Shrub encroachment alters sensitivity of soil respiration to temperature and moisture

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[1] A greater abundance of shrubs in semiarid grasslands affects the spatial patterns of soil temperature, moisture, and litter, resulting in fertile islands with potentially enhanced soil metabolic activity. The goal of this study was to quantify the microsite specificity of soil respiration in a semiarid riparian ecosystem experiencing shrub encroachment. We quantified the response of soil respiration to different microsite conditions created by big mesquite shrubs (near the trunk and the canopy edge), medium-sized mesquite, sacaton bunchgrasses, and open spaces. We hypothesized that soil respiration would be more temperature sensitive and less moisture sensitive and have a greater magnitude in shrub microsites compared with grass and open microsites. Field and incubation soil respiration data were simultaneously analyzed in a Bayesian framework to quantify the microsite-specific temperature and moisture sensitivities and magnitude of respiration. The analysis showed that shrub expansion increases the heterogeneity of respiration. Respiration has greater temperature sensitivity near the shrub canopy edge, and respiration rates are higher overall under big mesquite compared with those of the other microsites. Respiration in the microsites beneath medium-sized mesquites does not behave like a downscaled version of big mesquite microsites. The grass microsites show more similarity to big mesquite microsites than medium-sized shrubs. This study shows there can be a great deal of fine-scale spatial heterogeneity that accompanies shifts in vegetation structure. Such complexity presents a challenge in scaling soil respiration fluxes to the landscape for systems experiencing shrub encroachment, but quantifying this complexity is significantly important in determining overall ecosystem metabolic behavior.

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1. Introduction

[2] In arid and semiarid ecosystems worldwide, shifts in vegetation communities from grass to shrub dominated have been a major consequence of altered fire regimes, cattle grazing practices, and climate change [*Archer et al.*, 1988; *Archer*, 1989; *Brown and Archer*, 1989; *Buffington and Herbel*, 1965; *Van Auken*, 2000]. The resulting increase in the spatial heterogeneity of soil carbon cycling processes, such as soil respiration, will challenge our ability to scale from the plot to the ecosystem level [e.g., *Barron-Gafford et al.*, 2011]. Additionally, increased heterogeneity in the magnitude of soil respiration or the sensitivity of nonlinear processes, such as the temperature sensitivity of respiration, will impact our ability to predict how ecosystem-level carbon cycling will respond to climate change [e.g., *Zhang et al.*, 2004]. Lacking is a study that contributes to our understanding of how spatial heterogeneity created by shrub expansion will affect soil respiration, particularly one that quantifies the dynamics of both the magnitude and temperature sensitivity of soil respiration induced by the variety of microsites created by shrub expansion into semiarid grasslands.

[3] Shrub expansion into grasslands significantly redistributes soil CO_2 efflux activity on the landscape, creating respiration "hot spots" beneath shrub canopies [*Hibbard et al.*, 2001; *McCulley et al.*, 2004]. Individual shrubs tend to be more dispersed on the landscape than grasses, so more open space develops between shrub canopies [*Schlesinger et al.*, 1996], sometimes through processes termed desertification [*Ravi and D'Odorico*, 2009; *Ravi et al.*, 2009].

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Thus, these shrub hot spots are interspersed with open spaces largely devoid of surface litter, with much less root biomass and with very hot and dry microclimatic conditions [*Hibbard et al.*, 2001; *McCulley et al.*, 2004]. Remnant grasses located between shrubs contribute to this spatial heterogeneity because they are characterized by less surface litter, a more shallow rooting distribution, and warmer and drier microclimatic conditions [*Hibbard et al.*, 2001; *McCulley et al.*, 2004].

[4] The amplified carbon cycling activity beneath shrubs is due to deposition of high-quality litter on the soil surface, significant growth of woody root biomass, and a favorable (cool, wet) microclimate (fertile island effect) [*Belsky*, 1994; *Hibbard et al.*, 2001; *Liu et al.*, 2010; *McCulley et al.*, 2004; *Schlesinger et al.*, 1996; *Villegas et al.*, 2010a, 2010b; *Zou et al.*, 2007]. These factors also lead to the development of large soil microbial communities [*Cable et al.*, 2009]. Such microsite-specific effects on the soil should depend on shrub development, wherein smaller shrubs should affect soil less than larger shrubs because of less litter deposition, soil carbon and nitrogen, root growth, and soil shading [*McLain and Martens*, 2006; *Schlesinger et al.*, 1996; *Throop and Archer*, 2008]. Additionally, there can be significant spatial variations in soil carbon and nitrogen beneath large shrub canopies (more near the trunk) [*Throop and Archer*, 2008]. The density of roots is greater near the trunk under the shrub canopies compared with that in an open space [*Belsky*, 1994], suggesting there is a gradient in root density and root respiration with increasing distance from the trunk. However, the effect of shrub size on soil respiration has not been explored in semiarid encroached communities. This is significant because a major challenge to understanding the impact of shrub expansion on ecosystem source-sink dynamics is quantifying the threshold of shrub development when soil respiration is altered from grassland to woodland states [*Scott et al.*, 2006].

[5] One aspect of this threshold that can hinder the predictability of soil carbon fluxes is how the different microsites created by shrubs, grasses, and open space alter soil microclimate (moisture and temperature). Soil moisture stimulates microbial respiration in semiarid systems by enhancing substrate availability and microbial biomass turnover [*Fierer and Schimel*, 2002; *Saetre and Stark*, 2005]. Moisture can also increase autotrophic respiration by stimulating plant production [*Tang and Baldocchi*, 2005; *Tang et al.*, 2005]. Respiration typically increases exponentially with temperature [*Lloyd and Taylor*, 1994], and the temperature sensitivity of respiration is reduced by low substrate availability [*Gershenson et al.*, 2009], low soil moisture [*Conant et al.*, 2004], and high soil temperatures [*Chen and Tian*, 2005; *Davidson et al.*, 2006] [*Cable et al.*, 2008, 2011]. However, in semiarid ecosystems, the effect of temperature is more complex because of interactions with highly variable soil moisture conditions [*Cable et al.*, 2008] and nutrient quality and quantity [*Davidson and Janssens*, 2006; *Fernandez et al.*, 2006; *McLain and Martens*, 2006]. Rigorous quantification of how soil moisture and temperature affect the magnitude and temperature sensitivity of soil respiration in semiarid encroached ecosystems is critical for predicting the impacts on soil carbon cycling.

