

Temperature and precipitation controls over leaf- and ecosystem-level CO₂ flux along a woody plant encroachment gradient

GREG A. BARRON-GAFFORD*†, RUSSELL L. SCOTT‡, G. DARREL JENERETTE§, ERIK P. HAMERLYNCK‡ and TRAVIS E. HUXMAN*†

*Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, USA, †B2 Earthscience, Biosphere 2, University of Arizona, Tucson, AZ 85721, USA, ‡USDA-Agricultural Research Service, Southwest Watershed Research Center, Tucson, AZ 85719, USA, §Department of Botany and Plant Sciences, University of California Riverside, Riverside, CA 92521, USA

Abstract

Conversion of grasslands to woodlands may alter the sensitivity of CO₂ exchange of individual plants and entire ecosystems to air temperature and precipitation. We combined leaf-level gas exchange and ecosystem-level eddy covariance measurements to quantify the effects of plant temperature sensitivity and ecosystem temperature responses within a grassland and mesquite woodland across seasonal precipitation periods. In so doing, we were able to estimate the role of moisture availability on ecosystem temperature sensitivity under large-scale vegetative shifts. Optimum temperatures (T_{opt}) for net photosynthetic assimilation (A) and net ecosystem productivity (NEP) were estimated from a function fitted to A and NEP plotted against air temperature. The convexities of these temperature responses were quantified by the range of temperatures over which a leaf or an ecosystem assimilated 50% of maximum NEP (Ω_{50}). Under dry pre- and postmonsoon conditions, leaf-level Ω_{50} in C₃ shrubs were two-to-three times that of C₄ grasses, but under moist monsoon conditions, leaf-level Ω_{50} was similar between growth forms. At the ecosystems-scale, grassland NEP was more sensitive to precipitation, as evidenced by a 104% increase in maximum NEP at monsoon onset, compared to a 57% increase in the woodland. Also, woodland NEP was greater across all temperatures experienced by both ecosystems in all seasons. By maintaining physiological function across a wider temperature range during water-limited periods, woody plants assimilated larger amounts of carbon. This higher carbon-assimilation capacity may have significant implications for ecosystem responses to projected climate change scenarios of higher temperatures and more variable precipitation, particularly as semiarid regions experience conversions from C₄ grasses to C₃ shrubs. As regional carbon models, CLM 4.0, are now able to incorporate functional type and photosynthetic pathway differences, this work highlights the need for a better integration of the interactive effects of growth form/functional type and photosynthetic pathway on water resource acquisition and temperature sensitivity.

Keywords: eddy covariance, mesquite (*Prosopis velutina*), net ecosystem exchange, photosynthesis, respiration, temperature optima, vegetative change, woody plant encroachment

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Introduction

Many climate models forecast increasing terrestrial air temperatures and rainfall variability (Christensen *et al.*, 2007), renewing interest in plant responses to changing temperatures and thermal stress in conjunction with water stress (Gunderson *et al.*, 2000; Medlyn *et al.*, 2002a, b; Hikosaka *et al.*, 2006; Lloyd & Farquhar, 2008; Sage *et al.*, 2008, 2011; Montpied *et al.*, 2009). Understanding leaf-level seasonal photosynthetic temperature responses is essential for modeling ecosystem carbon

balance and predicting carbon cycle responses to climate change (Hikosaka *et al.*, 2007), however, there are currently very few data describing how plant responses to temperature vary seasonally, and this dynamic is not often captured in ecosystem models (Kull, 2002). Furthermore, Bonan *et al.* (2011) noted that the latest version of the larger-scale Community Land Model, CLM 4.0, now simulates CO₂ assimilation by the plant canopy and uses estimations of plant functional type distributions (Lawrence *et al.*, 2011), but the model still misestimates plant productivity. As models become better equipped to estimate regional carbon dynamics across multiple functional types, we need to augment these efforts with targeted measures of seasonal

Correspondence: Greg A. Barron-Gafford, tel. +1 520 548 0388, fax +1 520 621 9190, e-mail: gregbg@email.arizona.edu

variations in plant responses to environmental drivers so as to improve model parameterization.

Plant photosynthetic rates (A) display temperature optima (T_{opt}) in accordance with the Arrhenius function, beyond which rates decline depending on the plant's tolerance characteristics (Farquhar *et al.*, 1980; Leuning, 2002; Sage *et al.*, 2011). Over the short-term (seconds to hours), biochemical limitations determine light-limited (Leuning, 2002) and light-saturated (Sage & Kubien, 2007) photosynthetic rates, whereas in the longer-term (weeks to months), plants can acclimate to growth temperature. Nighttime leaf respiration (R_{Leaf}) and A can also have distinct acclimation rates, depending on the degree of daytime vs. nighttime warming (Mooney *et al.*, 1978; Berry & Björkman, 1980; Loveys *et al.*, 2003; Atkin *et al.*, 2006; Campbell *et al.*, 2007) such that warmer temperatures increase the ratio of R_{Leaf} : A because R_{Leaf} responds exponentially whereas A decreases at temperatures beyond T_{opt} (Atwell *et al.*, 1999). Improved understanding of the factors underlying variation in R_{Leaf} : A across functional groups can be used to extrapolate leaf-level temperature sensitivity to ecosystem functioning from diel to seasonal scales.

Such analyses are especially important for mixed-vegetation ecosystems experiencing climate change

(Weiss & Overpeck, 2005) and transitions in community structure (Archer, 1994). In southwestern North America, woody plant encroachment has converted nearly 60 million ha of C_4 semiarid grasslands into shrub- or woodland savanna ecosystems, producing an extensive mixed system comprised of competing native C_4 grasses and C_3 shrubs that differ in fundamental photosynthetic properties, water use efficiency, and thermal tolerances (Van Auken, 2000, 2009; McClaran, 2003). This sets up a model system for studying the trade-offs in resource acquisition (ecosystem productivity and growth) and resource-use efficiency, particularly since seasonally scarce water and frequent high temperatures characterize these ecosystems. Kirschbaum (2004) proposed that warming alone is likely to favor C_4 species in mixed ecosystems, partially because C_4 plants usually outperform C_3 plants at higher temperatures and under drier soil conditions (Fig. 1; Björkman *et al.*, 1975; Berry & Björkman, 1980; Sage *et al.*, 2011). However, predicting whether C_3 or C_4 plants will dominate under projected temperature and precipitation regimes can be confounded by variation in growth form traits such as rooting depth (Enquist *et al.*, 2007). Aridland C_4 grasses are often hemicryptophytes that allocate fewer resources toward root biomass, while co-occurring

