

The sensitivity of ecosystem carbon exchange to seasonal precipitation and woody plant encroachment

D. L. Potts · T. E. Huxman · R. L. Scott ·
D. G. Williams · D. C. Goodrich

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Abstract Ongoing, widespread increases in woody plant abundance in historical grasslands and savannas (woody encroachment) likely will interact with future precipitation variability to influence seasonal patterns of carbon cycling in water-limited regions. To characterize the effects of woody encroachment on the sensitivity of ecosystem carbon exchange to seasonal rainfall in a semi-arid riparian setting we used flux-duration analysis to compare 2003-growing season NEE data from a riparian grassland and shrubland. Though less seasonally variable than the grassland, shrubland NEE was more responsive to monsoon rains than anticipated. During the 2004-growing season we measured leaf gas exchange and collected leaf tissue

for $\delta^{13}\text{C}$ and nitrogen content analysis periodically among three size classes of the dominant woody-plant, *Prosopis velutina* and the dominant understory species, *Sporobolus wrightii*, a C_4 bunchgrass, present at the shrubland. We observed size-class and plant functional type independent patterns of seasonal plant performance consistent with greater-than-anticipated sensitivity of NEE in the shrubland. This research highlights the complex interaction between growing-season precipitation, plant-available alluvial groundwater and woody plant abundance governing ecosystem carbon balance in this semi-arid watershed.

Keywords Flux-duration analysis · Photosynthesis · Woody encroachment · Precipitation variability

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D. L. Potts · T. E. Huxman
Ecology and Evolutionary Biology, University of Arizona,
Tucson, AZ 85721, USA
e-mail: huxman@email.arizona.edu

D. L. Potts (✉)
Ecology and Evolutionary Biology, University of California,
321 Steinhaus Hall, Irvine, CA 92697, USA
e-mail: dpotts@uci.edu

R. L. Scott · D. C. Goodrich
Southwest Watershed Research Center, USDA-ARS,
Tucson, AZ 85719, USA
e-mail: rscott@tucson.ars.ag.gov

D. C. Goodrich
e-mail: dgoodrich@tucson.ars.ag.gov

D. G. Williams
Renewable Resources and Botany, University of Wyoming,
Laramie, WY 82071, USA
e-mail: dgw@uwyo.edu

Introduction

How climate may influence ecosystem function has been a focal point in the development of the ecosystem concept in ecology (Lindeman 1942; Odum 1969; Rosenzweig 1968; Golley 1993). While the relationship of vegetation community composition to global patterns of temperature and rainfall are well established and long recognized (Koeppen 1936; Bailey 1996), evaluating dynamic ecosystem processes that derive from those vegetation patterns in response to variability in climate remains a central focus (Weltzin et al. 2003; Enquist et al. 2003; Huxman et al. 2004b). Additionally, assessing ecosystem responses to future climate variability requires both reductionist and synthetic approaches to understand the mechanistic processes that underlie whole-system function (Weltzin et al. 2003).

In water-limited regions, precipitation arrives in discrete “pulses” that may trigger episodes of biotic activity (Noy-Meir 1973). Characteristics of rainfall events such as size and seasonal timing may interact with soils and vegetation to affect the duration and magnitude of the resulting periods of biotic activity (Schwinning and Ehleringer 2001; Snyder et al. 2004; Reynolds et al. 2004; Huxman et al. 2004a; Potts et al. 2006). For example, a small pulse may percolate through a coarse-textured soil to reach the roots of a deeply rooted shrub and stimulate photosynthesis while the same-sized pulse in a fine-textured soil may influence only soil water content in the near-surface and not be utilized by deeply rooted shrubs (Fravolini et al. 2005).

Pulses and their effects are scale dependent (Schwinning and Sala 2004) and may range from a small storm triggering microbial activity with a duration of a few hours (Cable and Huxman 2004) to interannual and decadal variation in precipitation associated with phenomena such as the El Niño Southern Oscillation and the Pacific Decadal Oscillation that can impact fire frequency and intensity (Swetnam and Betancourt 1998). In the semi-arid southwestern United States annual precipitation is roughly divided evenly between two intermediate-scale pulses of water: cool season precipitation associated with frontal storms (November–March) and warm season precipitation associated with the North American Monsoon during July–September (Adams and Comrie 1997). Regional predictions of future climate suggest that in addition to increased totals, rainfall may become even more variable (Giorgi et al. 1998). Changes in seasonal rainfall regime likely will interact with other global-change factors, such as changes in landscape vegetation cover, to affect ecosystem functions such as biosphere–atmosphere exchanges of material and energy.

An important contributor to broad-scale vegetation change in semi-arid regions worldwide is the expansion and increasing density of woody plants in historical grasslands and savannas (Archer et al. 2001). This phenomenon, termed “woody encroachment” (Goodale and Davidson 2002) has been attributed to grazing by livestock, altered fire regimes, atmospheric enrichment of CO₂ and climate change (McPherson 1997; Van Auken 2000). The potential consequences of woody encroachment include increased net primary productivity (House et al. 2003), increased spatial heterogeneity of soil resources (Schlesinger et al. 1990; Reynolds et al. 1999) and increases in mean rooting depth (Jackson et al. 1996). Of particular concern is the potential for regional increases in woody plant abun-

dance to alter North America’s terrestrial carbon budget (Pacala et al. 2001; Goodale and Davidson 2002; Jackson et al. 2002; Asner et al. 2003; Houghton 2003) and to affect changes in regional hydrologic cycling (Wilcox et al. 2003; Huxman et al. 2005). However, little is known of how woody encroachment interacts with present precipitation variability to affect processes underlying ecosystem CO₂ and H₂O exchange.

