ECOSYSTEMS

Antecedent Conditions Influence Soil Respiration Differences in Shrub and Grass Patches

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ABSTRACT

Quantifying the response of soil respiration to past environmental conditions is critical for predicting how future climate and vegetation change will impact ecosystem carbon balance. Increased shrub dominance in semiarid grasslands has potentially large effects on soil carbon cycling. The goal of this study was to characterize the effect of antecedent moisture and temperature conditions on soil respiration in a grassland now dominated by shrubs. Continuous measurements of soil respiration, soil temperature, and soil moisture were made over the entire summer of 2005 within distinct vegetation microsites in this shrubland community—under grasses, shrubs, and in open spaces. We analyzed these data within a Bayesian framework that allowed us to evaluate the time-scale over which antecedent conditions influence soil respiration. The addition of antecedent conditions explained an additional 16% of the variation in soil respiration. High soil moisture during the preceding month increased respiration rates in both the grass and shrub microsites. However, the time period over which antecedent soil moisture influenced the temperature sensitivity of soil respiration was shorter in the shrub compared to the grass microsites (1 vs. 2 weeks, respectively). The depth of moisture was important; for example, for respiration under shrubs, near-surface moisture was more influential on the day of the respiration measurement but subsurface moisture was more influential on the antecedent time scale. Although more mechanistic studies are required, this study is the first to reveal that shrub encroachment changes the time scales over which soil moisture and temperature affect soil respiration.

Key words: ecohydrology; lag effects; pulse response; shrub encroachment; Sonoran desert; temperature sensitivity.

INTRODUCTION

The response of ecosystem processes to variation in environmental conditions is important to understand in light of recent and future changes in vegetation (Archer and others 2001) and climate (Christensen and others 2007). Toward understanding the potential impacts of such changes, it is important to quantify how the ecosystem process of interest (for example, soil respiration) responds to variation in antecedent conditions (for example, past soil water and/or temperature). This study explores how changes in vegetation associated with recent shrub encroachment potentially impact soil respiration and its relationship with antecedent drivers in a semiarid shrubland community. Previous studies found that antecedent soil moisture is critical for predicting soil respiration in semiarid ecosystems (Sponseller 2007; Cable and others 2008; Casals and others 2009; Ma and others 2012). These studies, however, arbitrarily define the antecedent conditions by choosing a fixed integration period without considering any potential lag effects. We propose that the antecedent conditions and their effects are more complex, and simultaneous estimation of lag times, integration periods, relative importance of past time periods, and antecedent effects will improve our predictive understanding of ecosystem processes such as soil respiration.

Quantification of the *antecedent conditions*—the relevant past state/values of the driving variable(s) of interest (such as soil water)—involves the *integration period* and the *lag time* (Figure 1). The integration period defines the time scale over which the antecedent conditions operate (for example, soil water conditions over the ''past 2 weeks''). The lag time describes the past time over which the driving variable has the greatest influence on the current response of interest (for example, ''4 days ago'', curves 3 and 4, Figure 1). The relationship between the process and the antecedent driver may not always involve a time lag, such that the current conditions dominate the response (curves 1 and 2,
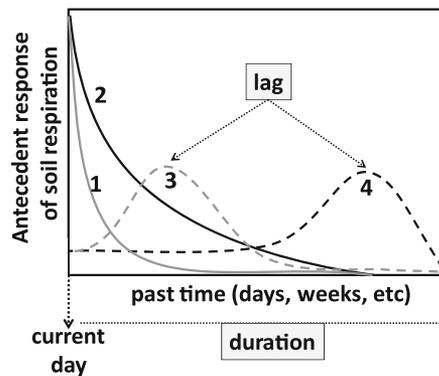
	1	2	3	4
Duration and lag descriptions	Short duration No lag time Current conditions important	Intermediate duration No lag time Current conditions important	Intermediate duration Short lag time Current conditions less important	Long duration Long lag time Current conditions less important
Microbial vs. root dominated	microbial	microbial	grass root	shrub root
surface vs. deep dominated	surface	surface & subsurface	subsurface	deep

Figure 1. Four primary antecedent responses of soil respiration. *Line 1* This is a short duration with no lag time and current conditions are important, which is likely associated with microbial dominated respiration or respiration from surface/near-surface soil layers. *Line 2* This is an intermediate duration with no lag time and current conditions are important, which is also mostly associated with microbial respiration and respiration originating from surface and subsurface soil layers. It is possible for shallow roots to have this response as well if they can respond quickly to current moisture/temperature conditions. *Line 3* This is an intermediate duration with a short lag time and current conditions are less important. This response is associated with grass root respiration because their roots are found in the subsurface soil layers. *Line 4* This is a long duration with a long lag time and current conditions are less important. This response is associated with shrub root respiration because they tend to have deep rooting systems.

Figure 1). The integration period and lag time combine to describe the relative importance of past conditions. The *antecedent effect* describes the direction and degree to which the antecedent conditions impact the process of interest. If an antecedent effect does not exist, then the integration period and lag time are irrelevant.

The response of soil respiration to antecedent conditions should depend on the primary location or depth in the soil where root or microbial activity occurs. The environment of deeper soil layers is less variable than surface layers; for example, it takes longer for soil water to reach deeper layers, but the water is retained longer (Schwinning and Ehleringer 2001; Schenk and Jackson 2002b). The temperature of deeper soil layers tends to be fairly stable, with small diurnal and seasonal changes, and cool relative to surface layers. In the surface layers, availability of soil water is highly ephemeral due to evaporation, and soil temperatures tend to be more variable, with large daily and seasonal cycles. Deeper soil layers are primarily occupied by plant roots, and shallow surface layers are occupied by both roots and non-rhizosphere associated microbes (Schenk and Jackson 2002a; Cable and others 2009).

The relative dominance of roots versus microbes could impact the antecedent response of soil respiration. In addition to being exposed to different environments, roots and microbes tend to respond differently to moisture and temperature, and they have different life spans and acclimation times. The long life span and acclimation time of roots (Palta and Nobel 1989; Kubiske and others 1998; Pavon and Briones 2000; Tang and others 2005; Zhang and others 2009) may lead to a longer integration time and lag period than the short-lived, rapidly acclimating microbes (Luo and others 2001; Fierer and Schimel 2003; Davidson and Janssens 2006; Atkin and others 2008). Microbial respiration also tends to be more moisture and temperature sensitive than root respiration, with large and rapid responses of microbial respiration to water addition and temperature increases (Qi and others 2002; Xu and others 2004). Therefore, we hypothesize that respiration from surface soil layers, particularly those dominated by microbes, will have a short integration period and no lag time, so current conditions are more important than antecedent conditions (curve 1, Figure 1). With increases in microbial biomass and organic matter for microbial consumption, we hypothesize a lengthening of the integration period (curve 2, Figure 1). Further, we hypothesize that respiration from deeper soil layers, which are dominated by roots, will have a long

integration period and a long lag time, with a relatively low importance of environmental conditions on the current day (curves 3 and 4, Figure 1). Roots found closer to the surface should have a shorter lag time and integration period (curve 3, Figure 1) compared to deeper roots (curve 4, Figure 1).

The presence of different plant functional types may affect the antecedent response of soil respiration because of the impact on the depth distribution of soil activity. For example, relative to neighboring grasses, woody plants or shrubs have more belowground biomass (Cox and others 1986; Schenk and Jackson 2002b), particularly in deeper soil layers (Midwood and others 1998), and support greater microbial biomass near the surface (Hibbard and others 2001; McLain and Martens 2006; Brantley and Young 2008; Cable and others 2009). The soil temperature and moisture depth profiles beneath shrubs also differ from those beneath grasses, where the shrub canopies are more effective than grasses at shading the soil and intercepting rainfall. Therefore, soil respiration under shrubs likely originates from both surface and deeper soil layers, and the microbes in the surface layers have a larger organic matter pool to decompose. We hypothesize that the antecedent response of respiration under shrubs will be a qualitative mixture of curves 2 and 4 (Figure 1). Soil respiration under grasses likely originates more from the surface layers where there is a small organic matter pool, so we hypothesize that the antecedent response under grasses will be a qualitative mixture of curves 1 and 3 (Figure 1).