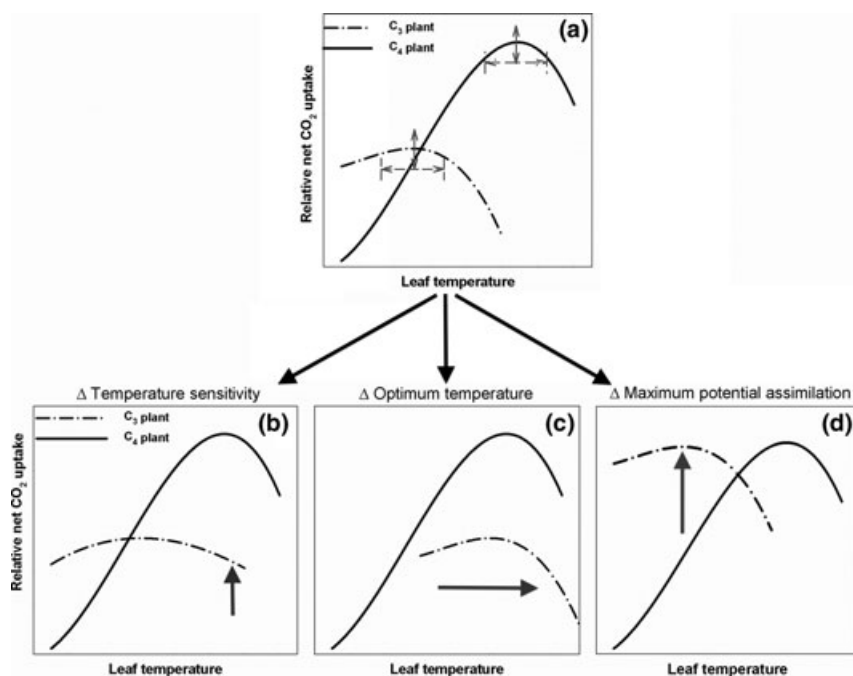


Fig. 1 (a) Classic temperature responses of plants with C_3 or C_4 photosynthetic pathway, re-drawn from Berry & Björkman (1980) and Sage *et al.* (2011), and (b–d) potential shifts in these assumed sensitivities in the C_3 plant if it were a deeper rooted shrub. The widespread vegetative change of woody plant encroachment is yielding a mosaic landscape of mixed pathway and growth form. As such, we may find relaxed thermal sensitivities at higher temperatures (b), a shift in optimal temperatures beyond those limited temperature typical of C_3 plants (c), an increase in maximum potential for assimilation (d; leveling the playing field among C_3 and C_4 plants), or some combination of these changes.

woody C₃ shrubs are phanerophytes with greater belowground investment (Raunkjær, 1977; Esser, 1995). Thus, C₄ grasses may be more constrained phenologically since they must initiate root growth following the onset of seasonal rains (Carpenter, 1956).

Changes in vertical root distributions and depths attendant with woody plant encroachment into semiarid grasslands may alter ecosystem-scale water balance by increasing the depth and amount of soil water extracted for transpiration, thereby shifting sensitivity of ecosystem evapotranspiration to seasonal precipitation (Scott *et al.*, 2000; Hultine *et al.*, 2006; Jenerette *et al.*, 2011). This switch in water has been shown to drive carbon dynamics as ecosystems experience vegetative change. Grassland ecosystem carbon uptake and respiration are more responsive than woodlands to initial seasonal rains and to those following summer dry spells (Potts *et al.*, 2006; Scott *et al.*, 2006; Jenerette *et al.*, 2009). Thus, the physical structure and the facultative phreatophytic nature of encroaching woody plants complicate predictions of community responses to projected climate change based on plant photosynthetic pathway (Kirschbaum, 2004; see review by Sage & Kubien, 2007).

Figure 1 illustrates potential departures from these classic assumptions about C₃ vs. C₄ plants' leaf-scale temperature sensitivity that may result from differences in growth form. Relative to C₄ grasses, increased rooting depth in woody C₃ plants may reduce CO₂ assimilation sensitivity to higher temperatures by ameliorating high-temperature moisture stress (Fig. 1b). Reduced sensitivity to high vapor pressure deficit, which typically coincides with higher temperatures, has been documented in semiarid woody plants relative to grasses (Barron-Gafford *et al.*, 2007; Potts *et al.*, 2008). Similarly, reduced moisture stress in C₃ shrubs may allow for an increase in T_{opt} beyond that typical of C₃ plants (Fig. 1c), a greater maximum potential for CO₂ assimilation (thereby leveling the playing field among C₃ and C₄ plants; Fig. 1d), or some combination of these responses. Therefore, a critical gap in our ability to estimate whole ecosystem and model regional temperature sensitivities remains tied to our understanding of component plant sensitivities as they relate to photosynthetic pathway and growth form.

Quantifying rates of A and R_{Leaf} across a wide temperature ranges allows for determination of T_{opt} for A , maximum A and R_{Leaf} rates, and the temperature range over which A and R_{Leaf} approach optimum (Ω). A trade-off exists in that some plants maintain lower, but similar A across a large temperature range, whereas others have higher A across a narrower temperature range, as seen in C₃ and C₄ plants, respectively (Berry & Björkman, 1980; Sage & Kubien, 2007; Sage *et al.*,

2011). Much has been done to understand how T_{opt} and maximum A rates respond to water status, but this tradeoff highlights the importance of understanding the breadth of a temperature response, given that the temperature tolerance range is at least as important as the peak amplitude in determining a plant's carbon-assimilation potential. Furthermore, a paired analysis of leaf- and ecosystem-scale temperature sensitivity provides the opportunity to more fully quantify differences between leaf- and whole-ecosystem-scale functioning.

Here, we explore the controls of temperature and precipitation on leaf- and ecosystem-scale CO₂ flux of a grassland that recently began experiencing woody plant expansion and a fully encroached woodland ecosystem. We quantified temperature sensitivity by measuring the convexity of the net CO₂ uptake temperature response function and using the change in convexity across distinct growing-season periods as a metric for plant and ecosystem precipitation responsiveness. We addressed the following questions: (i) are photosynthesis and respiration differentially sensitive to temperature or soil moisture? (ii) how does the temperature sensitivity of net CO₂ uptake in these ecosystems change through varying seasonal precipitation and temperature patterns? and (iii) are the dynamics of plant temperature sensitivity influenced by ecological setting (e.g., do grasses perform the same within a grassland and a woodland)? Answering these questions will provide a better understanding of leaf to whole-ecosystem temperature response scaling and the predictability of the effects of climate change on carbon and water cycling, as mediated by the consequences of woody plant encroachment across semiarid regions.