Changes in ecosystem carbon balance associated with woody encroachment may be estimated by measurements of net ecosystem exchange of CO₂ (NEE) using eddy-covariance (Baldocchi 2003). In water-limited ecosystems, pulse events preceded by dry conditions may produce NEE fluxes orders of magnitude larger than those before the pulse (Huxman et al. 2004b; Xu et al. 2004; Scott et al. 2006). Huxman et al. (2004c) suggest flux-duration analysis as an approach to comparing ecosystem carbon dynamics using NEE time-series.

Analogous to flow-duration analysis in hydrology (Searcy 1959; Vogel and Fennessy 1995; Smakhtin 2001; Potts and Williams 2004; Lane et al. 2005), flux-duration analysis ranks and assigns a frequency to NEE time-series values in the form of cumulative frequency distribution. In water-limited systems, flux-duration analysis incorporates episodic periods of high activity associated with rainfall pulses and extended periods of low activity associated with dry conditions into a single calculation (Huxman et al. 2004c). Flux-duration analysis complements traditional time series and cumulative approaches in the interpretation of tower-based ecosystem exchange data by yielding a probabilistic description of fluxes for a given period of interest.

The first objective of this research was to characterize the effects of woody plant abundance on the sensitivity of ecosystem carbon exchange to seasonal rainfall in a riparian setting. We predicted that in comparison with a grassland system, NEE in a shrubland would be less sensitive to summer rainfall associated with the North American Monsoon, owing to the ability of woody plants to access alluvial groundwater. Our second objective was to understand how the physiological sensitivity to summer precipitation of different plant functional types and woody plants of different size-classes influence whole-ecosystem patterns of CO₂ exchange with the atmosphere. We predicted that in a riparian shrubland, deeply rooted mature woody plants would be less sensitive to shallow soil moisture associated with summer rainfall than shallowly rooted smaller woody plants and bunchgrasses.

Methods

Site description

Study sites were located within the San Pedro National Riparian Conservation Area adjacent a perennial reach of the San Pedro River, approximately 12 km east of Sierra Vista, AZ, USA. Woody plant cover in the San Pedro has increased dramatically during recent decades (Turner et al. 2003). Watershed-wide, mesquite cover increased by 410% during the period 1973–1992 (Kepner et al. 2000). In riparian areas, this increase likely resulted from several interacting processes that include grazing by cattle (Skartvedt 2000), changes in the flood-frequency regime and channel morphology of the river (Stromberg 1998), and declines in fire frequency (Blank et al. 2003).

Scott et al. (2006) provide an in depth description of the research sites used in this investigation. Briefly, the grassland and shrubland sites were located within 1 km of one another on an alluvial terrace at an elevation of 1,230 m. During 2003, depth to groundwater measured by observation wells was approximately 2.8 m at the grassland and 6.5 m at the shrubland (Scott et al. 2006). Soils at the sites consist mainly of sandy-loams interspersed with clay and gravel lenses derived from alluvium deposited by the nearby river.

Within the San Pedro basin, the early growing season (April–June) is characterized by hot, dry conditions. During July–September, the North American Monsoon delivers approximately 60% of annual precipitation in the form of spatially discrete, high intensity convective storms. Based on the dewpoint temperature definition of the National Weather Service (<http://www.wrh.noaa.gov/twc/monsoon/monsoon.php>), the 2003 monsoon began on July 13 (DOY 194). During 2003, the period for which we present NEE data, July–September precipitation totaled 118 mm at the sites. During 2004, the period for which we measured plant physiological attributes, monsoon atmospheric conditions began on DOY 191 and July–September precipitation totaled 120.9 mm. It should be noted that the 2004 summer precipitation total includes a 31 mm contribution in the third week of September from dissipating Tropical Storm Xavier.

Vegetation at the grassland site was dominated by big sacaton (*Sporobolus wrightii*) with a canopy height of approximately 1 m. Sacaton is a C₄ bunchgrass associated with riparian-influenced grasslands in the southwestern United States (Richter et al. 2002). During 2003, the grassland growing-season plant area index (PAI) varied from 1.0 to 2.5 (Scott et al. 2006). The shrubland site was a co-dominant stand of velvet

mesquite (*Prosopis velutina* Woot.) and big sacaton. Velvet mesquite is deciduous and is regarded as a deeply rooted, facultative phreatophyte (Snyder and Williams 2000). Mesquite at the shrubland ranged in height from 0.5 to 6 m. We surveyed mesquite heights within 30 m of the tower and found heights to be approximately normally distributed around a mean of 3.5 m (SD = 1.28, $n = 90$); total canopy cover during 2003 was approximately 55% (Scott et al. 2006). At the shrubland site, sacaton dominated the understory and inter-shrub spaces. During the 2003 growing season, total PAI ranged from 1.1 to 1.5 at the shrubland site (Scott et al. 2006).