MATERIALS AND METHODS

Field Study

The research site is a semiarid riparian shrubland located on an old alluvial terrace of the San Pedro River Basin in southeastern Arizona, near the town of Sierra Vista (1200 m asl), where mean summer temperature is 26°C and mean annual rainfall is 358 mm. Annual rainfall has a bimodal distribution, where 60% falls between June to September (monsoon season) and the remainder falls between December and March (Scott and others 2004). The site is a medium-dense shrub-grass ecosystem with a mix of velvet mesquite (*Prosopis velutina*) and sacaton bunchgrass (*Sporobolus wrightii*) (Scott and others 2006). The relative covers of each major microsite type are: small to medium-sized (up to 1 m tall) mesquite (30%), large-sized (1–4.5 m tall) mesquite (20%), sacaton bunchgrass (22%), open

ground with litter (11%), open ground without litter (11%), and other types of ground cover (5%). From DOY 170 to 290 in 2005, continuous measurements of soil respiration, soil moisture, and soil temperature were made beneath two large-sized mesquite (>3 m tall), two bunchgrasses, and in two open spaces devoid of surface litter for a total of six measurement locations.

Soil respiration collars (PVC, 25.4 cm diameter) placed to 5 cm depth were installed in six locations (two replicates each under grasses, in open space, and under shrubs). Automated respiration measurements were made using clear acrylic domes attached to each collar. Opening and closing of the domes over the collar were actuated using a pneumatic cylinder controlled by a datalogger (CR10X, Campbell Scientific, Inc, Logan, UT). Each chamber was fitted with 2.5 mm wide, 25 mm-long capillary tubing vented to the atmosphere to relieve pressure differentials (Hutchinson and Mosier 1981; Davidson and others 2002). A small 4.5-V microfan provided minor mixing of air within the chamber, and a thermocouple was installed to measure chamber temperature while the lid was closed. A 5-min measurement procedure was triggered every 30 min for each collar. The procedure began with the lid closing slowly, which created a closed loop system wherein chamber air was circulated with a pump, through a gas analyzer (LI-6262, CO_2 and H_2O analyzer, LiCOR Inc., Lincoln, NE, USA). A low flow rate (0.8 l min^{-1}) was used to minimize disturbance to the soil boundary layer. CO_2 concentrations increased in the chamber over the 5-min period, and the first 30 s (nonsteady-state period) of data were discarded. Given the low flux rates in this system, the build-up of CO_2 in the chamber over this period of time was always linear. The CO_2 concentration data were converted to flux density (FCO$_2$; μmol m^{-2} s^{-1}) with the following equation:

$$\text{FCO}_2 = \frac{dC}{dt} \cdot \frac{\left(10 \cdot V \cdot Po \cdot \left(1 - \frac{Wo}{100}\right)\right)}{\left(R \cdot S \cdot (T_0 + 273.15)\right)},$$

where $\frac{dC}{dt}$ is the slope of [CO$_2$] with time (sec), V is the chamber volume (cm^3), Po is the initial pressure (kPa), Wo is the initial water vapor mole fraction (mmol mol^{-1}), R is the universal gas constant, To is the initial air temperature (°C), and S is the soil surface area (cm^2) (Pearcy and others 1990; LI-COR 2010). Daily-integrated soil respiration was computed by assuming that each flux measurement was representative of its corresponding 30-min period, and summing the 30-min fluxes over each 24-h period.

Within 5 cm of each chamber, soil moisture probes (% volume, ECH$_2$O probes, Decagon Devices, Inc., Pullman, WA; probes were calibrated in the lab for the soils at the field site) were installed at two depths (1–4 and 6–16 cm), and soil thermocouples were installed at 2.5 and 11 cm to record temperature (°C). Hereafter, we will refer to the two depths as "surface" and "subsurface". Precipitation data were collected with a tipping bucket rain gauge (TE525, Texas Electronics), and other basic meteorological data (air temperature, relative humidity, PAR, and so on) were collected on a nearby (<20 m away) eddy covariance tower described elsewhere (Scott and others 2006).

DATA ANALYSIS

We took an approach similar to Cable and others (2011) to analyze the daily integrated soil respiration data, but the model herein explicitly quantifies antecedent moisture and temperature and their effects on the magnitude and the temperature sensitivity of daily respiration. We apply the model to learn how the antecedent conditions and their effects differ between microsite types. We assumed that roots of both functional types (grass and shrub) can extend into open space soils. Thus, we explicitly model soil respiration for each vegetated microsite type, and we model soil respiration in the open space as a mixture of the predicted respiration dynamics in the grass and shrub microsites. This approach serves to significantly reduce the number of model parameters compared to an approach that explicitly models the open space independent of the vegetated microsites (we tried this parameter-rich version, but the increase in model fit (R^2) was less than 1%). The mixture approach also allowed us to quantify the relative importance of grasses and shrubs for understanding soil respiration responses on a landscape scale. We describe the important elements of our model below; see Table 1 for a list of the model parameters.

We defined the likelihood of the observed daily soil respiration (R^{obs}; mmol m^{-2} day^{-1}) by assuming that R^{obs} is log-normally distributed such that for day i ($i = 1, 2,…,120$) and collar c ($c = 1, 2,…,6$):

$$\ln(R_{i,c}^{\text{obs}}) \sim \text{Normal}\left(\mu\text{LR}_{i,c}, \sigma^2\right) \qquad (1)$$

μLR is the mean (or predicted) log soil respiration rate and σ^2 describes the observation variance. The model for μLR is based on an Arrhenius-type function described by Lloyd and Taylor (1994) as modified in Cable and others (2011). Thus, for each

Table 1. Parameters Associated with Model Parts Found in Equations 1–9

Parameter	Description	Equations
μLR	Predicted log respiration rates, daily integrated scale (mmol m^{-2} d^{-1})	1, 2, 3
τ	Precision for the respiration data	1
LRb	Log respiration base rate (Rb) at 25°C (mmol m^{-2} d^{-1})	2, 5
Eo	Energy of activation and temperature sensitivity of Rb (K)	2, 5
Q^{10}	Temperature sensitivity of soil respiration calculated from Eo	
To	Temperature sensitivity (K)	2
a_1	Base respiration rate under average soil moisture and VPD conditions (mmol m^{-2} d^{-1})	5
a_2	Current soil moisture effect	5
a_3	Antecedent soil moisture effect	5
a_4	Antecedent soil temperature effect	5
a_5	VPD effect	5
a_6	Current and antecedent moisture interaction effect	5
b_1	Base energy of activation under average soil moisture conditions (K)	5
b_2	Current soil moisture effect	5
b_3	Antecedent soil moisture effect	5
b_4	Current and antecedent moisture interaction effect	5
f	mixture weight for the relative contribution of grass vs. shrub respiration	3
p	Mixture weight of surface vs. deep conditions. A different p was used for soil temperature (current and antecedent) and soil moisture (current and antecedent). For VPD, this is the mixture weight of average daytime VPD vs. average night and day VPD	4
w	Daily and weekly memory weights	6
ϵ_i	Daily random effects	8

collar c associated with a vegetated microsite (m = mesquite or grass):

$$\mu LR_{i,c} = \ln\left(Rb_{i,c}\right)$$
$$+ Eo_{i,c}\left(\frac{1}{298.15 - To_m} - \frac{1}{(\bar{T}_{i,c} + 273.15) - To_m}\right) \quad (2)$$

where Rb is the "base" respiration rate at 25°C, Eo (Kelvin) is analogous to an energy of activation term, To (K) is a microsite-specific temperature sensitivity parameter, and T is the "average" soil temperature (°C) as described in equation (4). As noted above, we assume that the respiration response in the open space is a mixture of the grass and mesquite respiration responses, such that for each collar c associated with an open microsite:

$$\mu LR_{i,c} = f \cdot \mu LR_{i,c,\text{grass}} + (1 - f) \cdot \mu LR_{i,c,\text{mesquite}} \quad (3)$$

where f and $(1-f)$ describe the relative contribution of grass and mesquite, respectively, respiration to open space respiration. The notation on the right, $\mu LR_{i,c,m}$ for m = grass or mesquite, indicates that the function in equation (2) is evaluated at the environmental data associated with each open space collar c, but the grass and mesquite respiration-related terms (Rb, Eo, and To) are used in equation (2).

In equation (2), μLR is described as a function of soil temperature (T), and the slope (first derivative) of this function reflects the sensitivity of R to changes in T. The slope depends on Eo and To, and we specifically focus on Eo as an index of the microsite-specific temperature sensitivity of R, where larger values of Eo indicate greater sensitivity (steeper slope). In equation (2), $\bar{T}$ represents the weighted average of T measured at two depths; the weights p and $(1-p)$ describe the relative importance of T measured at 2.5 and 11 cm, respectively, and a value of p close to 1 indicates that soil respiration is more strongly coupled to surface compared to subsurface temperature. Thus, for day i, collar c, depth z ($z = 1$ for 2.5 cm, $z = 2$ for 11 cm), and microsite m associated with c:

$$\bar{T}_{i,c} = p_m \cdot T_{i,c,z=2.5\,\text{cm}} + (1 - p_m) \cdot T_{i,c,z=11\,\text{cm}} \quad (4)$$

We allow p to vary by m (for m = grass, mesquite, or open) because the microsites may differ in the relative importance of each depth given potential differences in the depth-distributions of roots and microbes (Cable and others 2009). Note that p is an estimated parameter, and the R data will inform the relative importance of each depth.