Methods

Study sites and species

Two riparian sites within the San Pedro National Riparian Conservation Area in southeastern Arizona represent end members of a woody plant encroachment gradient (Scott *et al.*, 2006). The historic grassland site (31.562 N, 110.140 W) is located on an alluvial terrace at an elevation of 1230 m, bordering the San Pedro River. The grassland was dominated by sacaton bunchgrass (*Sporobolus wrightii*), but many small velvet mesquites (*Prosopis velutina*) now inhabit the site due to recent woody encroachment. Within a 200 m diameter of the site's eddy covariance tower, bunchgrass canopy cover is ca. 65%, with a mean bunchgrass height of 1 m; mesquite cover is ca. 25%, with a mean height of 2 m, and the remaining 10% is bare soil. The plant area index (PAI) for the site varied from 1.0 in the premonsoon to a peak of 2.5 in the monsoon (Scott *et al.*, 2006), and mean depth to groundwater at the grassland was 2.5 m (Scott *et al.*, 2006). The fully

encroached, mesquite woodland study site (31.667 N, 110.178 W) is located on an old alluvial terrace of the San Pedro River at an elevation of 1200 m (Scott *et al.*, 2004), about 12 km downstream and north of the grassland site. This site is dominated by large velvet mesquite (ca. 70% canopy cover and 7 m mean canopy height), with an understory primarily of sacaton bunchgrass (ca. 24% understory cover) with scattered graythorn shrubs (*Zizyphus obtusifolia*) and ephemeral annual herbaceous species, most commonly *Viguiera dentata* (Yepez *et al.*, 2003) within 200 m of the site's eddy covariance tower. Growing-season PAI varied from ca. 1.2 to 2.0, and the average depth to groundwater was ca. 10 m (Scott *et al.*, 2004).

Leaf-level measurements of gas and water exchange

Leaf-level gas exchange was measured during the day and night on five *S. wrightii* grasses and *P. velutina* mesquites at each of the two sites during each measurement period. Measurements spanned a nearly 30 °C range of air temperatures (T) within a LI-6400 portable photosynthesis system (LI-COR, Lincoln, NE, USA). A small, white reflective A-frame cap was set upon the top of the leaf chamber cuvette to help minimize heat gain by the chamber, while still allowing for thermal dissipation by the chamber's cooling fans. A spot measurement of A at ambient temperature was made to serve not only as an indicator of plant performance under ambient conditions but also as a metric against which to compare the temperature response curve. Finding a similar reading prior to the initialization of the response curve and at that same temperature later during the response curve confirmed that no short-term perturbations had been induced by the measurement procedure. After this spot measurement, the block temperature was set to 5 °C to drop the chamber temperature to its lowest reachable temperature. Once the chamber had stabilized at its lowest temperature, the two infrared gas analyzers within the instrument were matched, and the data were logged. The chamber's block temperature was increased in 3–5 °C increments, and the plant was given time to stabilize in response to these changes in cuvette T until the maximum potential temperature in the chamber was reached. Throughout, leaf temperature was measured using a fine-wire type-T thermocouple pressed to the underside of the leaf within the chamber. All measurements were conducted at ambient CO₂ (375 ppm). It was often necessary to add a small amount of water to the instrument's CO₂ scrubber to provide sufficient moisture at higher temperatures and to buffer excessive vapor pressure deficits, although care was taken to avoid condensation in the measurement tubes.

Nighttime measures of leaf-level respiration (R_{Leaf}) were made in the hours prior to sunrise. Leaf-level net photosynthesis (A) was measured within the mid-morning to midday hours (10:00–13:00) at a consistent irradiance of 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$, as delivered by the LI-6400 red–blue light source (LI-6400-02b). All measurements were conducted on intact leaves on the southern face of the plant midway up the canopy, with five *P. velutina* and five *S. wrightii* individuals sampled for each measurement suite at each site. These mea-

surements were repeated during three periods throughout the growing season: the premonsoon drought (DOY 171–173), monsoon peak (DOY 223–225), and postmonsoon dry-out (DOY 284–286). Measurements among these three seasonal periods were key in identifying (i) the upregulation in photosynthetic capacity, (ii) any change in temperature sensitivity in response to the prolonged presence of available soil moisture, and (iii) acclimation potential as seasonal rains dissipated and the system dried out again.

Eddy covariance measurements

We have used the eddy covariance method to monitor ecosystem-scale CO₂, water vapor, and energy fluxes at the grassland from 2003 to 2007 and continuously at the woodland since 2001; details of the micrometeorological instrumentation and data processing are fully described elsewhere (Scott *et al.*, 2004, 2006). Briefly, the 3 m (grassland) and 13 m (woodland) towers log all necessary variables to calculate 30 min averages of net ecosystem exchange of CO₂ (NEE; $\mu\text{mol m}^{-2} \text{s}^{-1}$), along with measures of air temperature, vapor pressure deficit (VPD), air pressure, incoming photosynthetic photon flux density (PPFD), net short and long wave radiation, and precipitation. We made use of these data to estimate ecosystem-scale gross ecosystem exchange (GEE) by: $\text{GEE} = R_{\text{Eco}} - \text{NEE}$, where R_{Eco} is ecosystem respiration, derived from the nighttime NEE data and following procedures outlined by Reichstein *et al.* (2005). We used the simple transformation of $\text{NEP} = -\text{NEE}$, where NEP refers to net ecosystem productivity so that the ecosystem-scale data are on the same sign convention as those of the physiological leaf-level data. In order to eliminate nighttime CO₂ flux data when there was poor turbulent mixing, we limited the data pool to measurements made when the friction velocity (u^*) was >0.10 and $0.20 \text{ m}^{-2} \text{s}^{-1}$ for the grassland and woodland, respectively (Scott *et al.*, 2006).

All resulting eddy covariance data from the growing season were divided into three 30 day periods encompassing the leaf-level measurement periods: premonsoon (DOY 140–180), monsoon (DOY 190–230), and postmonsoon (DOY 280–320) periods (Fig. 2). These three seasonal blocks characterized periods of extreme temperatures but little precipitation (premonsoon), a period of warm days, but relatively abundant precipitation (130 mm; monsoon), and a dry period that occurs after the monsoon has ended in which evaporative demand (characterized by VPD and temperature) is lower (postmonsoon). Maximum air temperatures (T_{max}) average 35 °C and daytime VPD averages 2.5 kPa during the premonsoon, but drop dramatically with the onset of the summer monsoon, averaging 24 °C and 1.2 kPa, respectively, illustrating a separation between the dominant period of extreme temperature stress (premonsoon) and the principal period of precipitation input (monsoon). There was <2.5 mm of precipitation during the postmonsoon, yet average VPD increased only slightly to 1.4 kPa because air temperatures were much lower (averaging 15 °C), yielding a lower evaporative demand on the ecosystems.

