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Climate change alters growing season flux dynamics in mesic grasslands

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Abstract Changing climate could affect the functioning of grassland ecosystems through variation in climate forcings and by altering the interactions of forcings with ecological processes. Both the short and long-term effects of changing forcings and ecosystem interactions are a critical part of future impacts to ecosystem ecology and hydrology. To explore these interactions and identify possible characteristics of climate change impacts to mesic grasslands, we employ a low-dimensional modeling framework to assess the IPCC A1B scenario projections for the Central Plains of the United States; forcings include increased precipitation variability, increased potential evaporation, and earlier growing season onset. These forcings are also evaluated by simulations of vegetation photosynthetic capacity to explore the seasonal characteristics of the vegetation carbon assimilation response for species at the Konza Prairie in North Central Kansas, USA. The climate change simulations show decreases in mean annual soil moisture and and carbon assimilation and increased variation in water and carbon fluxes during the growing season. Simulations of the vegetation response show increased variation at the species-level instead of at a larger class scale, with important heterogeneity in how individual species respond to climate forcings. Understanding the drivers and relationships behind these ecosystem responses is important for understanding the likely scale of climate change impacts and for exploring the mechanisms shaping growing season dynamics in grassland ecosystems.

Keywords Konza Prairie · Ecohydrology · Low-dimensional modeling · Nonlinear interactions · Soil moisture feedback

1 Introduction

Climate change may have profound impacts on the ecology and hydrology of grassland ecosystems. Increased variability and long-term change to the properties of climate forcings may alter mass and energy flux dynamics and induce change at many scales of ecosystem functioning (Suyker et al. 2003; Fay et al. 2008). Driving variables shape ecosystem dynamics; forcings such as precipitation and solar radiation play critical roles in creating the spatial and temporal heterogeneity of landscapes and are affected by diverse influences such as feedbacks and biotic processes (Claussen et al. 2001; Ivanov et al. 2008). These interactions are not stable and the response of mass and energy fluxes to driving variables differs across levels of support (Brunsell and Gillies 2003; Riley et al. 2009). Understanding the way changing climate alters ecosystem interactions may provide insight on the possible intricacies of future ecosystem functioning.

The interplay between driving variables and ecosystem responses is often evaluated at long timescales, which provides a useful time step but can also overlook

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critical information that exists at shorter scales. Ecosystem variables are also less likely to show statistically-significant change at longer scales, delaying identification of the direction and rate of the ecosystem response. Relating processes at different timescales and sensitivities, therefore, is of particular importance for identifying the nature of ecosystem responses (D'Odorico et al. 2000; Laio et al. 2002; Daly and Porporato 2006). Studies outlining the probability of extreme events (Fay et al. 2008), moisture allocation during drydown periods (Teuling et al. 2006a, b; Milly 1994), plant-scale analyses of C_3 and C_4 photosynthesis (Vico and Porporato 2008), and water flux coupling to surface processes (Ridolfi et al. 2000a) are examples of the diversity of topics within this focus. Representation of feedbacks and atmospheric coupling extend this further (Brunsell and Gillies 2003); defining the scales of ecosystem functioning aids in more-directed application of processes and variability. We suggest this background knowledge provides substantial background information on the critical spatial and temporal scales of ecosystem change.

The relationships governing nonlinear surface processes may be assessed using low-dimensional modeling techniques. The strength of these approaches is their ability to simulate climate forcings as the framework of ecosystem flux dynamics at small and large scales. Low-dimensional models have been applied to precipitation and water flux variability (Daly and Porporato 2005, 2006; Koster and Suarez 1999) and also to spatiotemporal water-limitation and flux depression (Ridolfi et al. 2000b; Porporato et al. 2001). They have been used to identify how relationships between vegetation and environment govern spatial vegetation patterns in the Kalahari grassland in Southwest Africa (Porporato et al. 2003) and hydrology of the Konza prairie in North Central Kansas (Porporato et al. 2004). Recently, the authors used a similar low-dimensional technique to assess seasonal sensitivities of mass and energy fluxes to climate forcings as a way of characterizing differences in ecosystem processes across the Kansas River Basin precipitation gradient (Petrie and Brunsell 2011).

Mesic grasslands exhibit dynamic responses to climate forcings at short timescales. Variation and disturbance are, in many ways, normal for grasslands and resulting heterogeneity is an important component of how these ecosystems function (Knapp et al. 1998; Collins et al. 2002). Local ecology also feeds back at differing scales, producing specialized function and niche development (Collins et al. 2002). The ecologic role of vegetation, for example, is one of many parts. It is affected by forcings, feeds back on them, and changes in response over time. Water and carbon fluxes are both drivers and products of these processes and are often upscaled to represent large-scale ecosystem responses (Betts et al. 1997). Photosynthesis, for example, varies in sensitivity to precipitation at different states of water limitation (Petrie and Brunsell 2011) and provides information on how ecosystems are shaped over long timescales. Determining which variables are likely to show elastic responses to future climate scenarios is a necessary extension of this earlier analysis and may offer insight on the effect climate change will have on mesic grasslands.

Global Climate Model (GCM) projections for the Central United States were evaluated by Brunsell et al. (2010) for the Intergovernmental Panel on Climate Change (IPCC) A1B climate change scenario. Central Plains ecosystems are projected to experience an increase in mean surface temperature and higher precipitation variability (fewer events of higher magnitude), slightly decreased mean annual precipitation, and earlier growing season onset (Brunsell et al. 2010). These compliment other projections for the Central Plains (Houghton 2001). Studies by Richardson et al. (2009) and Monson et al. (2005) have explored earlier onset conditions for temperate Harvard and arid Colorado forests; their results suggest differing water availability and ecosystem flux responses to altered seasonal conditions and earlier growing season onset. How an altered growing season could affect mesic grasslands, an intermediate between the temperate east and arid west, is unknown. We expect simulations for the Central United States to reflect increased short-term variability of soil moisture and also increased average amplitude between productive early-season and summer drydown periods within individual years, similar to the results of Angert et al. (2005).

To explore potential states of mesic grasslands under changing climate, we focus on the effects of increased precipitation variability, earlier growing season onset, and heightened potential evaporation as climate drivers of seasonal water flux dynamics, growing season length, and carbon assimilation for semiarid forb and grass species. Specific goals are: (1) To characterize the individual and aggregate effects of decreased precipitation timing and increased magnitude, heightened potential evaporation, and earlier growing season onset on seasonal carbon assimilation and soil moisture availability; (2) to determine how seasonality in photosynthetic capacity might act as a critical variable that illustrates variation in the vegetation response to changing climate; and (3) to explore carbon assimilation responses of Konza Prairie vegetation to changing forcings and earlier growing season onset. This furthers prior analysis of climatic and ecologic variability across the Central Plains in Petrie and Brunsell (2011) by characterizing how driving mechanisms and responses interact at short to long timescales within the Konza Prairie region and assessing the possible effects of changing climate on mesic grassland ecology.

2 Site

This study simulates precipitation dynamics of the Konza Prairie mesic grassland in the Central Plains of the United States (40° N, 99.5° W). Precipitation timing (λ: events day^{-1}) and magnitude ($\frac{1}{\alpha}$: depth event^{-1}), along with seasonal potential evaporation, drives the ecology and hydrology of this region (Petrie and Brunsell 2011). Low annual rainfall (84 cm year^{-1} at Konza; 70 cm year^{-1} for the larger region) promotes dry-mesic grasslands of C_4 grasses and C_3 grass and forb species (Fay et al. 2000). These areas are heavily influenced by soil moisture dynamics and fire suppression (Harpole and Tilman 2006; Nippert and Knapp 2007). Annual Net Primary Production (ANPP) in the Konza Prairie is dominated by relatively few, abundant species while spatially-small microclimates have higher species diversity (Knapp et al. 1998). Soils in the region tend to have mollic properties that vary with topography and composition, often with active depths of 1 m or more.

