Gross primary production variability associated with meteorology, physiology, leaf area, and water supply in contrasting woodland and grassland semiarid riparian ecosystems

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[1]   Understanding ecosystem-atmosphere carbon exchanges in dryland environments has been more challenging than in mesic environments, likely due to more pronounced nonlinear responses of ecosystem processes to environmental variation. To better understand diurnal to interannual variation in gross primary productivity (GPP) variability, we coupled continuous eddy-covariance derived whole ecosystem gas exchange measurements with an ecophysiologic model based on fundamental principles of diffusion, mass balance, reaction kinetics, and biochemical regulation of photosynthesis. We evaluated the coupled data-model system to describe and understand the dynamics of 3 years of growing season GPP from a riparian grassland and woodland in southern Arizona. The data-model fusion procedure skillfully reproduced the majority of daily variation GPP throughout three growing seasons. While meteorology was similar between sites, the woodland site had consistently higher GPP rates and lower variability at daily and interannual timescales relative to the grassland site. We examined the causes of this variation using a new state factor model analysis that partitioned GPP variation into four factors: meteorology, physiology, leaf area, and water supply. The largest proportion of GPP variation was associated with physiological differences. The woodland showed a greater sensitivity than the grassland to water supply, while the grassland showed a greater sensitivity to leaf area. These differences are consistent with hypotheses of woody species using resistance mechanisms, stomatal regulation, and grassland species using resilience mechanisms, leaf area regulation, in avoiding water stress and have implications for future GPP sensitivity to climate variability following wood-grass transitions.

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1.   Introduction

[2]   The complexity of soil-vegetation-atmosphere interactions results in distinct patterns of ecological variability at timescales ranging from subhourly to millennial [*Braswell et al.*, 2005; *Hetherington and Woodward*, 2003; *Katul et al.*, 2001; *Richardson et al.*, 2007]. While models describing the variability of photosynthesis or gross primary production (GPP), a key component in terrestrial-atmosphere CO_2 exchanges, for mesic terrestrial systems have had many successes [*Richardson et al.*, 2007; *Siqueira et al.*, 2006], understanding the controls on GPP in semiarid

and arid regions has been more challenging [*Mu et al.*, 2007; *Wang et al.*, 2007]. Hydrologic variability interacts strongly and nonlinearly with ecological variability and improving linkages between hydrologic and ecologic processes will lead to a more robust understanding of carbon cycle dynamics in dryland regions [*Jenerette and Lal*, 2005]. In semiarid and arid regions the lack of available water may tighten the coupling between the meteorology and biota leading to increased ecological variability; however the relative importance of the physical drivers and the biological responses for the resulting ecological variability is poorly understood. Therefore, attributing GPP variation in water-limited regions to biological and physical components will lead to an improved understanding of ecosystem function and the potential to better assess ecological responses to global changes [*Brummer et al.*, 2008; *Mahecha et al.*, 2007; *Richardson et al.*, 2007; *Stoy et al.*, 2006, 2008].

[3]   In many dryland regions woody plant encroachment into historic grasslands is occurring rapidly [*Archer*, 1995; *Briggs et al.*, 2005]. These shifts have large implications

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for both hydrology and carbon cycling [*Huxman et al.*, 2005; *Knapp et al.*, 2008]. How these contrasting plant functional types respond to environmental variability will likely affect the future organization and dynamics of these systems [*D'Odorico et al.*, 2007; *Gunderson*, 2000; *Wiegand et al.*, 1998]. Drylands frequently exhibit alternative stable states between grass and woody dominated conditions [*Carpenter et al.*, 2001; *D'Odorico et al.*, 2007; *Kefi et al.*, 2007; *Rietkerk and van de Koppe*, 2008] and transitions in both directions have been observed [*Briggs et al.*, 2005; *Cox and Allen*, 2008]. Linking the organizational properties of these systems with a mechanistic understanding of ecophysiological dynamics has been lacking. Ecophysiological differences between grass and woody dominated ecosystems likely result in contrasting strategies for managing environmental variation and may influence transitions between woody and grass dominated states. We hypothesize that the better access to deeper soil water resources by woody plants compared to grasses leads to both a greater total photosynthetic capacity [*Huxman et al.*, 2005] and a strategy of increased resistance to environmental variation in woodlands. In contrast, the more dynamic phenology and sensitivity to near-surface water availability of grasses is hypothesized to lead a greater variability in GPP [*Knapp and Smith*, 2001; *Novick et al.*, 2004] and a strategy of increased resilience to environmental variation in grasslands. We propose these contrasting strategies for managing environmental variation, resistance dominant, preventing structural and capacity changes, and resilience dominant, allowing structural and capacity changes, will be associated with greater stomatal regulation and sensitivity to water supply in the woodland and a contrasting greater leaf area regulation in the grassland.

[4] Partitioning observed GPP variation into several broad state factors provides a synthetic approach for understanding ecological variability and facilitates comparisons between woodland and grassland dominated ecosystems. State factor approaches were initially used for understanding soil formation [*Jenny*, 1941, 1980], and more broadly, state factor models have been considered a general approach for understanding ecosystem dynamics [*Amundson and Jenny*, 1997]. Several recent applications have used state factor models to characterize diverse components of ecosystem functioning [*Jones et al.*, 2006; *Perakis and Hedin*, 2007; *Vancleve et al.*, 1991], and the approach has been implicit in several recent attempts to separate the dynamics of CO_2 soil-vegetation-atmosphere transfers (SVATs) into climate and biologic determinants [*Hui et al.*, 2003; *Richardson et al.*, 2007; *Stoy et al.*, 2006; *Williams and Albertson*, 2005]. We explored a general state factor approach attributing the variation in GPP to variation in four broad factors: meteorology, biochemical physiology, leaf area, and water supply. These four factors describe how meteorology (vapor pressure, light availability, temperature, and CO_2 concentration), plant water supply, plant physiology (the biochemical parameters describing photosynthesis, see Table 2), and leaf area individually and interactively control GPP variation. These factors are not necessarily a correlative but a mechanistic grouping of variables affecting GPP. This approach of using broad factors complements analyses that

partition variation into specific variables [*Duursma et al.*, 2009; *Williams et al.*, 2008]. While not providing direct predictive ability of future responses, this approach should allow for a better understanding of the sources of ecological variability.