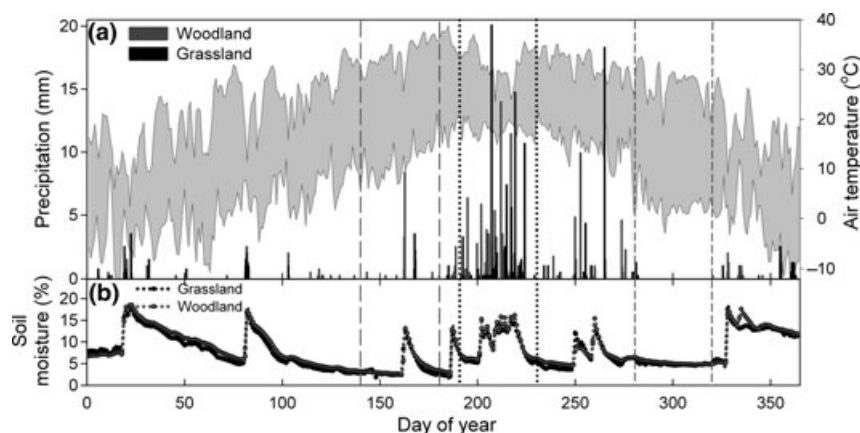


Fig. 2 (a) Precipitation within the grassland and woodland and average daytime maximum and minimum temperatures among the two ecosystems. (b) Surface soil moisture at the grassland and woodland throughout the entire annual cycle. Long-dashed vertical lines indicate the beginning and end of the premonsoon (DOY 140–180), dotted lines bracket the monsoon (DOY 190–230), and short-dashed lines indicate the beginning and end of the postmonsoon (DOY 280–320).

When constructing the subset of data for temperature sensitivity analysis, all NEP data from the day of a precipitation event and from the subsequent 5 days were removed to avoid capturing spikes in biological activity in response to wetting (Jenerette *et al.*, 2008). All remaining NEP data within each site were separated into eleven 2.5 °C-temperature bins from 10 to 37.5 °C. Within each bin, NEP was regressed against PPFD to assess temperature effects at different light levels across the day and season (Huxman *et al.*, 2003), such that a light-saturated NEP rate for each temperature bin was obtained using the following nonlinear, least-squares regression equation using SIGMAPLOT 11.0 (SPSS, Chicago, IL, USA):

$$\text{NEP} = \left(\frac{\alpha_e' * \text{PPFD} * \text{NEP}_{\text{sat}}}{\text{NEP}_{\text{sat}} + (\alpha_e' * \text{PPFD})} \right) - R_e, \quad (1)$$

where α_e' is the apparent quantum yield of the ecosystem ($\text{mol CO}_2 \text{ mol}^{-1}$ quanta), NEP_{sat} is the net CO_2 exchange at light saturation ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), and R_e is the mean respiratory net CO_2 exchange at $\text{PPFD} = 0 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (after Ruimy *et al.*, 1995). All 15 individual bins' average of T and NEP_{sat} were plotted for each site within each seasonal period to assess the temperature response function of daytime CO_2 assimilation for each ecosystem.

Determination of temperature optima and range of highly operational temperatures and statistical analysis

A_{max} and NEP_{max} were estimated from the single peak of a temperature response curve fit to the data, and the optimum temperature (T_{opt}) was the temperature at which that A_{max} occurred. To fit this data, a custom model was developed in MATLAB 2009b (MathWorks, Natick, MA, USA), based on the energy of activation and deactivation model first presented by Leuning (2002) for estimating the temperature sensitivity of maximum catalytic rate of the enzyme Rubisco and the maximum electron transport rate. The model code will be made

available online within the MATLAB user-community-generated program area, at <http://www.mathworks.com/matlabcentral/fileexchange/>. The model estimates a peak in the temperature response function and allows asymmetry in the sub- and supra-optimal portions of the curve.

An estimate of the convexity of the temperature response curve was developed by quantifying the range of temperatures over which a leaf or ecosystem was assimilating 50% (Ω_{50}) and 75% (Ω_{75}) of maximum net CO_2 uptake (A_{max} and NEP_{max} , respectively). Ω_{50} and Ω_{75} illustrate the difference between the upper and lower temperatures at which A_{max} and NEP_{max} declined by 50% and 75%, respectively. These two measures were used because changes in Ω_{50} illustrate variation in the temperature sensitivity at the edge of the plant's or ecosystem's functional range and the Ω_{75} illustrates a plant or ecosystem's ability to assimilate carbon in the range of temperatures most immediate to its temperature optima. The Q_{10} of R_{Leaf} was calculated similarly to Giardina & Ryan (2000), where Q_{10} = the reaction rate at $T + 10$ °C / reaction rate at T . T was set to the common temperature of 25 °C in this study, and rates of R_{Leaf} at this common temperature ($R_{\text{Leaf}25}$) were also used for interspecific and inter-seasonal comparisons. The Q_{10} of R_{Eco} and rates of R_E at 25 °C (R_{E25}) were calculated in the same manner as was leaf-scale respiration.

A split-plot, repeated-measures analysis of variance (STATISTIX v. 8.0; Analytical Software, Tallahassee, FL, USA) was used to test for differences in leaf-level physiological parameters of A_{max} , T_{opt} , Ω_{50} and Ω_{75} , and R_{Leaf} between the grassland and woodland, three sampling periods, and two species. The between-treatment (whole-plot) effect was growth form (mesquite vs. grass), using the growth form-by-replicate interaction as the whole-plot error term and a significance level (α) of 0.05. The within-treatment (subplot) effects were seasonal periods (premonsoon, monsoon, postmonsoon) and the growth form-by-season interaction, using the growth form-by-season-by-replicate interaction as the error term.