[6] The fertile island effect occurs in nearly every type of semiarid ecosystem undergoing shrub encroachment [e.g., *Van Auken*, 2000], but the effect on respiration may not be universal across these ecosystems. Much of our understanding of how shrub encroachment impacts soil processes is from semiarid upland or mesic ecosystems [e.g., *Briggs et al.*, 2005; *Throop and Archer*, 2007]. Semiarid riparian grasslands are also experiencing shrub expansion [e.g., *Scott et al.*, 2006], likely with different consequences for soil processes compared with other ecosystems. For example, shrub encroachment in mesic grasslands tends to reduce soil respiration because of lower autotrophic respiration rates and an increase in the temperature sensitivity of respiration [*McCarron et al.*, 2003]. On the whole, however, higher respiration is observed in semiarid riparian ecosystems [*McLain and Martens*, 2006] relative to upland ecosystems [*Potts et al.*, 2008]. In fact, all aspects of the impact of shrub encroachment on soil carbon processes may be enhanced in riparian systems because large-sized shrubs can access the shallow water table [*Scott et al.*, 2003; *Scott et al.*, 2004; *Snyder and Williams*, 2000]. These shrubs are less water stressed, more productive, and deposit more leaf litter compared with shrubs that do not access groundwater or compared with grasslands [*Potts et al.*, 2008; *Scott et al.*, 2006]. Thus, although riparian woodlands show a large carbon sink potential, the soil respiration dynamics may prove to offset this effect of shrub dominance [*Scott et al.*, 2006].

[7] The goal of this study is to quantify the microsite-specificity of soil respiration "characteristics" (i.e., microclimatic effects on the rate magnitude and water and temperature sensitivities) in a semiarid riparian ecosystem experiencing shrub encroachment. Understanding these patterns is critical for scaling plot to ecosystem-scale CO_2 effluxes and for better predicting changes in soil carbon dynamics with shrub expansion and climate change. We identified five soil microsites representing the microclimate and litter conditions created by spatial variations in plant canopies due to shrub encroachment into grasslands: beneath large-sized shrub canopies (both near the trunk base and near the canopy edge), beneath medium-sized shrub canopies (hereafter medium shrubs), beneath grass canopies, and in intercanopy spaces (hereafter open).

[8] We hypothesized that soil respiration in cool, moist, nutrient-rich microsites will have a greater magnitude and be more sensitive to temperature while being less sensitive to moisture compared with soils in warm, dry, nutrient-poor microsites. Therefore, we expect soil respiration properties to follow a trend from large shrubs (cool, moist, nutrient-rich microsites), to medium shrubs, to grass, to open space (hot, dry, nutrient-poor microsites). We also expect greater within-microsite variations in the magnitude and sensitivities of respiration beneath the large shrubs because of spatial variations in root and litter distributions under the canopy. Root respiration is likely higher near the trunk versus the canopy edge under large shrubs [e.g., *Belsky*, 1994]. Root respiration tends to be more sensitive to temperature than microbial respiration [*Boone et al.*, 1998], so we hypothesize that respiration near the trunk will be more sensitive to temperature compared with near the canopy edge. We conducted field measurements of soil respiration in a shrubland system, which were complemented by respiration measurements of soils incubated at four temperatures and two moisture levels. A Bayesian statistical approach was utilized to combine the two data sets to quantify the response of respiration rates and the sensitivity of respiration to soil

temperature and moisture. Toward improving the respiration models, we explored incorporating the effects of the Enhanced Vegetation Index (EVI) to account for changes in ecosystem vegetation "activity" on soil respiration. This analysis approach allowed for seamless integration of the two data sets, and the incubation data were used to help inform the temperature sensitivity parameters in the respiration model.

2. Methods

[9] This study was conducted in a semiarid riparian system in the Sonoran Desert. We made field measurements of soil respiration (R), moisture, and temperature, and we performed lab incubations with intact soil cores at four temperature and two soil moisture levels. The incubations were used to help quantify the temperature response of respiration under low-moisture conditions, the "typical" condition of semiarid systems. Both the field and incubation data directly informed the temperature sensitivity parameters used to model respiration (see below). Field measurements were made over a growing season. A hierarchical Bayesian framework was employed that allowed for simultaneous analysis of all the data associated with the field and the incubation measurements and full accounting of model and data uncertainty.

2.1. Site Description

[10] The research site is a riparian shrubland located on an old alluvial terrace of the San Pedro River in southeastern Arizona, near Sierra Vista (1200 m above sea level (asl)). The area is characterized by a semiarid climate with a mean annual precipitation of 350 mm and a mean summer temperature of 26°C [*Scott et al.*, 2004]. Annual precipitation has a bimodal distribution, in which 60% falls during the monsoon season (June to September) and most of the remainder falls between November and March [*Scott et al.*, 2004]. The site supports a matrix of velvet mesquite (*Prosopis velutina*) (1–4.5 m tall) and sacaton bunchgrass (*Sporobolus wrightii*) [*Scott et al.*, 2006]. The mesquite shrubs vary in height, and we categorize medium-sized mesquites as those between 1.5 and 3 m tall and big mesquites as those >3 m tall. The depth to groundwater is about 7 m and is accessed only by medium-sized and big mesquites [*Potts et al.*, 2006]. The primary microsites and their relative cover on the landscape are medium-sized mesquite (30.1%), big mesquite (20.4%), bunchgrass (22.2%), open ground with litter (11.2%), open ground without litter (11.0%), and other types of ground cover (5.1%). For exploratory modeling analysis, 16 day Moderate Resolution Imaging Spectroradiometer (MODIS) EVI data were used as a proxy for ecosystem leaf area index during the growing season in 2005, as *Scott et al.* [2006] found a linear relationship between the two measures. Precipitation was collected with a tipping bucket rain gauge (TE525, Texas Electronics) on a nearby (within 20 m) eddy covariance tower.

2.2. Soil Respiration: Field Measurements

[11] Soil collars (PVC pipe, 10.16 cm diameter) were installed in the soil (5 cm deep) in microsites created by shrubs, grasses, and open space. That is, collars were installed beneath five medium-sized mesquite shrubs, beneath five sacaton bunchgrasses, in three open spaces devoid of litter, and beneath five big mesquite shrubs. Two collars were installed under each big mesquite shrub; one was placed within 50 cm of the main trunk and the other within 25 cm of the canopy edge (under the canopy). Hereafter, we refer to the microsites as near the main trunk of big mesquite (BM-T), near the canopy edge of big mesquite (BM-C), medium mesquite (MM), sacaton bunchgrass (grass), and open space (open).

[12] Measurements of soil CO_2 flux were made with a closed-loop static chamber system (Li-820, LICOR, Lincoln, Nebraska) from 0800 to 0930 nearly biweekly from 2 June to 2 October 2005 (using methods of *Cable et al.* [2008]). The dry CO_2 concentration data were converted to flux density with volume and area corrections [*Pearcy et al.*, 1990]. Within 10 cm of the soil collars, we made spot measurements of soil temperature (at two depths: 2 and 12 cm) (DiGi-Sense, Eutech Instruments, Vernon Hills, Illinois) and soil moisture (integrated over 0–12 cm, % volumetric water content; CS620 HydroSense, Campbell Scientific, Logan, Utah). Soil moisture on each sampling day was determined from the average of three separate measurements made within 10 cm of each other at each soil collar. Litter depth was measured with a ruler (in centimeters) from the top of the soil to the litter surface. Root mass was measured by extracting soil cores (0–10 cm) from each microsite (n = 3 per microsite), sieving out and hand picking the roots and weighing the dry root mass.