We extend the original Lloyd and Taylor (1994) function by modeling the base rate (Rb) and temperature sensitivity (Eo) as a function of antecedent

and current soil water content (*AntW* and *W*, respectively) and antecedent soil temperature (*AntT*) (Cable and others 2008). We also include an effect of vapor pressure deficit (VPD) on *Rb* to implicitly account for potential aboveground controls on *R* (Ekblad and others 2005; Carbone and others 2008):

$$
\begin{aligned}
\log(Rb_{i,c}) &= a_{1m} + a_{2m} \cdot W_{i,c} + a_{3m} \cdot AntW_{i,c} \\
&\quad + a_{4m} \cdot AntT_{i,c} + a_{5m}i + a_{6m} \\
&\quad \cdot \left(W_{i,c} \cdot AntW_{i,c}\right) \\
Eo_{i,c} &= b_{1m} + b_{2m} \cdot AntT_{i,c} + b_{3m}i, c + b_{4m} \\
&\quad \cdot AntW_{i,c} + b_{5m} \cdot \left(W_{i,c} \cdot AntW_{i,c}\right)
\end{aligned}
\tag{5}
$$

The microsite-specific parameters *a* and *b* are only allowed to differ between grass and mesquite. Recall that open space is mixture of the two vegetated microsites such that equation (5) is evaluated at the environmental conditions corresponding to each open space collar, but the grass and shrub *a* and *b* parameters are used according to equation (3). The a_1 and b_1 parameters represent the microsite-specific base rate and temperature sensitivity, respectively, under average moisture, antecedent moisture, antecedent temperature, and VPD (*Rb* model only) conditions. That is, *W*, *AntW*, *AntT*, and VPD are mean-centered, wherein the mean for each variable, across all days and microsites, was subtracted from each original observed value. The parameters a_2–a_6 and b_2–b_5 describe the main effects of the corresponding environmental driver (that is, *W*, *AntW*, *AntT*, VPD), and a_6 and b_5 describe the current (*W*) and antecedent soil water (*AntW*) interaction effects. Because Q_{10} values are typically reported in the literature to describe the temperature sensitivity of respiration, we calculated the Q_{10} to simplify comparisons with other ecosystems, where:

$$
Q_{10_{i,c}} = e^{Eo_{i,c}\left(\frac{1}{\overline{T}_{i,c}-5-To_m} - \frac{1}{\overline{T}_{i,c}+5-To_m}\right)}
\tag{6}
$$

Similar to soil temperature, *W*, *AntW*, and *AntT* represent weighted averages of soil moisture and temperature at two depths (surface vs. subsurface), and VPD is a weighted average of the maximum daytime and daytime average VPD. For each variable, there is a mixture weight (*p*) that describes the importance of the surface conditions (or maximum VPD), and $1-p$ is the importance of the subsurface layers (or average VPD). For each variable, *p* varies by microsite (grass, shrub, or open), and the mixture is computed analogous to equation (4). We allow the open space to have independent

p's (not a mixture of shrub and grass) because the depth of roots and microbes may differ between grass, mesquite, and open microsites, potentially leading to a difference in the importance of the depth of soil moisture and temperature.

We assumed that temperature operates and affects respiration on a faster time scale (daily) than soil water (weekly), and thus we computed *AntT* over past days and *AntW* over past weeks. For example, *AntW* is modeled as a weighted average of past soil water conditions, such that the antecedent conditions associated with day *i*, collar *c*, microsite *m*, and depth *z* (that is, shallow vs. subsurface) are:

$$
AntW_{i,c,z} = \sum_{k=1}^{N\,\text{weeks}} w_{k,m} \cdot \overline{W}_{i,k,c,z}
\tag{7}
$$

We summed over the past *N* weeks, where $k = 1$ is the "current" week, which goes from day $i-6$ to day *i*; by trial and error, we set *Nweeks* = 10, which was sufficiently long to capture the integration time and lags associated with the different microsites. Because we summed with respect to weeks, $\overline{W}_{i,k,c,z}$ is the weekly mean soil water averaged over days $i-7\,k + 1$ to $i-7\,k + 7$. The importance of soil water experienced different weeks into the past is given by the weights, *w*. We assigned Dirichlet priors to the microsite-specific vector of *w*'s to obey the constraints $0 \leq w_{k,m} \leq 1$ and $\sum_{k=1}^{N\,\text{weeks}} w_{k,m} = 1$. $AntT_{i,c,z}$ is computed similarly to equation (7), except we summed the product of daily weights and daily temperature ($T_{i,c,z}$) from the current day to the 6 days ago (*Ndays* = 7). Following equation (4), $AntW_{i,c}$ and $AntT_{i,c}$ in equation (5) are computed as weighted averages of the surface ($AntW_{i,c,1}$ and $AntT_{i,c,1}$) and subsurface ($AntW_{i,c,2}$ and $AntT_{i,c,2}$) antecedent values.

The above equations essentially describe a multilevel nonlinear regression model (for example, Gelman and Hill 2006), which we implemented in a Bayesian framework. Thus, we specified independent and relatively noninformative (diffuse) priors for all unknown parameters. Normal densities with large variances were used for a_1–a_6 and b_2–b_5; a uniform distribution on the interval (0,1) was used for *f* and the *p*'s associated with each variable (*W*, *AntW*, *T*, *AntT*, VPD); wide uniform densities were used for the standard deviation (σ). Lloyd and Taylor (1994) suggest that *Eo* and *To* are relatively conserved across a variety of ecosystem types. Thus, we used semi-informative normal distribution priors for *To* and b_1 ("base" *Eo*) with means given by the Lloyd and Taylor (1994) estimates (227.13 and 308.56 K, respectively) and

relatively large variances (1,000) (Cable and others 2011). As required, we restricted To to occur between 0 and 285 K (285 K is slightly lower than the minimum measured T).

We evaluated three additional versions of the model, and we refer to the above model as the *final model*. We compare this final model to: (1) a *simple model* that does not include antecedent effects, and the open microsite is assigned its own parameters; (2) a *random effects model* that implements the same assumptions as the simple model, but that incorporates day random effects; and (3) an *antecedent microsites model* which is the same as the final model, but this parameter-rich version allows for the open microsite to have its own parameters such that open space is not modeled as a mixture of the vegetated microsites. Previous work found substantial temporal variation in respiration, even after accounting for time varying environmental drivers (Cable and others 2008); thus, comparison of the simple model and the random effects model quantifies the potential importance of residual daily variation, and comparison of the final model and the random effects model lends insight into how much of the residual daily variation in R can be attributed to antecedent effects. Comparison of the final model and the antecedent microsites model quantifies how well the mixing model approach works for describing respiration in open spaces. For the simple and the day random effects models, equation (5) becomes:

$$\log(Rb_{i,c}) = a_{1m} + a_{2m} \cdot W_{i,c} + a_{5m} \cdot VPD_i$$
$$Eo_{i,c} = b_{1m} + b_{3m}i, c \tag{8}$$

For the random effects model, we also incorporated day random effects (ϵ) by modifying equation (2):

$$\mu LR_{i,c} = \ln(Rb_{i,c})$$
$$+ Eo_{i,c}\left(\frac{1}{298.15 - To_m} - \frac{1}{(T_{i,c} + 273.15) - To_m}\right) + \varepsilon_i \tag{9}$$

The ϵ_i are modeled as coming from a normal distribution with mean zero and an unknown variance term that is estimated. For the antecedent microsites model, we do not employ equation (3); we allow To and the a's and b's in equation (5) to vary by all three microsites.

The seasonal dynamics of Rb and Q_{10} were predicted using the parameter estimates associated with the final model and the daily environmental data. That is, we computed Rb and Q_{10} based on equations (2), (5), and (6) for each day i given the posterior results for a and b, the predicted daily VPD, and the predicted microsite-level daily means for W, $antW$, and $antT$.

All models were programmed in the Bayesian statistical software package WinBUGS (Spiegelhalter and others 2002). For each model, we ran three parallel Markov chain Monte Carlo (MCMC) chains for approximately 10,000 iterations, and we used the built-in Brooks–Gelman–Rubin (BGR) diagnostic tool to evaluate convergence of the chains to the posterior distribution (Brooks and Gelman 1998; Gelman 2004b). We discarded the first 4,000 burn-in samples, yielding an independent sample of greater than 5,000 values for each parameter from the joint posterior distribution (see for example, Gelman 2004a, b; Gamerman and Hedibert 2006). We present the posterior mean and 95% credible interval (95% CI, defined by the 2.5th and 97.5th percentiles of the posterior distribution) for each parameter of interest.

