

# Temperature and precipitation controls over leaf- and ecosystem-level CO<sub>2</sub> 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 CO<sub>2</sub> 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 ( $\Omega_{50}$ ). Under dry pre- and postmonsoon conditions, leaf-level  $\Omega_{50}$  in C<sub>3</sub> shrubs were two-to-three times that of C<sub>4</sub> grasses, but under moist monsoon conditions, leaf-level  $\Omega_{50}$  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 C<sub>4</sub> grasses to C<sub>3</sub> 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

Received 19 September 2011 and accepted 24 October 2011

## 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 CO<sub>2</sub> 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

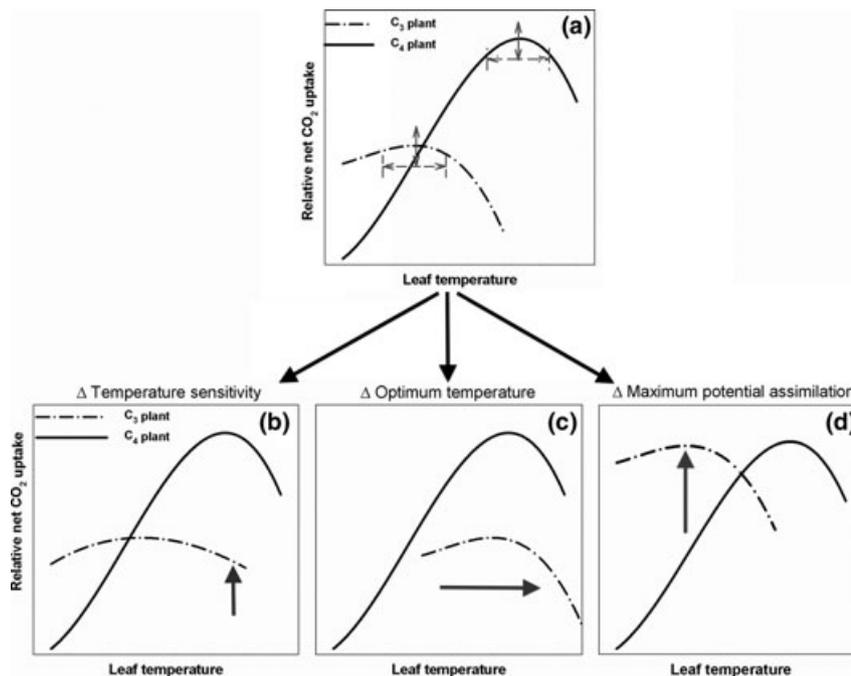
Correspondence: Greg A. Barron-Gafford, tel. +1 520 548 0388, fax +1 520 621 9190, e-mail: gregbg@email.arizona.edu

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

Plant photosynthetic rates ( $A$ ) display temperature optima ( $T_{\text{opt}}$ ) 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 ( $R_{\text{Leaf}}$ ) 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  $R_{\text{Leaf}}: A$  because  $R_{\text{Leaf}}$  responds exponentially whereas  $A$  decreases at temperatures beyond  $T_{\text{opt}}$  (Atwell *et al.*, 1999). Improved understanding of the factors underlying variation in  $R_{\text{Leaf}}: A$  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  $C_3$  shrubs are phanerophytes with greater belowground investment (Raunkjær, 1977; Esser, 1995). Thus,  $C_4$  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 semi-arid 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  $C_3$  vs.  $C_4$  plants' leaf-scale temperature sensitivity that may result from differences in growth form. Relative to  $C_4$  grasses, increased rooting depth in woody  $C_3$  plants may reduce  $CO_2$  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  $C_3$  shrubs may allow for an increase in  $T_{opt}$  beyond that typical of  $C_3$  plants (Fig. 1c), a greater maximum potential for  $CO_2$  assimilation (thereby leveling the playing field among  $C_3$  and  $C_4$  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 ( $\Omega$ ). 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  $C_3$  and  $C_4$  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  $CO_2$  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  $CO_2$  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  $CO_2$  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 CO<sub>2</sub> (375 ppm). It was often necessary to add a small amount of water to the instrument's CO<sub>2</sub> 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.