2.3. Soil Respiration: Incubations of Intact Cores

[13] In June 2005, prior to the onset of the monsoon, five replicates of paired soil cores (extracted from 0 to 10 cm) were collected from the five microsites used in the field study (BM-C, BM-T, MM, grass, and open), yielding 50 cores (2 cores per replicate × 5 replicates × 5 microsites). Each core was extracted with its own 5.1 cm diameter, 10 cm long PVC tube with one end open. Cores were kept intact and on ice until returning to the lab for flux measurements. Thus, respiration from the cores is a combination of heterotrophic and autotrophic activities since roots were not removed. However, we acknowledge that root respirations may not have been occurring at their peak level because the roots were severed from carbon inputs from the leaves. Soils were kept in these tubes, and one of the paired cores (per pair) was brought to average moisture conditions observed in the field by adding 10 mL of water to achieve volumetric water content of about 5.1%. The other core in the pair did not receive additional water so the moisture content was less than 5.1%. Within 24 h of collection in the field, all soil cores were put in a growth chamber, and CO_2 flux was measured as in the field with an Li-820, but in a controlled environment at each of four constant temperatures: 15°C, 25°C, 35°C, and 45°C. The cores were allowed to equilibrate to each temperature for 1 h prior to CO_2 measurements. All of the measurements were completed within 48 h of being collected in the field. Prior incubation work has shown that the respiration rates from soils at this site remain unchanged up to 48 h after field collection [*Cable et al.*, 2009].

2.4. Statistical Analyses

[14] To evaluate differences in soil respiration, soil moisture, and soil temperature among microsites (measurement day times microsite comparison for each variable), we

Table 1. Descriptions of the Abbreviations From the Model and the Microsite Identification

Microsite Abbreviation	Description	
BM-T	big mesquite near the trunk	
BM-C	big mesquite near the canopy edge	
MM	medium-sized mesquite	
grass	sacaton bunchgrass	
open	intercanopy spaces	
Model Parameter	**Description**	**Equation and Units**
$\mu LR_{i,d}$	mean predicted respiration rates for observation i and data set d (field or incubation)	Equation (1), μmol m^{-2} s^{-1}
τ_d	precision for each data set d	Equation (1)
LRb_i	predicted base respiration rate or respiration at 25°C	Equations (2) and (4), μmol m^{-2} s^{-1}
Eo	energy of activation	Equation (2), K
To_m	temperature sensitivity of respiration	Equations (2) and (4), K
$\overline{T}_i$	soil temperature data (weighted by depth)	Equations (2) and (3), °C converted to K
ε_c	random effects associated with soil collar	Equation (2)
γ_t	random effects associated with measurement day	Equation (2)
p_m	weight for each microsite m associated with the weighted soil temperature function	Equation (3)
$a_{1,m}$	LRb under average soil moisture and EVI conditions	Equation (4), μmol m^{-2} s^{-1}
$a_{2,m}$	microsite-specific effect of soil moisture on LRb	Equation (4)
$a_{3,m}$	microsite-specific effect of EVI on LRb	Equation (5)
$b_{1,m}$	microsite-specific To under average soil moisture conditions	Equation (4), K
$b_{2,m}$	microsite-specific effect of soil moisture on To	Equation (4)
$\overline{W}$, $\overline{EVI}$	average soil moisture and EVI across all microsites and over all measurement days	Equations (4) and (5), % for soil moisture
W_i	soil moisture data	Equation (4), %
EVI_i	EVI data	Equation (5)

conducted analyses of variance (ANOVAs) with the JMP statistical software (SAS, Cary, North Carolina). However, we used a hierarchical Bayesian (HB) approach to rigorously quantify the response of respiration to temperature and moisture across the five microsites. We also explored incorporating the EVI into the model because aboveground and belowground plant phenologies are often correlated [*Reichstein et al.*, 2003; *Steinaker and Wilson*, 2008], and thus we expect the EVI to reflect potential temporal changes in ecosystem-scale soil autotrophic respiration. We simultaneously analyzed the field and incubation data such that the incubation data informed the temperature sensitivity parameters in the model for the field data.

[15] The HB framework has three primary components: (1) the data model that describes the likelihood of observed respiration data associated with the field and incubation studies; (2) the process model that includes a nonlinear respiration model, which is applied to both data sets and process uncertainty; and (3) the parameter model that specifies prior distributions for process model parameters and variance terms. These three components were combined to generate posterior distributions of parameters [see *Cable et al.*, 2011; *Clark*, 2005; *Wikle*, 2003] that lend insight into the factors controlling soil respiration. We utilized a model similar to that of *Cable et al.* [2011], but the model herein explicitly accommodates both field and incubation data, and it uses a slightly different approach for quantifying the temperature and moisture effects. The variables and parameters used in the model are also defined in Table 1.

2.4.1. Data Model

[16] First we define the likelihood function for observed soil respiration rates (R^{obs}) associated with the two data sets (note that there is a different likelihood for the field and incubation data). The R^{obs} is lognormally distributed such that for data set d (d = 1 for field, 2 for incubation) and observation i (i = 1, 2, …, 317 for the field data; i = 1, 2, …, 200 for the incubation data):

$$\ln\left(R^{\mathrm{obs}}_{i,d}\right) \sim \mathrm{normal}\left(\mu LR_{i,d}, \sigma_d\right). \tag{1}$$

Thus, $\mu LR_{i,d}$ is the mean (or latent) log soil respiration rate specific for observation i and data set d, and σ_d is the standard deviation that describes the observation variability associated with each data set.

2.4.2. Process Model

[17] A process model is specified for $\mu LR_{i,d}$ based on a modified version of an Arrhenius-type function described by *Lloyd and Taylor* [1994] and as modified by *Cable et al.* [2011]. In the model for the field data, we incorporated random effects to describe process errors associated with variability between soil collars within each microsite and between measurement days. First we describe the model for the field data (d = 1); for observation i associated with collar c (five collars per microsite), day t (14 days), and microsite m (five microsites):

$$\mu LR_i = LRb_i + Eo\left(\frac{1}{298.15 - To_m} - \frac{1}{\left(\overline{T}_i + 273.15\right) - To_m}\right) + \varepsilon_c + \gamma_t, \tag{2}$$

where $LRb = \ln(Rb)$ is the log base rate (i.e., Rb is the "base" respiration rate at 25°C), Eo (Kelvin) is analogous to an energy of the activation term, To (Kelvin) is a temperature sensitivity parameter, and $\overline{T}$ is the "average" soil temperature (°C converted to K) as described in equation (3). The collar and day random effects are denoted by ε and γ, respectively, and we assumed that each group of random effects comes

from a normal distribution with a mean of zero and standard deviations of σ_ε and σ_γ, respectively. We implemented sum-to-zero constraints for the collar random effects (small group size) according to the "sweeping" algorithm, which ensures accurate estimates of σ_ε and σ_γ [*Gilks and Roberts*, 1996].