Historical climate change in the Central Plains produced greater overall effects on grassland ecology than is expected for contemporary climate change (Woodhouse and Overpeck 1998), but the rapid onset and direction suggested by current projections may still have disruptive effects (Brunsell et al. 2010). Variation in the distribution of precipitation, for example, may result in increased frequency of extreme hydrologic events, disrupting vegetation functioning and soil stability in agricultural regions (Fay et al. 2008; Rosenberg et al. 1999). More intensive irrigation requirements may be realized for sustaining agriculture in some cases and hasten the depletion of aquifer resources (Rosenberg et al. 1999). Land class compositions may also be affected; drier conditions could limit current woody vegetation encroachment, which increased by 154% from 1939–1985 at Konza (Briggs et al. 2005). At present, native and invasive species both constitute a sizable portion of the land area of the Central Plains. Elevated atmospheric CO_2 concentrations may be another driving variable in the climate change problem, with effects that are difficult to generalize and are highly species-specific (Drake et al. 1997; Geeske et al. 2001). Understanding the primary drivers and scales of the ecosystem response is an important part of planning for the future use and management of grassland resources.

3 Methods

To assess the effects of climate change on mesic grasslands, we focus on identifying the effects of changing climate drivers of less frequent precipitation event timing (λ) and higher magnitude ($\frac{1}{\alpha}$), increased potential evaporation (E_p), and earlier growing season onset identified from Brunsell et al. (2010)'s simulations for the Central Great Plains. In the first part of this study, we focus on changing precipitation timing and magnitude, potential evaporation, and growing season onset as the major drivers of ecosystem flux dynamics and the effect their estimated variation has on simulated water and carbon fluxes. In the second, we implement measurements of photosynthetic capacity as a critical parameter that governs the vegetation response to altered soil moisture and potential evaporation in the model, and apply this framework to explore the relation of potential carbon assimilation and climate forcings in Konza Prairie vegetation.

3.1 Precipitation simulation and model framework

The basis for the simulation of precipitation and water fluxes in are based on D'Odorico et al. (2000) and Laio et al. (2001), respectively. The model is implemented at the daily timestep, where soil moisture and potential evaporation are the main variables used to simulate daily evaporation and transpiration. Soil moisture is influenced by precipitation inputs at the beginning of the time step and is reduced at the end of the time step from the magnitude of the mass fluxes and from a soil moisture leakage function that incorporates the soil properties included in Table 1 (Ridolfi et al. 2000a). The soil moisture value is then implemented within the next time step.

Precipitation was used to force the model using a Poisson process of event timing and magnitude, with daily Monte Carlo generation of precipitation (D'Odorico et al. 2000). Timing and magnitude values for Central Plains grasslands were calculated in the same manner as Petrie and Brunsell (2011), using United States Historical Climatology Network (USHCN) daily precipitation data averages from stations within 1.5° latitude and longitude from the Konza

Table 1 Model parameterizations

Name	Parameter	Value	Units
Soil matric potential	ψ	−.00034	MPa
n/a	b	4.05	n/a
n/a	c	11.1	n/a
Hydraulic conductivity	K_s	175	cm d^{-1}
Soil porosity	n	0.4	n/a
n/a	β	12.1	n/a
Hygroscopic point	θ_h	0.12	$m^3\ m^{-3}$
Reduction point	θ^*	0.37	$m^3\ m^{-3}$
Field capacity	θ_{fc}	0.42	$m^3\ m^{-3}$
Wilting point	θ_w	0.17	$m^3\ m^{-3}$
Soil evaporation at θ_w	S_w	0.08	cm d^{-1}
Soil active depth	Zr	100	cm
Potential evaporation curve amplitude	δ_{et}	0.75	n/a
Potential evaporation phase shift	ψ_{et}	2.62	d^{-1}
Potential evaporation sinusoid frequency	ω_{et}	0.02	d^{-1}
Control event timing	λ	0.225	events d^{-1}
Scenario event timing	λ	0.185	events d^{-1}
Control event magnitude	$\frac{1}{\alpha}$	0.95	cm $event^{-1}$
Scenario event magnitude	$\frac{1}{\alpha}$	1.14	cm $event^{-1}$
Control mean evapotranspiration	E_{p0}	0.280	cm d^{-1}
Scenario mean evapotranspiration	E_{p0}	0.308	cm d^{-1}
Control growing season onset	n/a	90	d^{-1}
Scenario growing season onset	n/a	75	d^{-1}
Early and late peak mean WUE	WUE_0	0.12	µmol C mmol H_2O^{-1}
Early and late peak curve amplitude	δ_{WUE}	0.13	n/a
Early and late peak sinusoid frequency	ω_{WUE}	0.03	d^{-1}
Early peak phase shift	ψ_{WUE}	5.0	d^{-1}
Late peak phase shift	ψ_{WUE}	2.3	d^{-1}

Prairie (Williams et al. 2006) [http://cdiac.ornl.gov/epubs/ndp/ushcn/usa.html]. Simulations of 500 years output daily values of soil evaporation, transpiration, carbon assimilation, and soil moisture (Fig. 1). Values used for control and climate change simulations are shown in Table 1.

In climate change simulations, precipitation was varied by timing (λ) and magnitude ($\frac{1}{\alpha}$) with negligible change to mean annual values. Calculated Konza $\lambda = 0.225$ and $\alpha = 1.05$ for control simulation 'A' were varied by 9 and 8.25% ($\lambda = 0.205$; $\alpha = 0.966$) for the 'B' simulation and 18 and 16% ($\lambda = 0.185$; $\alpha = 0.877$) for the 'C' simulation. These simulations produced mean annual precipitation of 70.0 cm, 70.2 cm, and 70.2 cm, respectively, with slightly varying yearly totals. As discussed in Petrie and Brunsell (2011), soil moisture feeds back on its sensitivity to λ and α within the temporal unit of analysis; dry conditions are most-affected by event timing and wet conditions are most-affected by event magnitude. It is unclear how sensitive mesic grassland water and carbon fluxes are to small variations in precipitation such as those expected from the IPCC A1B scenario.

3.2 Water and carbon flux simulation

To simulate vegetation growth, we scale potential carbon and water fluxes by a metric that resembles the temporal evolution of vegetation functioning through the growing season. This vegetation functioning (fv) metric increases from 0.0% to 100% for 30 days at the start of the growing season, reaches a maximum of 100% during the growing season, and is depleted for 20 days up to the date of senescence, where it falls to 0.0% until the following growing season begins. Water stress events, defined in the model as sustained soil moisture below the vegetation wilting point ($\theta \leq \theta_w$), reduce the vegetation functioning metric to 0% and negate all vegetation fluxes for the remainder of the simulated growing season. This represents the impact of extreme drydown conditions on local ecology, which may become more frequent and intense in future climate scenarios (Brunsell et al. 2010).

Daily maximum carbon assimilation (A_p) is calculated as:

$$A_p = E_p \cdot WUE \quad (1)$$

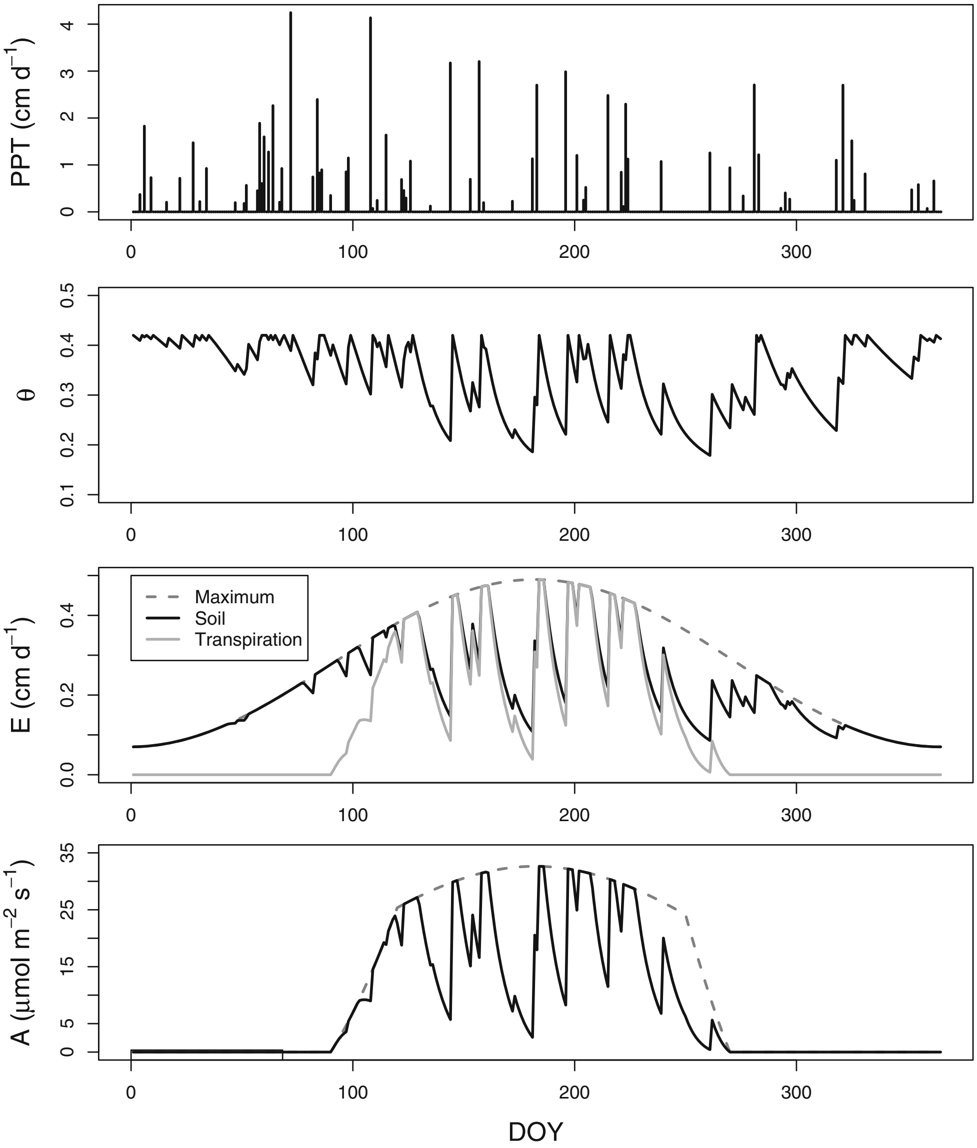

Fig. 1 One year of modeled precipitation (*top*) and resulting volumetric soil moisture, water, and carbon fluxes (*bottom*). Water fluxes are partitioned between transpiration and soil evaporation

where daily E$_p$ [cm d^{-1}] is calculated from Milly (1994) as:

$$E_p = \left(E_{p0}/nZr\right) \cdot \left[1 + \delta_{et} \cdot \sin\left(\omega_{et} \cdot h_{day} + \phi_{et}\right)\right] \qquad (2)$$

where E_{p0} is mean annual E_p, nZr is the active soil depth [cm], δ_{et} is the amplitude about $\frac{E_{p0}}{nZr}$, ω_{et} is the frequency of the sinusoid [d^{-1}], h_{day} is the hydrologic day, and ϕ_{et} is the phase shift. The vegetation functioning metric induces seasonality in maximum assimilation at the beginning and end of the growing season. Transpiration is calculated from carbon assimilation as:

$$Tr = A \cdot \frac{1}{WUE} \qquad (3)$$

where WUE is the water-use efficiency of vegetation [µmol C mmol H$_2$O $^{-1}$] calculated from photosynthetic capacity simulations and A is carbon assimilation [µmol m^{-2} d^{-1}] calculated in a piecewise manner from (Laio et al. 2001) as:

$$\begin{aligned} &if \quad \theta \le \theta_w; \quad && A = 0.0 \\ &if \quad \theta_w \le \theta < \theta^*; \quad && A = \left(\frac{\theta - \theta_w}{\theta^* - \theta_w}\right) \cdot A_p \\ &if \quad \theta \ge \theta^*; \quad && A = A_p \end{aligned} \qquad (4)$$

where A$_p$ is potential assimilation [µmol m^{-2} d^{-1}], θ is volumetric soil moisture [m^3 m^{-3}], θ_h is the hygroscopic point, θ_w is the wilting point of vegetation, and θ^* is the soil moisture at which plant fluxes begin to be reduced. Evaporation is decoupled from transpiration and is calculated in a piecewise manner from Laio et al. (2001) as:

$$
\begin{aligned}
&\mathit{if}\ \ 0 < \theta \le \theta_h; && Es = 0\\
&\mathit{if}\ \ \theta_h < \theta \le \theta_w; && Es = S_w \cdot ((\theta - \theta_h)/(\theta_w - \theta_h))\\
&\mathit{if}\ \ \theta_w < \theta \le \theta^*; && Es = S_w + (E_p - E_w)\\
& && \quad \cdot \left((\theta - \theta_h)\big/(\theta_w - \theta_h)\right)\\
&\mathit{if}\ \ \theta > \theta^*; && Es = E_p
\end{aligned} \tag{5}
$$

where S_w is soil evaporation at the wilting point of vegetation. These values are theoretical parameterizations for model simulation of fluxes. Total evaporation (E, cm d^{-1}) is the sum of Es and Tr, weighted by vegetation functioning:

$$E = Es \cdot (1 - fv) + Tr \cdot fv \tag{6}$$

where fv is the vegetation functioning. Each of these model outputs are simulated at the daily time step.

3.3 Photosynthetic capacity and water-use efficiency

An important variable shaping vegetation water and carbon fluxes in the model is water-use efficiency (WUE, $\frac{\delta A}{\delta E}$). Water-use efficiency is the slope of the carbon assimilation-transpiration curve and its variation is a product of sensitivities of stomatal conductance to surface temperature, vapor pressure, and seasonal phenology (Monson et al. 1986; Nippert et al. 2009). Measurements of carbon assimilation and transpiration reflect varying nonlinear sensitivities of vegetation photosynthesis to external forcings and carbon flux dynamics are an emergent property of the photosynthetic capacity of vegetation. These measurements also reflect the compatibility of vegetation to temporal variation in and magnitude of moisture availability. The relation of transpiration to evaporation responds strongly to soil moisture variation, although the vegetation control plays an important role in the overall magnitude of carbon and water fluxes.

We implement vegetation photosynthetic capacity as a seasonally-varying parameter to estimate how changes to the temporal variation in potential carbon assimilation and soil moisture might influence the partitioning of growing season carbon assimilation and also mean annual values. These simulations may also help identify the likely spatial scale of the ecosystem response. For example, variation in plant phenology and external forcings (parameterized in this study as potential carbon assimilation) produces different carbon assimilation patterns between vegetation species (Epstein et al. 1996; Emmerich 2007). The photosynthetic pathway of vegetation may be an important variable; large-scale shifts in vegetation dominance, including C_3 woody vegetation and C_4 grasses at Konza, could be driven by phenologic responses to changing climate (Epstein et al. 1996; Emmerich 2007). Photosynthesis and carbon assimilation during dry, warm summers (Monson et al. 1986; Nippert et al. 2007; Niu et al. 2005) and mild, wet springs varies between species (Vermeire et al. 2009) and may be negated in cases of water limitation, even under an enhanced early growing season (Makela et al. 1996; Niu et al. 2005; Nippert et al. 2007). While treating photosynthetic capacity as a critical parameter in the model simplifies vegetation dynamics, this treatment allows the modeling framework to produce insight on how climate simulations and vegetation phenology impact ecological functioning at smaller spatial scales.

To explore how vegetation and environment interact across the growing season, we implement vegetation photosynthetic capacity in the model as water-use efficiency simulations (Fig. 2). The first employs water-use efficiency as a constant (WUE = 0.12) to isolate climate forcings. The second simulations vary WUE as out-of-phase sine functions at a daily scale to explore the timing of WUE maximum and minimum on carbon assimilation, calculated as:

$$WUE = WUE_0 \cdot \left[1 + \delta_{WUE} \cdot \sin\left(\omega_{WUE} \cdot h_{day} + \phi_{WUE}\right)\right] \tag{7}$$

where WUE_0 is the annual mean WUE, δ_{WUE} is the amplitude about WUE_0, ω_{WUE} is the frequency of the sinusoid [d^{-1}], h_{day} is the hydrologic day, and ϕ_{WUE} is the phase shift. These values are shown in Table 1. The third implementation of water-use efficiency is introduced below.