We compared models using two different approaches. First, the four models were compared by using equation (2) to generate replicated data associated with each observation of soil respiration (Gelman 2004b), which produced predictive distributions for each respiration observation in the dataset, for each model. A model that fits the data perfectly would yield observed respiration data versus predicted (replicated) data that fall exactly along the 1:1 line. The R^2 value from a regression of the observed versus predicted data serves as an informal index of model fit, but it does not account for differences in model complexity between the models. Thus, we also computed the posterior predictive loss (D), which is the sum of a goodness of fit term (G) plus a model complexity (penalty) term (P) (Gelfand and Ghosh 1998). The model with the lower D is preferred, which can be due to a better model fit (low G value) and/or lower model complexity (low P value).

RESULTS

Data Description

The summer rainy period (monsoon) of 2005 spanned DOY 200 to 255, and during this time, VPD and air temperature declined (Figure 2). During the onset of the monsoon, soil respiration increased nearly 9-, 3-, and 2-fold for the shrub, grass, and open microsites, respectively (Figure 3A). During this time, soil moisture content (% v/v) also increased from zero to about 7, 10, and 17% in open, grass, and shrub microsites, respectively (Figure 3D, E). In all three microsites, soil temperature at both depths decreased by about
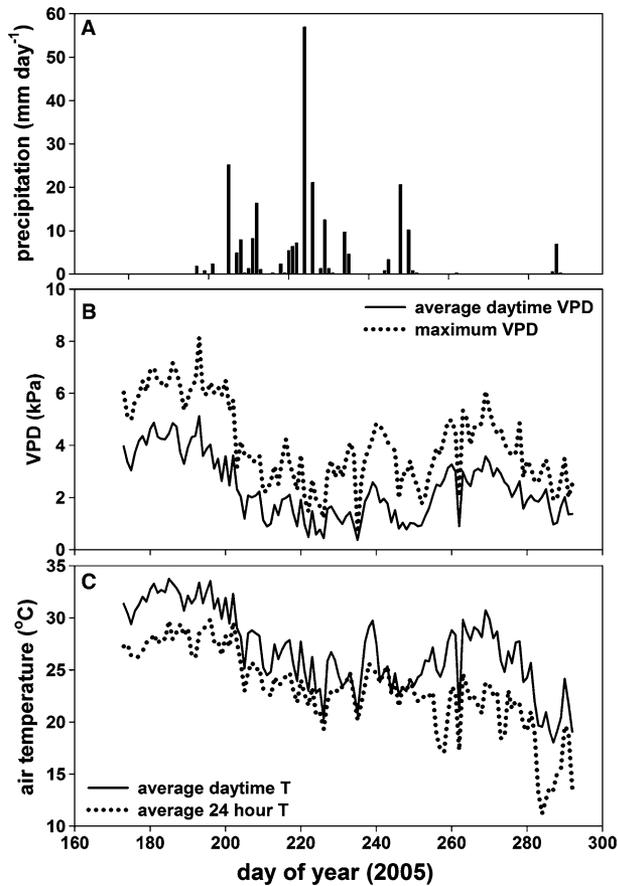
Figure 2. Climate characteristics for the research site during the summer of 2005: **A** total daily precipitation (mm d^{-1}), **B** average daytime and maximum VPD (kPa), and **C** average daytime and average 24 h air temperature (°C).

10°C after the onset to the middle of the monsoon, when the soil was coolest (Figure 3B, C).

MODEL RESULTS

Model Evaluation

Compared to the simple model, incorporation of day random effects improved the model fit (simple model $R^2 = 0.71$ vs. random effects model $R^2 = 0.93$; Figure 4A vs. B). Thus, 22% of the variation in soil respiration can be explained by residual daily random effects. The final model ($R^2 = 0.87$) fit the respiration data better than the simple model, but did not fit as well as the day random effects model. However, the final model was able to explain about two-thirds of the residual daily variation. The final model and the antecedent microsites model fit the data equally well ($R^2 = 0.87$ for both models; Figure 4C vs. D). That is, the increased complexity (that is, due to addition of open space parameters)
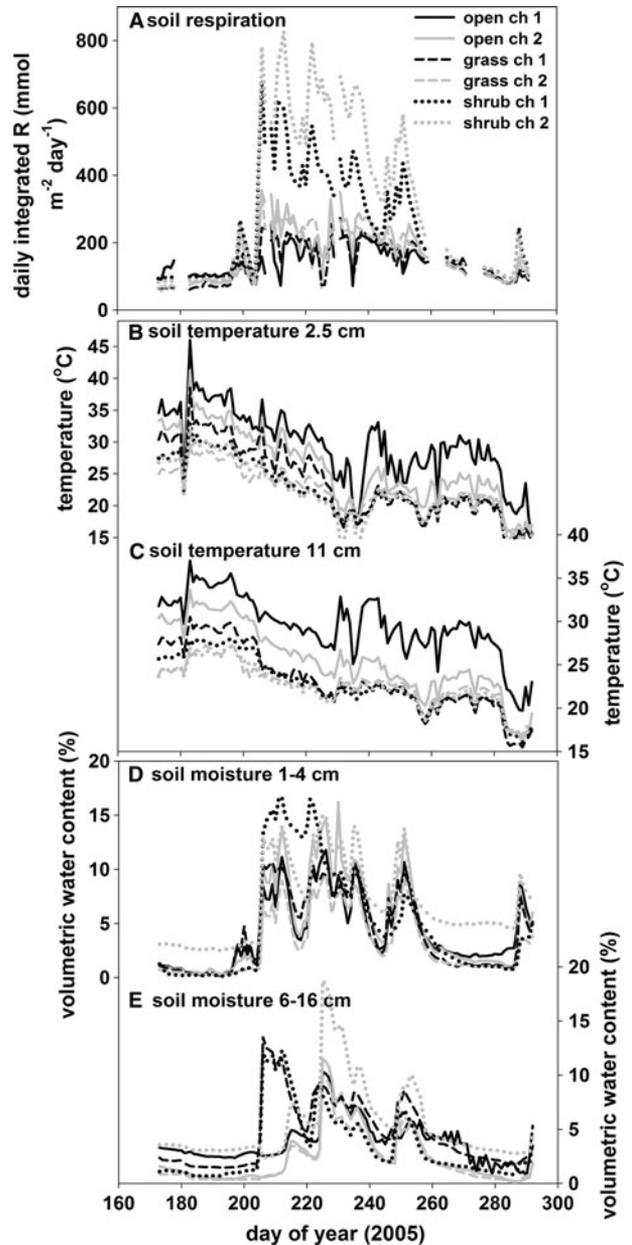

Figure 3. Soil respiration and soil environmental characteristics associated with each respiration chamber in each microsite during the growing season of 2005: **A** daily integrated soil respiration (mmol m^{-2} d^{-1}), daily average soil temperature (°C) measured at **B** 2.5 cm, and **C** 11 cm, and daily average soil moisture (%) measured from **D** 1–4 cm, and **E** 6–16 cm.