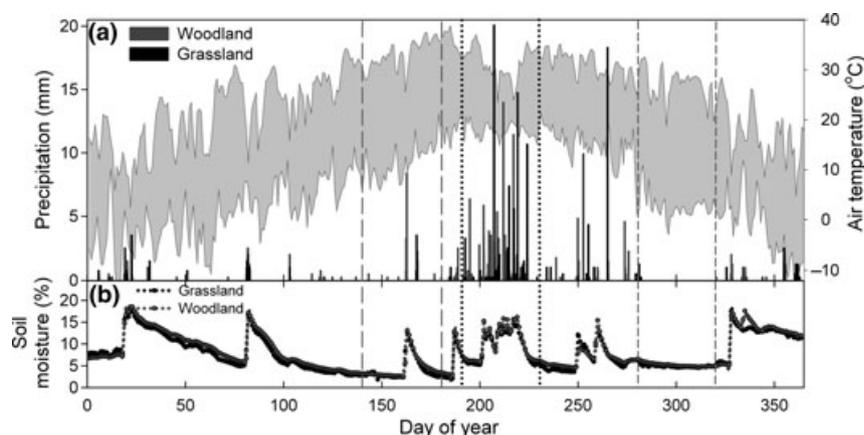
Nighttime measures of leaf-level respiration ( $R_{\text{Leaf}}$ ) were made in the hours prior to sunrise. Leaf-level net photosynthesis ( $A$ ) was measured within the mid-morning to midday hours (10:00–13:00) at a consistent irradiance of 1500  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , as delivered by 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 CO<sub>2</sub>, 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 CO<sub>2</sub> (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  $R_{\text{Eco}}$  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 CO<sub>2</sub> 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 ( $T_{\text{max}}$ ) 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  $\alpha_e'$  is the apparent quantum yield of the ecosystem ( $\text{mol CO}_2 \text{ mol}^{-1}$  quanta),  $\text{NEP}_{\text{sat}}$  is the net  $\text{CO}_2$  exchange at light saturation ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ), and  $R_e$  is the mean respiratory net  $\text{CO}_2$  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  $\text{NEP}_{\text{sat}}$  were plotted for each site within each seasonal period to assess the temperature response function of daytime  $\text{CO}_2$  assimilation for each ecosystem.

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

$A_{\text{max}}$  and  $\text{NEP}_{\text{max}}$  were estimated from the single peak of a temperature response curve fit to the data, and the optimum temperature ( $T_{\text{opt}}$ ) was the temperature at which that  $A_{\text{max}}$  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% ( $\Omega_{50}$ ) and 75% ( $\Omega_{75}$ ) of maximum net  $\text{CO}_2$  uptake ( $A_{\text{max}}$  and  $\text{NEP}_{\text{max}}$ , respectively).  $\Omega_{50}$  and  $\Omega_{75}$  illustrate the difference between the upper and lower temperatures at which  $A_{\text{max}}$  and  $\text{NEP}_{\text{max}}$  declined by 50% and 75%, respectively. These two measures were used because changes in  $\Omega_{50}$  illustrate variation in the temperature sensitivity at the edge of the plant's or ecosystem's functional range and the  $\Omega_{75}$  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  $R_{\text{leaf}}$  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  $R_{\text{leaf}}$  at this common temperature ( $R_{\text{leaf}25}$ ) were also used for interspecific and inter-seasonal comparisons. The  $Q_{10}$  of  $R_{\text{eco}}$  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  $A_{\text{max}}$ ,  $T_{\text{opt}}$ ,  $\Omega_{50}$  and  $\Omega_{75}$ , and  $R_{\text{leaf}}$  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 ( $\alpha$ ) 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 CO<sub>2</sub> uptake