[18] Equation (2) describes μLR as a monotonically increasing function of soil temperature (T), and the slope (first derivative) of this function reflects the sensitivity of R to changes in soil temperature (T). The slope depends on Eo and To, and we specifically focus on To as an index of the microsite-specific temperature sensitivity of R, in which larger values of To indicate greater sensitivity (steeper slope). In equation (2), $\overline{T}$ represents the weighted average of T measured at two depths; the weights p and $1 - p$ describe the relative importance of T measured at 2 cm and at 12 cm, respectively. For example, a value of p close to 1 indicates that bulk soil respiration is more strongly coupled to surface temperature (2 cm) compared with the subsurface temperature (12 cm). Thus, for field soil temperature (T), observation i, depth z ($z = 1$ for 2 cm, $z = 2$ for 12 cm), and microsite m associated with i,

$$\overline{T}_i = p_m T_{i,1} + (1 - p_m) T_{i,2}. \tag{3}$$

We allow p to vary by m because the microsites may differ in the relative importance of each depth for R given potential differences in the depth distributions of root and microbial activity [*Cable et al.*, 2009]. Note that p is an estimated parameter, and equation (3) allows the R data to determine the relative importance of each depth.

[19] We extend the original function in the work by *Lloyd and Taylor* [1994] by modeling the base rate (LRb) and temperature sensitivity (To) as functions of volumetric soil water content (W) such that for observation i and microsite m,

$$\begin{aligned} LRb_i &= a_{1m} + a_{2m}\left(W_i - \overline{W}\right) \\ To_i &= b_{1m} + b_{2m}\left(W_i - \overline{W}\right) \end{aligned}, \tag{4}$$

We also explored modeling LRb as a function of the EVI to examine the potential influence of aboveground plant activity on R:

$$LRb_i = a_{1m} + a_{2m}\left(W_i - \overline{W}\right) + a_{3m}\left(\mathrm{EVI}_i - \overline{\mathrm{EVI}}\right). \tag{5}$$

[20] The a_1 parameter represents the microsite-specific log base rate under average moisture conditions ($\overline{W}$ is the observed mean W across all days and microsites; equations (4) and (5)) and the average EVI ($\overline{\mathrm{EVI}}$ is the observed mean EVI across all days; equation (5)). Likewise, b_1 depicts the microsite-specific temperature sensitivity (To) under average moisture conditions. The a_2 and b_2 parameters, which also vary by microsite, describe the soil moisture main effects; thus, moisture has the potential to impact the magnitude and the temperature sensitivity of respiration. The a_3 parameter in equation (5) is the EVI main effect (for LRb), which is multiplicative on the regular scale (for Rb) and can be interpreted as scaling the base rate under average canopy cover conditions by the amount of root and/or microbial activity; there is no analogous argument for To, and thus we do not explore the potential impact of EVI on To.

[21] The model for the incubation data ($N = 200$) has the same format as the model for the field data described above, but the following modifications were made. The model did not include an EVI effect on the base rate, there are no random effects associated with collar or day, and the "average" temperature ($\overline{T}$) was set to the corresponding applied temperature (15°C, 25°C, 35°C, or 45°C). The same value of $\overline{W}$ was used, which was based on the field observations of W. Thus, the parameters for the base rate and temperature sensitivity functions are informed by both the field and incubation data sets; that is, a_1, a_2, b_1, b_2, and Eo are shared between the incubation and field models, while a_3, p, and the random effects variances were informed by the field data, and the data set-specific observation variances in equation (1) were informed by their corresponding data set.

2.4.3. Parameter Model

[22] The final stage in the HB modeling approach is the specification of the priors for the unknown parameters. We used independent and relatively noninformative (diffuse) priors for the a, b, and p parameters and all standard deviation terms. That is, normal densities with large variances were used for the a_1, a_2, a_3, and b_2 parameters; a uniform distribution on the interval (0,1) was used for p; wide uniform densities were used for the σ parameters; all distributions were parameterized according to the work by *Gelman* [2004a]. *Lloyd and Taylor* [1994] suggest that Eo and To (equation (2)) are relatively conserved across a variety of ecosystem types. Thus, we used semi-informative normal priors for Eo and b_1 with means given by the estimates of *Lloyd and Taylor* [1994] (308.56 and 227.13 K, respectively) and relatively large variances of 1000 [*Cable et al.*, 2011]. As required, we restricted b_1 (and thus To) to occur between 0 and 285 K (285 K is lower than the minimum measured soil temperature).

[23] The HB model was implemented in the Bayesian statistical software package WinBUGS [*Spiegelhalter et al.*, 2002]. For each model, we ran three parallel Markov chain Monte Carlo (MCMC) chains for ~12,000 iterations, and we used the Brooks-Gelman-Rubin (BGR) diagnostic tool to evaluate convergence of the chains to the posterior distribution [*Brooks and Gelman*, 1998; *Gelman*, 2004a]. We discarded the first 3000 burn-in samples, yielding an independent sample of ~9000 values for each parameter from the joint posterior distribution [see, for example, *Gamerman and Hedibert*, 2006; *Gelman*, 2004a, 2004b]. The presentation of results from the ANOVA includes means and standard errors, but we present posterior means and 95% credible intervals (CIs) for the HB results.

3. Results

3.1. ANOVA Results

3.1.1. Incubations

[24] Respiration rates were higher in wet soil compared with dry soil at all of the incubation temperatures (Figure 1). The respiration rates under wet conditions were highest at 35°C and 45°C (Figure 1). Soil from the open space tended to have the lowest respiration rates (Figure 1).

3.1.2. Root Mass and Litter Depth

[25] Litter depth near the trunk under big mesquite (microsite BM-T) was significantly higher than in the other

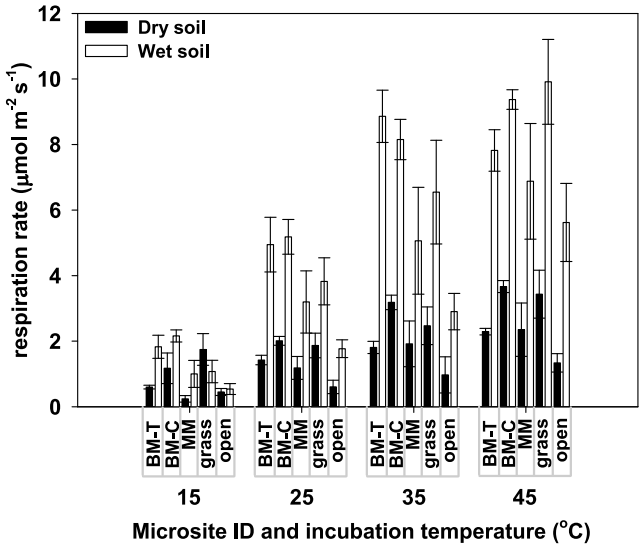

Figure 1. Means and standard errors for respiration rates from incubations conducted at four temperatures for intact cores from each of the five microsites at 5% water content (dark bars) and dry (white bars) conditions.

microsites. That is, litter depths under BM-T were 3.4, 4.4, and 8 times greater than under medium mesquite (MM), near the canopy edge of big mesquite (BM-C), and under grass, respectively ($F_{4,24}$ = 15.7232, $p < 0.0001$; Figure 2). The open microsite had little to no discernible litter. Likewise, root masses in the BM-T microsite were 3.2, 3.3, 4.7, and 10.9 times greater than in the BM-C, grass, MM, and open microsites, respectively ($F_{4,24}$ = 4.4711, p = 0.0096; Figure 2).