Results

Leaf-level measures of temperature and moisture sensitivity of net CO₂ uptake

The temperature response functions, maximum rates of assimilation (A_{\max}), and temperature at which A_{\max} was attained (optimum temperature; T_{opt}) for the dominant C₃ shrubs and C₄ grasses at both sites varied significantly between seasonal periods ($F_{2,40} = 575.20$ and 4.20 ; $P \leq 0.05$ for A_{\max} and T_{opt} , respectively). Variation in A_{\max} was linked to both the vegetative growth form and the physiographic position, as reflected in a significant three-way interaction ($F_{1,40} = 80.34$; $P \leq 0.001$; Fig. 3). Pooled across seasons and sites, A_{\max} was significantly greater in mesquites than grasses ($F_{2,40} = 4.20$; $P \leq 0.05$). Within both ecosystems, grasses responded more to monsoon onset and ending than mesquites in terms of A_{\max} (Fig. 3). Average grass A_{\max} more than doubled, increasing 118% and 143% within the grassland and woodland, respectively, in response to the monsoon. Subsequent dry downs yielded comparable decreases of 72% and 65% in these in the postmonsoon. Response of mesquite A_{\max} to the monsoon depended on physiographic setting; A_{\max} increased 47% within the grassland, and <5% within the woodland.

Within the grassland, grasses and mesquites had similar leaf-area basis maximum photosynthetic rates, although mesquites remained physiologically active across a wider temperature range during the premonsoon. During the monsoon, grass A_{\max} was 37% higher than mesquite, and A remained higher at all measured temperatures (Fig. 3b). Throughout the subsequent dry postmonsoon, mesquites had a 25% greater A_{\max} and

had near-peak rates of A across a wider range of temperatures within the grassland. Within the woodland ecosystem, mesquite A_{\max} was ca. 150% greater than grasses in the pre- and postmonsoon, but only ca. 5% greater in the monsoonal period (Fig. 3d–f).

Pooled T_{opt} was significantly higher in grasses (30.2 ± 0.4 °C) than mesquites (28.5 ± 0.5 °C; $F_{2,40} = 4.20$; $P \leq 0.05$), although there were differences in T_{opt} and A_{\max} within each growth form depending on the ecosystem in which it was found. T_{opt} was lower in bunchgrasses at the woodland site (28.4 °C) than in the grassland site (32.2 °C; Fig. 3d–f vs. a–c), illustrating the importance of the stage of woody plant invasion on temperature optima. By contrast, T_{opt} in mesquites did not differ between locations, suggesting no influence of the degree of stand development or tree size on T_{opt} .

Pooled across all periods and sites, Ω_{50} and Ω_{75} were significantly higher in mesquites than in grasses (Table 1; $F_{2,40} = 998.43$ and 2017.89 ; $P \leq 0.001$ for Ω_{50} and Ω_{75} , respectively; Fig. 3). Ω_{50} of A increased four-fold in grasses in the grassland and threefold in the woodland ecosystem, in response to the onset of the monsoon (Table 1, Fig. 3a/b, d/e). The temperature response convexity increased at the ending of the monsoon, yielding an average reduction in Ω_{50} and Ω_{75} by 60% in bunchgrasses from both ecosystems, although dry postmonsoon values remained higher than in the dry premonsoon. Because soil moisture levels were similar between these periods, temperature acclimation attained during the monsoon appears to have carried over in these grasses. Ω_{50} was ca. 40 °C in mesquites in the grassland and well over 40 °C in the woodland during the hot and dry premonsoonal period (Table 1, Fig. 3d). Mesquite Ω_{50} did not change significantly in

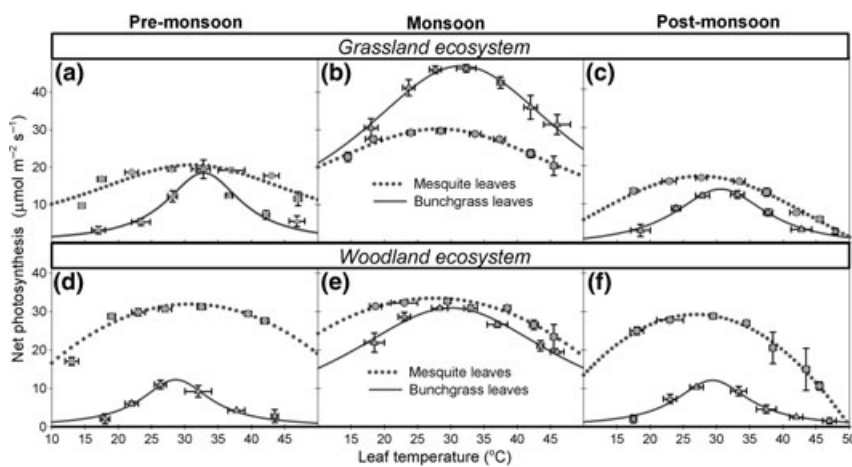


Fig. 3 (a–c) Leaf-level photosynthesis data for C₄ grasses and C₃ mesquites across the range of temperatures within the grassland ecosystem for the premonsoon, monsoon, and postmonsoonal periods. (d–f) Same as above but for the C₄ grasses and C₃ mesquites located in the woodland ecosystem. Data are species means ($n = 5$ leaves) within each seasonal period, and bars represent the standard error of the mean leaf temperature and net photosynthetic rate.

Table 1 Ecosystem-scale and leaf-scale temperature ranges (°C) across which ecosystems or leaves of the grass and mesquites within those ecosystems were able to conduct rates of net CO₂ assimilation at 50% (Ω_{50}) and 75% (Ω_{75}) of maximum uptake

Scale	Ecosystem	Ω_{50}			Ω_{75}		
		Premonsoon	Monsoon	Postmonsoon	Premonsoon	Monsoon	Postmonsoon
Ecosystem-scale	Grassland	11.5	14.6	19.8	6.9	8.1	10.9
	Woodland	24.0	27.9	21.6	14.5	17.7	12.0
Leaf-scale							
Bunchgrasses	Grassland	9.1	39.5	16.0	4.2	21.8	9.5
	Woodland	12.4	40.0	15.4	6.2	21.8	9.3
Mesquites	Grassland	37.8	39.9	30.8	27.0	30.9	21.6
	Woodland	>40.0	>40.0	32.8	30.9	34.4	23.5

response to the monsoon at either site. However, mesquite Ω_{75} increased an average of 13% across the sites, indicating a broadening of the area immediately around the temperature response peak. Reductions in Ω_{75} were about half the reductions seen for the grasses within these same ecosystems, illustrating a greater acclimation potential.