Collection and analysis of NEE

A 3-D, sonic anemometer (Model CSAT-3; Campbell Scientific Inc., Logan, UT, USA) and an open-path infrared gas analyzer (LI-7500, LI-COR Inc., Lincoln, NE, USA) were mounted on towers at 3 m at the grassland site and 6 m at shrubland to record wind speed and direction, temperature and the concentrations of water vapor and CO₂. Data were sampled at 10 Hz, averaged and calculated to 30-min covariances and recorded by a datalogger (CR5000, Campbell Scientific Inc.). Scott et al. (2006) provide additional details of tower-based instrumentation and analysis and on the methods used to process NEE data collected during 2003. By convention, positive NEE values indicate net carbon loss and negative NEE values indicate net carbon gain by the ecosystem.

We examined daylight flux data only and excluded NEE data from time periods when $u^* < 0.15$. Because we were interested in a cumulative probability distribution of flux, we did not gap-fill missing NEE values. In a more detailed analysis of flux source area size, Scott et al. (2003) found that fluxes in a nearby riparian woodland were usually representative (>90% of the daytime measurements) of the patch and within 200 m of the tower. By analogy, the locations of the towers in the grassland and shrubland were located within each vegetation patch so that the fetch in the predominant wind directions (north and south) exceeded 200–400 m. Due to the competing influences between instrument height and vegetation height and density (i.e., aerodynamic roughness), similar analyses of flux source area sizes revealed slightly smaller source area sizes for the grassland and shrubland.

To examine seasonal changes the dynamics of carbon exchange associated with the onset of monsoon precipitation, the 2003 growing season was divided into two approximately equal parts: a pre-monsoon period (DOY 135–194) and a monsoon period (DOY

195–255). This division is based on the beginning and the end of monsoon circulation according to local atmospheric conditions defined by the National Weather Service. To address the prediction that increased woody plant abundance would decrease ecosystem sensitivity to monsoon rainfall, we compared pre-monsoon and monsoon daylight fluxes at the two sites using flux-duration curves analogous to the stream flow duration curves calculated by Searcy (1959).

Briefly, NEE data for the period of interest at each site was assigned a rank in order of descending magnitude, positive to negative. An exceedence frequency (F) was calculated for each ranked value (r) according to the formula:

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

where n is the number of ranked NEE values for the period of interest. For example, the largest NEE value ($r = 1$) for a 50-h period ($n = 100$, 30-min averaged values) would have an exceedence frequency (F) equal to 1. Particular exceedence values are expressed using Q_F . The flux value exceeded 50% of the time (the median), therefore would be expressed as Q_{50} .

We used Kolmogorov–Smirnov (K–S) tests to compare pre-monsoon and monsoon cumulative frequency distributions to one another at each site and linear regression (JMP In Statistical Discovery Software Ver. 4, SAS Institute Inc., Cary, NC, USA) to correlate site specific pre-monsoon and monsoon cumulative frequency distributions to one another. If NEE was unresponsive to monsoon circulation, then the slope of the regression would be equal to 1. If monsoon rains stimulated NEE, then the slope of the regression would be greater than 1. The amount of stimulation (i.e., the sensitivity) is indicated as an increase in the slope. The slope of the linear correlation between pre-monsoon and monsoon cumulative frequency distributions therefore provides an index of the sensitivity of NEE to the monsoon that may be compared between sites.

Field measurements

At the shrubland site, we selected five individual mesquite plants in each of three size-classes and five individual sacaton plants for repeated measurements during 2004. Primary criteria for the selection of mesquite individuals were that they appeared in healthy condition and that they fit into one of the a priori size-classes (Table 1). Mid-sized sacaton plants situated in inter-canopy locations were selected to characterize the seasonal performance of the population. Canopy

Table 1 Canopy characteristics of each mesquite size-class expressed as mean \pm standard deviation ($N = 5$)

Size-class	Canopy characteristic	
	Height (m)	Mean diameter (m)
Small	1.10 \pm 0.29	1.13 \pm 0.43
Medium	2.93 \pm 0.32	2.32 \pm 0.45
Large	3.74 \pm 0.46	4.79 \pm 1.08

dimensions of each mesquite plant were estimated with a meter stick. Mean canopy diameter was calculated from measurements made on the cardinal compass directions.

We measured predawn plant water (ψ_{pd}) using a Scholander-type pressure chamber (PMS Instruments, Corvallis, OR, USA). Measurements were made between 01:30 and 02:30 hours. Mid-canopy leaves of mesquite and sacaton were cut with a sharp blade, placed in a plastic bag, sealed and stored in a plastic cooler before measurement with the pressure chamber. Measurements of ψ_{pd} were made prior to and after the onset of monsoon circulation on DOY 141, 181, 212 and 224.

To assess seasonal patterns of maximum individual rates of leaf gas exchange, we measured net CO_2 assimilation (A_{net}) and stomatal conductance of H_2O (g_s) between 0900 and 1100 hours periodically throughout the growing season (Naumburg et al. 2003). Diurnal measurements of *S. wrightii* in a similar, nearby riparian setting suggest that maximum leaf gas exchange rates occur in the mid-morning (D. L. Potts, unpublished data). We used a portable photosynthesis system (LI-6400, Li-Cor) on sun-lit leaves positioned in the middle canopy of each plant. Inside the measurement cuvette of the LI-6400, the red/blue light source was set to 1,500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and CO_2 concentration was set to 370 $\mu\text{mol mol}^{-1}$. 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 was estimated using a desktop scanner and imaging software (Scion Image, Scion Corp., Frederick, MD, USA).