3.1.3. Enhanced Vegetation Index

[26] The EVI increased from 0.21 at the beginning of the summer (day 150) to a peak of 0.41 near day 250, and then declined to 0.25 near day 280 (Figure 3). Canopy development, as indexed by the EVI, lagged behind the timing of the monsoon. The monsoon season in southern Arizona occurred between days 197 and 262 (Figure 3a).

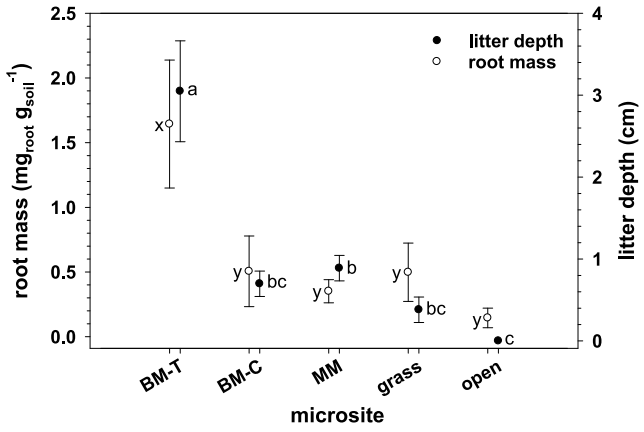

Figure 2. Means and standard errors for root biomass in the top 10 cm of the soil (open symbols) and litter depth (closed symbols) in each microsite. Letters denote statistical differences among microsites: a–c indicate the litter depth, and x and y indicate the root biomass comparisons.

3.1.4. Soil Respiration, Moisture, and Temperature

[27] The means and standard errors for the field-measured soil respiration, soil temperature, and soil moisture are given in Table 2; for simplicity, these statistics are shown for the three

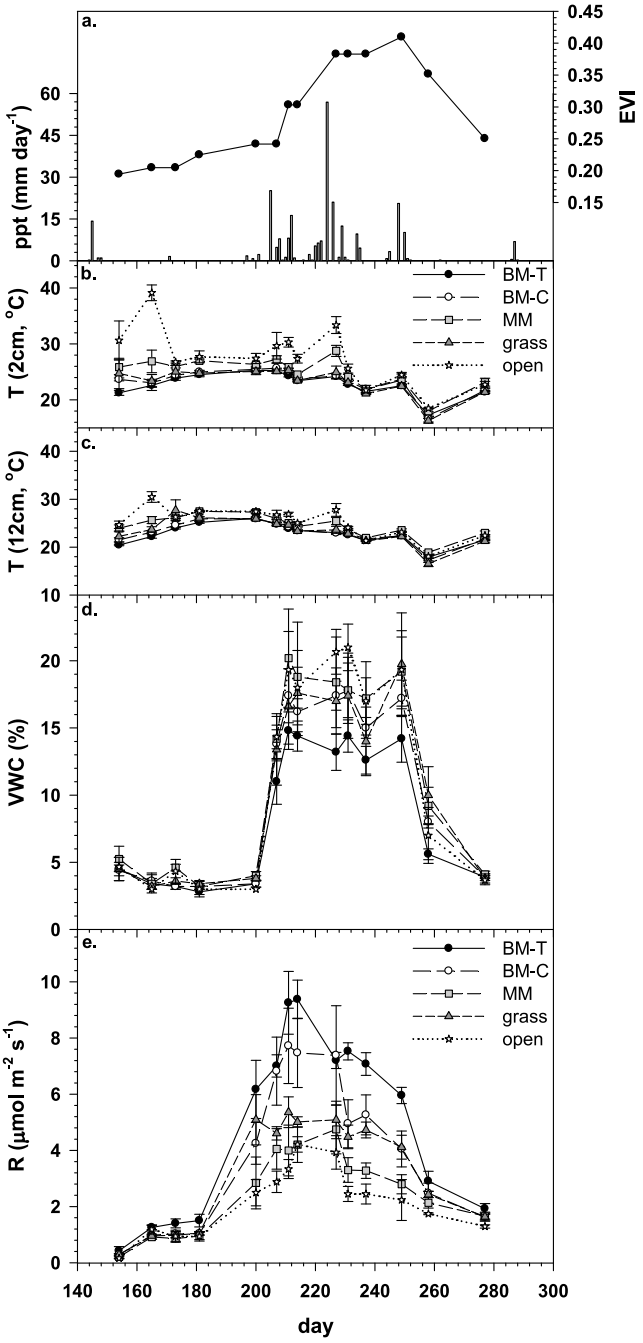

Figure 3. (a) The Enhanced Vegetation Index (EVI) for each measurement date in this study. The EVI is a landscape measure of vegetation cover (integrating over microsite or cover types), and larger values reflect greater canopy cover. Precipitation (ppt; mm day^{-1}) measured at the San Pedro, Arizona, research site. The means and standard errors for the following variables measured within each microsite: (b) soil temperature (T, °C) at 2 cm, (c) T at 12 cm, (d) volumetric soil water content (VWC, %) integrated from 0 to 12 cm, and (e) soil respiration rate (R, μmol m^{-2} s^{-1}).

Table 2. The Mean and Standard Errors (SEs) for Soil Respiration (R, μmol m^{-2} s^{-1}), Soil Temperature (T, °C) at 2 and 12 cm Depths, and Volumetric Soil Water Content (VWC, %) Between 0 and 10 cm for Big Mesquite Near the Canopy Edge (BM-C), Big Mesquite Near the Main Trunk (BM-T), Medium Mesquite (MM), Open Space (Open), and Sacaton Bunchgrass (Grass)[a]