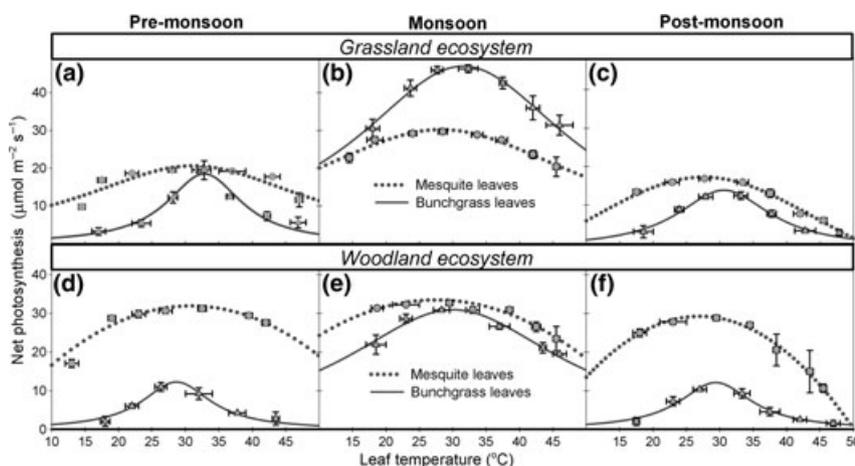
The temperature response functions, maximum rates of assimilation ( $A_{\max}$ ), and temperature at which  $A_{\max}$  was attained (optimum temperature;  $T_{\text{opt}}$ ) for the dominant C<sub>3</sub> shrubs and C<sub>4</sub> grasses at both sites varied significantly between seasonal periods ( $F_{2,40} = 575.20$  and  $4.20$ ;  $P \leq 0.05$  for  $A_{\max}$  and  $T_{\text{opt}}$ , 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  $T_{\text{opt}}$  was significantly higher in grasses ( $30.2 \pm 0.4$  °C) than mesquites ( $28.5 \pm 0.5$  °C;  $F_{2,40} = 4.20$ ;  $P \leq 0.05$ ), although there were differences in  $T_{\text{opt}}$  and  $A_{\max}$  within each growth form depending on the ecosystem in which it was found.  $T_{\text{opt}}$  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,  $T_{\text{opt}}$  in mesquites did not differ between locations, suggesting no influence of the degree of stand development or tree size on  $T_{\text{opt}}$ .

Pooled across all periods and sites,  $\Omega_{50}$  and  $\Omega_{75}$  were significantly higher in mesquites than in grasses (Table 1;  $F_{2,40} = 998.43$  and  $2017.89$ ;  $P \leq 0.001$  for  $\Omega_{50}$  and  $\Omega_{75}$ , respectively; Fig. 3).  $\Omega_{50}$  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  $\Omega_{50}$  and  $\Omega_{75}$  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.  $\Omega_{50}$  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  $\Omega_{50}$  did not change significantly in



**Fig. 3** (a–c) Leaf-level photosynthesis data for C<sub>4</sub> grasses and C<sub>3</sub> 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<sub>4</sub> grasses and C<sub>3</sub> 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 CO<sub>2</sub> assimilation at 50% ( $\Omega_{50}$ ) and 75% ( $\Omega_{75}$ ) of maximum uptake

Scale	Ecosystem	$\Omega_{50}$			$\Omega_{75}$		
		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  $\Omega_{75}$  increased an average of 13% across the sites, indicating a broadening of the area immediately around the temperature response peak. Reductions in  $\Omega_{75}$  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 CO<sub>2</sub> 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  $30.5 \pm 0.9$ ,  $30.5 \pm 0.6$ , and  $30.3 \pm 0.7$  °C in the premonsoon, monsoon, and postmonsoon, respectively, whereas  $NEP_{max}$  within the woodland was  $26.9 \pm 0.4$ ,  $22.2 \pm 0.3$ , and  $22.1 \pm 0.4$  °C throughout these same periods.  $\Omega_{50}$  and  $\Omega_{75}$  of NEP were greater in the woodland ecosystem than in the grassland, but  $\Omega_{50}$  increased 27% in the grassland compared to 16% in the woodland with the transition to the monsoon. During the postmonsoon,  $\Omega_{50}$  increased 35% in the grassland, indicating a relaxing of the temperature sensitivity, but decreased 23% in the woodland. The percentage increase in  $\Omega_{75}$  at the onset of the monsoon was greater in the woodland ecosystem (22%) than in the grassland (17%), although the relative changes in  $\Omega_{75}$  in response to the end of the monsoon was similar to  $\Omega_{50}$ .