Leaf carbon isotope and %N analysis

The carbon isotope ratio of leaf tissues provides a record of woody plant photosynthetic responses to environmental variation (Williams and Ehleringer 1996). Francey and Farquhar (1982) provide a widely accepted model of carbon isotope variation in photosynthetically fixed carbon. The ratio of ^{13}C – ^{12}C in

photosynthate ($\delta^{13}\text{C}_p$) is a function of the isotope ratio of the air surrounding the leaf ($\delta^{13}\text{C}_a$), the ratio of leaf internal to ambient CO_2 concentration (c_i/c_a), the diffusive fractionation of $^{13}\text{CO}_2$ in air ($a = 4.4\text{‰}$), and the fractionation by Rubisco ($b = 27\text{‰}$) in the form:

$$\delta^{13}\text{C}_p = \delta^{13}\text{C}_a - a - (b - a)c_i/c_a \quad (2)$$

Variation in observed isotopic ratios in leaf tissues can be attributed to environmental, physiological and genetic factors that affect c_i/c_a . In the case of limited water availability or high transpirational demand, stomata respond by closing and reducing the supply of CO_2 in the leaf thereby decreasing c_i/c_a and increasing $\delta^{13}\text{C}_p$ (Farquhar et al. 1989). Isotopic analysis of bulk leaf tissue combines recently assimilated photosynthate and structural carbohydrates and so reflects an integrated estimate of growing-season c_i/c_a .

Mature, sun-lit leaves positioned at middle canopy height were collected periodically for isotopic analysis during the 2004 growing season (DOY 141, 170, 205, 224, 248). Leaf samples were stored in paper envelopes and air dried in the laboratory. We homogenized individual leaf samples with a mortar and pestle. Leaf tissue was analyzed for $\delta^{13}\text{C}$ on a continuous flow gas-ratio mass spectrometer (Delta PlusXL, Finnigan MAT Inc., San Jose, CA, USA) coupled to an elemental analyzer (Costech, Valencia, CA, USA) at the University of Arizona Department of Geosciences. To evaluate the precision of the mass spectrometer an acetanilide standard (NBS-22 and USGS-24) was measured along with the leaf-tissue samples (-29.06‰ , $\text{SD} = 0.03$). Data are reported relative to the PDB carbonate standard using “delta” (δ) notation in parts per thousand (‰) (Craig 1957). In addition to reporting carbon isotope values, we report the nitrogen content of leaf samples ($\%N$) collected on DOY 224 using the same instrumentation.

Statistical analysis of plant physiological data

Plant physiological data were checked for normality and analyzed with JMP In Statistical Discovery software Version 4 (SAS Institute Inc.). We used repeated measures MANOVA to examine the dependence of ψ_{pd} , g_s and A_{net} and leaf tissue $\delta^{13}\text{C}$ on plant type, time and their interaction. The effect of time and its interaction with plant type are reported as univariate G–G epsilon F values. Variation in $\%N$ among plant functional type and mesquite size-classes were assessed using ANOVA.

Results

Sensitivity to the onset of the monsoon

Cumulative frequency distributions of NEE for the two sites illustrate a shift in the frequency and magnitude of carbon exchange with the onset of the monsoon (Fig. 1). In the grassland, cumulative frequency distributions of pre-monsoon and monsoon NEE fluxes were distinct (K–S test, $D = 0.48$, $P < 0.0001$, $n = 99$). NEE fluxes became both more positive and more negative during the monsoon. This is consistent with a system in which shallow soil wetting stimulates photosynthesis in plants and respiratory activity in both autotrophs and heterotrophs (Fig. 1, upper panel). During the monsoon, the frequency of daytime net carbon loss also increased in the grassland. This is illustrated by a leftward shift in the point where the cumulative frequency distribution crosses the zero value of NEE. Like the grassland, the cumulative