		R		T (2 cm)		T (12 cm)		VWC	
Days	Microsite	Mean	SE	Mean	SE	Mean	SE	Mean	SE
154 to 181	BM-C	0.83	0.09	24.0	0.3	23.8	0.4	3.60	0.21
	BM-T	1.18	0.12	23.3	0.4	23.3	0.5	3.40	0.23
	MM	0.76	0.08	26.5	0.5	26.0	0.4	4.05	0.30
	grass	0.85	0.07	24.5	0.6	25.1	0.7	3.65	0.21
	open	0.80	0.13	30.2	1.1	27.1	0.4	6.50	1.18
200 to 249	BM-C	5.99	0.43	23.2	0.4	22.7	0.3	15.23	0.69
	BM-T	7.45	0.28	23.3	0.6	23.1	0.3	12.38	0.67
	MM	3.65	0.24	25.3	0.4	24.7	0.3	16.23	1.20
	grass	4.83	0.17	24.1	0.3	24.0	0.3	13.15	1.19
	open	3.00	0.20	27.8	0.8	25.7	0.5	15.04	1.42
258 to 277	BM-C	2.05	0.23	21.8	0.5	21.3	0.3	4.00	0.39
	BM-T	2.41	0.25	25.1	1.3	23.5	0.7	4.15	0.51
	MM	1.89	0.14	26.8	2.2	23.9	1.0	4.75	0.62
	grass	1.99	0.15	19.1	0.9	19.2	0.9	6.56	1.40
	open	1.52	0.11	23.3	1.2	22.2	0.7	4.70	0.79

[a]Data were averaged for three precipitation periods: premonsoon (days 154–181), midmonsoon (days 200–249), and late monsoon (days 258–277).

distinct precipitation periods defining the summer season: premonsoon (dry period), midmonsoon (wet period), and late monsoon (semidry period). Within each microsite and precipitation period, soil temperature did not differ between the surface (2 cm) and subsurface (12 cm). Comparisons across microsites, however, showed that temperatures at 2 cm were lowest beneath the BM (mean ± SE: 22.9°C ± 0.3°C for BM-T; 23.4°C ± 0.3°C for BM-C) and the grass (23.4°C ± 0.3°C), highest in the open microsite (27.5°C ± 0.8°C), and intermediate under MM (24.9°C ± 0.5°C) ($F_{4,315}$ = 17.9790, $p < 0.0001$; $F_{4,315}$ = 8.3577, $p < 0.0001$, respectively). Despite some daily differences, soil moisture content across the microsites did not differ from each other throughout the season (Figure 3d). The highest soil moisture content across all microsites occurred during the midmonsoon period, between days 207 and 249 (Table 2, $F_{13,306}$ = 181.4597, $p < 0.0001$).

3.1.5. Seasonal Patterns in Soil Respiration

[28] In the premonsoon period (days 154–181), soil respiration rates were at their lowest for the summer season (time times microsite, $F_{13,247}$ = 174.1893, $p < 0.0001$; Figure 3e). Soil respiration rates increased on day 200, coinciding with a small rain event that marked the onset of the monsoon season (day 197, 1.8 mm; Figures 3a and 3e), and soil respiration remained near these high rates for the duration of the monsoon (days 200–249) (Figure 3e). Respiration rates began to decline around day 258, signifying the onset of the late-monsoon period (Figure 3e). Comparisons across microsites revealed that the highest mean respiration rates were observed beneath the BM-T, particularly after day 231 (monsoon period) (Figure 3e). Mean respiration rates were similar at the BM-C and grass microsites, and rates from the MM and open microsites were the lowest ($F_{4,247}$ = 48.0392, $p < 0.0001$).

3.2. Soil Respiration Characteristics: HB Model Results

[29] Unless otherwise specified, we present results from the model wherein the respiration base rate (Rb) is modeled only as a function of soil moisture (equation (4)). We focus on this model because we lack mechanistic insight into the link between ecosystem-scale EVI and microsite-specific plant production at this site. The nonlinear respiration model given by equations (1)–(4) fits the field data set fairly well and fits the incubation data set less well (observed versus predicted: field data R^2 = 0.94; incubation data R^2 = 0.40, Figure 4). The model likely fits the field data better because of the explicit incorporation of plot and day random effects and because there was more variation in soil moisture across the observed soil respiration values compared with the incubation data. The measurement day random effects (γ, equation (2)) were negative early in the premonsoon period and in the postmonsoon period and positive following the onset of the monsoon (Figure 5d), indicating that the mean model (equation (2), without random effects) overpredicted soil respiration (R) in the premonsoon and postmonsoon seasons and underpredicted R during the monsoon season.

3.2.1. Relative Importance of Temperature at Different Depths

[30] The posterior means for the microsite-specific p values were close to 0.5, indicating that soil temperatures at both depths (2 and 12 cm) were equally important for respiration in all the microsites (Table 3). However, the 95% credible intervals for p spanned nearly the entire range of possible values, from 0 to 1, indicating large uncertainties in the relative importance of each depth.

3.2.2. Base Soil Respiration Rate

[31] The base soil respiration rates at 25°C (i.e., log scale, LRb) under average soil water conditions (a_1) were highest for the BM-C, BM-T, and grass microsites, followed by the MM and open microsites (Table 3). On the regular scale, Rb associated with the BM microsites were 1.5, 1.6, and 1.16 times higher than those at the MM, open, and grass microsites, respectively (Table 3). Soil moisture positively affected Rb in all but the open microsite, and the effect was the largest in the BM microsites (Table 3). The model we explored with EVI effects (equation (5)) showed a significant positive effect of EVI (a_3) on Rb in the BM-T, MM, and grass microsites, but a minimal effect in the BM-C and open microsites.

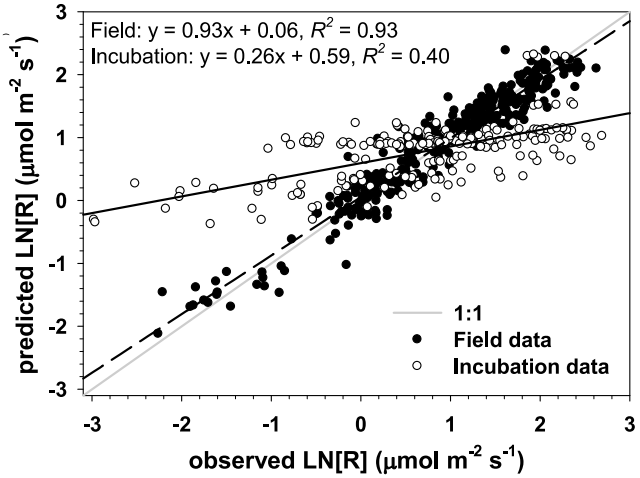

Figure 4. The comparison of observed versus predicted log respiration rates (LN[R]) for the field and incubation data. The 1:1 line is plotted in gray.