[5] Recent advances in nearly continuous whole-ecosystem monitoring, coupled carbon and water modeling, and robust data-model fusion tools have made possible the examination of the role of multiple factors involved in GPP variability. Eddy-covariance systems provide a relatively new data stream for quantifying whole ecosystem gas exchange [*Baldocchi*, 2003; *Goulden et al.*, 1996], as they yield direct estimates of net ecosystem exchange of CO_2 (NEE), the difference between respiratory losses and GPP [*Chapin et al.*, 2006; *Randerson et al.*, 2002]. Robust partitioning methods are available to separate NEE into both component carbon loss and uptake processes [*Desai et al.*, 2008; *Reichstein et al.*, 2005a]. Mechanistic ecosystem models that couple GPP with transpiration have been developed based on first principles of stomatal conductance, gas diffusion across a leaf boundary, and biochemical assimilation of CO_2 [*Dickinson et al.*, 1998; *Ivanov et al.*, 2008; *Katul et al.*, 2003; *Krinner et al.*, 2005; *Tuzet et al.*, 2003; *Woodward et al.*, 1995]. The application of this ecophysiological theory has gained prominence for describing instantaneous ecosystem dynamics and provides a strong foundation for understanding observed GPP variability from diurnal to interannual timescales [*Ivanov et al.*, 2008; *Luo et al.*, 2001; *Santaren et al.*, 2007; *Wang et al.*, 2007]. In the context of this quantitative theory of ecosystem gas exchanges the different factors of meteorology, physiology, leaf area, and water supply have strongly nonlinear and interactive effects on GPP. To couple eddy covariance data and ecophysiological theory, data-model fusion techniques are becoming widely used [*Bousquet et al.*, 1999; *Braswell et al.*, 2005; *Sacks et al.*, 2007; *Xu et al.*, 2006]. A key benefit of data-model fusion is the ability to estimate parameters for a model given an existing data stream and quantify uncertainty in both the estimated parameter and model performance. These three advances together provide tools necessary to partition GPP variability into state factors and allow for an expanded understanding of ecosystem dynamics.

[6] To identify the magnitude and causes of multiscale temporal variability of GPP we asked two linked questions: (1) how did growing season GPP in a riparian woodland and grassland ecosystem vary from daily to interannual timescales and (2) how did differences in meteorology, physiology, leaf area, and water supply, contribute to this variability? The semiarid riparian setting in a monsoon climate of our study area results in a growing season with a premonsoon period, characterized by hot and dry conditions, and a monsoon period that is wetter, cooler during the day, and has a substantially reduced vapor pressure deficit (VPD). Both ecosystems had access to groundwater and supplemented their water supply when near-surface soil water was lacking. Thus, an evaluation of these sites provided a unique opportunity to describe the dynamics of vegetation, test hypotheses regarding the effects of physical drivers and biological responses on ecosystem photosynthetic variability, and evaluate the potential for differences

Table 1. Meteorological Forcing Data for 3 Years at Each Site During the Growing Season[a]

Site	Year	PAR (mol/d)	VPD (kPa)	Air Temperature (°C)	Total Precipitation (mm)
Woodland	2003	24.1 (5.4)	−1.9 (1.5)	25.0 (6.2)	166
	2004	24.8 (5.0)	−1.9 (1.4)	23.8 (6.5)	102
	2005	24.4 (5.1)	−2.1 (1.5)	24.6 (6.3)	174
Grassland	2003	23.9 (5.4)	−1.9 (1.7)	24.0 (7.7)	168
	2004	24.2 (5.6)	−1.8 (1.5)	22.3 (8.3)	122
	2005	25.7 (6.4)	−1.9 (1.6)	23.7 (7.8)	215

[a]Mean and standard deviation.

in vegetation strategies for coping with environmental variation between these two communities.

2. Methods

2.1. Data Description

[7] Data for this study came from two riparian sites located along alluvial terraces of the San Pedro River in southern Arizona, USA. They consisted of: (1) a mesquite (*Prosopis velutina)* dominated woodland with a canopy cover of ∼75% and a peak LAI of about 1.8, and (2) a grassland dominated by the perennial bunchgrass Sacaton (*Sporobolus wrightii*) with a canopy cover of 65% and a peak LAI of 2.5 [*Scott et al.*, 2006]. The water table depth at the woodland and grassland were around 10 m and 2.5 m, respectively [*Scott et al.*, 2008]. The annual site water balances confirm that both sites access groundwater, making them less dependent on local precipitation inputs [*Scott et al.*, 2006, 2008; *Williams et al.*, 2006]. Extensive field physiological, biogeochemical, and hydrological studies have been conducted at these sites and throughout the region, providing a rich context for understanding ecosystem dynamics.

[8] Eddy covariance systems located at both sites measure NEE and associated meteorological patterns at half-hourly resolution. Tower instrumentation, data processing, and summaries of observed fluxes have previously been described [*Scott et al.*, 2004, 2006]. Briefly, an open-path infrared gas analyzer (IRGA) and a sonic anemometer were mounted on a tower above the plant canopies. From these instruments, measurements of atmospheric CO_2 concentration and the wind field were obtained at 10 Hz. The covariance between the vertical wind velocity and CO_2 concentrations were computed over 30-min intervals. The covariance was combined with a two-dimensional coordinate rotation and corrected for density fluctuations to produce an estimate of CO_2 flux (μmol C m^{-2} s^{-1}). An estimate of CO_2 storage change from the IRGA to the ground surface was determined using the CO_2 concentrations from the IRGA alone and this was added to the tower flux to estimate NEE. CO_2 exchange estimated by eddy covariance is sensitive to a number of environmental conditions and these data contain frequent gaps and spikes [*Baldocchi*, 2003; *Goulden et al.*, 1996; *Rannik et al.*, 2006; *Reichstein et al.*, 2005a]. A potential source of error, occurring usually at night, happens when there is insufficient atmosphere turbulence below the instrument height to accurately quantify the CO_2 exchange within the canopy and at the ground surface. In the topographically simple sites where our towers were located, the periods of atmospheric stability can be identified using the atmospheric friction velocity ($u*$), which commonly shows a correlation with measured fluxes below some threshold. To remove the bias associated with atmospheric friction velocity and other potential sources of error, we applied a filtering process that flagged individual cases based on the $u*$ threshold identified by *Scott et al.* [2006]. These thresholds were similar to the values identified using a complementary approach described by *Reichstein et al.* [2005a, 2005b]. Atmospheric stability is more frequently a problem at night requiring more data to be excluded than during the day. No gap-filling procedure was used to estimate missing data points as any such procedure would obscure the relationship between the model and NEE.