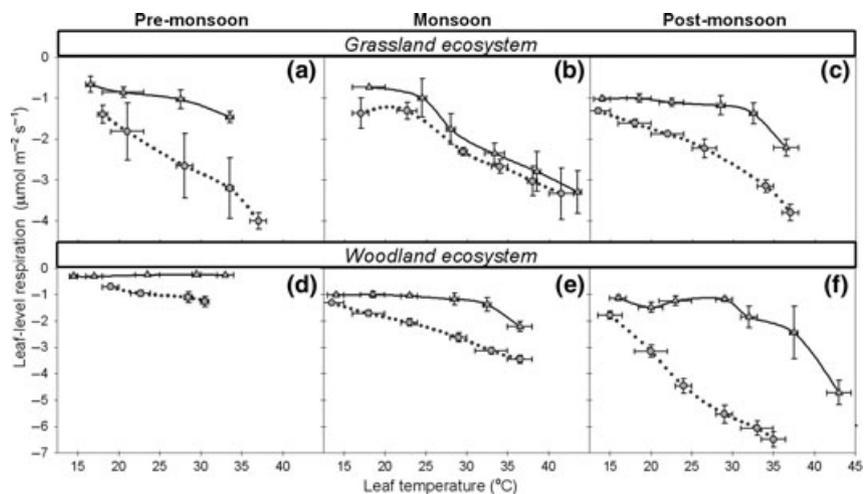
#### *Sensitivities of CO<sub>2</sub> efflux to variations in temperature and soil moisture*

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

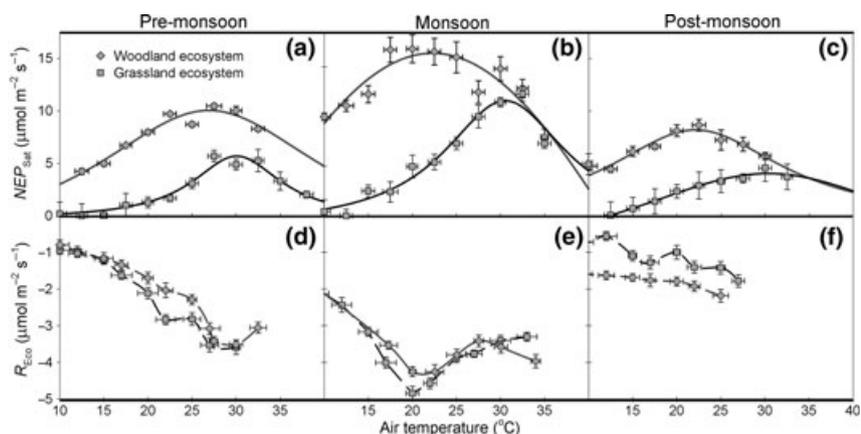
(Fig. 4a–c). In contrast,  $Q_{10}$  values and  $R_{Leaf25}$  rates increased significantly through time in grasses and mesquites at the woodland ecosystem (Fig. 4d–f), resulting in a significant site-by-period interaction ( $F_{2,40} = 71.41$ ;  $P \leq 0.001$ ).  $R_{Leaf25}$  rates were significantly 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 CO<sub>2</sub> 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 CO<sub>2</sub> 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 CO<sub>2</sub> assimilation across a broader temperature range. These ratios of CO<sub>2</sub> efflux to assimilation did not change in woodland mesquites or for the woodland ecosystem until ca. 25 °C, beyond which respiration increasingly dominated CO<sub>2</sub> exchange (Fig. 6c, d). In woodland mesquites,  $R_{Leaf} : A_{Gross}$  followed a similar pattern with increasing