of the antecedent microsites model did not result in an improved ability to predict respiration across all microsites. The posterior predictive loss (D) for the simple model was much larger than the D for the final model (130.8 vs. 63.8, respectively). The lower D value for the final model is attributed both lower G ($G = 29.0$ vs. 63.9, for the final vs. simple
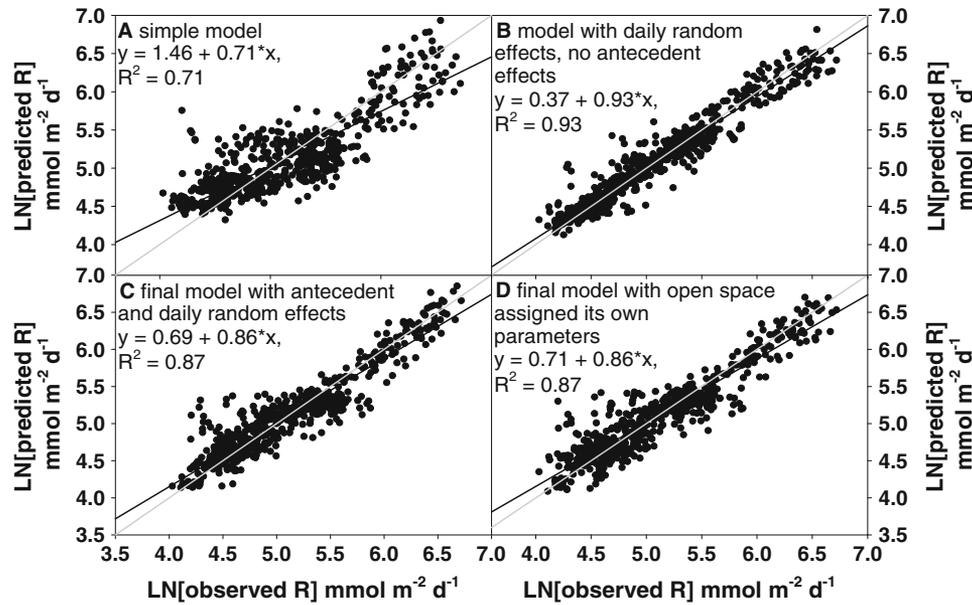
Figure 4. Comparison of predicted (posterior mean of predicted respiration) versus observed natural log respiration rates (*R*) from four models. The gray line in each panel is the 1:1 line. **A–C** are models in which the parameters for the open space respiration model are modeled as a mixture of grass and shrub microsites. Specifically, **A** the simple model without daily random effects or antecedent effects, **B** the model with daily random effects but no antecedent effects, **C** the final model that incorporates antecedent effects, but no daily random effects, and **D** the model that modifies the final model by assigning open space its own respiration parameters.

model, respectively) and a lower penalty term (*P* = 34.8 vs. 66.9, for the final vs. simple model, respectively). Thus, the final model is characterized by a better goodness-of-fit and is it not over-fitting the data.

Hereafter, all model results are reported for the final model, which incorporates antecedent effects and treats open microsite respiration as a mixture of grass and shrub microsites (equations 1–6, Figure 4C). Similarly, we focus on the grass and shrub microsite results because the open microsite results are essentially the same as the grass microsite. That is, respiration in the open space was more reflective of the grass than the mesquite microsites because *f* in equation (3) is closer to 1 than 0 (*f* = 0.87 [0.72, 0.99]). The only results we report for the open microsites are the importance of depth of moisture and temperature, as these were modeled as independent parameters for all three microsites.

Response of Respiration to Antecedent and Current Soil Moisture

Recall that *Rb* is the respiration rate at 25°C, which is the average field soil temperature measured during the study period. With respect to *Rb*, the effects of current (*W*) and antecedent (*antW*) soil water conditions were consistent between the two vegetated microsites (Figure 5A). For respiration under both grasses and shrubs, there was a significant positive effect of *W* ($a_2 > 0$; Table 2) indicating that wet current conditions are associated with high *Rb*. Conversely, there was a significant negative effect of *antW* ($a_3 < 0$; Table 2), indicating that wet antecedent conditions may actually reduce *Rb*; however, the significant negative interaction effect ($a_6 < 0$; Table 2) implies that both wet current and wet antecedent conditions enhance *Rb*.

The effects of *W* and *antW* on the temperature sensitivity of respiration (*Eo*) showed a less consistent pattern between the shrub and grass microsites (Figure 5B). For example, in contrast to the *Rb* response, wet antecedent conditions enhanced the *Eo* of respiration in shrub microsites ($b_3 > 0$ for shrub; Table 2) but not in grass microsites ($b_3 \cong 0$ for grass; Table 2). Also in contrast to the *Rb* response, *W* generally had a negative effect on *Eo* such that wet current conditions decreased *Eo*, but this effect was only statistically significant in the shrub microsite ($b_5 < 0$; Table 2). Similar to the *Rb* response, there was a significant positive interactive effect of *W* and *antW* on *Eo* in both microsites
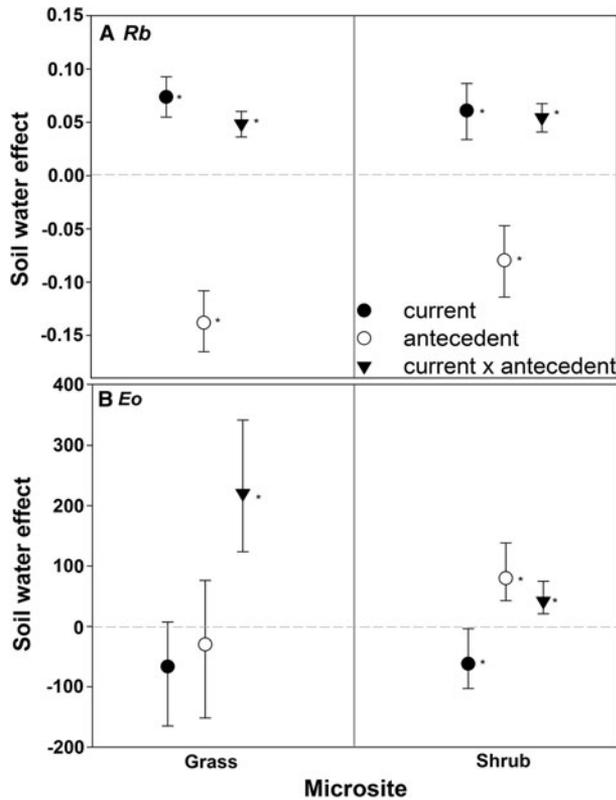
Figure 5. The posterior means and 95% credible intervals (CIs) for the effects of current soil water (parameters a_2, b_2; equation 4), antecedent soil water (a_3, b_3), and current × antecedent soil water (a_6, b_5) in the (**A**) base rate model for Rb (respiration at 25°C, equation 5) and the **B** temperature sensitivity model for Eo (akin to an energy of activation, equation 5) for the grass and shrub microsites. A positive effect (means and 95% CI > 0) indicates that higher soil water content increases Rb or Eo, and a negative effect (means and 95% CI < 0) indicates that higher soil water decreases Rb or Eo. The horizontal *gray dashed line* denotes zero, and if a CI overlaps zero, then the associated effect is non-significant; the *asterisks* show which parameters are significantly different from zero. The units for the soil water effects are log(mmol m^{-2} d^{-1})/% soil water for the LRb effects and Kelvin/% soil water for the Eo effects.

such that wet current and wet antecedent conditions increased Eo.

Characteristics of Antecedent Moisture Response

Given that *antW* is predicted to significantly affect Rb and Eo (Figure 5; Table 2), we evaluate the characteristics of this antecedent response. For Rb, the weights (*w*, equation 5) describing the relative importance of soil moisture at different times into the past share some similarities between the grass and

shrub microsites (Figure 6A). For example, the soil moisture conditions during the past week or two have the greatest effect on Rb (*w*'s relatively high), but the weights are generally low (*w* close to 0, little importance) for conditions occurring seven or more weeks into the past. However, the cumulative weights (Figure 6B) differ between shrubs and grasses at weeks two, three, six, seven, and eight (the 95% CIs for one microsite does not contain the posterior mean for the other microsite). For the grass microsite, the largest weights occurred one and two weeks in the past, suggesting a relatively short lag period, but there also appears to be a minor lag effect at about 6 weeks in the past (Figure 6A, B). The integration period of the antecedent response was about 7 weeks for the grass microsites, which marks the time scale at which the cumulative weights roughly converge to one (Figure 6B). For the shrub microsites, the 1st week was the most important (largest *w*), after which the weights drop off gradually over a 4-week period. There also appears to be a minor lag response in the shrub microsites that occurs around 9 weeks in the past (Figure 6A), and the cumulative weights indicate that the integration period was about 10 weeks (Figure 6B).

For Eo, the weekly weights showed that moisture in the current week was most important for the temperature sensitivity of respiration in the shrub microsite, and there was no detectable lag response (Figure 6C). The cumulative weights indicate an integration period of about four to six weeks in shrub microsites (Figure 6D). Conversely, moisture conditions occurring two to three weeks into the past were most important for Eo in the grass microsites, indicating a lag response of about two weeks (Figure 6C), and the cumulative weights show an integration period similar to that of shrubs (Figure 6C, D). For both Eo and Rb, and for both vegetated microsites, the estimated cumulative weights (Figure 6B, D) are significantly different then the prior weights, which assume equal importance of soil moisture on all past weeks, which is somewhat analogous to computing the average soil water content across this time period.