[9] For 2003–2005, growing season fluxes were extracted (days 150–280), which included both the pre-monsoon and the monsoon periods. In conjunction with the NEE measurements, we obtained patterns of photosynthetic photon flux density (μmol m^{-2} s^{-1} within the 400–700 nm wavelength range; LI-190 PAR sensor manufactured by Licor, Lincoln, NE), air temperature (°C), vapor pressure (kPa), and atmospheric CO_2 concentrations (ppm). Both sites experienced similar meteorology forcing over the 3 years (Table 1). Estimates of plant area were derived from empirical functions that use 16 day remotely sensed MODIS enhanced vegetation index as input [*Scott et al.*, 2006].

2.2. GPP Model

[10] A general theory of ecophysiological responses to hydrologic variability is dependent upon the constraints imposed by the biochemical demand for CO_2, and the diffusion-limited supply of CO_2 constrained by stomatal conductance (Figure 1a). A modeling approach based on this theory has been used for theoretical studies [*Katul et al.*, 2003; *Schwinning and Ehleringer*, 2001; *Tuzet et al.*, 2003], as the mechanisms for several land surface models [*Ivanov et al.*, 2008; *Santaren et al.*, 2007; *Wang et al.*, 2007], and forms the basis for process-oriented dynamic global vegetation models [*Bonan et al.*, 2003; *Krinner et al.*, 2005; *Woodward et al.*, 1995; *Woodward and Lomas*, 2004]. The linkage of these models has been suggested appropriate for understanding carbon cycling responses to water limitation [*Katul et al.*, 2003]. Because the reduction of parameters is essential for deriving a useful coupling between eddy covariance data and theory [*Braswell et al.*, 2005; *Wang et al.*, 2001], we strategically simplified the classic model to generate a form that could be compared with eddy covariance data.

[11] The rate of water movement across the leaf was described as a diffusion process, which was associated with a gradient in water potentials (Ψ_L, Ψ_A for leaf and air kPa, normalizing for atmospheric pressure P) between two pools
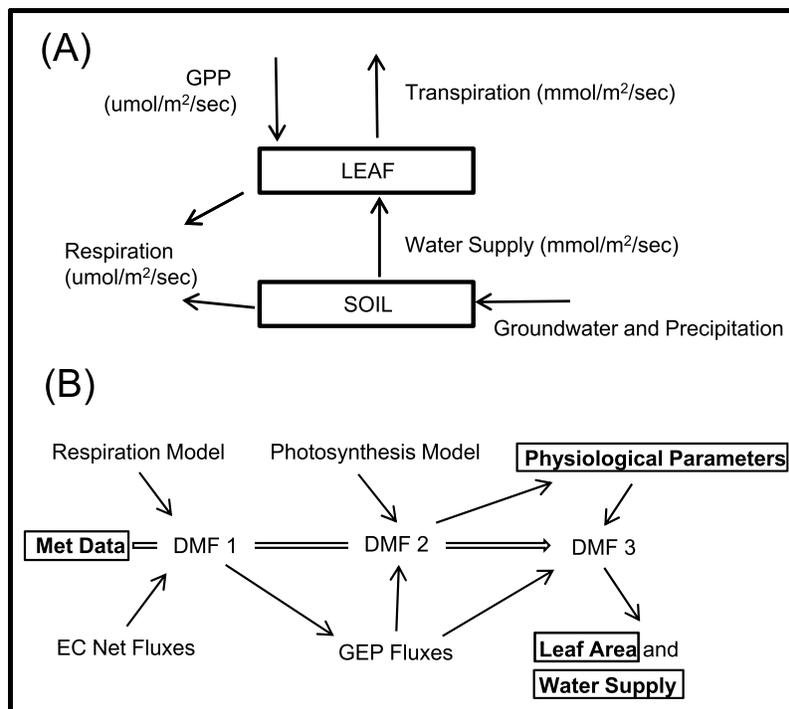
Figure 1. Model schematic showing the (a) coupled carbon and water fluxes with the linkage of the biochemical demand and atmospheric supply photosynthesis models and the (b) hierarchical partitioning of the model inversions into a three step procedure.

and a conductance across the interface. In these analyses, we assumed leaf stomatal conductance was always much lower than canopy conductance and the effects of canopy on terrestrial-atmosphere exchanges could be excluded to focus on the stomatal control of conductance [*Katul et al.*, 2003]. Water content in the leaf was assumed to be saturated, and the saturated vapor pressure was calculated using the Buck model [*Buck*, 1981]. With an estimate of a maximum stomatal conductance (G_{max}, mmol m^{-2} s^{-1}), the atmospheric water demand (Θ_d, mmol m^{-2} s^{-1}) was calculated as:

$$\Theta_d = G_{max}(\Psi_L - \Psi_A)/P \qquad (1)$$

[12] Because we were conducting the data-model fusion for riparian sites that had access to groundwater, we assumed the supply of water (Θ_s, mmol m^{-2} s^{-1}) could be described by a single parameter related to the strength of the ecosystem-groundwater coupling. Differences in water supply may reflect both differences in plant hydraulic capacity and access to the groundwater. This assumption greatly reduced the complexity of the hydrologic cycle, which otherwise would entail a detailed description of soil moisture and root dynamics. From this simplified model, the rate of transpiration was either the water supply to the leaf or atmospheric demand. If the demand for transpiration was equal to or less than supply then the actual stomatal conductance was the maximum stomatal conductance. If transpiration was supply limited, plants adjust leaf stomatal conductance such that demand did not exceed supply; this has been described as the physical limitation to transpiration and is a basis for regulation of leaf stomatal conductance [*Katul et al.*, 2003]. The reduced stomatal conductance (G_w)

was identified by rearranging the diffusion equation and including the water supply rate (Θ_s) and total leaf area (LAI, m^2 m^{-2}):

$$G_w = \frac{\Theta_S}{LAI(\Psi_L - \Psi_A)/P} \qquad (2)$$

[13] Carbon assimilation (A, μmol m^{-2} s^{-1}) rates can be regarded as the interaction between a biochemical demand and a diffusion-limited supply for CO$_2$. With stomatal conductance defined from hydrologic limitation (where the conductance for water and CO$_2$ are factored based on the difference in molecular weights), the gross assimilation of CO$_2$ can be computed from two equations describing diffusion and biochemical processes. Both the supply and demand are directly related to the internal leaf CO$_2$ concentration (C_i, ppm). With increasing C_i, the biochemical assimilation rate increases and the demand for CO$_2$ increases, however, at the same time the diffusion gradient decreases and the resulting supply for CO$_2$ decreases. A fundamental challenge with developing whole ecosystem physiological models is the inability to directly validate or measure C_i. However, with two unknowns, C_i and A, and two models describing both variables, diffusion and biochemical assimilation, we can jointly solve for both unknowns for a given set of parameters and environmental conditions. The diffusion-limited assimilation is described by:

$$A = G_c(C_i - C_o) \qquad (3)$$

where G_c is stomatal conductance for CO$_2$, which is corrected from G_w based on differences in diffusivity

between CO_2 and H_2O [*Farquhar and Sharkey*, 1982], and C_o is atmospheric CO_2 concentration, which we assume here is equivalent to leaf boundary layer CO_2.