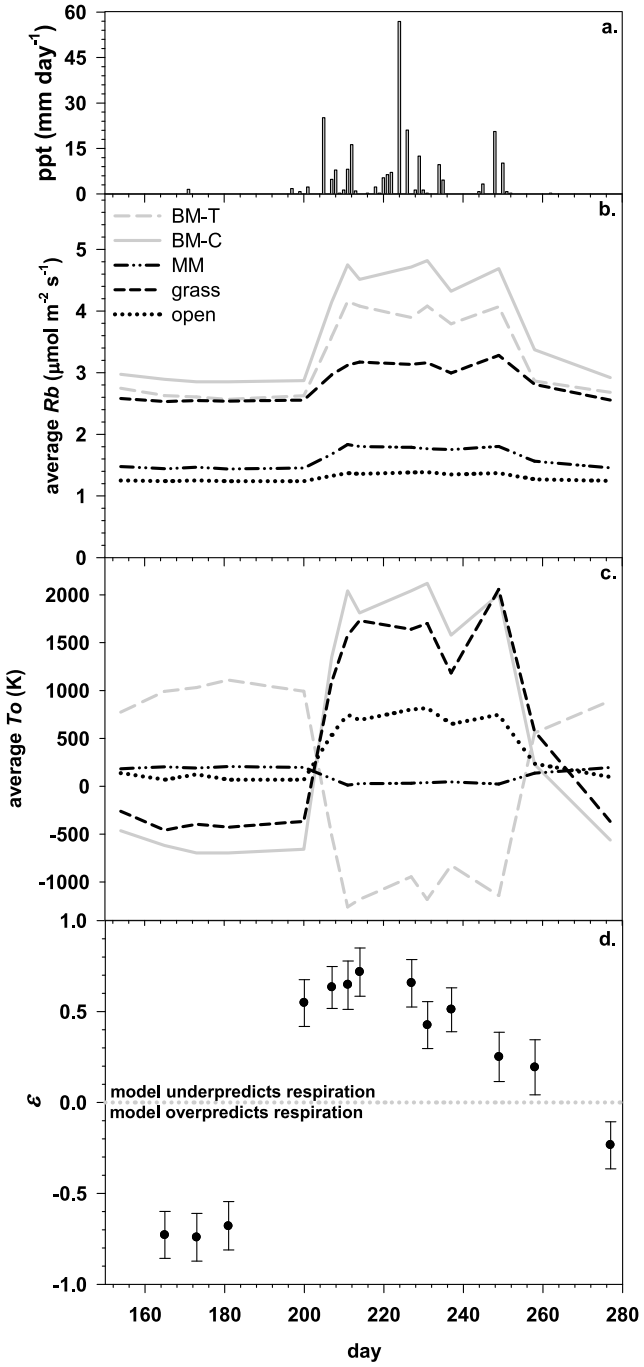

Figure 5. (a) Precipitation (ppt) measured at the research site (also shown in Figure 4). Posterior means for (b) the predicted base rate (*Rb*, equation (4) and (c) the temperature sensitivity (*To*, equation (4) over the growing season for each microsite. (d) The posterior mean and 95% credible interval for the day random effects (γ, equation (2)). For Figure 5d, values less than zero (gray dotted line) indicate dates the model overpredicts respiration and values greater than zero indicate dates the model underpredicts respiration; if the 95% CI's overlap zero, then the model predicts respiration well (no bias).

3.2.3. Temperature Sensitivity

[32] The posterior mean for the energy of the activation-type parameter (*Eo*) was 281.5 K (95% CI: [216.6, 347.7]). For the microsite-specific temperature sensitivity parameter (*To*), the "base" value (b_1; *To* under average soil water conditions) was similar across the microsites (Table 3); that is, the posterior mean for a particular microsite was contained within the 95% CIs for the other microsites. Soil water increased the temperature sensitivity in the BM-C, grass, and open microsites and decreased the sensitivity in the BM-T microsite (Table 3). Soil moisture did not have an effect on *To* in the MM microsite (Table 3). This explains some of the patterns in the mean predicted *To* values over the summer (Figure 5c). For example, *To* in the BM-T microsite decreased significantly from the premonsoon (dry) to the monsoon (wet) period (Figure 5c); in contrast, *To* in the BM-C, grass, and open microsites increased significantly, and *To* in the MM microsite remained relatively unchanged (Figure 5c).

4. Discussion

[33] A greater abundance of shrubs in semiarid grasslands affects the spatial patterns of soil temperature, moisture, and litter, resulting in fertile islands with enhanced soil metabolic activity [*Cable et al.*, 2009; *Schlesinger et al.*, 1996]. The goal of this study was to quantify the microsite specificity of soil respiration in a semiarid riparian ecosystem experiencing shrub encroachment and to understand changes in the sensitivity of metabolic processes to primary drivers. We examined the response of soil respiration associated with five different microsite conditions created by shrubs, grasses, and open spaces in a semiarid riparian ecosystem undergoing shrub expansion. Our hierarchical Bayesian analysis revealed that the presence of big mesquite affected the spatial heterogeneity of respiration "characteristics," such that respiration was more temperature sensitive near the canopy edge and respiration rates were higher under the big mesquites and grasses, relative to the open and medium mesquite microsites (Table 3 and Figure 5c). This does not support our hypotheses that greater temperature sensitivity will be associated with greater root density near the trunk, but it does support our hypothesis that the magnitude of soil respiration under large shrubs should be greater than that of the other microsites.

[34] One of the most interesting results was the spatial heterogeneity in the seasonal patterns of the temperature sensitivity (*To*) of respiration beneath the big mesquite (Figure 5c). The integration of the incubation and field data in our analysis helped to reveal these patterns. The microsites had opposing responses over the growing season, wherein the sensitivity of soil respiration in the big mesquite canopy edge, the open space, and the grass microsites increased during the monsoon period but it decreased in the big mesquite trunk microsite and remained unchanged in the medium mesquite microsite (Figure 5c). Given that the major abiotic drivers of soil respiration (soil temperature and soil moisture) were similar between the canopy and trunk positions under the big mesquite canopies (Figures 3b–3e), we suspect the difference in sensitivity between these two microsites is due to variation in heterotrophic versus autotrophic activity. It is likely that autotrophic or root-derived respiration dominates near the trunk of the mesquite given

Table 3. Posterior Means and 95% Credible Intervals (in Brackets) for Parameters in the Base Rate Model (*LRb*, equation (4)) and the Temperature Sensitivity Model (*To*, equation (4))[a]

Parameter	BM - T	BM - C	MM	Grass	Open
p	0.48 [0.01, 0.98]	0.42 [0.01, 0.97]	0.35 [0.008, 0.94]	0.52 [0.02, 0.98]	0.57 [0.03, 0.99]
a_1	1.20^{A} [0.96, 1.41]	1.12^{A} [0.89, 1.33]	0.42^{B} [0.18, 0.66]	0.99^{A} [0.78, 1.21]	0.24^{B} [0.005, 0.45]
a_1*	3.34 [2.62, 4.09]	3.11 [2.43, 3.80]	1.53 [1.19, 1.93]	2.71 [2.17, 3.37]	1.27 [1.00, 1.57]
a_2	$\mathbf{0.04^{A}}$ [0.02, 0.05]	$\mathbf{0.04^{A}}$ [0.02, 0.06]	$\mathbf{0.01^{B}}$ [0.002, 0.03]	0.005^{B} [−0.009, 0.02]	$\mathbf{0.02^{B}}$ [0.002, 0.03]
a_3	$\mathbf{6.34^{A}}$ [1.39, 11.0]	4.25^{A} [−0.89, 8.95]	$\mathbf{6.78^{A}}$ [1.93, 11.5]	$\mathbf{7.15^{A}}$ [2.29, 11.9]	4.87^{A} [−0.34, 9.85]
b_1	175 [67.3, 279]	82.9 [0.73, 282]	161 [51.5, 219]	228 [111, 284]	269 [185, 285]
b_2	173.2^{A} [68.1, 268]	-163^{B} [−296, −124]	-10.7^{C} [−30.8, 0.15]	144^{D} [68.7, 260]	36.3^{A} [20.2, 105]