**Fig. 4** (a–c) Leaf-level respiration ( $R_{\text{Leaf}}$ ) 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.

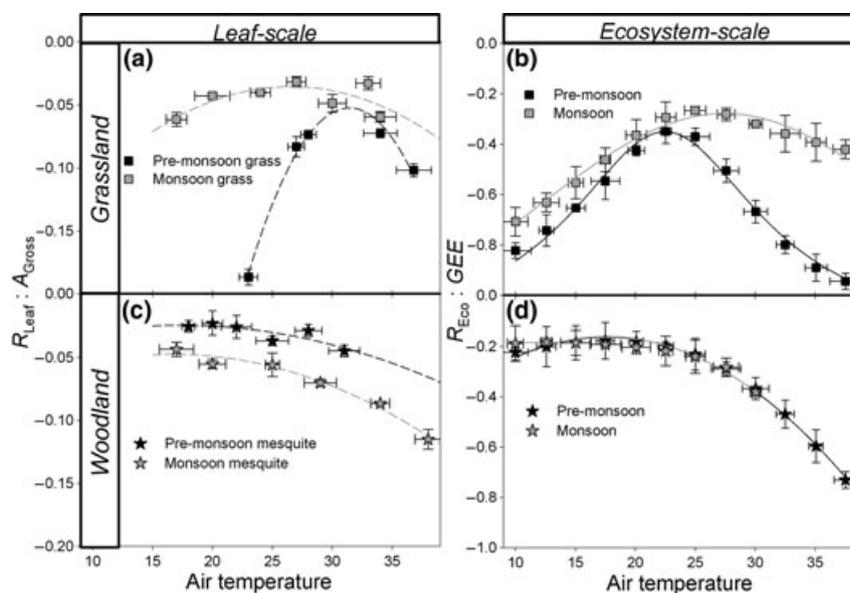


**Fig. 5** (a–c) Net ecosystem productivity (NEP) throughout the premonsoon, monsoon, and postmonsoonal periods across the range of temperatures that the grassland (black circles) and woodland (gray triangles) experienced. (d–f) Ecosystem respiration ( $R_{\text{Eco}}$ ) across these same seasonal periods are shown for both sites. Data are presented in the traditional plant-physiological manner, where  $\text{CO}_2$  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  $R_{\text{Eco}}$  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,  $R_{\text{Eco}}$ : 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  $\text{CO}_2$  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 ( $R_{\text{Leaf}} : A_{\text{Gross}}$ ) 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 ( $R_{\text{Eco}} : \text{GEE}$ ) 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  $\text{CO}_2$  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  $\text{CO}_2$  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 $\text{CO}_2$ 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 ( $\Omega_{50}$  of  $A$ ; Fig. 3). This illustrates a significant departure from the classic assumptions of  $\text{C}_3$  vs.  $\text{C}_4$  temperature sensitivity (Fig. 1a; Berry & Björkman, 1980; Sage *et al.*, 2011; Sage & Kubien, 2007), as the  $\text{C}_3$  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  $\text{C}_4$  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  $\text{C}_3$  vs.  $\text{C}_4$  performance at higher temperatures probably follows deeper rooting and a greater utilization of groundwater in the  $\text{C}_3$  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  $\text{CO}_2$  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). Pre-dawn 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  $NEP_{max}$  ( $\Omega_{50}$ ) 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  $NEP_{max}$  ( $\Omega_{75}$ ) was greater in the woodland than the grassland  $\Omega_{50}$  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  $\Omega_{50}$  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  $\Omega_{50}$ , in contrast to  $\Omega_{75}$  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 CO<sub>2</sub> 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 CO<sub>2</sub> flux and the role of precipitation in moderating that sensitivity, projected climate change scenarios will probably differentially influence future CO<sub>2</sub> 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 C<sub>3</sub> 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, C<sub>3</sub> shrubs outperformed C<sub>4</sub> grasses by way of maintaining a broader thermal range of function and ability to perform near-peak rates of CO<sub>2</sub> assimilation within periods of limited precipitation.
- 2 Contrary to expectations based on photosynthetic pathway alone (Fig. 1a), young C<sub>3</sub> shrubs are better able to assimilate more CO<sub>2</sub> than C<sub>4</sub> 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.

## Acknowledgements

This work was supported by Philecology Foundation of Fort Worth, Texas, and NSF-DEB 04189134 and 0414977 to T. E. H. Additional support was provided by the USDA-ARS and by SAHRA (Sustainability of semi-Arid Hydrology and Riparian Areas) under the STC Program of the National Science Foundation, Agreement No. EAR-9876800. The authors thank J. L. Bronstein, D. L. Venable, and R. L. Minor for providing insightful comments on the manuscript. The authors also thank A. Tyler and R. Bryant for assistance with measurements and equipment maintenance.