[14] The biochemical demand for C_3 vegetation (as at the woodland) is potentially limited by electron transport, which depends primarily on light availability, or carboxylation, which depends on primarily CO_2 concentrations. These two processes are described by the biochemical assimilation model [*Farquhar et al.*, 1980]. *Katul et al.* [2003] provide the canonical description as:

$$A = \frac{\alpha_1(C_i - \Gamma^*)}{(C_i + \alpha_2)} - R_L \quad (4)$$

[15] For electron-transport limited photosynthesis, α_1 and α_2 are modeled as:

$$\alpha_1 = \alpha_q l e_m \quad (5)$$

$$\alpha_{21} = 2\Gamma^* \quad (6)$$

and for carboxylation-limited photosynthesis α_1 and α_2 are modeled as:

$$\alpha_1 = V_{cmax} \quad (7)$$

$$\alpha_2 = k_c\left(1 + \frac{O_i}{k_o}\right) \quad (8)$$

[16] In this model C_i is the internal CO_2 concentration, Γ^* is the compensation point for CO_2, R_L is leaf respiration, I is photosynthetically active radiation, α_q is the leaf absorptivity for I, e_m is the maximum quantum efficiency, V_{cmax} is the maximum carboxylation capacity of Rubsico, k_c and k_O are Michaelis-Menton constants for CO_2 fixation and O_2 inhibition, and O_i is leaf oxygen concentration. To simplify, we treated both α_q and e_m as the single parameter quantum use efficiency (Q_e). When modeling carboxylation-limited photosynthesis, we did not have sufficient information to describe O_i and therefore collapsed the α_2 into a single parameter, k_c. The resulting model describes photosynthesis using four parameters (Γ^*, Q_e, V_{cmax}, k_c) and two variables (I and C_i). At the whole ecosystem scale, GPP is modeled by multiplying the resulting A and leaf area.

[17] The C_4 photosynthetic pathway for the grassland site differs from the C_3 pathway in the woodland by several mechanism, the most important being an initial carbon fixation by PEP-carboxylase, which greatly increases the efficiency of internal CO_2 use and secondarily an altered quantum use efficiency that decreases the oxygenation reaction of Rubisco and consequent photorespiration thereby reduces the CO_2 compensation point [*Lambers et al.*, 1998]. To account for the differences in C_4 physiology we used a common modification to the C_3 biochemical model presented in equation 4 [*Collatz et al.*, 1992]. In the C_4 specific model biochemical assimilation is described by:

$$A = \min\begin{Bmatrix} J_i \\ J_c \\ J_e \end{Bmatrix} - R_L \quad (9)$$

where

$$J_i = \alpha_q l \quad (10)$$

$$J_c = K_{C4}C_i \quad (11)$$

$$J_e = V_{cmax} \quad (12)$$

[18] J_i is the light dependent reaction, described by α_q, a quantum use efficiency, and I, photosynthetically active radiation. J_c is the C_i limited rate, described by K_{C4}, a rate constant and C_i. J_e is the maximum Rubisco capacity, described by V_{cmax} a single maximum rate constant. The resulting C_4 biochemical demand model describes photosynthesis using three parameters (α_q, K_{C4}, and V_{cmax}) and two variables (I and C_i).

[19] Several simplifications of the biophysical modeling approach did not appear to negatively impact the performance of the model throughout the growing season. These simplifications allowed for a reduced number of parameters, which was essential for comparison with eddy covariance data [*Braswell et al.*, 2005; *Wang et al.*, 2001]. Rather than explicitly modeling soil water dynamics, we considered the water available for transpiration to be derived entirely from near-surface groundwater. Previous research at this site has shown relative insensitivity of the woodland to growing season precipitation events [*Potts et al.*, 2008]. Due to more extensive and deeper root systems, the degree of connection between the near-surface groundwater is likely to be stronger for the woodland than the grassland systems [*Scott et al.*, 2006; *Stromberg et al.*, 1996; *Williams et al.*, 2006]. The lack of an explicit soil moisture model may have been more critical for describing the dynamics of heterotrophic respiration in the NEE separation [*Davidson et al.*, 1998; *Reichstein et al.*, 2005b]. In developing our initial GPP/R separation we included a precipitation event component to respiration (see below). A second simplification was not explicitly modeling the maximum quantum yield (J_{max}) in C_4 photosynthesis. As in the work of *Katul et al.* [2003], we allowed V_{cmax} to determine the upper bound on total photosynthesis rather than specifying a maximum for both electron transport and carboxylation. Preliminary analyses showed J_{max} could not be well constrained; periods of high light availability were associated with stomatal closure, reduced C_i, and therefore consistent photosynthetic limitation by the carboxylation step and the V_{Cmax} parameter. The current model is sensitive to light-limited assimilation at low light levels by explicitly modeling quantum yield, which is the primary determinant of the light reaction at low light levels. A third simplification, treating the canopy as a single layer, was generally appropriate because these sites had relatively low LAI. Initial studies dividing the canopy into multiple layers did not appreciably affect the results. A fourth simplification of the model was not explicitly describing temperature sensitivities for photosynthesis. This simplification resulted in the typical 8−10 model parameters describing temperature sensitivity [*Leuning*, 1997] being reduced to two. Nonlinearities associated with temperature dependence can vary substantially

Table 2. Parameters, Symbols, Units, and Ranges Included in the Model Inversion for Each Sample Period

Symbol	Description	Unit	Range for Inversion
Θ_r	water supply from root to leaf	mmol m^{-2} s^{-1}	0–100
Gw	maximum stomatal conductance for water	mmol m^{-2} s^{-1}	0–10
α_q	quantum use efficiency for electron transport (C$_3$, C$_4$)		0–100
Γ^*	CO$_2$ compensation point (C$_3$)	μmol m^{-2} s^{-1}	0–1000
V$_{cmax}$	maximum rate of carboxylation (C$_3$,C$_4$)	μmol m^{-2} s^{-1}	0–1000
k$_c$	half saturation coefficient for photosynthesis (C$_3$)	μmol m^{-2} s^{-1}	0–10000
k$_{c4}$	rate constant (C$_4$)		0–100
R$_l$	leaf respiration	μmol m^{-2} s^{-1}	0.01–7.5

between plant species [*Leuning*, 1997, 2002; *Medlyn et al.*, 2002]. Furthermore, leaf temperatures were not well described and likely vary throughout the canopy and between communities. Previous studies have found substantial heterogeneity in both the microclimate and photosynthesis that occurs within the vegetation canopy [*Baldocchi et al.*, 2002; *Niinemets*, 2007; *Tissue et al.*, 2006]; while others have suggested a more tightly regulated leaf temperature [*Helliker and Richter*, 2008; *Roden and Pearcy*, 1993]. For sites located in more complicated topographies and denser canopies, a better understanding of the interactions between the canopy and the microclimate will likely be needed [*Bohrer et al.*, 2005]. The applicability of these simplifications and the uncertainties they generate can help guide experiments to better constrain model parameters.