Ecosystem-scale measures of temperature and moisture sensitivity of net CO₂ uptake

The temperature response function of NEP differed significantly between the grassland and mesquite woodland and varied among the seasonal periods; NEP was greatest within the monsoon and lowest in the cooler postmonsoon, regardless of ecosystem (Fig. 5a–c). The temperature maximum NEP (NEP_{max}) within the grassland was essentially unchanged throughout the growing season with values of 30.5 ± 0.9 , 30.5 ± 0.6 , and 30.3 ± 0.7 °C in the premonsoon, monsoon, and postmonsoon, respectively, whereas NEP_{max} within the woodland was 26.9 ± 0.4 , 22.2 ± 0.3 , and 22.1 ± 0.4 °C throughout these same periods. Ω_{50} and Ω_{75} of NEP were greater in the woodland ecosystem than in the grassland, but Ω_{50} increased 27% in the grassland compared to 16% in the woodland with the transition to the monsoon. During the postmonsoon, Ω_{50} increased 35% in the grassland, indicating a relaxing of the temperature sensitivity, but decreased 23% in the woodland. The percentage increase in Ω_{75} at the onset of the monsoon was greater in the woodland ecosystem (22%) than in the grassland (17%), although the relative changes in Ω_{75} in response to the end of the monsoon was similar to Ω_{50} .

Sensitivities of CO₂ efflux to variations in temperature and soil moisture

Within the grassland ecosystem, Q_{10} values for leaf respiration differed significantly between the two growth forms, with no significant changes through time

(Fig. 4a–c). In contrast, Q_{10} values and R_{Leaf25} rates increased significantly through time in grasses and mesquites at the woodland ecosystem (Fig. 4d–f), resulting in a significant site-by-period interaction ($F_{2,40} = 71.41$; $P \leq 0.001$). R_{Leaf25} rates were significantly greater in mesquites than in the grasses across all seasonal periods, regardless of the ecosystem ($F_{1,40} = 276.95$; $P \leq 0.001$).

Variation in ecosystem respiration (R_{Eco}) rate and temperature sensitivity depended on the seasonal period (Fig. 5d–f). Q_{10} during the premonsoon was 1.54 and 1.53 in the grassland and woodland, and R_{Eco} at 25 °C (R_{Eco25}) was similar (-2.9 and -2.6 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively) among these systems. During the monsoon, the temperature responses of R_{Eco} were especially curvilinear beyond ca. 23 °C in both ecosystems (Fig. 5e). R_{Eco25} was similar between the two ecosystems during the monsoon, but R_{Eco} rates beyond 30 °C were greater in the woodland than the grassland. Postmonsoon, the temperature sensitivity of R_{Eco} was greater in the grassland than the woodland ($Q_{10} = 1.43$ vs. 1.26, respectively), but actual rates of efflux were 46% greater in the woodland ($R_{Eco25} = -1.5$ and -2.2 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively; Fig. 5f).

The ratios of respiration rates to gross CO₂ exchange were calculated to estimate the relative carbon balance across all temperatures for both the leaf- and ecosystem-scale (Fig. 6). At the leaf- and ecosystem-scales, both individual grasses and the grassland itself exhibited a peak in this ratio indicating that respiratory efflux was a greater component of net CO₂ exchange at lower and higher temperatures (Fig. 6a, b). During the monsoon, the convexity of these functions eased, illustrating an increased capacity to conduct net CO₂ assimilation across a broader temperature range. These ratios of CO₂ efflux to assimilation did not change in woodland mesquites or for the woodland ecosystem until ca. 25 °C, beyond which respiration increasingly dominated CO₂ exchange (Fig. 6c, d). In woodland mesquites, $R_{Leaf} : A_{Gross}$ followed a similar pattern with increasing

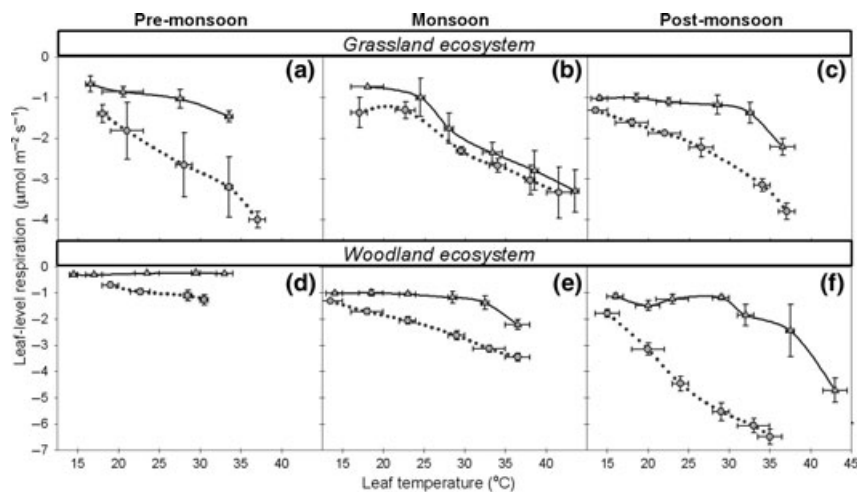


Fig. 4 (a–c) Leaf-level respiration (R_{Leaf}) data for C_4 grasses and C_3 mesquites across the range of temperatures within the grassland ecosystem for the premonsoon, monsoon, and postmonsoonal periods. (d–f) Same as above but for the C_4 grasses and C_3 mesquites located in the woodland ecosystem. Data are species means ($n = 5$ leaves) within each seasonal period, and bars represent the standard error of the mean leaf temperature and respiration rate.

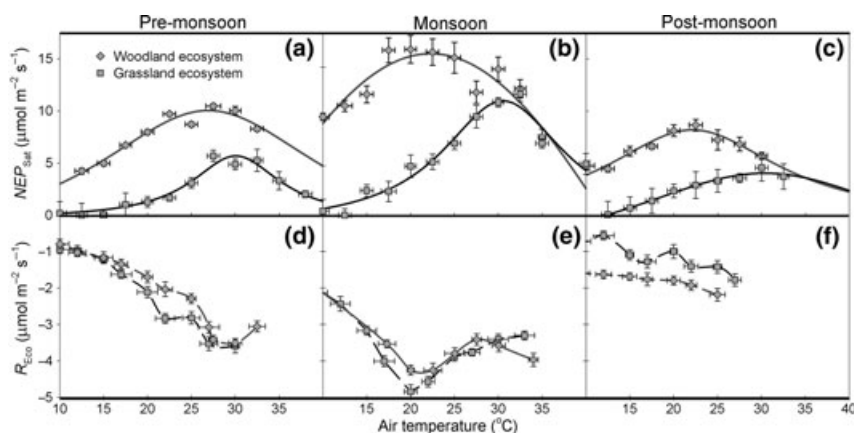


Fig. 5 (a–c) Net ecosystem productivity (NEP) throughout the premonsoon, monsoon, and postmonsoonal periods across the range of temperatures that the grassland (black circles) and woodland (gray triangles) experienced. (d–f) Ecosystem respiration (R_{Eco}) across these same seasonal periods are shown for both sites. Data are presented in the traditional plant-physiological manner, where CO_2 assimilation is represented as positive and respiratory loss as negative, rather than in atmospheric notation, to aid in comparison with leaf-level data. Data are ecosystem-scale means ($n = 5$ days) within each seasonal period, and bars represent the standard error of the mean air temperature and NEP or R_{Eco} rate.

temperature during the premonsoon and monsoonal periods, although the ratio was consistently more negative at each measurement temperature during the monsoon (Fig. 6c). At the ecosystem-scale, R_{Eco} : GEE in the woodland were consistent across all cooler temperatures, but every 1°C increase in air temperature beyond 25°C yielded a 16% reduction in capacity of the woodland for net CO_2 uptake (Fig. 6d). These rates and patterns were unaffected by seasonal moisture dynamics.