3.4 Konza Prairie vegetation

To assess the role of vegetation in the ecosystem response, we implement water-use efficiency for Konza Prairie species (one C_4 grass, *Andropogon gerardii*, and two C_3 forbs, *Salvia pitcherii* and *Ambrosia psilostachya*) and also for C_3 and C_4 vegetation classes. A difference at the vegetation class scale would suggest differences in photosynthetic pathways may be likely to influence species composition and grassland functioning at the landscape-scale. If effects are instead more realized for individual species, this may suggest future climate scenarios will drive change in grasslands in a more subtle way. This distinction is important for identifying the future research questions that are likely to provide insight on grassland responses.

Carbon assimilation and transpiration measurements for Konza vegetation were taken in-situ during the 2008 growing season on days 155, 168, 182, 196, and

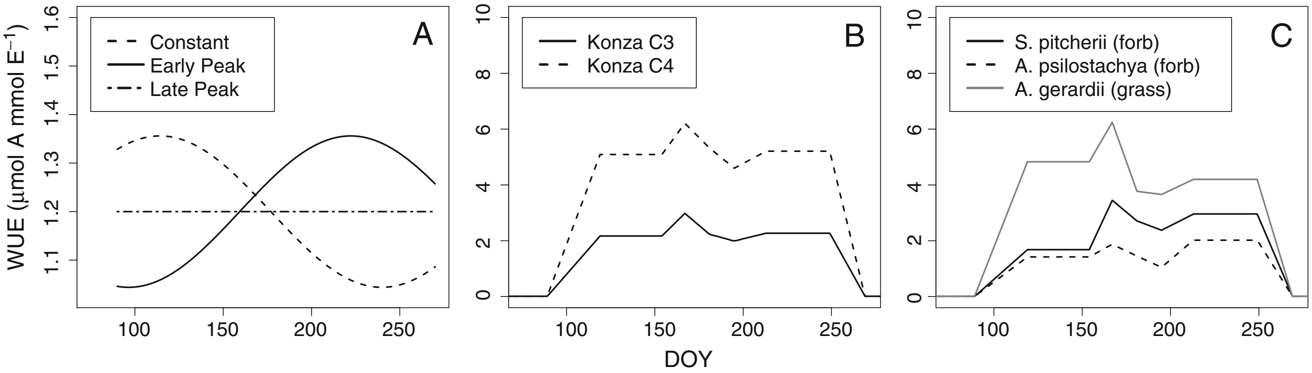

Fig. 2 Variation in photosynthetic capacity expressed as water-use efficiency for (Panel A) constant value and out-of-phase sine curves, (Panel B) Konza C_3 and C_4 vegetation, and (Panel C) *S. pitcherii*, *A. psilostachya*, and *A. gerardii* species (*right*). Reference growing season onset date is Julian day 90 and date of senescence is Julian day 270. Panels B and C have 30 day maturation periods beginning at start date and 20 day periods of decline leading to senescence

214. Over this period, 287 instantaneous measurements of photosynthesis [μmol m^{-2} s^{-1}] and transpiration [mmol m^{-2} s^{-1}] were made for C_3 vegetation and 180 were made for C_4. These include 24 measurements of photosynthesis and transpiration for *S. pitcherii*, 41 for *A. psilostachya*, and 40 for *A. gerardii*. To estimate daily values of water-use efficiency, linear change was assumed between measurements and was scaled at the beginning and end of each growing season (Fig. 2). This variability defines the interaction of climate forcings and vegetation at a fundamental level, helping to identify the temporal scales that underlie the ecosystem response to climate forcings.

4 Results

4.1 Changing forcing mechanisms

The effects of increased mean potential evaporation ($\overline{Ep}$), earlier growing season onset, and higher precipitation variation (fewer events of greater magnitude with the same annual mean) were analyzed for their effects on water-stress event frequency and also mass fluxes of water and carbon. Control simulations suggest water stress periods ($\theta \leq \theta_w$) of more than 20 days occur in approximately 2% of years at Konza. For Konza vegetation simulations, the implemented water stress

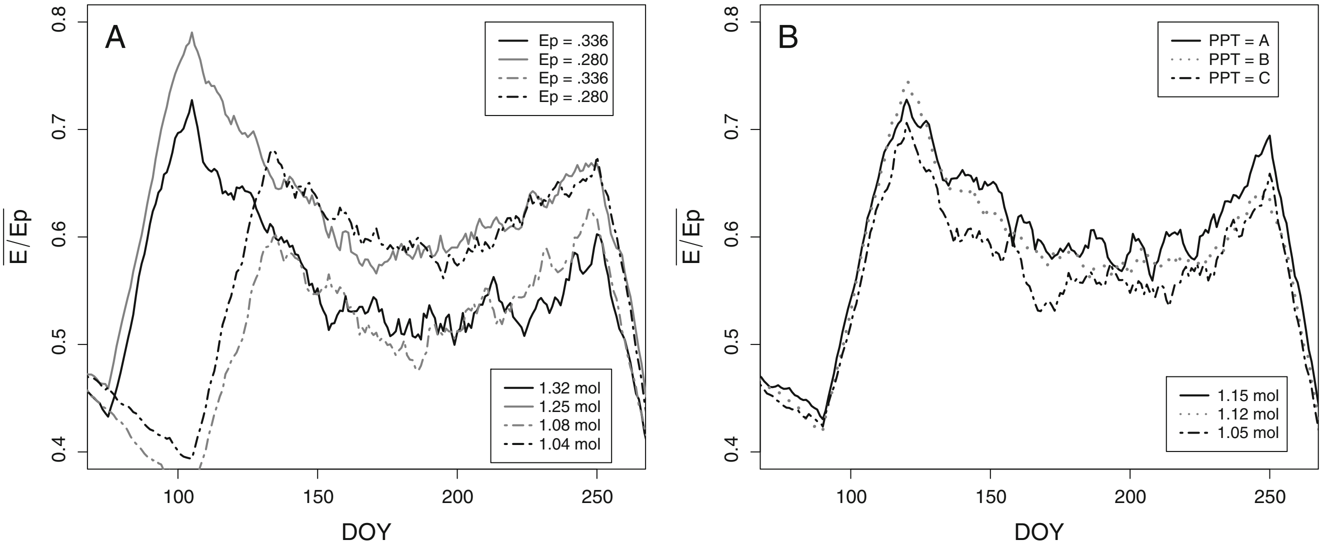

Fig. 3 (Panel A) Effects of potential evaporation and growing season onset simulations on evaporative fraction and total carbon assimilation (mol m^{-2} y^{-1}); (Panel B) precipitation timing and magnitude simulations on evaporative fraction and total carbon assimilation (mol m^{-2} y^{-1})

resilience of 15 days maintains full growing season in approximately 90–97% of simulated years.

Control simulations are shown in Fig. 3 and focus on the effects of forcing combinations on the seasonal dynamics of water and carbon fluxes. These show little deviation from the expected responses. Increased potential evaporation and precipitation variability both increase average daily spring water and carbon fluxes and reduce them in the drier summer through reduced soil moisture availability (panels A and B). This variability produces a negative relationship between annual carbon assimilation and precipitation variance, although it is difficult to assess the interaction between heightened potential evaporation and precipitation variability in individual years. Model simulations of increased precipitation variance and potential evaporation did not produce a notable increase in the number of water stress events in the A1B scenario (not shown), but did interact with potential evaporation to alter soil moisture availability and water fluxes (Fig. 3).

Earlier growing season onset reduces soil moisture availability later in the growing season, suggesting it could be important for scaling mass fluxes and influence the magnitude of water stress events (Fig. 4). These simulations produce change at a lower magnitude than is suggested by the results of Monson et al. (2005) for arid Colorado forests but are, however, a likely response in a less-arid climate. This suggests that sensitivity of water fluxes to forcings varies throughout the growing season and that mean values are an aggregate of small-scale variability between individual years or on even shorter timescales such as periods of altered soil moisture availability.