2.3. Analysis

[20] To identify the parameters of the model describing GPP based on 30 min values of I, VPD, temperature, and C$_o$, we developed an inversion or data-model fusion procedure based on the likelihood function and Markov-chain Monte-Carlo (MCMC) [*Braswell et al.*, 2005; *Gamerman and Lopes*, 2006; *Santaren et al.*, 2007; *Xu et al.*, 2006]. By using the MCMC approach, rather than identifying a single value for each parameter, posterior distributions of parameters were generated, yielding confidence intervals in model performance and allowing the resulting forward estimation of model output to be directly quantified. This method is consistent with Bayesian approaches by using an uninformative uniform prior probability within the permissible range and a prior probability of 0.0 outside the range. Data-model agreement was defined by the log likelihood function, which is more appropriate than a least squares approach for eddy covariance data [*Braswell et al.*, 2005; *Sacks et al.*, 2007]. We assumed the error in the data-model relationship was both independent of time and normally distributed. Because the error is unknown, it was estimated for each step of the optimization. Rather than include the error term as an inverted parameter, we estimated the most likely value based on an optimization of the likelihood function using the procedure described by *Braswell et al.* [2005]. Following the MCMC protocol, the model was initialized with a randomized value for all parameters, fluxes were estimated, and the likelihood function was evaluated. New candidate parameter were based on the prior accepted parameters, and candidate parameters were accepted based on the ratio of likelihoods between the candidate and most recently accepted parameters. To facilitate the optimization, potential parameter values were restricted to a permissible range that was defined to capture a broad range of realistic values (Table 2). After a "burn-in"

period, a stable chain occurs with the set of accepted values determining an estimate of the posterior parameter distribution. After extensive evaluation of the procedure, we ran the optimization for 150,000 iterations and used the final 50,000 iterations to generate the posterior distributions.

[21] We constructed our inversions using a hierarchical or stepwise structure that allowed us to sequentially include new sources of variability and more accurate sets of parameters [*Wu and David*, 2002]. These stages included (1) estimation of ecosystem R model parameters; (2) estimation of leaf physiological model parameters; and (3) estimation of leaf area and water supply (Figure 1b). We developed estimates of daytime ecosystem R by inverting the nighttime flux data against an Arrhenius ecosystem R model that accounted for potential precipitation-induced pulses of respiration [*Jenerette et al.*, 2008] and projected this model to the daytime. This temperature-sensitivity approach for separating eddy covariance data into R and GPP is a modification of a standardized approach [*Desai et al.*, 2008; *Makela et al.*, 2008; *Reichstein et al.*, 2005a; *Wohlfahrt et al.*, 2005]. Estimates of R parameters were identified independently at 5 day intervals, and daytime GPP values were derived from NEE observations by subtracting the modeled daytime R. At the second stage, we identified five "gold standard" days in the growing season of each year. These days had complete records and did not show any appreciable effects of stomatal reduction to water limitation. Using these gold standard data, we implemented the model inversion procedure to acquire the photosynthetic parameters for each site independently. Finally, we used the physiological parameters as input to an inversion procedure to identify leaf area and water supply at 5 day intervals. This hierarchical approach of using multiple levels of model inversion allowed us to use the relative constancy in the vegetation community to obtain physiological parameters and then identify the more rapidly changing water and leaf area parameters. As a check on the performance of the overall data-model fusion procedure we generated 10,000 realizations of the model NEE patterns using the posterior distributions of all parameters and compared these results with observed NEE through regression analysis.

[22] With a suitable model-data correspondence, we used the resulting distributions of parameters to identify the magnitude, distribution, and sources of uncertainty in the resulting estimates of GPP. We evaluated the distribution of modeled GPP and estimated the uncertainty associated with each factor as the ratio simulated total GPP for each factor and the mean of the total distribution of simulated GPP. For comparison at growing season scales, we estimated the total growing season GPP for each year and the corresponding uncertainty. To identify GPP temporal variability within and

A – Woodland Site
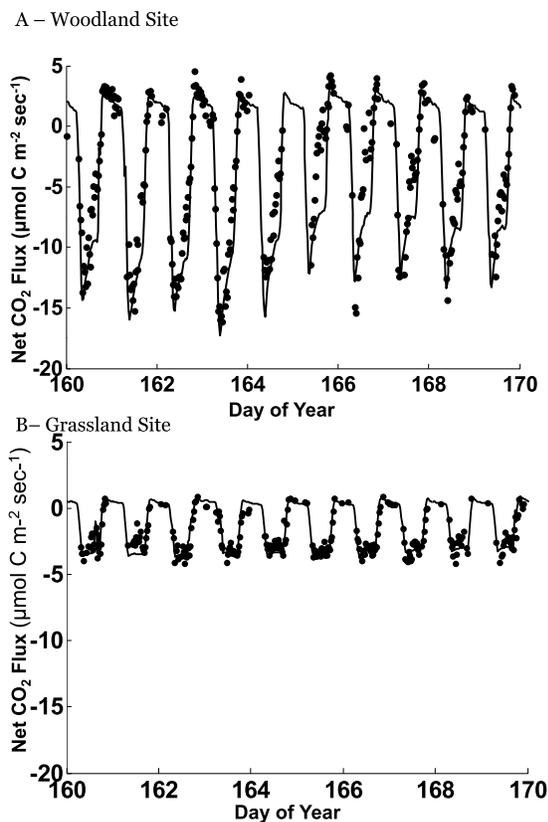
B– Grassland Site

Figure 2. A 10 day example of modeled NEE versus observations for the premonsoon season in 2003 at the (a) woodland site and (b) grassland site.

between growing seasons we computed the semivariance between daily GPP during each growing season. Semivariance (γ_h) describes the variability between data separated by a scale lag (h) and is calculated as:

$$\gamma_h = \frac{1}{2n(h)} \sum_{i=1}^{n_h} (x_i - x_{i+h})^2 \qquad (13)$$

where x_i and x_{i+h} are two data separated by the temporal lag, h. Semivariance has frequently been used to describe spatial variability [*Dent and Grimm*, 1999; *Ewers and Pendall*, 2008; *Meisel and Turner*, 1998] but is also appropriate for temporal data [*Carmona-Moreno et al.*, 2005; *Florin et al.*, 2009].

