with shallow soil moisture during the monsoon. Access to mineralized nutrients in shallow soil layers may provide one advantage of shallow soil moisture uptake by larger mesquite during the monsoon. Overall, our observations of the effects of rainfall variability on mesquite physiology are broadly consistent with those of other investigations that have examined the role of plant size and physiological responsiveness to precipitation in arid land shrubs (Donovan and Ehleringer 1992, 1994, de Soyza et al. 1996).

Micro-site differences in soil respiration (R_s) are consistent with well-documented patterns of R_s in semiarid shrublands associated with "islands of fertility" (e.g., Schlesinger et al. 1996). The seasonally dependent nature of these differences (Table 3, micro-site \times season) suggests that mesquite density, through its impact on the distribution of micro-site types, may influence the responsiveness of ecosystem respiration to rainfall. For example, R_s was similarly low during the pre-monsoon in both shrublands, suggesting that differences in NEE

during this period were due to differences in CO₂ assimilation by photosynthesis. However, during the monsoon period, the trend was for increased R_s in the riparian shrubland, especially in sub-canopy locations (Fig. 6A, B). Greater rates of sub-canopy R_s during the monsoon, coupled with a greater abundance of sub-canopy micro-sites, could combine to partially offset monsoonal increases in CO₂ assimilation by photosynthesis in the riparian shrubland. The effect of these factors contributing to greater ecosystem respiration in the riparian shrubland would be, as we observed, to reduce the sensitivity of daytime NEE in response to monsoonal rainfall.

Upland and riparian shrublands differ in their sensitivity of NEE to rainfall and these differences are attributable to site differences in shrub physiological sensitivity, soil respiration, and physiography. The observations support the conclusion that deep sources of soil moisture accessible to plants alter the relationship between growing-season precipitation and ecosystem productivity. In the riparian shrubland where groundwater was available to plants, seasonal patterns of NEE might be seen as illustrative of seasonal CO₂ dynamics in

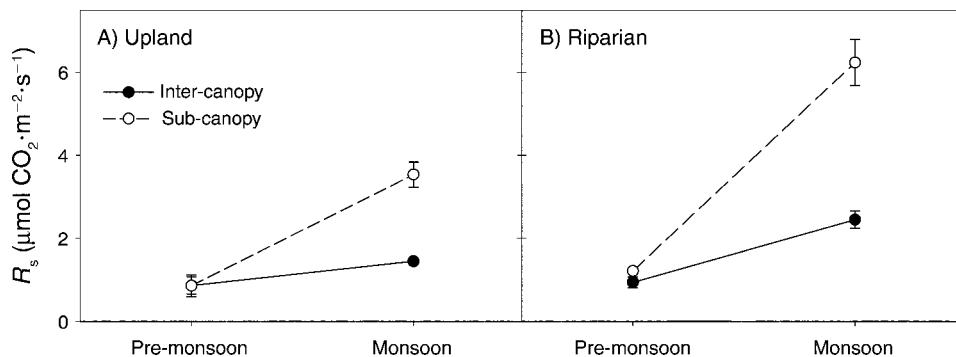


FIG. 6. Pre-monsoon and monsoon mid-morning soil respiration (R_s , mean \pm SE) in inter-canopy (solid symbols, solid line) and sub-canopy (open symbols, dotted line) micro-sites in (A) an upland and (B) a riparian mesquite shrubland.

TABLE 3. Mean square (MS), degrees of freedom (df), *F* statistics (*F*), and corresponding *P* values (*P*) of an ANOVA statistical analysis of soil respiration (R_s) in contrasting mesquite shrublands.

Factors	MS	df	<i>F</i>	<i>P</i>
R_s				
Site	0.77	1, 1	13.82	0.002
Micro-site	1.41	1, 1	25.40	0.0001
Season	6.97	1, 1	125.2	0.0001
Site × micro-site	0.04	1, 1	0.74	0.40
Site × season	0.12	1, 1	2.11	0.16
Micro-site × season	0.79	1, 1	14.26	0.0016
Site × micro-site × season	0.02	1, 1	0.44	0.51

Notes: Site refers to upland vs. riparian landscape settings. Micro-site refers to open area vs. mesquite sub-canopy R_s measurements. Season refers to measurements of R_s during the pre-monsoon period (day of year 173–175) and the monsoon period (day of year 227–231).

an upland shrubland following an extremely wet winter. For example, given a winter in which greater amounts of deep soil moisture recharge occurred, we might expect early growing season mesquite performance in the upland shrubland to more closely match that of riparian mesquite, with the result being a decline in upland ecosystem carbon exchange sensitivity to monsoonal rains.

In the present study, we were logistically constrained to limit our observations to two shrublands during a single, albeit, climatically typical growing season. Given these constraints, caution is warranted in extrapolating our findings to other shrublands or to years of extreme high or low precipitation. However, we observed seasonal patterns of shrub water status, leaf gas exchange, and soil respiration and NEE that strongly support the hypothesis that physiography and rainfall interact to effect CO_2 exchange in mesquite-dominated shrublands. This research highlights the interplay between physiographic constraints on woody plant performance and micro-site controls on soil respiration that together influence the sensitivity of NEE to rainfall. Accounting for these factors, along with a consideration of the temporally dynamic influence of deep vs. shallow soil moisture, will be required for a more complete synthesis of ecosystem metabolic responses to climate variability.

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