Discussion

Extensive reviews of leaf-level research suggests that C_4 species should outperform C_3 individuals at warmer temperatures given inherent properties associated with their photosynthetic pathways (Berry & Björkman, 1980; Kirschbaum, 2004; Sage & Kubien, 2007; Sage *et al.*, 2011). Recent patterns of extensive woody plant expansion into grasslands provide an opportunity to quantify the influence that traits associated with

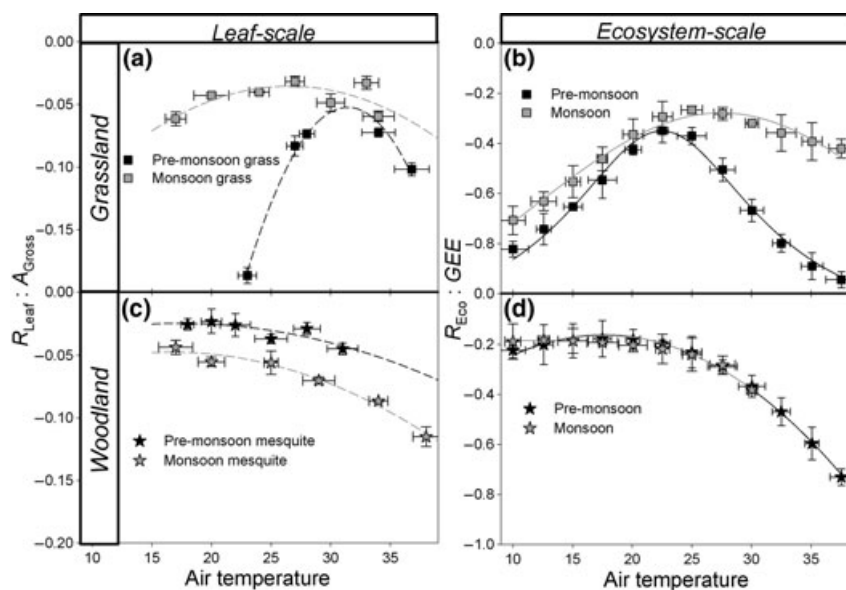


Fig. 6 The ratio of leaf-level respiration to gross photosynthesis ($R_{Leaf} : A_{Gross}$) across a range of temperatures for the dominant vegetation within the grassland (a) and mesquite woodland (c) during the premonsoon (gray squares) and the monsoonal (black squares) periods. The ratio of ecosystem-level respiration to gross photosynthesis ($R_{Eco} : GEE$) across a range of temperatures for the grassland (b) and mesquite woodland (d) during the premonsoon (gray squares) and the monsoonal (black squares) periods. Data are presented in the traditional plant-physiological manner, where CO_2 assimilation is represented as positive and respiratory loss as negative, rather than in atmospheric notation, to aid in comparison with leaf-level data. Data are either leaf-level species means (a, c; $n = 5$ leaves) or ecosystem-scale means (b, d; $n = 5$ days) within each seasonal period, and bars represent the standard error of the means.

different growth forms, such as rooting depth, play in modulating these sensitivities to temperature stress. By quantifying net CO_2 exchange across a range of temperatures at the leaf- and ecosystem-scale within multiple seasonal periods of differing environmental conditions, we were able to evaluate the relative roles of temperature and available soil moisture in controlling ecophysiological functioning in systems dominated by contrasting photosynthetic pathways. As regional carbon models, such as the widely used CLM4, are now poised to incorporate functional type (Lawrence *et al.*, 2011) and photosynthetic pathway differences (Bonan *et al.*, 2011) into large-scale estimates of carbon cycling, this work highlights the need for a better integration of the interactive effects of growth form and photosynthetic function on water resource acquisition, and thus temperature sensitivity.

The role of temperature and precipitation input in limiting leaf-scale net CO_2 uptake

We found that grasses were only able to physiologically outperform juvenile mesquites during the wet monsoon. In dry, nonmonsoon periods, mesquites maintained higher assimilation rates at every measurement temperature and were able to maintain function across a range of temperatures that were twice that of grasses

within the grassland (Ω_{50} of A ; Fig. 3). This illustrates a significant departure from the classic assumptions of C_3 vs. C_4 temperature sensitivity (Fig. 1a; Berry & Björkman, 1980; Sage *et al.*, 2011; Sage & Kubien, 2007), as the C_3 shrubs were able to maintain both a higher maximum rate of assimilation (Fig. 1d) and photosynthetic function across a greater temperature range (*sensu* Fig. 1b) than co-occurring C_4 grasses. By maintaining physiological function across a wider temperature range during water-limited periods, encroaching mesquites were assimilating large amounts of carbon, whereas grass function was limited to a very narrow temperature band.

The disparity between expected and measured differences of C_3 vs. C_4 performance at higher temperatures probably follows deeper rooting and a greater utilization of groundwater in the C_3 mesquites at these sites (Hultine *et al.*, 2004). VPD between a leaf and the air rises exponentially as temperatures increases, and this increase can lead to reduced stomatal conductance, diminished intercellular CO_2 and, ultimately, A (Berry & Björkman, 1980; Monteith, 1995; Fredeen & Sage, 1999; Medlyn *et al.*, 2002a; Sage *et al.*, 2008). However, significant transpirational evaporative cooling near the leaf surface has been shown in canopies of other semi-arid riparian trees (Barron-Gafford *et al.*, 2007). Predawn water potentials, a measure of plant water status,

illustrated that mesquites within this woodland were not significantly hindered by increases in VPD, likely because of mesquites' deeper access to groundwater (Potts *et al.*, 2008). Therefore, although C_4 plants have evolved to perform under conditions of higher temperatures within water-limited systems, a shift toward deeper soil water utilization appears to allow C_3 mesquites to outcompete their C_4 counterparts across dry seasonal periods. Together, these findings suggest broader temperature function accompanies access to deeper water sources, providing a physiological mechanism to the means by which woody plants transform vegetative cover of historic grasslands. To date, broader temperature function has not been highlighted as a potential factor in woody plant expansion, but further analysis in other invasive woody species should be conducted to quantify the universality of the mechanism.