[23] The variability of GPP associated with premonsoon and monsoon periods within the growing season was evaluated through comparisons between DOY 150–180 and DOY 220–250. We computed the proportional change in GPP, leaf area, water supply, VPD, and light between these two seasons using 1000 simulations from the posterior distributions of all parameters. In all analyses we assumed physiological parameters were consistent through time.

[24] To understand the causes of GPP variation, we developed a fully factorial state factor based sensitivity analysis to identify the dependence of GPP variability on the individual and interactive variation in meteorology, physiology, leaf area, and water supply. The physiology factor was composed of the combination of all physiological

parameters. Meteorology was composed of daily patterns of PAR, VPD, and C_o. Leaf area and water supply were single variables. The factorial analysis modeled the carbon exchanges for 50 possible combinations of each factor, these combinations were obtained from daily meteorology, or the distributions of inverted parameters. This approach allowed only realistic combinations of meteorology, such as consistent daily trends in light and VPD, rather than exploring the entire potential space of parameters and variables. This grouping of variables also had a practical aspect: this limited suite of sensitivity analyses resulted in 6,250,000 unique simulations for the woodland and grassland sites. A fully factorial analysis of all possible variable combinations would be computationally challenging. To identify the variation associated with each factor for the grassland and woodland sites individually we computed the mean response for each instance of the factor and then computed the variance among all instances of the factor. A similar analysis was conducted for all pairs and three-way combinations of factors.

3. Results

[25] The data-model fusion procedure was able to couple the observed subhourly variability from eddy covariance measurements with an ecophysiological model that simultaneously estimated stomatal conductance, photosynthesis, and respiration (Figure 2 and Table 3). For all sampling periods, the confidence interval for the slope and intercept of the model-data relationships included 1.0 and 0.0, respectively. The model inversion procedure performed similarly in the woodland (mean $r^2 = 0.62$) and the grassland (mean $r^2 = 0.66$). Following the whole ecosystem NEE data-model comparisons, we focused on better understanding the dynamics of GPP. The diurnal dynamics of GPP on most days displayed responses characteristic of water-limited systems, exhibiting a maximum photosynthetic rate before solar noon and a hysteresis in photosynthesis response to light. The hysteresis of the photosynthesis-light response often resulted in substantially larger morning assimilation rates than in the afternoon for the same amount of light. The magnitude of this hysteresis was larger for the woodland than the grassland. The uncertainty in GPP was associated primarily with uncertainty in the physiological responses. Leaf area and water supply contributed similarly to the uncertainty and was an order of magnitude less than plant physiology (Figure 3). Uncertainties in all components of physiology, water availability, and leaf area factors were higher in the woodland than the grassland. The resulting total growing season GPP showed distinct rates and vari-

Table 3. Goodness-of-Fit Statistics From Regression Analysis Between the Observed and Modeled NEE[a]

Site	Year	r^2	Intercept	Slope
Woodland	2003	0.64–0.75	−1.6–4.3	0.56–1.32
	2004	0.49–0.66	−0.16–3.58	0.55–1.22
	2005	0.49–0.72	−1.65–3.35	0.63–1.37
Grassland	2003	0.46–0.83	−0.04–2.23	0.48–3.56
	2004	0.35–0.69	−0.65–2.38	0.40–2.70
	2005	0.45–0.82	−0.05–2.76	0.51–3.52

[a]The 95% confidence intervals are shown derived from bootstrapped model runs using the posterior distribution of inversely fitted parameters.
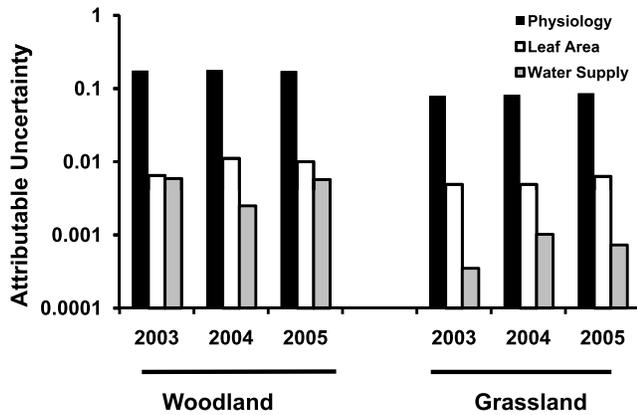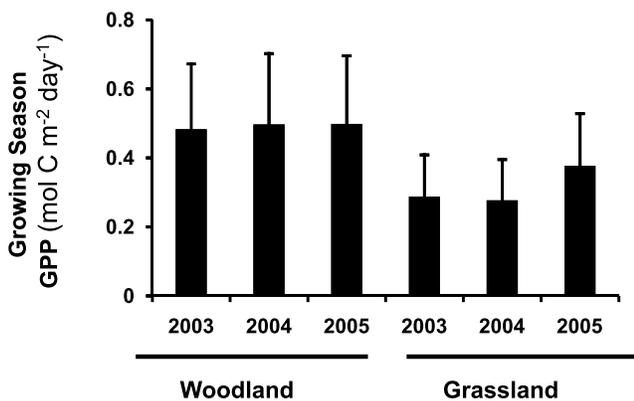
Figure 3. Contribution of each source to model simulation uncertainty. Each bar represents the width of the 95% confidence interval in estimated GPP associated with each source scaled by the median estimate of GPP.

ability between the woodland and grassland (Figure 4) with the woodland whole growing season GPP consistently higher and less variable than the grassland.
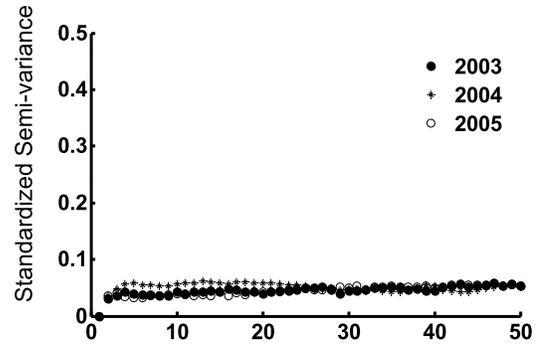
[26] The patterns of GPP variability exhibited differences in the temporal scale between the daily, growing season, and interannual responses between the woodland and grassland when computed over the entire growing season (Figure 5). At lags as small as 2 days, the grassland and woodland exhibited marked differences with the grassland having a higher mean semivariance and higher interannual variation. With increasing lags, the woodland and grassland patterns diverged further. The woodland had a consistently stable semivariance for lags up to 50 days with little difference between years. The grassland semivariance generally continued to increase with increasing lags; each year had a unique semivariance pattern ranging from nearly continuous increases in semivariance (2003 and 2004) to a rapid rise followed by a plateau (2005). Beyond the shortest lags, the woodland dominated ecosystem was more stable (or less variable) within and between growing seasons than the grassland dominated ecosystem.