## References

- Archer S (1994) Woody plant encroachment into southwestern grasslands and savannas: rates, patterns and proximate causes. In: *Ecological Implications of Livestock Herbivory in the West* (eds Vavra M, Laycock W, Pieper R), pp. 13–68. Society for Range Management, Denver, CO, USA.
- Atkin OK, Scheurwater I, Pons TL (2006) High thermal acclimation potential of both photosynthesis and respiration in two lowland *Plantago* species in contrast to an alpine congener. *Global Change Biology*, **12**, 500–515.
- Atwell B, Kriedemann P, Turnbull C (1999) *Plants in Action: Adaptations in Nature, Performance in Cultivation*. MacMillan Education Australia Pty Ltd., South Yarra.
- Backlund P, Schimel D, Janetos A, Hatfield J, Ryan MG, Archer SR, Lettenmaier D (2008) Introduction to the effects of climate change on agriculture, land resources, water resources, and biodiversity in the United States. In: *A Report by the U.S. Climate Change Science Program and Subcommittee on Global Change Research* (ed. Walsh M), 10 p. Washington, DC, USA.
- Barron-Gafford GA, Grieve KA, Murthy R (2007) Leaf- and stand-level responses of a forested mesocosm to independent manipulations of temperature and vapor pressure deficit. *New Phytologist*, **174**, 614–625.
- Barron-Gafford GA, Scott RL, Jenerette GD, Huxman TE (2011) The relative controls of temperature, soil moisture, and plant functional group on soil CO<sub>2</sub> efflux at diel, seasonal, and annual scales. *Journal of Geophysical Research – Biogeosciences*, **116**, G01023, doi: 10.1029/2010JG001442.
- Berry J, Björkman O (1980) Photosynthetic response and adaptation to temperature in higher plants. *Annual Review of Plant Physiology*, **31**, 491–543.
- Björkman O, Mooney HA, Ehleringer JR (1975) *Photosynthetic Responses of Plants from Habitats with Contrasting Thermal Environments: Comparison of Photosynthetic Characteristics of Intact Plants*. Carnegie Institute Washington Yearbook, Vol 74, pp. 743–748. Carnegie Institute, Washington.
- Bonan GB, Lawrence PJ, Oleson KW *et al.* (2011) Improving canopy processes in the Community Land Model version 4 (CLM4) using global flux fields empirically inferred from FLUXNET data. *Journal of Geophysical Research – Biogeosciences*, **116**, doi: 10.1029/2010JG001593.
- Braswell BH, Schimel DS, Linder E, Moore B (1997) The response of global terrestrial ecosystems to interannual temperature variability. *Science*, **278**, 870–872.
- Campbell C, Atkinson L, Zaragoza-Castells J, Lundmark M, Atkin O, Hurry V (2007) Acclimation of photosynthesis and respiration is asynchronous in response to changes in temperature regardless of plant functional group. *New Phytologist*, **176**, 375–389.
- Carpenter JR (1956) *An Ecological Glossary*. Hafner Publishing Company, New York.
- Christensen JH, Hewitson B, Busuioc A *et al.* (2007) Regional climate projections. In: *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL), pp. 847–940. Cambridge University Press, Cambridge, UK/New York, NY, USA.
- Cubasch U, Meehl GA, Boer GJ *et al.* (2001) Projections of future climate change. In: *Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change* (eds Houghton JT, Ding Y, Griggs DJ, Noguer M, van der Linden PJ, Dai X, Maskell K, Johnson