4.2 Seasonally-varying photosynthetic capacity

To assess how differences in the timing and amplitude of photosynthetic capacity influences the temporal distribution of carbon assimilation, we simplify water-use efficiency dynamics as out-of-phase sine curves with

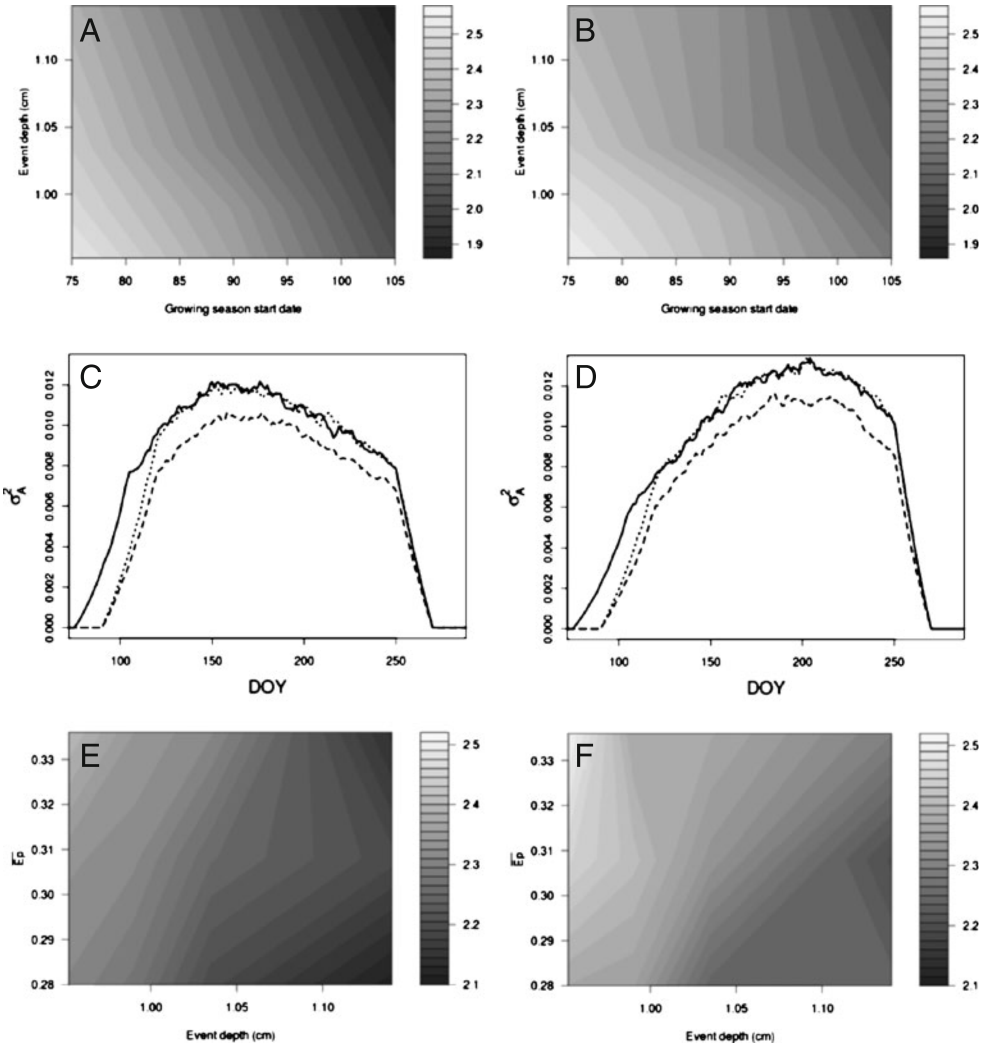

Fig. 4 (Panel A) Effects of changing precipitation timing and magnitude (denoted by event depth value) and growing season onset on carbon assimilation (mol m^{-2} y^{-1}) simulations of an early peak in photosynthetic capacity and (Panel B) late-peak simulations; (Panel C) precipitation on the temporal variance of carbon assimilation for early-peak simulations and (Panel D) late-peak simulations; (Panel E) precipitation timing and magnitude and mean evaporation on carbon assimilation (mol m^{-2} y^{-1}) for early-peak simulations and (Panel F) for late-peak simulations

early and late peaks (Fig. 2). We are also interested in how this variation in sensitivity to external climate forcings upscales to shape mean annual values, which may offer insight on the long term effects of the A1B scenario.

Results from the early and late peak water-use efficiency simulations are shown in Fig. 4. Early peak simulations (panels A and E) show a uniform response to precipitation variation, potential evaporation, and growing season onset. Late peak simulations show less-uniformity in annual mean carbon assimilation between drivers, but assimilate more carbon overall (panels B and F). This is illustrative of the type of control photosynthetic capacity may have on the sensitivity of carbon assimilation to soil moisture; early peak simulations incur less-variation in assimilation during the spring and during the summer, while late peak simulations show a higher mean annual carbon assimilation and variance due to summer correlation between potential evaporation and maximum water-use efficiency, which produces higher variability and magnitude in mass fluxes than in early-peak simulations. This suggests that variation in photosynthetic capacity and vegetation phenology may be a critical variable that controls the vegetation response to soil moisture availability and would play an important role in the vegetation response to an altered growing season, especially one with increased variability in soil moisture.

4.3 Konza Prairie vegetation

Exploring the vegetation response at Konza is the third part of this study and focuses on water-use efficiency simulations from measurements of photosynthesis for C_3 and C_4 vegetation. There was large variation in measurements of photosynthetic capacity within C_3 and C_4 classes and very little similarity in the simulated response, especially in years of lower and higher than average precipitation totals (not shown). We did not see results that suggest the pathway differences between C_3 and C_4 photosynthesis are a major driver of the ecosystem response for the A1B climate scenario.

The species-level is a better scale for assessing climate change impacts to mesic grasslands. We believe projections for future increases in potential evaporation and precipitation variability are more-likely to induce small shifts to critical habitat and species functioning than they are widespread ecosystem change. To explore this hypothesis, we employ water-use efficiency parameterizations for two C_3 forb (*S. pitcherii* and *A. psilostachya*) and one C_4 grass (*A. gerardii*) species at Konza to assess their responses to climate simulations (Fig. 2, Panel C). Three scenarios are assessed for three separate climate scenarios; control ($\overline{Ep} = 0.28$, precipitation scenario 'A'), climate change ($\overline{Ep} = 0.31$, precipitation scenario 'C'), and climate change with earlier growing season onset (day 75 instead of day 90).

Konza species show variation at the annual scale (Fig. 5), which illustrates the relationship between average annual precipitation and carbon assimilation. Annual assimilation is influenced by the climate influence on soil moisture, how the photosynthetic capacity of vegetation correlates to periods of soil moisture availability and potential evaporation, and how the seasonality of photosynthetic capacity and potential evaporation influences the feed back on soil moisture. These dynamics create highly variable carbon assimilation totals in individual years of simulation (illustrated by the scatter in Fig. 5) and in mean annual values.

S. pitcherii shows the most-varied response to the climate change scenarios (Fig. 5, panels A and B). This is, in part, due to the large difference in photosynthetic capacity for *S. pitcherii* between the early and late growing season, which increases the elasticity of annual carbon assimilation to variation in soil moisture variability. *S. pitcherii* shows the largest change in in slope of the carbon assimilation regression line for all simulations.

A. psilostachya has a less elastic response to climate change and earlier onset simulations than *S. pitcherii*, illustrated by a lower change in slope of the carbon assimilation line (Fig. 5, panels C and D). This is a product of the low variability in water-use efficiency displayed by *A. psilostachya*, which may create a response that is most similar to the control simulations in Fig. 3.

A. gerardii shows an intermediate response between *S. pitcherii* and *A. psilostachya* (Fig. 5, panels E and F). The slope of annual carbon to precipitation for *A. gerardii* is increased for both climate change simulations and shows a strong response to low and high extremes in annual precipitation. Total assimilation is increased in earlier growing season onset simulations, but is most-increased for years of higher than average precipitation. This is likely a product of *A. gerardii* having the highest amplitude between early and late season water-use efficiency maxima and minima (Fig. 2).

Calculated r^2 values show poor correlation between annual precipitation and carbon assimilation for all Konza species simulations, with the highest r^2 value of 0.33 for *A. psilostachya* control simulations. The variance between annual carbon assimilation values in Figure 5 also illustrates this. This poor correlation is an expected result of the varied influences on vegetation carbon assimilation and the likely importance of these interactions daily to seasonal temporal scales.