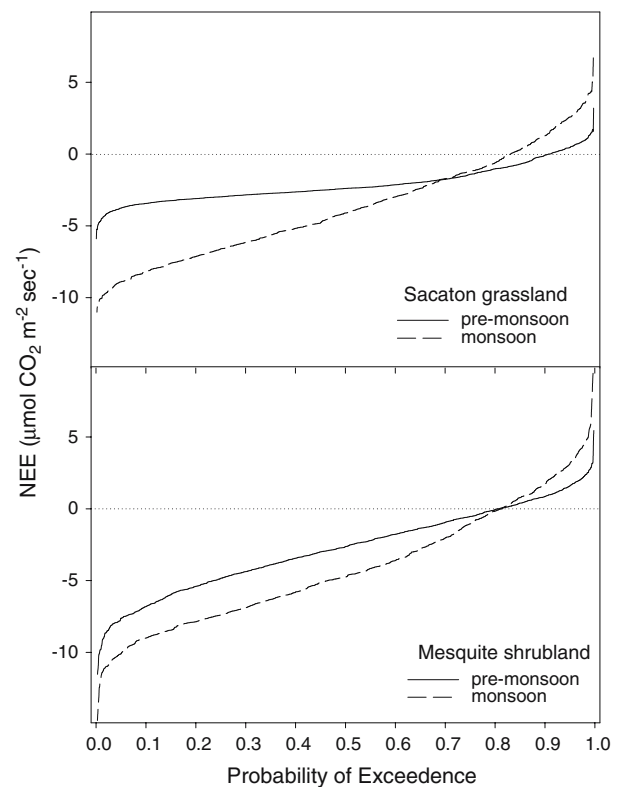


Fig. 1 Cumulative frequency distributions of daytime net ecosystem exchange of CO_2 (NEE) generated using flux-duration analysis (Huxman et al. 2004c) in a sacaton grassland (upper panel) and mesquite shrubland (lower panel) prior to and during the monsoon (solid and dashed line, respectively). Negative NEE indicates net assimilation of CO_2 by the atmosphere. The dotted horizontal line indicates compensation between photosynthetic and respiratory processes

frequency distributions of fluxes in the shrubland were seasonally distinct (K–S test, $D = 0.25$; $P = 0.003$, $n = 99$). Similar to the grassland, positive NEE fluxes became more positive (consistent with an increase in respiratory activity) and negative NEE fluxes became more negative (consistent with an increase in photosynthetic activity) (Fig. 1, lower panel). In contrast to the grassland, the frequency of net carbon loss remained virtually unchanged in the shrubland.

To quantify the sensitivity of net ecosystem exchange to the onset of summer rains at each site we used least squares linear regression to compare the cumulative frequency distributions of NEE prior to

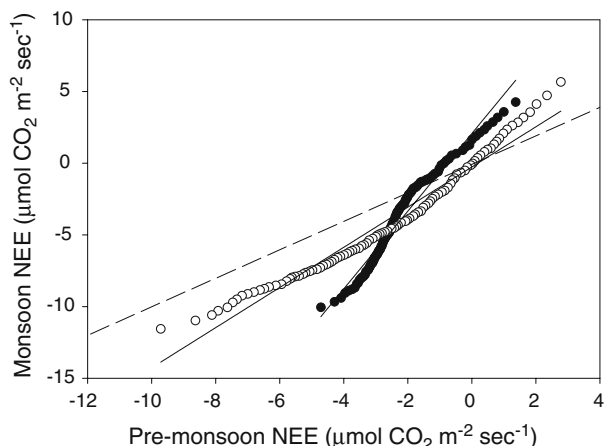


Fig. 2 Linear correlation of NEE cumulative frequency distributions prior to and during the monsoon in a riparian sacaton grassland (filled circles) and a mesquite shrubland (open circles). The dashed line is the 1:1 line. Slope magnitude represents an index of NEE sensitivity to the monsoon

and after the onset of the monsoon (Fig. 2). The slope of the linear regression in the grassland (mean = 2.71, 95% confidence interval 2.60–2.81, $n = 99$) was distinct from that of the shrubland (mean = 1.40; 95% confidence interval = 1.35–1.45, $n = 99$). The greater slope in the grassland suggests that NEE at this site was more sensitive to the onset of the monsoon. However, in contrast with our prediction, the regression slope of the shrubland excluded the null hypothesis value of 1 suggesting that woody plants may dampen but not preclude NEE sensitivity to the monsoon.

Vegetation response to the monsoon

In the shrubland, seasonal patterns of predawn leaf water potential (ψ_{pd}) varied among plant functional types and mesquite size-classes (Table 2, plant type \times time). Between May 20 (DOY 141) and June 29 (DOY 181), ψ_{pd} declined among all plant types consistent with decreasing soil moisture availability and increasing transpiration demand from rising daytime temperatures, high vapor pressure deficits and full development of the canopy (Fig. 3, lower panel). This decline was most pronounced among the smallest mesquite size-class and sacaton bunchgrasses. Comparing ψ_{pd} values on June 29 (DOY 181) and July 30 (DOY 212; Fig. 3, lower panel) illustrates that mesquite size-class and plant functional type interacts with the onset of summer precipitation to differentially affect plant water status (plant type \times time, Table 2). Small mesquite and sacaton bunchgrass ψ_{pd} responded strongly to the onset of monsoonal circulation and precipitation. The response of ψ_{pd} to summer rainfall

Table 2 Mean square (MS), degrees of freedom (df), F statistic (F), corresponding P values from the repeated measures MANOVA statistical analysis of predawn leaf water potential

Factors		MS	df	F	P value
ψ_{pd}	Plant type	10.6	3,9	31.8	<0.0001
	Plant type \times time	0.08	9,17	3.35	0.015
	Time	3.68	3,7	0.0096	0.01
g_s	Plant type	10.87	3,8	29.01	<0.0001
	Plant type \times time	0.364	9,23	2.36	0.047
	Time	0.364	3,24	15.19	<0.0001
A_{net}	Plant type	5.43	3,8	14.49	0.001
	Plant type \times time	0.50	12,32	2.29	0.03
	Time	0.50	4,32	10.42	<0.0001
$\delta^{13}C$	Plant type	318.1	3,10	1,060.3	<0.0001
	Plant type \times time	0.82	10,33	1.81	0.09
	Time	0.82	3,33	9.27	<0.0001
$\delta^{13}C$ (mesquite-only)	Plant size	1.87	2,6	5.42	0.045
	Plant type \times time	0.77	6,18	0.69	0.66
	Time	0.77	3,18	8.40	0.0009