Importance of Soil Moisture at Different Depths

For Rb, the importance of moisture in the surface versus subsurface soil differed between the three microsites (Figure 7A). In the shrub microsite, surface moisture was most important for Rb on the current time scale ($P > 0.5$; see definition of P in equation (4) applied to W and *antW*) but subsurface moisture was most important on the antecedent time scale ($P < 0.5$; Figure 7A). In the grass mi-

Table 2. Predicted Values for the Respiration Model Parameters (equation 5) Where Rb is the Base Respiration Rate at 25°C and Eo is akin to an Energy of Activation or Temperature Sensitivity of Respiration

Parameter	Grass	Shrub
To (K)	160 [126, 189]	184 [149, 215]
a_1 Base respiration rate (Rb) (log scale) under average soil water conditions	[A]5.01 [4.98, 5.07]	[B]5.50 [5.41, 5.65]
a_2 Current soil moisture effect on log(Rb)	**[A]0.07** [0.06, 0.09]	**[A]0.06** [0.04, 0.09]
a_3 Antecedent soil moisture effect on log(Rb)	**[A]−0.14** [−0.17, −0.11]	**[B]−0.08** [−0.11, −0.04]
a_4 Antecedent temperature effect on log(Rb)	**[A]−0.01** [−0.02, −0.007]	**[B]0.03** [0.004, 0.07]
a_5 VPD effect on log(Rb)	−0.003 [−0.05, 0.04]	**−0.14** [−0.21, −0.08]
a_6 Current x antecedent soil water effect on log(Rb)	**[A]0.05** [0.04, 0.06]	**[A]0.05** [0.04, 0.07]
b_1 Base Eo under average soil water conditions	280 [219, 345]	306 [246, 368]
b_2 Antecedent soil temperature effect on Eo	53.7 [−29.1, 144]	**106** [35.7, 214]
b_3 Current soil water effect on Eo	−67.7 [−143, 14.8]	**−57.0** [−115, −9.32]
b_4 Antecedent soil water effect on Eo	−29.9 [−142, 88.9]	**77.6** [39.3, 141]
b_5 Current x antecedent soil water effect on Eo	**[A]228** [127, 351]	**[B]37.9** [12.6, 73.5]
d_{VPD} (below 0.5 = maximum VPD important, above 0.5 = average VPD important)	0.47 [0.02, 0.97]	0.06 [0.002, 0.24]

Bolded values denote parameters that are statistically different from zero (not relevant for a_1 and b_1), and the superscripted letters (A, B) denote differences between grass and shrub. The parameter estimates for the soil moisture, antecedent moisture, and interaction effects can be found in Figure 5.

crosite, the importance of surface versus subsurface depths for Rb was indistinguishable (wide 95% CI for P that contained 0.5) on the current time scale, but surface moisture was more important on the antecedent time scale ($P \cong 1$; Figure 7A). In the open space, subsurface soil moisture was more important than surface moisture on both time scales ($P < 0.5$; Figure 7A).

For Eo, the importance of the two depths for each time scale (current and antecedent) could not be discerned (wide 95% CIs for P that contained 0.5) for the grass and shrub microsites (Figure 7A). Similar to Rb, Eo in the open microsite was more sensitive to subsurface soil moisture on both time scales ($P < 0.5$; Figure 7A).

Response of Respiration to Antecedent Temperature

For Rb, high antecedent soil temperature (*antT*) decreased respiration rates in the grass microsites ($a_4 < 0$), but increased respiration in the shrub microsites ($a_4 > 0$; Table 2). The importance of surface versus subsurface *antT* for Rb could not be discerned in any microsite (wide 95% CIs for P that contained 0.5; Figure 7B). High *antT* increased Eo in the shrub microsites (Table 2). On the current time scale, the surface temperature was more important for Eo in the grass and open microsites ($P > 0.5$; Figure 7B), and the deep temperature was most important in the shrub microsite ($P < 0.5$, Figure 7B).
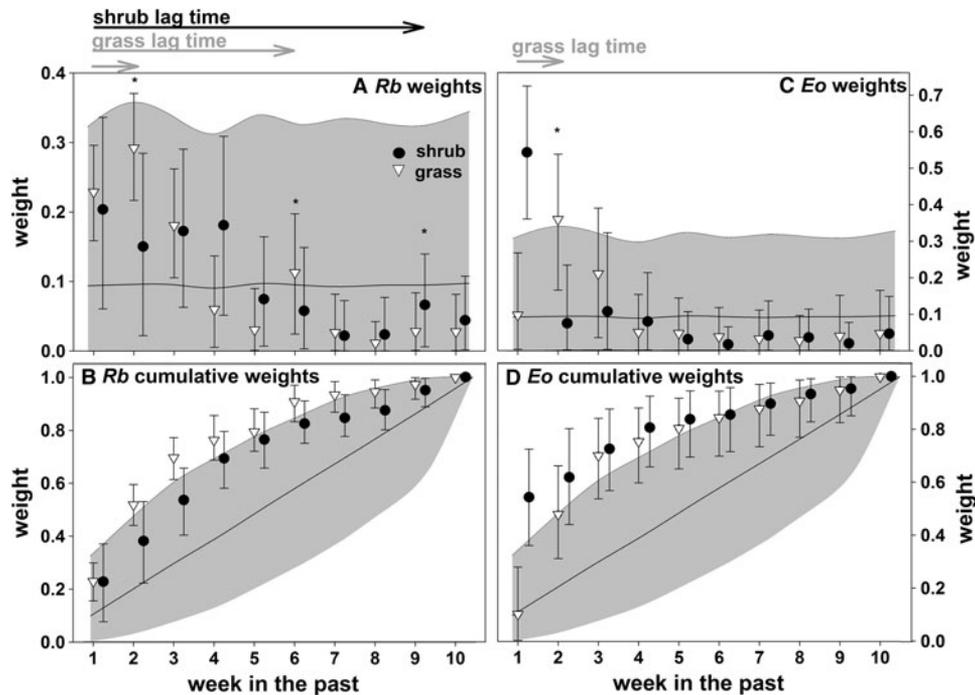
Figure 6. The posterior mean and 95% credible intervals (CIs) for the antecedent weights (*w*, equation 7) associated with antecedent soil moisture for the base rate (**A**, *Rb*) and temperature sensitivity (**C**, *Eo*) for the grass and shrub microsites. The *asterisks* denote ''peaks'' in the weights that indicate potential lag times, which are also shown with *arrows* above (**A**) and (**B**). The *black arrow* is for the shrub and the *grey arrows* are for the grass. The cumulative weights are shown in (**B**) for the *Rb* and (**D**) for *Eo*. The *grey areas* with the *black lines* denote the mean and 95% CI for the weights based on the non-informative Dirichlet prior. Note that, the predicted weights are different and more resolved than the prior weights.

Although *antT* significantly affected *Rb* and *Eo*, the relative importance of temperature on different days into the past could not be discerned because the 95% CIs for the daily weights (*w*'s) were relatively wide (see Appendix Figure 1 in supplementary material). Thus, we could not clearly identify lag effects or the integration times associated with the antecedent temperature response. However, for *Rb*, there is a slight trend suggesting that soil temperature 2 days in the past is most important for the grass microsite (see Appendix Figure 1 in supplementary material).

Response of Respiration to Vapor Pressure Deficit

There was a significant negative effect of VPD on *Rb* in the shrub microsites such that high VPD appears to reduce soil respiration ($a_5 < 0$; Table 2). The effect of VPD was not significant in the grass microsites ($a_5 \cong 0$; Table 2).

Seasonal Dynamics of Rb and Q_{10}

For all three microsites, the predicted daily temperature sensitivity (Q_{10}) was about 1 prior to the onset of the monsoons, but it decreased slightly to about 0.5 during the first rainy period (DOY 190-239), and varied between about 2 and 0.5 during the rainy period from DOY 240-250 (Figure 8A–C). After DOY 250, the monsoon period is over, and the Q_{10} values increase to about 2 (Figure 8A–C). Respiration in the shrub microsites tended to have higher Q_{10} values than the grass and open microsites. Further, a sharp increase in Q_{10} values, approaching approximately 4, occurred in the shrub microsites in conjunction with a final rain even around DOY 290 (Figure 8C).

The seasonal patterns in *Rb* suggest that base respiration rate in the open microsites is fairly unresponsive to rain events because large spikes in *Rb* are not observed following rains (Figure 8D). However, *Rb* increases following the onset of the monsoon season, and it remains relatively constant at approximately 190–210 mmol m^{-2} s^{-1} for the duration of the monsoon (Figure 8D). *Rb* in the grass microsites shows greater temporal variation compared to the open microsites such that *Rb* in the grass microsites rapidly increases with the onset of the monsoon, and *Rb* is more variable during the

monsoon period (Figure 8E). The range of predicted Rb values over the study period, however, are similar between the open and grass microsites (~190–230 mmol m^{-2} s^{-1}, Figure 8D, E). Rb in the shrub microsites exhibited the most dynamic behavior (Figure 8F). That is, pre-monsoon Rb was low and constant, but a large increase occurred with the onset of the monsoon, large spikes were predicted in response to individual rain events (Figure 8F), and the responsiveness of Rb to rain events persisted until the end of the monsoon (after DOY 290, Figure 8F). Rb values in the shrub microsite during the monsoon were significantly larger (200–900 mmol m^{-2} s^{-1}, Figure 8F) than those in the grass and open microsites.