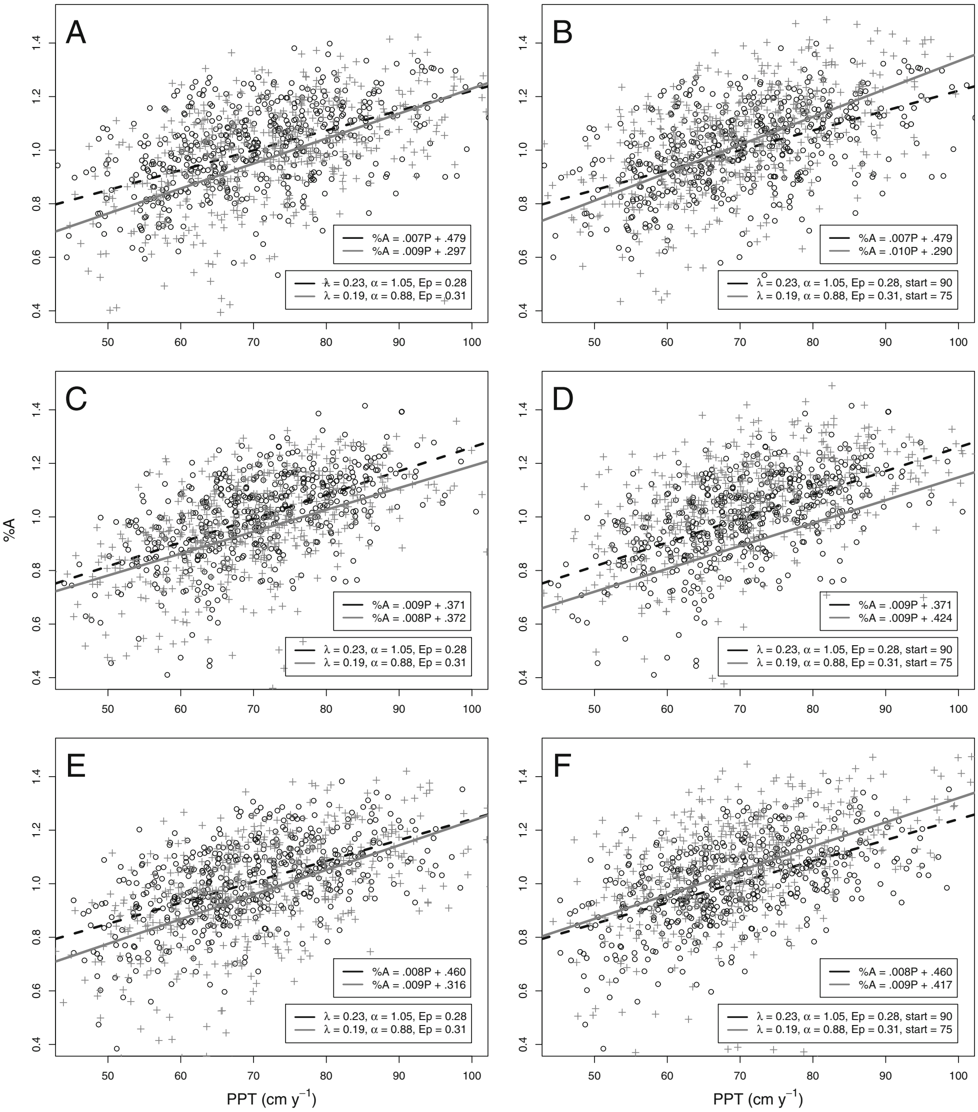

Fig. 5 Annual carbon assimilation divided by average annual carbon assimilation (mol m^{-2} y−1) vs. total annual precipitation (cm y^{-1}) for (Panel A) control and climate change simulations for *S. pitcherii* and with earlier growing season onset (Panel B); (Panels C and D) *A. psilostachya*; and (Panels E and F) *A. gerardii*. Trendlines for each simulation are shown, where P is annual precipitation and A is the carbon assimilation fraction

To explore the influence of the climate change and earlier onset conditions on assimilation through the growing season, we evaluate mean daily values for climate change and climate change with earlier onset simulations against the control scenario for *S. pitcherii*, *A. psilostachya*, and *A. gerardii* (Fig. 6). These illustrate the aggregate impact of the climate forcings, vegetation phenology, and feedbacks on how carbon is assimilated through the growing season at a scale that is better for identifying temporal periods of stability and change. Figure 6 illustrates a highly varied response between species and also a dissimilarity in response to early growing season onset conditions, which influences carbon assimilation later in the growing season. Altered partitioning of carbon fluxes and soil moisture feedbacks may be an important for realizing the implications of climate change, especially at shorter temporal scales.

5 Discussion

This study presents two foci for exploring climate change in mesic grasslands. The first is characterizing the aggregate effects of increased precipitation variability, increased potential evaporation, and earlier growing season onset as drivers of seasonal water and carbon flux dynamics at the Konza Prairie. The second introduces measurements of seasonally-varying photosynthetic capacity as a way to simulate vegetation dynamics and assess their impact on carbon assimilation within the climate scenarios. The purpose of this discussion