- CA), pp. 525–582. Cambridge University Press, Cambridge, UK/New York, NY, USA.
- Enquist BJ, Kerkhoff AJ, Huxman TE, Economo EP (2007) Adaptive differences in plant physiology and ecosystem paradoxes: insights from metabolic scaling theory. *Global Change Biology*, **13**, 591–609.
- Esser LL (1995) *Sporobolus wrightii*. In: *Fire Effects Information System*. USDA, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. Available at: <http://www.fs.fed.us/database/feis/plants/graminoid/spowri/all.html> (accessed 10 November 2011).
- Farquhar GD, von Caemmerer S, Berry JA (1980) A biochemical model of photosynthetic CO<sub>2</sub> assimilation in leaves of C<sub>3</sub> species. *Planta*, **149**, 78–90.
- Fredeen AL, Sage RF (1999) Temperature and humidity effects on branchlet gas-exchange in white spruce: an explanation for the increase in transpiration with branchlet temperature. *Trees-Structure and Function*, **14**, 161–168.
- Giardina CP, Ryan MG (2000) Evidence that decomposition rates of organic carbon in mineral soil do not vary with temperature. *Nature*, **404**, 858–861.
- Gunderson CA, Norby RJ, Wullschlegel SD (2000) Acclimation of photosynthesis and respiration to simulated climatic warming in northern and southern populations of *Acer saccharum*: laboratory and field evidence. *Tree Physiology*, **20**, 87–96.
- Hikosaka K, Ishikawa K, Borjigidai A, Muller O, Onoda Y (2006) Temperature acclimation of photosynthesis: mechanisms involved in the changes in temperature dependence of photosynthetic rate. *Journal of Experimental Botany*, **57**, 291–302.
- Hikosaka K, Nabeshima E, Hiura T (2007) Seasonal changes in the temperature response of photosynthesis in canopy leaves of *Quercus crispula* in a cool-temperate forest. *Tree Physiology*, **27**, 1035–1041.
- Hultine KR, Koepke DF, Pockman WT, Fravolini A, Sperry JS, Williams DG (2006) Influence of soil texture on hydraulic properties and water relations of a dominant warm-desert phreatophyte. *Tree Physiology*, **26**, 313–323.
- Hultine KR, Scott RL, Cable WL, Goodrich DC, Williams DG (2004) Hydraulic redistribution by a dominant, warm-desert phreatophyte: seasonal patterns and response to precipitation pulses. *Functional Ecology*, **18**, 530–538.
- Huxman T, Turnipseed A, Sparks J, Harley P, Monson R (2003) Temperature as a control over ecosystem CO<sub>2</sub> fluxes in a high-elevation, subalpine forest. *Oecologia*, **134**, 537–546.
- Jenerette GD, Barron-Gafford GA, Guswa AJ, McDonnell JJ, Camilo-Villegas J (2011) Organization of complexity in water limited ecohydrology. *Ecohydrology*, doi: 10.1002/eco.217.
- Jenerette GD, Scott RL, Barron-Gafford GA, Huxman TE (2009) Gross primary production variability associated with meteorology, physiology, leaf area, and water supply in contrasting woodland and grassland semiarid riparian ecosystems. *Journal of Geophysical Research*, **114**, doi: 10.1029/2009JG001074.
- Jenerette GD, Scott RL, Huxman TE (2008) Whole ecosystem metabolic pulses following precipitation events. *Functional Ecology*, **22**, 924–930.
- Kirschbaum MUF (2004) Direct and indirect climate change effects on photosynthesis and transpiration. *Plant Biology*, **6**, 242–253.
- Kull O (2002) Acclimation of photosynthesis in canopies: models and limitations. *Oecologia*, **133**, 267–279.
- Lawrence DM, Oleson KW, Flanner MG *et al.* (2011) Parameterization improvements and functional and structural advances in version 4 of the Community Land Model. *Journal of Advances in Modeling Earth Systems*, **3**, M03001, doi: 10.1029/2011MS000045:27.
- Leuning R (2002) Temperature dependence of two parameters in a photosynthesis model. *Plant, Cell and Environment*, **25**, 1205–1210.
- Lloyd J, Farquhar GD (2008) Effects of rising temperatures and [CO<sub>2</sub>] on the physiology of tropical forest trees. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **363**, 1811–1817.
- Loveys BR, Atkinson LJ, Sherlock DJ, Roberts RL, Fitter AH, Atkin OK (2003) Thermal acclimation of leaf and root respiration: an investigation comparing inherently fast- and slow-growing plant species. *Global Change Biology*, **9**, 895–910.