This tapping into subsurface water allows for the sustained water supply needed to support the stimulated photosynthetic capacity developed by high leaf nitrogen. In turn, this higher leaf nitrogen can also support more stress-tolerant leaves. Ultimately, this water stress avoidance would facilitate C_3 expansion into C_4 dominated grasslands when deeper soil water resources are available. Consistent with these findings, Braswell *et al.* (1997) found semiarid C_4 grasslands experience reductions in NDVI, a proxy for vegetative activity, in warmer years, whereas C_3 wooded-grasslands, such as the one in this study, had the opposite response. Collectively, these results (i) underscore the variability in ecosystem CO_2 source/sink strength in response to climatic changes depending on the vegetative composition of ecosystems, (ii) suggest that increased temperature may negatively impact plant growth and increase water stress principally in grassland ecosystems, and (iii) are applicable across a range of physiographic positions.

The role of temperature and precipitation input in limiting ecosystem net CO_2 uptake

For grasslands, precipitation was a major limiting resource for NEP, as seen in the 104% increase in maximum NEP (NEP_{max}) with the onset of the monsoon. The increase in average NEP_{max} of the woodland (ca. 57%) in response to the onset of the monsoon was significantly lower than that of the grassland, and woodland rates of NEP were greater across the range of temperatures the ecosystems experienced (Fig. 5a–c). Given that surface soil moisture increased ca. 55% in the monsoon, the ratio of increase in productivity in response to precipitation ($\Delta NEP_{max} : \Delta \text{soil moisture}$) was nearly 2 : 1 in the grassland but only 1 : 1 in the woodland. This markedly larger stimulation in NEP

underscores the greater dependency of the grassland on ambient precipitation, consistent with prior findings (Potts *et al.*, 2006; Jenerette *et al.*, 2009). When the grassland was more water-limited in the premonsoon, NEP rates only reached 50% of NEP_{max} (Ω_{50}) within a narrow 11 °C range of temperatures, whereas the woodland did so across a 24 °C range (Table 1). In fact, the range of temperatures across which NEP was 75% of NEP_{max} (Ω_{75}) was greater in the woodland than the grassland Ω_{50} throughout the premonsoon and monsoonal periods, further demonstrating a reduced temperature sensitivity of the woodland in all seasonal periods of varying soil moisture. Grassland and woodland Ω_{50} increased 27% and 16%, respectively, in response to the monsoon, indicating that NEP_{max} was much more responsive to rains than the breadth of the temperature response function. The onset and ending of the monsoon yielded the greatest changes in grassland temperature sensitivity in Ω_{50} , in contrast to Ω_{75} in the woodland (Table 1). The results illustrate a significant expansion of the entire temperature range over which the grassland could conduct NEP, but only an extension in the range of temperatures over which the woodland carried out near-peak NEP (Fig. 5).

Notably, the results presented concerning the temperature sensitivity and seasonably variable responses of NEP ignore targeted measurements of the sensitivity of heterotrophic respiration, roots, and stems. Such component measurements will also provide great insight into the overall ecosystem-scale response to temperature but were beyond the scope of this manuscript. Measurements of the temperature sensitivity of soil respiration (R_{soil}) under mesquites and grasses in a companion upland shrubland have illustrated a complex seasonal pattern of microhabitat-specific differences in R_{soil} in response to varied soil moisture and plant phenology and a strong hysteretic temperature response (Barron-Gafford *et al.*, 2011). Rates of R_{soil} under mesquites averaged 40% greater than under grasses during the monsoon and cumulative, ecosystem-scale R_{soil} was nearly twice that under mesquites than grasses.

Conclusions

C_4 grasses were only able to physiologically outperform encroaching C_3 mesquites when soil moisture was relatively abundant (monsoon) and in an ecosystem where the mesquites were only recently established (grassland). In drier seasonal periods, mesquites had higher rates of A across every measurement temperature and were able to maintain net carbon gain across a range of temperatures twice that of grasses within a grassland

ecosystem. These differences were even more pronounced in the woodland where mesquites were more established and the water table depths greatly exceeded grass rooting depth. In terms of ecosystem-scale responses of net CO₂ flux to temperature, the grassland was nearly twice as sensitive to temperature as the woodland, and the greater access of the woodland to subsurface water allowed for a relaxation of the ecosystem's dependence on precipitation for carbon assimilation. As recently noted by Jenerette *et al.* (2011), there is a pressing need to better quantify coupled semiarid ecosystem productivity and hydrologic functioning during periods of water limitation so that widely used regional scale carbon models can better estimate current and future productivity in ecosystems of mixed growth form and photosynthetic pathways (Bonan *et al.*, 2011).

Given these interspecific differences in temperature sensitivity of CO₂ flux and the role of precipitation in moderating that sensitivity, projected climate change scenarios will probably differentially influence future CO₂ source/sink status of ecosystems depending on the dominant vegetative cover. The arid and semiarid ecosystems of western North America are predicted to experience warmer day- and nighttime temperatures (Cubasch *et al.*, 2001; Tebaldi *et al.*, 2006; Christensen *et al.*, 2007; Backlund *et al.*, 2008). In addition to becoming warmer, western North America has experienced a decrease in precipitation of ca. 15% since 1900 (Cubasch *et al.*, 2001). Models are also forecasting reduced and more variable precipitation (Tebaldi *et al.*, 2006; Christensen *et al.*, 2007; Backlund *et al.*, 2008) and higher interannual variability in the amount precipitation within the North American summer monsoon (Cubasch *et al.*, 2001). Based on these projections, we suggest:

- 1 The rate of C₃ shrub invasion will accelerate across the Southwest, especially in regions where deeper soil moisture is available. Due to their greater access to deeper soil water, C₃ shrubs outperformed C₄ grasses by way of maintaining a broader thermal range of function and ability to perform near-peak rates of CO₂ assimilation within periods of limited precipitation.
- 2 Contrary to expectations based on photosynthetic pathway alone (Fig. 1a), young C₃ shrubs are better able to assimilate more CO₂ than C₄ grasses through unfavorable periods. As such, areas now relatively unoccupied by mesquite, such as upland semiarid grasslands along mountain fronts, are likely to be more prone to shrub expansion.
- 3 Currently encroached/transformed grasslands are likely to remain so. Furthermore, these encroached

lands will likely be more resilient to climatic perturbations of short-term drought under warmer atmospheric temperatures.

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