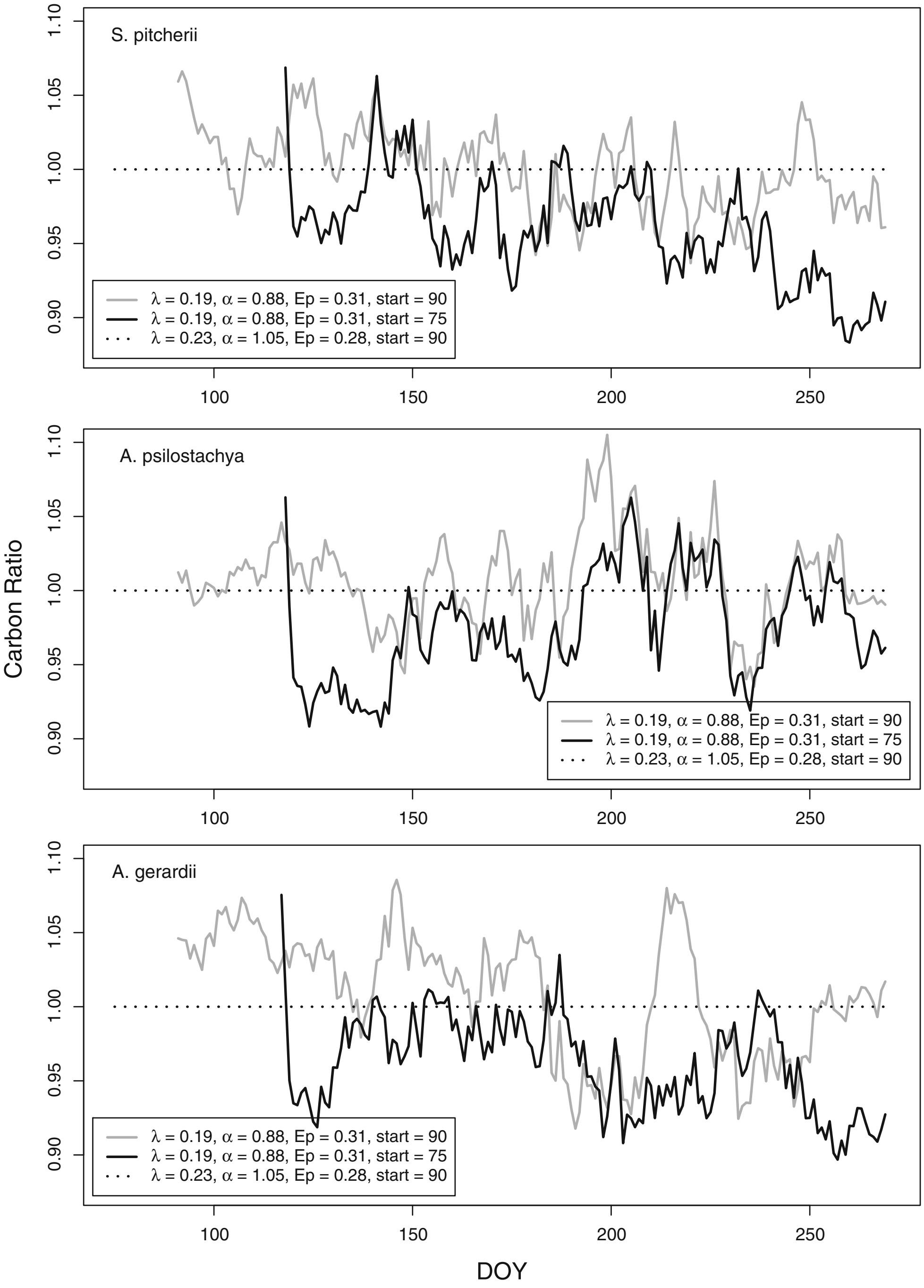

Fig. 6 Ratio of 500 years of simulated average daily carbon assimilation for climate change scenarios to that of a control scenario for Konza Prairie vegetation *S. pitcherii*, *A. psilostachya*, and *A. gerardii* species. Climate change drivers of decreased precipitation timing (λ), increased precipitation magnitude ($\frac{1}{\alpha}$), increased potential evaporation (Ep), and earlier growing season date of onset are evaluated, where a baseline of 1.0 corresponds to the control simulation. Earlier growing season onset dates that are earlier than the control scenario have been omitted from this figure

is to illustrate the direct findings of these simulations, explore the implications of altered flux dynamics, and identify opportunities for sharpening analysis of climate variability in semiarid ecosystems.

5.1 Climate forcing

Climate change simulations produce some expected responses of water and carbon fluxes to forcing variation and also illustrate unique components of ecological functioning and responses in the Konza Prairie. General effects to major relationships are understood: decreased precipitation event timing and increased event magnitude increases early-season soil moisture availability and reduces it later in the growing season, while potential evaporation increases mass fluxes and acts to intensify the feedback between water fluxes and soil moisture (Petrie and Brunsell 2011). This results in increased variability between early and late-season water fluxes (Fig. 3, panel B) that is amplified by increased potential evaporation (panel A). Earlier growing season onset also influences this feedback by reducing summer and late-season soil moisture availability, especially where increased precipitation variability increases early-season water fluxes.

Seasonally-varying photosynthetic capacity simulations assess the interaction of vegetation and environmental conditions in shaping water and carbon fluxes through the growing season. Of these interactions, the transpiration feedback on soil moisture and the timing and magnitude of water-use efficiency maxima and minima are critical for ecosystem carbon assimilation. The feedback relationship is illustrated in Fig. 4, panels E and F; carbon assimilation is partitioned differently between simulations of early and late-season peak in photosynthetic capacity. This suggests the optimal relationship between potential evaporation, soil moisture, and vegetation phenology varies by the temporal scale of analysis. Increased variability in the climate system can generally be assessed to have an amplified negative effect when paired with high seasonal variation in vegetation photosynthetic capacity or other governing variables.

Increased variability in soil moisture dynamics will influence the seasonal properties of vegetation carbon assimilation through increased variance at daily to annual scales. At the annual scale, Konza grasslands can initially expect greater annual average carbon assimilation at the price of more inter-annual and seasonal variability (Fig. 3). This benefit is negated as seasonal drydown conditions are amplified by climate forcings and is especially notable in cases where photosynthetic capacity was simulated with a late-season peak (Figs. 3 and 4). This suggests an intermediate response between that of temperate eastern and arid western U.S. of Richardson et al. (2009) and Monson et al. (2005) that will likely be scaled by long term climate forcings. Increased variability in precipitation timing and magnitude beyond the A1B scenario projections that further amplifies the intensity and frequency of extreme environmental conditions could also be realized (Julien and Sobrino 2009). We expect the general impact of climate change to be an intensification of beneficial and deleterious extremes of soil moisture availability, especially where influenced by a more elastic vegetation feedback.

5.2 Konza vegetation and climate change

Changing climate is likely to reshape ecological interactions in the Konza Prairie. Much of this response may be at the species-scale; Konza vegetation exhibits strong heterogeneity to climate simulations both between (Fig. 5) and within species (Fig. 6). Variability at the species scale in Fig. 6 exemplifies the possible dynamic created by the A1B scenario: carbon assimilation shows large temporal variation in response to changing drivers but average daily assimilation values are within 10% of control simulations. It also suggests a trend where species with differing vegetative controls on carbon assimilation, such as *S. pitcherii* and *A. gerardii* photosynthetic capacity simulations (Fig. 2), can produce both similar and differing trends in seasonal carbon assimilation depending on the climate scenario (Fig. 6). This is important for assessing the roles of microclimate, vegetation phenology and variation in flux dynamics in shaping longer-term changes in species composition and local ecology. The varied responses in this analysis suggest mesic grasslands are not likely to show a landscape-scale response to a moderate climate projection such as the A1B scenario. It is important, however, to remember these systems exist in a constant state of response to continuous and discrete external forcings. Change will instead be a product of increased ecosystem flux variability and the long-term response of smaller scale vegetation processes and interactions.

Due to observed heterogeneity in the species simulations, we expect the response of mesic grasslands to be most-pronounced in cases where additional variables, such as site characteristics or microclimate, induce a dominate control on ecosystem flux dynamics. Fire frequency has been and will remain a primary driver of native and invasive species composition at Konza and the surrounding region, but it may have a lessening impact on the spread of invasive woody species and the response of grasses as a more variable climate influences periods between discrete fire events. We also expect longer-term change in local ecology to respond at different timescales and with a good deal of inter-annual variability, similar to modeled vegetation carbon assimilation in Fig. 6. Disruption at these smaller scales may prove to be a critical driver of ecosystem functioning; the Konza Prairie maintains species diversity within specialized niches that are maintained by heterogeneity in ecosystem conditions (Knapp et al. 1998; Harpole and Tilman 2006). Climate change may produce conditions where small scale ecosystem functioning may alter critical relationships that ultimately influence the larger ecosystem, much in the same way fire suppression has altered species composition at Konza and promoted an increase in invasive woody species. How these small deviations influence vegetation optimality and competition may provide further insight on mesic grassland stability as climate change progresses.

Feedbacks from altered surface processes and energy flux partitioning may upscale to affect large-scale processes. Climatic variation, including the moderate simulations presented in this paper, has the effect of adjusting the partitioning of latent and sensible energy, which feeds back on climatology and may influence long-term climate and extreme events (Pielke 2001; Riley et al. 2009). Information theory and Maximum Entropy Production frameworks may also provide insight on how flux partitioning and biotic dynamics interact and feed back on the earth system, with possible impacts on the coupling between hydrology and entropy production and optimization of surface energy partitioning (Jaynes 1957; Cowan 2002; Kleidon 2009). How these conceptual frameworks such as these could identify pertinent issues shaping energy partitioning and climatic gradients could be an important component of planning for climate change impacts to the earth system.

6 Conclusions

Climate change will affect mesic grassland functioning as increased precipitation variance, increased potential evaporation, and earlier growing season onset induce greater variation in growing season soil moisture availability. Observed heterogeneity in the hydrologic and vegetation responses to the climate simulations suggests smaller-scale interactions are likely to define larger-scale responses in mesic grasslands and will vary as climate change becomes more pronounced. We expect these changes to be most-pronounced where environmental variables such as microclimate maintain community assemblages and ecosystem flux dynamics. These results suggest more focused studies of how the ecosystem interactions and feedbacks within small-scale systems could change in future climate scenarios and ultimately define larger scale responses.