Plant type refers to grasses and mesquite in different size classes

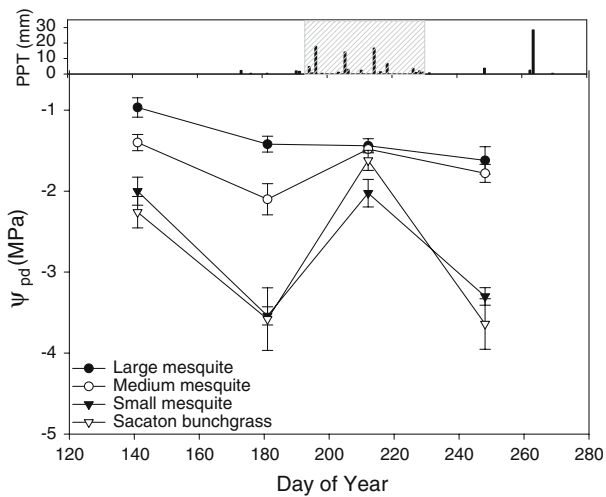


Fig. 3 Upper panel 2004 growing season precipitation expressed in mm by event. The hatched portion of the figure indicates the period of atmospheric conditions associated with the North American Monsoon. Lower panel predawn leaf water potential (ψ_{pd}) of sacaton bunchgrass and mesquite trees in three size-classes during the 2004-growing season. Error bars indicate SE

was dampened in the medium size-class while ψ_{pd} among the largest mesquite size-class was unchanged. By early September (DOY 248), small mesquite and sacaton returned to their pre-monsoon (DOY 181) states while the larger mesquite classes exhibited a water status consistent with access to stable sources of soil moisture.

Stomatal conductance of water vapor (g_s) varied significantly during the growing season among plant types (Table 2, plant type \times time). On May 20 (DOY 141), mesquite in all three size-classes had similar, low levels of conductance (Fig. 4, middle panel). As the pre-monsoon period progressed, size-classes diverged—larger mesquite plants increased g_s while the smallest mesquite plants maintained low values, similar to those observed in sacaton. After the onset of the monsoon (~DOY 212), g_s increased among the smallest mesquite plants and the bunchgrasses but remained unchanged among the larger shrubs. Among mesquite, g_s peaked on DOY 224 and was followed by a decline on DOY 248, consistent with increasing vapor pressure deficits and drying surface soils through the end of the period of monsoon circulation on DOY 233. Though we cannot say definitively whether g_s responded to the precipitation associated with dissipating Tropical Storm Xavier around DOY 260 (Fig. 3, upper panel), g_s on DOY 269 was similar among all plant types to values observed before the start of the monsoon.

Mid-morning patterns of leaf carbon assimilation (A_{net}) were influenced by plant type, time and their interaction (Table 2). Prior to the monsoon, A_{net}

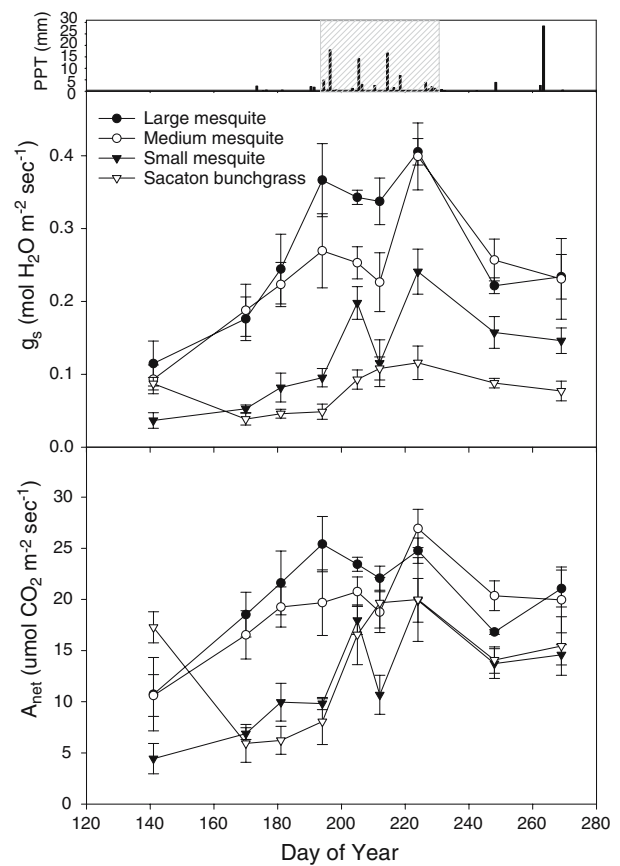


Fig. 4 Upper panel as in Fig. 3. Middle panel mid-morning leaf stomatal conductance (g_s expressed in $\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$). Lower panel mid-morning net assimilation of CO_2 by leaves (A_{net} expressed as $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). Here, positive values indicate assimilation of CO_2 by the leaf

among large and medium individuals increased steadily while smaller mesquite plants maintained low levels of photosynthesis (Fig. 4, lower panel). Leaf gas exchange among the medium-sized mesquite plants suggests similar performance to the large size-class prior to the monsoon and sensitivity to the onset of summer rains similar to small size-class (Fig. 4).