[a]The five microsites (BM-T, BM-C, MM, grass, and open) are defined in Table 1. The parameters in the *LRb* model are p (the importance of soil temperature at 2 cm; equation (3)), a_1 (base rate at 25°C under average soil water conditions), a_2 (soil water main effect), and a_3 (EVI effect in equation (5). Also shown is a_1* = $\exp(a_1)$, the predicted base rate at 25°C under average conditions on the regular scale (μmol m^{-2} s^{-1}). The parameters in the *To* model are b_1 (temperature sensitivity under average soil water conditions) and b_2 (soil water main effect). Boldfaced values are means that are significantly different from zero (only relevant for b_2, a_2, and a_3), and different superscript letters denote statistical differences among microsites.

that there was significantly more root biomass near the trunk compared to the canopy edge. This is supported by the fact that the temperature sensitivity of autotrophic respiration has been shown differ relative to heterotrophic respiration [*Boone et al.*, 1998]. Yet, quantifying the temperature sensitivity of root respiration is a relatively underexplored area of research. These microsite-dependent differences in the base rate and its temperature sensitivity suggest that shrub expansion could significantly affect the spatial variability in root and soil respiration.

[35] We expected, but did not find, that respiration characteristics (magnitude, temperature sensitivity, and moisture sensitivity) in the medium mesquite microsites should be most similar to those of the big mesquite microsites (e.g., Table 3 and Figures 3, 5b, and 5c). Interestingly, these characteristics in medium mesquite microsites were more similar to those of the open microsite (Table 3). Soils beneath medium mesquites had high soil microbial biomasses, similar to big mesquite soils [*Cable et al.*, 2009], which should result in high respiration rates and potentially high moisture sensitivity [e.g., *Fierer and Schimel*, 2003]. However, other soil characteristics, which are shared with those of the open microsite, may be more important in affecting the patterns in soil respiration characteristics that we observed in this study. For example, medium mesquites have low root biomass, a thin litter layer (Figure 2), and low microbial carbon use and efficiency and substrate quality [*Cable et al.*, 2009], and these characteristics are associated with low soil respiration.

[36] Taken together, this suggests that, in the medium mesquite microsites, the ability of microbes to use different sources of carbon (substrate use and efficiency) and the amount of roots and litter play a more important role in affecting respiration than microbial biomass. For example, low-quality litter and inefficient microbes may decrease the temperature sensitivity of respiration [*Fierer et al.*, 2005]. The magnitude of soil respiration and its moisture sensitivity may be impacted by functionally limited microbes and low root biomass. The medium mesquite microsite is unique relative to the other microsites in this study, and it appears to represent a "transition microsite" in the grassland to shrubland conversion. *Potts et al.* [2008] found that photosynthesis is higher for medium mesquite than for sacaton bunchgrasses at the site where the present study occurred. Combined with low soil respiration, this indicates that the medium-sized mesquite may be important for enhancing ecosystem carbon gain during shrub expansion.

[37] We would like to note that although this study contributed significant information about how shrub expansion affects soil respiration, two aspects of our study highlight major knowledge gaps. First, a significant amount of additional variation in respiration was explained by the day random effects, which suggests there were important, temporally varying factors affecting soil respiration that we did not measure. The day random effects significantly differed from zero for each measurement day (Figure 3). We found that the low fluxes that occur early in the growing season are typically hard to predict [*Cable et al.*, 2008] because there is little variation in moisture or temperature during this time (Figure 3). Additionally, the onset of the monsoon may be an important period for processes that occur after long dry periods, such as development of new roots and growth of microbial biomass [e.g., *Austin et al.*, 2004]. Taken together, we suggest that future research focus on the controls of respiration during dry periods, which is the primary state of desert systems, and during the onset of rainy periods.

[38] Through exploratory modeling analysis, we wanted to account for development of seasonal vegetation cover by using MODIS EVI (Enhanced Vegetation Index) as a proxy for ecosystem-level autotrophic activity [*Reichstein et al.*, 2003; *Steinaker and Wilson*, 2008]. The EVI had a significantly positive effect on respiration rates in the big mesquite trunk, medium mesquite, and grass microsites, but a minimal effect in the big mesquite canopy and open microsites (Table 3). Although EVI was not incorporated into the primary model because microsite-specific EVI data were not available, we believe that this may be a good metric of ecosystem-level phenology and root development. Moreover, while it might seem appealing to include EVI at the level of individual microsites, this would not accurately reflect how the aboveground canopies translate to belowground influences in this semiarid system. While canopies of individual plants may show regular or clumped arrangements, it appears that the root systems overlap to a greater degree [*Fonteyn and Mahall*, 1978; *Phillips and Macmahon*, 1981; *Schenk and Jackson*, 2002], and thus the ecosystem-level EVI is expected to be more indicative of the potential influence of the vegetation on soil respiration. We think that further exploration of the impact of plant productivity on respiration in these systems is a fruitful area of research.

5. Conclusions

[39] Predicting how ecosystem carbon balance will change with shrub expansion depends on properly scaling processes such as the magnitude and temperature sensitivity of soil

respiration. Such scaling often relies on assumptions of how these processes relate to vegetation cover and the size or density distributions represented during vegetation transitions. This study shows that there can be a great deal of fine-scale spatial heterogeneity that accompanies shrub expansion, such as variation within the canopies of large-sized shrubs, between different shrub size classes, and between distinctly different microsite types (shrubs, grass, and open space). Given the extensive cover of mesquite in this system (~50%), their impact on respiration may be important. In particular, we show that the characteristics of soil respiration, such as temperature sensitivity, can vary significantly from the trunk to the canopy edge of large shrubs, likely due to the relative activity of autotrophs versus heterotrophs, with autotrophic respiration likely dominating near the trunk. This may be linked to the ability of big mesquites to use groundwater, which may allow them to maintain high root activity relative to plants that do not access groundwater. We also show that medium mesquite microsites do not behave like a downscaled version of big mesquite microsites. In fact, the grass microsites show more similarity to big mesquite microsites than medium-sized shrub microsites. Thus, spatial patterns in the magnitude of soil respiration are expected to differ from the spatial patterns in the temperature and moisture sensitivities of soil respiration. This spatial heterogeneity will present challenges in scaling soil respiration fluxes to the ecosystem level in riparian ecosystems experiencing shrub encroachment, but it is characteristic of such landscapes and thus cannot be ignored during such scaling processes.

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