- McClaran MP (2003) A century of vegetation change on the Santa Rita Experimental Range. In: *Santa Rita Experimental Range: One-Hundred Years (1903–2003) of Accomplishments and Contributions* (eds McClaran MP, Ffolliott PF, Edminster CB), pp. 16–33. U.S. Department of Agriculture Forest Service, Ogden, UT.
- Medlyn BR, Dreyer E, Ellsworth D *et al.* (2002a) Temperature response of parameters of a biochemically based model of photosynthesis. II. A review of experimental data. *Plant, Cell and Environment*, **25**, 1167–1179.
- Medlyn BR, Loustau D, Delzon S (2002b) Temperature response of parameters of a biochemically based model of photosynthesis. I. Seasonal changes in mature maritime pine (*Pinus pinaster* Aot.). *Plant, Cell and Environment*, **25**, 1155–1165.
- Monteith JL (1995) A reinterpretation of stomatal responses to humidity. *Plant, Cell and Environment*, **18**, 357–364.
- Montpied P, Granier A, Dreyer E (2009) Seasonal time-course of gradients of photosynthetic capacity and mesophyll conductance to CO<sub>2</sub> across a beech (*Fagus sylvatica* L.) canopy. *Journal of Experimental Botany*, **60**, 2407–2418.
- Mooney HA, Björkman O, Collatz GJ (1978) Photosynthetic acclimation to temperature in desert shrub, *Larrea divaricata*. I. Carbon-dioxide exchange characteristics of intact leaves. *Plant Physiology*, **61**, 406–410.
- Potts DL, Huxman TE, Scott RL, Williams DG, Goodrich DC (2006) The sensitivity of ecosystem carbon exchange to seasonal precipitation and woody plant encroachment. *Oecologia*, **150**, 453–463.
- Potts DL, Scott RL, Cable JM, Huxman TE, Williams DG (2008) Sensitivity of mesquite shrubland CO<sub>2</sub> exchange to precipitation in contrasting landscape settings. *Ecology*, **89**, 2900–2910.
- Raunkiaer C (1977) Life forms of plants and statistical plant geography. In: *History of Ecology* (ed. Egerton FN III). Arno Press, New York (Reprint of the 1934 ed. Published by Clarendon Press, Oxford).
- Reichstein M, Falge E, Baldocchi D *et al.* (2005) On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm. *Global Change Biology*, **11**, 1424–1439.
- Ruimy A, Jarvis PG, Baldocchi DD, Saugier B (1995) CO<sub>2</sub> fluxes over plant canopies and solar radiation: a review. *Advances in Ecological Research*, **26**, 1–68.
- Sage RF, Kocacinar F, Kubien DS (2011) C<sub>4</sub> photosynthesis and temperature. In: *C<sub>4</sub> Photosynthesis and Related CO<sub>2</sub> Concentrating Mechanisms* (eds Raghavendra AS, Sage RF), pp. 161–195. Springer, Dordrecht, The Netherlands.
- Sage RF, Kubien DS (2007) The temperature response of C<sub>3</sub> and C<sub>4</sub> photosynthesis. *Plant, Cell and Environment*, **30**, 1086–1106.
- Sage RF, Way DA, Kubien DS (2008) Rubisco, Rubisco activase, and global climate change. *Journal of Experimental Botany*, **59**, 1581–1595.
- Scott RL, Edwards EA, Shuttleworth WJ, Huxman TE, Watts C, Goodrich DC (2004) Interannual and seasonal variation in fluxes of water and carbon dioxide from a riparian woodland ecosystem. *Agricultural and Forest Meteorology*, **122**, 65–84.
- Scott RL, Huxman TE, Williams DG, Goodrich DC (2006) Ecohydrological impacts of woody-plant encroachment: seasonal patterns of water and carbon dioxide exchange within a semiarid riparian environment. *Global Change Biology*, **12**, 311–324.
- Scott RL, Shuttleworth WJ, Goodrich DC, Maddock T (2000) The water use of two dominant vegetation communities in a semiarid riparian ecosystem. *Agricultural and Forest Meteorology*, **105**, 241–256.
- Tebaldi C, Hayhoe K, Arblaster JM, Meehl GA (2006) Going to the extremes: An inter-comparison of model-simulated historical and future changes in extreme events. *Climatic Change*, **79**, 185–211.
- Van Auken OW (2000) Shrub invasions of North American semiarid grasslands. *Annual Review of Ecology and Systematics*, **31**, 197–215.
- Van Auken OW (2009) Causes and consequences of woody plant encroachment into western North American grasslands. *Journal of Environmental Management*, **90**, 2931–2942.
- Weiss JL, Overpeck JT (2005) Is the Sonoran Desert losing its cool? *Global Change Biology*, **11**, 2065–2077.
- Yepez EA, Williams DG, Scott RL, Lin GH (2003) Partitioning overstory and under-story evapotranspiration in a semiarid savanna woodland from the isotopic composition of water vapor. *Agricultural and Forest Meteorology*, **119**, 53–68.