Leaf tissue isotopic variation and nitrogen content

In the shrubland, a significant amount of variation in leaf tissue stable carbon isotope ratios ($\delta^{13}\text{C}$) was explained by plant type using a statistical model that compared C_4 sacaton to C_3 mesquite (Table 2). In a statistical model that included C_3 mesquite and excluded the distinctive isotopic values of the C_4 sacaton, size-class explained a significant amount of variation in $\delta^{13}\text{C}$ (Table 2). Leaf tissue $\delta^{13}\text{C}$ values in sacaton and the smallest mesquite were constant throughout the growing season (Fig. 5, bottom panel). Among largest mesquite there was a gradual trend towards increasing

isotopic discrimination during the course of the growing season.

Late-monsoon (DOY 224) leaf nitrogen (%N) indicated significant plant functional type differences between sacaton and mesquite (Fig. 5, inset). A comparison of %N among size-classes of mesquite indicated that the largest shrubs possessed leaves relatively rich in nitrogen while medium and small shrubs were indistinguishable from one another.

Discussion

We predicted that increases in rooting depth associated with woody encroachment coupled with shallow alluvial groundwater would decouple shrubland NEE dynamics from the onset of summer rains associated with the North American Monsoon. In contrast with our prediction, flux-duration analysis revealed that shrubland NEE did respond to the monsoon, though to a lesser degree than the grassland (Figs. 1, 2). Huxman et al. (2004c) used flux-duration analysis of NEE data to compare theoretical growing-season cumulative frequency distributions of carbon exchange in a coniferous forest (Niwot Ridge, CO, USA) and a semi-arid grassland (Jornada Basin, NM, USA). This comparison succinctly illustrated the difference between the coniferous forest in which snowmelt-dominated soil moisture declined steadily throughout the growing season and the semi-arid grassland in which soil moisture was dependent on episodic rainfall pulses.

In the present study, we compared seasonal patterns of NEE from two sites that differed in woody plant abundance. Apparent access to alluvial groundwater by the largest mesquite in the shrubland acts to

partially decouple ecosystem carbon exchange from precipitation inputs. The seasonal shift in NEE that we observed at the shrubland can be related to the dependence of smaller mesquite and sacaton bunchgrasses to shallow soil moisture availability. Together, these data illustrate the complex influence of woody plants on seasonal patterns of ecosystem carbon exchange.

Overall, seasonal patterns of $\delta^{13}\text{C}$ support the idea that mature mesquite shrubs had access to abundant moisture throughout the growing season (Fig. 5). However, whole-tissue isotopic analysis did not reflect seasonal differences in plant performance among mesquite size-classes (Table 2). This is surprising given the wide range of seasonal variation in g_s between medium and smaller size-classes of mesquite. Carbon isotope analysis of soluble leaf sugars in mesquite showed that when the signature of structural carbon is removed, $\delta^{13}\text{C}$ may be used to track short term changes in plant performance following experimental irrigation (Fravolini et al. 2005).

Leaf nitrogen content is positively correlated with photosynthesis (Tjoelker et al. 2005). Differences in leaf nitrogen content among plant types could contribute to the plant type differences in A_{net} . Indeed, there were plant functional type and mesquite size-class differences in leaf %N measured during the middle growing season (Fig. 6). However, given observed patterns of ψ_{pd} and that differences in %N were not observed between the smaller size-classes of mesquite, water, not nitrogen, should be considered the primary controller of seasonal patterns of plant performance in this system. Differences in %N among size-classes of mesquite suggest the possibility that symbionts of large mesquite positioned on roots in the phreatic zone of the soil fix proportionately more nitrogen than those of the smaller size-classes in this ecosystem (Jarrell and Virginia 1990).

Early in the season (DOY 141), sacaton had high A_{net} suggesting that this bunchgrass may have been accessing soil moisture stored in the soil profile from winter and spring rains. A_{net} represents a balance of gross photosynthesis and leaf respiration. Thus, higher rates of respiration in actively growing leaf tissue early in the growing season could mask or accentuate photosynthetic variation among plant types. In deciduous mesquite, lower A_{net} during the early growing season may indicate high levels of leaf respiration or differences in construction costs between the C_3 shrubs and the C_4 bunchgrass. During the middle growing season, sacaton leaves had lower %N than mesquite (Fig. 6 inset) suggesting functional type differences in leaf construction costs.