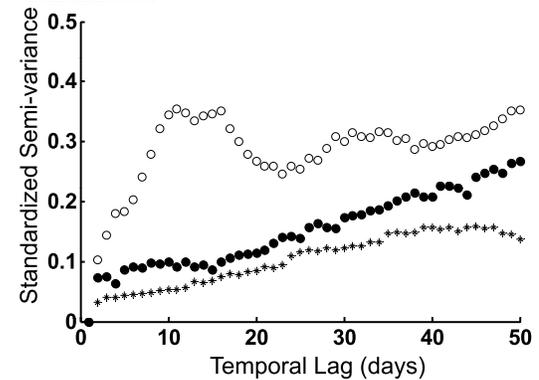[27] The effects of the monsoon were subtle in the woodland but much more pronounced in the grassland

Figure 5. Median semivariance of GPP throughout the entire growing season for the (a) woodland site and (b) grassland site. Semivariances were estimated up to 50 day lags.

(Figure 6). For both sites, key environmental differences between premonsoon and monsoon seasons were a decrease in VPD and light availability. In the woodland, the transition to the monsoon season had no detectable effect on GPP, a slightly increased leaf area and either no effect or slightly decreased water supply. In the grassland, the monsoon was associated with large increases in GPP (up to 1.4 times

Figure 4. Estimated GPP (mean and 95% confidence intervals) for each sampling period estimated from data-model inversion.
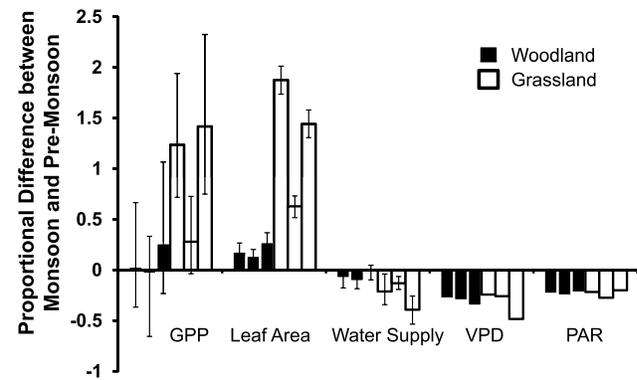
Figure 6. The change (median and 95% confidence interval) in GPP, leaf area, water supply, VPD, and PAR from premonsoon and monsoon periods of the growing season. Change is computed as the difference from monsoon and premonsoon scaled by the premonsoon value. Positive values represent increases in the variable from premonsoon to monsoon.
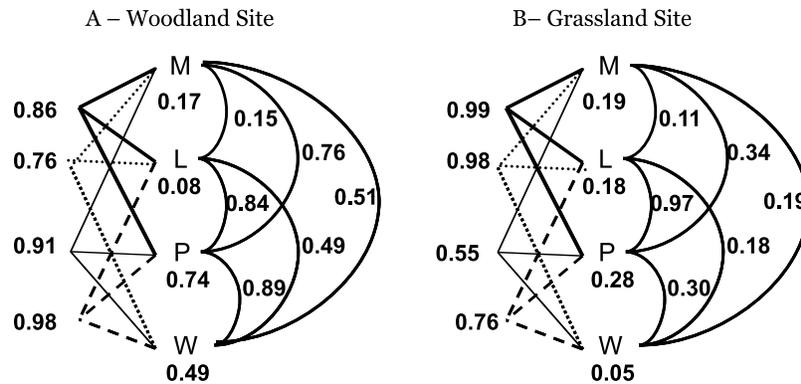
Figure 7. Proportion of total variability identified in a state factor sensitivity analysis separated into meteorology (M), leaf area (L), physiology (P), and water supply (W) for the (a) woodland site and (b) grassland site. The value under each symbol for each factor is the variation observed for this factor alone. The values to the right show the variation observed for the two factors connected by the line. The values to the left show the variation observed for the three factors connected. The variability is derived from the entire 3 years of information.

premonsoon), leaf area (up to 1.7 times premonsoon), and slight decreases in water supply.

[28] By conducting a fully factorial sensitivity analysis we were able to identify the contribution of each factor to overall variation (Figure 7). For GPP the differences in the physiological parameters were the single largest contributor to GPP variation at both sites. This factor was followed in decreasing order by meteorology, water supply, and then leaf area in the woodland and meteorology, leaf area, and then water supply in the grassland. The amount of variation related to combinations of factors was more complex with the effects of multiple factors not simple linear combinations of the individual factor. For the woodland, several combinations of two factors yielded similar results. For the combination of three factors, the woodland had the most variation explained with the meteorology factor excluded while the least amount of variation was explained with the physiological factor excluded. For the grassland, the most variation was observed with the water supply factor excluded and the least variation was observed with the leaf area factor excluded. These differences highlight the nonlinearities associated with combinations of factors compared to factors observed in isolation. A surprising result was the differential sensitivity of the grassland and woodland to water supply and leaf area. The woodland was more sensitive to water supply by a factor of 10 than the grassland while the grassland was more sensitive to leaf area than the woodland by more than a factor of 2 (Figure 7).

4. Discussion

[29] Our coupled empirical and modeling approach allowed for a mechanistically based simplification of ecosystem dynamics that could be directly linked with high resolution environmental sensing. The hierarchical approach to data-model fusion can potentially improve the recovery of model parameters when using sensor based data streams. This approach provided a robust approach for identifying the magnitude and determinants of ecosystem variation at multiple temporal scales (Figure 2 and Table 3). The overall correspondence between the model and obser-

vations suggests the simplifications to the physiological and hydrological dynamics were not overly detrimental to the analysis. This was particularly encouraging as the C_i variable recovered by the inversion procedure can be affected by strong gradients within a canopy and counter gradient transfers. While we conducted an extensive analysis of uncertainty in the model parameters, we did not directly incorporate potential uncertainty in the data streams. Data uncertainty enters the analysis through the NEE measurements used for inversions and the meteorological data used as a forcing. NEE data are generally characterized by relatively high uncertainty, while the meteorological data at the sensor location are generally more accurate [*Goulden et al.*, 1996; *Medlyn et al.*, 2005]. Both sources of data suffer from unknown errors in extrapolation through the measurement footprint. As the footprints in these sites were generally homogeneous we expect this uncertainty to be low. While assuming a minimal data uncertainty seems reasonable for the present study, such assumptions should be explored for extrapolating the model in either time, with future or historic meteorological projections, or space, to regional analyses of shrub-grass ecosystem dynamics.