DISCUSSION

The goal of this study was to quantify how soil respiration responds to antecedent soil moisture and temperature—in terms of integration times, lag times, and antecedent effects (for example, Figure 1)—across microsites created by two plant functional types (grasses and shrubs) defining a semiarid shrubland. Comparisons of different respiration model formulations indicated that the inclusion of day random effects improved model fit, but these terms are nonmechanistic, limiting our ability to predict respiration dynamics over seasonal time scales, on days not represented in the dataset, or under novel conditions (Cable and others 2008, 2011). In this study, incorporation of antecedent conditions, in the absence of day random effects, explained an additional 16% of the variability in soil respiration relative to a simple model without these effects (Figure 4). Importantly, antecedent effects explained all but 5% of the residual variation that was explained by the day random effects. Thus, the antecedent response of respiration explains much of the day-to-day variability in soil respiration, and incorporating antecedent factors allowed us to predict seasonal patterns of soil respiration rates and the temperature sensitivity of soil respiration.

High soil water on the day of measurement (or *current* soil water) increases soil respiration in all three microsites (under grass, under shrubs, and in open spaces), and this response is amplified under wet antecedent conditions (positive current × antecedent soil water interaction effect, Figure 5; Table 2). That is, soil respiration response to a rain event is higher during a wet period, like during the monsoon, compared to a dry period. Despite minor differences in the importance of soil moisture one to 2 weeks in the past, respiration rates in both the
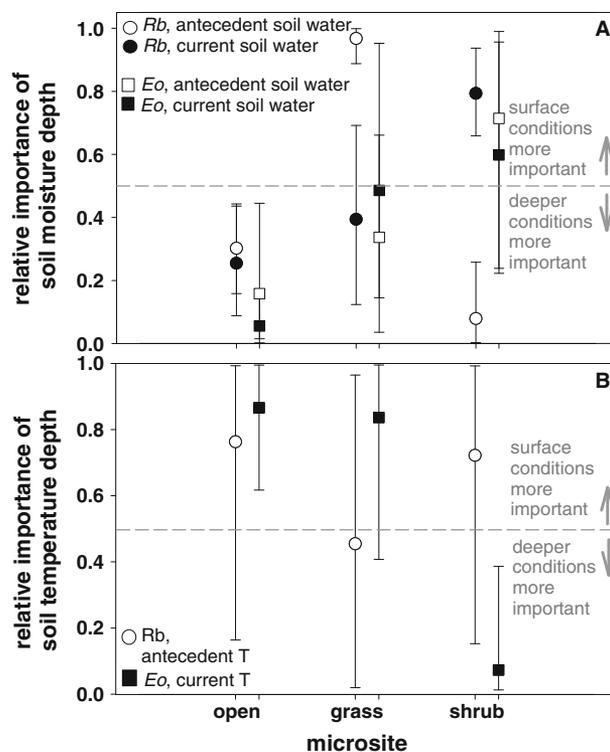

Figure 7. The posterior means and 95% credible intervals (CIs) for the importance of the surface versus deep depth of soil **A** moisture and **B** temperature conditions for the grass, open and shrub microsites with respect to the base rate and temperature sensitivity (equation 5). Values above 0.5 signify the importance of surface conditions and values below 0.5 signify the importance of deep conditions.

grass and shrub microsites show antecedent responses similar to the conceptual responses depicted by a mixture of lines 1, 2, 3, and 4 in Figure 1. Although, the response denoted by lines 1 and 2 (no obvious lag response) swamped out any dominant lag response depicted by lines 3 and 4 (Figure 6A). However, small increases in the importance of soil water conditions six and nine weeks in the past (similar to lines 3 and 4) for the grasses and shrubs (Figure 6A), respectively, suggest a very minor lagged response possible reflecting delayed root activity. Based upon our initial assumptions about the antecedent responses (Figure 1), the importance of moisture in recent weeks and the slow, multi-week drop off in the importance weights (Figure 6A), suggests that microbial respiration may be an important component of respiration in this system. Indeed, when water is sufficiently available, microbial respiration from wet mesquite soils can be sustained for longer than 80 days (Martens and McLain 2003).
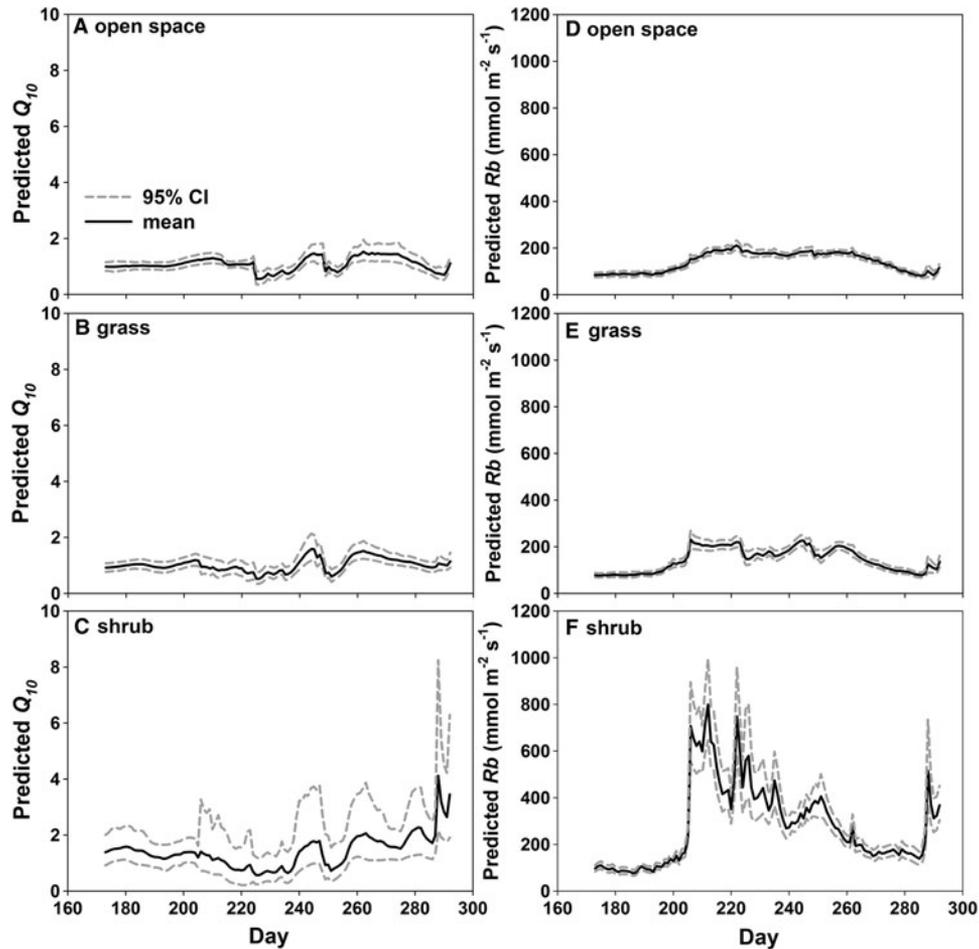
Figure 8. Mean (*solid black lines*) and 95% credible intervals (*dashed grey lines*) for the predicted (**A–C**) daily temperature sensitivities (Q_{10} values calculated from predicted Eo values) and (**D–F**) soil respiration rates at 25°C (Rb equation 2) for soil respiration in (**A**, **C**) open space, (**B**, **D**) grass, and (**C**, **F**) shrub microsites.

With regard to the microbial response, despite lower microbial biomass and substrate quality and quantity under grasses (Cable and others 2009), the antecedent responses of respiration rates in grass and shrub microsites were similar (Figure 6). The main differences were subtle, but the cumulative weights diverge three weeks into the past such that the integration period associated with antecedent soil water was longer for shrubs than grasses (Figure 6B). This subtle difference may be due to the higher nutrient quality and quantity under shrubs, which could sustain microbial respiration for a longer time. The similarity of the responses, however, may be related to the fact that the ratio of microbial biomass to substrate availability is conserved across these microsites (Cable and others 2009). Thus, the dry nature of the system might make it such that, regardless of the substrate conditions, respiration responds to water availability on multiple time scales (for example, days to weeks). Substrate limitation on microbial respiration may only develop after very long periods of sustained moisture availability (Martens and McLain 2003; McLain and Martens 2006).