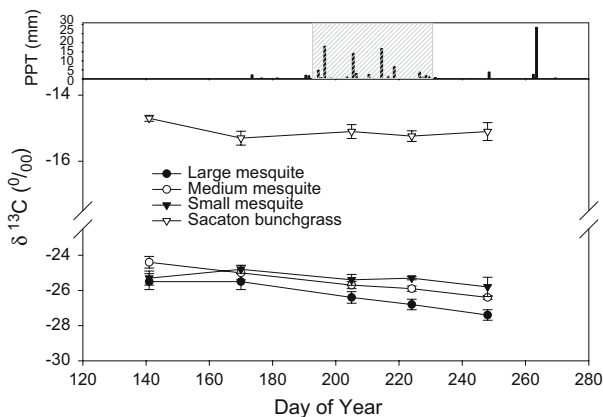


Fig. 5 Upper panel as in Fig. 3. Lower panel leaf tissue stable carbon isotope ratio ($\delta^{13}\text{C}$) expressed in parts per thousand. Increasingly negative values of $\delta^{13}\text{C}$ are suggestive of more favorable plant water status

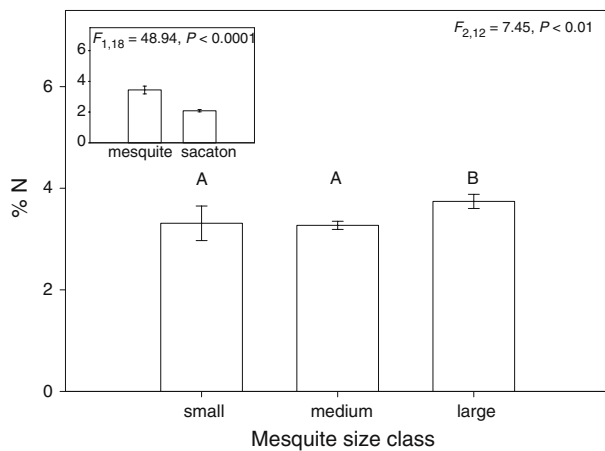


Fig. 6 Inset mean (\pm SE) late monsoon (DOY 224) leaf nitrogen content (%N) by plant functional type and ANOVA results. The comparison of plant functional types considers all mesquite size-classes as a single functional type. Main figure mean (\pm SE) late monsoon (DOY 224) leaf nitrogen content (%N) by mesquite size-class and ANOVA results. Capital letters indicate groups with different mean values (pairwise Student's *t* test, $P < 0.05$)

The greater-than-expected response of mesquite shrubland vegetation to summer precipitation may lend support to the Facilitation Optima model of woody encroachment (Teague and Smit 1992; House et al. 2003). The model predicts an increase in net primary production (NPP) associated with the facilitation of grass productivity by intermediate densities of woody plants. Alternatively, an increase in NPP at intermediate stages of woody encroachment may be due to a more complete utilization of environmental resources by a greater diversity of plant functional types and woody plant size-classes present in the shrubland would yield the same pattern. In the shrubland, ψ_{pd} data supports vertical partitioning of soil moisture suggesting more complete utilization of resources by the diversity of plant functional types and woody plant size-classes present there.

Our measurement of sensitivity was based on NEE that in turn represents the balance of photosynthetic and respiratory processes in the ecosystem. This investigation demonstrates that plant photosynthetic performance may drive seasonal patterns of daytime NEE. A shift in ecosystem respiration associated with increases in woody plant abundance could also affect seasonal patterns of daytime NEE. Despite efforts to quantify the contribution of woody plants to belowground carbon pools and their effects on soil carbon pools (Jackson et al. 2002), little is known regarding the effects of woody encroachment on ecosystem respiration fluxes (representing the metabolism of contributions from aboveground plant tissues, roots and soil heterotrophs, all potentially critical controllers of

ecosystem carbon balance (Valentini et al. 2000). In a southern Texas upland mesquite savanna, McCulley et al. (2004) determined that woody plants intensified belowground carbon cycling by simultaneously increasing soil carbon and soil respiration rates. However, Scott et al. (2006) reported on 2003 fluxes from the woody encroachment gradient in the present study and found that rates of ecosystem respiration in the shrubland were similar to those of the grassland. This supports the idea that at least under the climate conditions that prevailed during 2003, ecosystem-level changes in photosynthesis rather than respiration may shape seasonal shifts in NEE.

Late-summer precipitation associated with dissipating tropical cyclones is an irregular, but significant, climatic feature in the southwestern United States with potentially important consequences to hydrologic systems (Merritt and Wohl 2003). A lack of plant physiological response to Tropical Storm Xavier suggests late-season rainfall associated with these storms may not be “biologically significant” (sensu Reynolds et al. 2004). We suggest that in the case of late-season precipitation, phenology constrains plant responses (Fig. 3, middle, lower panels). Phenological canalization is a constraint to woody plant growth in response to experimental irrigation in the Mojave Desert (Comstock and Ehleringer 1986; Snyder et al. 2004). If future climate change is accompanied by an increase in the frequency of tropical cyclones, the consequences to Sonoran desert ecosystems may not include a significant, direct photosynthetic response by plant communities.

The findings of this research suggest that carbon dynamics in shrublands may be less sensitive to intra-annual precipitation variability than grasslands. Size-class distribution of woody plants may play an important role in constraining seasonal dynamics of shrubland carbon exchange. From the perspective of riparian ecosystem management, these results suggest that patterns of ecosystem productivity may be constrained by seasonal rainfall, even in systems dominated by facultative phreatophytes such as velvet mesquite and big sacaton. Finally, the independent physiological responses of different mesquite size-classes to precipitation associated with the North American Monsoon may provide insight into more effective woody plant control strategies for riparian vegetation managers.

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