[30] Differences between the woodland and grassland communities were observed in the dynamics of GPP at daily, seasonal and interannual scales, and these dynamics could be directly partitioned between meteorology, physiology, leaf area, and water supply. The estimated magnitudes of GPP in the woodland were consistently higher than in the grassland (Figure 4), consistent with a hypothesis that the deeper access to groundwater allows for a higher GPP. However, this higher rate of photosynthesis depended on a sufficiently high C_i; stomatal closure due to a relatively limited supply of water to the leaf compared to atmospheric demand substantially reduced photosynthesis from maximum rates especially in the afternoons. In contrast, the grassland did not exhibit the degree of afternoon GPP reduction suggesting it did not experience a limitation of water supply to the canopy when atmospheric demand was highest. This whole ecosystem observation coincides with a nearby experiment on semiarid grasses where at the leaf level, the midday depression was not commonly observed

[Ignace et al., 2007]. The higher access to groundwater and higher maximum capacity for GPP by the woodland, was associated with a higher regulation of leaf water loss than the grassland. The variability in assimilation rates were related both to differences in the temporal scale and community type (Figure 5). At short time scales, both the woodland and the grassland had similar responses to environmental variability. As the time scale increased, the responses were dominated by community differences. Grassland GPP was nearly ten times more variable than the woodland at scales more than a few weeks. These findings were further supported by comparing premonsoon with monsoon season (Figure 6), where the woodland showed little difference in GPP or leaf area, while the grassland had larger increases in both. The reduction in water supply at both sites is consistent with previous findings of drawdown of the water table between these seasons that recovers later in the year [Scott et al., 2004, 2008]. Inferred from the data-model analysis, the large within and between growing season variability in the grassland was caused primarily by variations in leaf area. Compared to other ecosystems, the riparian woodland exhibited a surprising amount of stability: some woodlands have been shown to vary as much as 100% [Goulden et al., 1996]. The stability in this riparian woodland was likely due to stability of the water table in the alluvial aquifer, which is buffered by inflows from the vast basin aquifer that surrounds it. The resulting analysis for these semiarid ecosystems supported the hypothesis that meteorology, while driving ecosystem processes, is strongly affected by nonlinear biological responses. Our results are consistent with expectations that biological responses to environmental variation are equally or even more important than the magnitudes of the environmental variation for physical terrestrial-atmosphere material and energy exchanges [Polley et al., 2008; Richardson et al., 2007; Rocha and Goulden, 2008].

[31] The multiple-factors approach compared alternative hypotheses as described by each state factor in determining growing season GPP variation. By examining contrasting woodland and grassland ecosystems in a riparian environment with access to groundwater, we were able to effectively separate the effects of meteorology, physiology, leaf area, and water supply. Conducting the state factor sensitivity analysis allowed for a quantitative comparison of the contrasting factors affecting variation in GPP (Figure 7). This approach partitioned multiple variables into conceptually related factors and facilitated understanding the different causes of GPP variation. Physiological differences were associated with the largest amount of variation between sites, while meteorological differences were associated with the least amount of variation. This result is consistent with the conclusions found in a mesic forest site, where a similar sensitivity analysis was conducted [Richardson et al., 2007]. However, in a landscape-scale analysis of an African savannah system, the importance of vegetation type was most strongly attributed to daily and seasonal variation, not annual scale variability [Williams and Albertson, 2005]. However, variation in the annual total of assimilation as described by Williams and Albertson [2005] is strongly affected by growing season length, while the interannual variation as we describe here is only within the growing season. Traditionally, state-factor models have been consid-

ered a phenomenological concept [Amundson and Jenny, 1997]. We suggest that examining the sensitivity of a mechanistic data-model fusion analysis and partitioning the factors into explicit variables and parameters provides a mechanistic framework for understanding the state factors. We found GPP variability was mostly attributable to the nonlinear responses to meteorological variability rather than meteorological variation itself. Nonlinearities in the combined effects of individual factors further highlighted the interactions between factors were as important as the individual factors by themselves.

[32] Comparing the two community types, the state factor analysis suggests the woodland was surprisingly more sensitive to water supply than the grassland (Figure 7). With more extensive and deeper root system, we had expected the woodland to be less sensitive to water supply than the grassland. However, the availability of water does not necessarily lead to reductions in the ratio between supply capacity to the leaf and atmospheric demand. The increased variability attributable to water supply in the woodland compared to the grassland is reflected again in the larger hysteresis responses of the woodland than the grassland observed both in the data and model (Figure 2). This hysteresis is associated with stomatal closure, which is in part determined by the balance between the atmospheric demand and supply of water to the leaf. Thus, the greater sensitivity to water supply in the woodland could be interpreted not necessarily as a limitation in the availability of water to the roots but rather as a limitation in the hydraulic capacity of the trees, which transport water from the water table at ~10 m through woody tissues to leaves at 3–7 m above the ground. In contrast, the grassland had a higher sensitivity to changes in leaf area than the woodland. Rather than adjusting daily physiology, the grassland adjusted leaf area. This is supported by the increased importance of leaf area in the grassland compared to the woodland. These differences are representative of alternative strategies for coping with variation in available water and atmospheric demand: either adjust stomatal conductance or adjust leaf area. These differences are consistent with a general model of how woodlands and grasslands manage carbon-water exchanges: woodlands maintain a consistent leaf area, strongly regulate stomata, and thus may be more resistant to drought conditions while grasslands strongly regulate leaf area, minimally regulate stomata, and thus may be more resilient to drought conditions. These different mechanisms are directly related to observed levels of within and between season variability; by changing leaf area the grassland can have a broader range of response to environmental fluctuations than the woodland. How these differences in resistance and resilience strategies will affect long-term sustainability of both grass or woody dominated states system is an open question. However, these results highlight a potential consequence of woody plant encroachment into grasslands: the increased stability of woodlands may lead to a decreased ability to acclimate to climate variability compared to grasslands.

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