We also suggest that root respiration is not negligible at this site. For example, if microbial respiration was the primary contributor to total soil respiration, we would expect a greater importance of surface compared to subsurface or deeper moisture because microbes are concentrated very close to the surface (0–5 cm) (Cable and others 2009). Yet, subsurface moisture (6–16 cm), which coincides with layers high in root biomass (Cable unpublished data), was important for respiration under shrubs on the antecedent time scale and was always important in open spaces (which have low microbial biomass) (Figure 7A). Lastly, the minor importance of moisture 6 and 9 weeks in the past for grass and shrub microsites, respectively (Figure 6A), is likely a root response.

Roots are generally characterized by long life spans and acclimation times relative to microbes (Palta and Nobel 1989; Kubiske and others 1998; Pavon and Briones 2000; Tang and others 2005; Zhang and others 2009). These differences between roots and microbes suggest that roots likely have a longer lag period compared to microbes (Luo and others 2001; Fierer and Schimel 2003; Davidson and Janssens 2006; Atkin and others 2008). Although roots respond more slowly to moisture than microbes, a lag of several weeks (as estimated here) is likely long enough to elicit a root respiration response (for example, Nobel 1997). However, the lag time in this study is fairly muted, as indicated by the slight increase in the importance weights on days 6 and 9 for the grasses and shrubs, respectively (Figure 6A). More detailed studies are required to mechanistically tease-apart the contribution of roots versus microbes to the antecedent soil respiration response, and to explore the prevalence of lagged responses of respiration to rain events.

The sensitivity of soil respiration to atmospheric vapor pressure deficit (VPD) also suggests that root respiration significantly contributed to soil respiration, at least on the current time scale in the shrub microsites. High maximum daily VPD was associated with reduced respiration rates (Table 2), which suggests a potential link between respiration and canopy photosynthesis. High VPD reduces stomatal conductance and photosynthesis of the shrubs and grasses as this site (Scott and others 2004), potentially reducing the amount of photosynthate allocated the roots and root exudation (for example, Bowling and others 2002). Others observed lags in soil respiration of up to several days with changes in VPD (Bowling and others 2002), potentially resulting from lags in photosynthate transport time from leaves to roots. However, we did not find a significant effect of antecedent VPD.

We assumed the effects of antecedent soil temperature would occur on the order of days rather than weeks. High soil temperatures two to three days in the past decreased respiration rates in the grass microsites (Table 2). A decline in respiration rates under high antecedent temperature has been observed in other semiarid ecosystems (Cable and others 2008), and we suspect this is related to low substrate availability for microbial activity in the grass microsites (Davidson and Janssens 2006). Decreased sensitivity of respiration rates with higher soil temperature can also be related to acclimation processes (Davidson and Janssens 2006), but it is unclear why this would only occur in the grass microsites.

Similar to respiration rates, the positive effect of past and current soil moisture on the temperature sensitivity of respiration was consistent across all microsites (Figures 5B, 6C). Subsurface moisture on both time scales influenced temperature sensitivity of respiration in the open microsites, but in the grass and shrub microsites the depth of soil moisture was less important for temperature sensitivity compared to its effect on respiration rates (Figure 7A). Relative to grasses, shrubs shorten the duration of the antecedent effect of soil moisture on the temperature sensitivity of respiration by 1 week, wherein the most recent week is the most important. For grasses, however, moisture two to three weeks in the past was most important (Figure 6C, D).

Overall, it appears that the temperature sensitivity of soil respiration under shrubs was more coupled to recent rainfall events, but respiration rates responded to moisture on a longer time scale (Figure 6A vs. C). However, under grasses and in open spaces, the temperature sensitivity and respiration rates responded to moisture on similar time scales. Thus, our initial assumption that the temperature sensitivity and base respiration rates would have similar antecedent responses was supported, but for only two of the microsites. These findings further support the mechanism we propose herein, that microbes drive the temperature sensitivity of respiration in this system. For example, shrubs support a larger microbial biomass pool and have highly decomposable litter (Cable and others 2009), both of which are expected to enhance the temperature sensitivity of microbial respiration (Davidson and Janssens 2006). The difference in the response of the temperature sensitivity versus the base respiration rates to antecedent moisture may be significant for modeling carbon dynamics, and requires that each component of the respiration response be considered separately. Lastly, we did not differentiate between intrinsic versus apparent temperature sensitivity, but the response of each sensitivity component to moisture and temperature may differ (Davidson and others 2012), particularly in extreme environments, like deserts. Future work should focus on differentiating between these two aspects of temperature sensitivity.

Three primary patterns emerge from examining the seasonal dynamics of respiration rates (Rb) and the temperature sensitivity (presented as Q_{10} values) (Figure 8). The first is that the precipitation pulse events affect the base respiration rates to a greater extent than the temperature sensitivity in the shrub microsites (Figure 8C, F). The base res-

piration rates are very responsive to rain events, but the temperature sensitivities show more gradual changes over the summer (Figure 8C, F). However, the opposite occurs in the grass and open microsites, where the temperature sensitivity is more responsive to the rain events but the base respiration rates show more gradual trends over the summer (Figure 8A, B, D, E). The second pattern is that respiration rates in the shrub microsites are more responsive to precipitation pulses compared to the grass and open microsites. In fact, soil respiration rates in the open microsites are not responsive to pulses. This supports our idea that respiration in the open microsites is root dominated, because root respiration is likely less impacted by pulses of moisture and comparatively more responsive to long periods of high soil moisture (Milchunas and Lauenroth 2001). The third pattern is that the shrubs support higher soil respiration rates and temperature sensitivities than the grass and open microsites (Figure 8). This behavior of soil respiration in shrub microsites likely reflects the influence of higher microbial biomass, substrate availability and quality, and higher root biomass (Cable and others 2009). A final observation is that the temperature sensitivities in the shrub microsites strongly increase in response to a rain event occurring during the dry post-monsoon period (after a long dry period, around DOY 290, Figure 8C). Differences in the pulse driven responses of the temperature sensitivity and the respiration rates across microsites are likely due to the differences in the primary controls of each. Under optimal soil moisture and temperature conditions, respiration rates are proportional to carbon availability and the biomass of respiring organisms. Controls on the temperature sensitivity are more complex due to interacting processes related to enzyme kinetics (Davidson and Janssens 2006).

Grasses appear to have a greater effect on soil respiration than their cover would suggest. We hypothesized that respiration in open space would be a mixture of grass and shrub root respiration given the presence of roots from each vegetation type, the absence of surface litter, and very low microbial biomass in open spaces. Regardless of time scale (current or antecedent), open space soil respiration only responds to subsurface soil moisture (Figure 7A), where roots tend to be located in this system. We compared predictions from the models where open space respiration is a mixture of grass and shrub soil respiration, versus open space receiving its own parameters that are estimated independently from the grass and mesquite

microsites. The models predicted the respiration rates equally well, indicating that the additional complexity introduced by treating open space independently does not improve our ability to predict soil respiration in this microsite type (Figure 4C vs. D). Surprisingly, about 75% of the soil respiration in open space appears to be derived from grass roots. This is likely due to rooting architecture of the shrubs and grasses at this site. Due to the relatively shallow ($\sim$6.5 m depth) water table, most mesquite roots extend to this water source whereas the bunchgrasses cannot access the water table given their shallower root systems (maximum rooting depth $\sim$3 m) (Scott personal communication). This results in bunchgrass roots dominating inter-canopy near-surface soils and apparently playing an important role in bare soil respiration at this site.

CONCLUSIONS

In this semiarid riparian shrubland, we showed that high soil moisture over the past month increases the magnitude of soil respiration in shrub and grass microsites. The integration time of the effect of antecedent soil moisture on respiration rates at 25°C is longer than the effect on the temperature sensitivity. Moreover, shrubs shorten the time period over which antecedent soil moisture affects the temperature sensitivity of respiration compared to grasses. The relative response of roots versus microbes cannot be wholly discerned, but the effect of VPD and subsurface soil moisture on soil respiration in shrub microsites suggests the importance of roots, but the responsiveness of respiration rates to rainfall suggests the importance of microbes. Lastly, we show that open space devoid of litter is dominated by grass root respiration, imparting a larger effect of grasses on soil carbon flux than previously thought. This study suggests that the temporal scale of environmental variability is critical in understanding respiration dynamics in shrublands. We provide a framework for quantifying antecedent effects on respiration, which can be applied to other ecophysiological processes, and this study addresses the need to incorporate antecedent effects of decomposition dynamics in empirical models to better describe predictors of soil respiration (Reichstein and others 2003).

ACKNOWLEDGMENTS

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