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References

Angert A, Biraud S, Bonfils C, Henning C, Buermann W, Pinzon J, Tucker C, Fung I (2005) Drier summers cancel out the CO_2 uptake enhancement induced by warmer springs. PNAS 31(102):10,823–10,827

Betts R, Cox P, Lee S, Woodward F (1997) Contrasting physiological and structural vegetation feedbacks in climate change simulations. Nature 387:796–799

Briggs J, Knapp A, Blair J, Heisler J, Hoch G, Lett M, McCarron J (2005) An ecosystem in transition: causes and consequences of the conversion of mesic grassland to shrubland. Bioscience 55:243–254

Brunsell N, Gillies R (2003) Scale issues in land-atmosphere interactions: implications for remote sensing of the surface energy balance. Agric For Meterol 117(3–4):203–221. doi:10.1016/S0168-1923(03)00064-9

Brunsell N, Jones A, Jackson T, Feddema J (2010) Seasonal trends in air temperature and precipitation in ipcc ar4 gcm output for Kansas, USA: evaluation and implications. Int J Climatol 30:1178–1193. doi:10.1002/joc.1958

Claussen M, Brovkin V, Ganapolski A (2001) Biogeophysical versus biogeochemical feedbacks of large-scale land cover change. Geophys Res Lett 28(6):1011–1014

Collins S, Glenn S, Briggs J (2002) Effect of local and regional processes on plant species richness in tallgrass prairie. Oikos 99:571–579

Cowan I (2002) Fit, fitter, fittest; where does optimisation fit in? Silva Fenn 3(36):745–754

Daly E, Porporato A (2005) A review of soil moisture dynamics: from rainfall infiltration to ecosystem response. Environ Eng Sci 22(1):9–24

Daly E, Porporato A (2006) Impact of hydroclimatic fluctuations on the soil water balance. Water Resour Res 42:1–11

D'Odorico P, Ridolfi L, Porporato A, Rodriguez-Iturbe I (2000) Preferential states of seasonal soil moisture: the impact of climate fluctuations. Water Resour Res 36(8):2209–2219

Drake B, Gonzalez-Meler M, Long S (1997) More efficient plants: a consequence of rising atmospheric CO_2? Annu Rev Plant Physiol Plant Mol Biol 48:609–639

Emmerich W (2007) Ecosystem water use efficiency in a semiarid shrubland and grassland community. Rangeland Ecol Manag 60:464–470

Epstein H, Laurenloth W, Burke I, Coffin D (1996) Ecological responses of dominant grasses along two climactic gradients in the great plains of the united states. J Veg Sci 7:777–788

Fay P, Carlisle J, Knapp A, Blair J, Collins S (2000) Altering rainfall timing and quantity in a mesic grassland ecosystem: design and performance of rainfall manipulation shelters. Ecosystems 3:308–319

Fay PA, Kaufman DM, Nippert JB, Carlisle JD, Harper CW (2008) Changes in grassland ecosystem function due to extreme rainfall events: implications for responses to climate change. Glob Chang Biol 14(7):1600–1608. doi:10.1111/j.1365-2486.2008.01605.x

Geeske J, Chapin III F, Chiariello N, Thayer S, Field C (2001) Species-specific responses of plant communities to altered carbon and nutrient availability. Glob Chang Biol 7:435–450

Harpole W, Tilman D (2006) Non-neutral patterns of species abundance in grassland communities. Ecol Lett 9:15–23

Houghton J (2001) The science of global warming. Interdiscip Sci Rev 4(26):247–257

Ivanov VY, Bras RL, Vivoni ER (2008) Vegetation-hydrology dynamics in complex terrain of semiarid areas: 1. A mechanistic approach to modeling dynamic feedbacks. Water Resour Res 44(3). doi:10.1029/2006WR005588

Jaynes E (1957) Information theory and statistical mechanics. Phys Rev 106:620–630

Julien Y, Sobrino J (2009) Global land surface phenology trends from gimms database. Int J Remote Sens 13:3495–3513

Kleidon A (2009) Nonequilibrium thermodynamics and maximum entropy production in the earth system. Naturwissenschaften 96:653–677

Knapp A, Briggs J, Hartnett D, Collins S (eds) (1998) Grassland dynamics: long-term ecological research in tallgrass prairie. LTER

Koster R, Suarez M (1999) A simple framework for examining the interannual variability of land surface moisture fluxes. J Clim 12(7):1911–1917

Laio F, Porporato A, Ridolfi L, Rodriguez-Iturbe I (2001) Plants in water-controlled ecosystems: active role in hydrologic processes and response to water stress - II. Probabilistic soil moisture dynamics. Adv Water Resour 24(7): 707–723

Laio F, Porporato A, Ridolfi L, Rodriguez-Iturbe I (2002) On the seasonal dynamics of mean soil moisture. J Geophys Res–Atmospheres 107(D15). doi:10.1029/2001JD001252

Makela A, Berninger F, Hari P (1996) Optimal control of gas exchange during drought: theoretical analysis. Ann Bot 77(5):461–467

Milly P (1994) Climate, soil water storage, and average annual water balance. Water Resour Res 7(30):2143–2156

Monson R, Sackschewsky M, Williams III G (1986) Field measurements of photosynthesis, water-use efficiency, and growth in *Angropyron smithii* (C_3) and *Bouteloua gracilis* (C_4) in the colorado shortgrass steppe. Oecologia 68: 400–409

Monson R, Sparks J, Rosentiel T, Scott-Denton L, Huxman T, Harley P, Turnipseed A, Burns S, Backlund B, Hu J (2005) Climatic influences on net ecosystem CO_2 exchange during the transitions from wintertime carbon source to springtime carbon sink in a high-elevation, subalpine forest. Oecologia 146:130–147

Nippert J, Knapp A (2007) Soil water partitioning contributes to species coexistence in tallgrass prairie. Oikos 116:1017–1029

Nippert J, Fay P, Knapp A (2007) Photosynthetic traits in C_3 and C_4 grassland species in mesocosm and field environments. Environ Exp Bot 60:412–420

Nippert J, Fay P, Carlisle J, Knapp A, Smith M (2009) Ecophysiological responses of two dominant grasses to altered temperature and precipitation regimes. Acta Oecol 35:400–408

Niu S, Yuan Z, Zhang Y, Liu W, Zhang L, Huang J, Wan S (2005) Photosynthetic responses of C_3 and C_4 species to seasonal water variability and competition. J Exp Bot 421(56):2867–2876

Petrie M, Brunsell N (2011) The role of precipitation variability on the ecohydrology of grasslands. Ecohydrology p. doi:10.1002/eco.224

Pielke R (2001) Influence of the spatial distribution of vegetation and soils on the prediction of cumulus convective rainfall. Rev Geophys 39:151–177

Porporato A, Laio F, Ridolfi L, Rodriguez-Iturbe I (2001) Plants in water-controlled ecosystems: active role in hydrologic processes and response to water stress - III. Vegetation water stress. Adv Water Resour 24(7):725–744

Porporato A, Laio F, Ridolfi L, Caylor K, Rodriguez-Iturbe I (2003) Soil moisture and plant stress dynamics along the Kalahari precipitation gradient. J Geophys Res–Atmospheres 108(D3). doi:10.1029/2002JD002448

Porporato A, Daly E, Rodriguez-Iturbe I (2004) Soil water balance and ecosystem response to climate change. Am Nat 164(5):625–632

Richardson A, Hollinger D, Dail D, Lee J, Munger J, O'Keefe J (2009) Influence of spring phenology on seasonal and annual carbon balance in two contrasting new england forests. Tree Physiol 29:321–331

Ridolfi L, D'Odorico P, Porporato A, Rodriguez-Iturbe I (2000a) Duration and frequency of water stress in vegetation: an analytical model. Water Resour Res 36(8):2297–2307

Ridolfi L, D'Odorico P, Porporato A, Rodriguez-Iturbe I (2000b) Impact of climate variability on the vegetation water stress. J Geophys Res–Atmospheres 105(D14):18,013–18,025

Riley W, Biraud S, Torn M, Fischer M, Billesbach D, Berry J (2009) Regional co2 and latent heat surface fluxes in the southern great plains: measurements, modeling, and scaling. J Geophys Res 114

Rosenberg N, Epstein D, Wang D, Vail L, Srinivasan R, Arnold J (1999) Possible impacts of global warming on the hydrology of the Ogallala aquifer region. Clim Change 4(42):677–692

Suyker A, Shashi B, Burba G (2003) Internnual variability in net CO_2 exchange of a native tallgrass prairie. Glob Chang Biol 9:255–265

Teuling A, Uijlenhoet R, Hupet F, Troch P (2006a) Impact of plant water uptake strategy on soil moisture and evapotranspiration dynamics during drydown. Geophys Res Lett 33(3). doi:10.1029/2005GL025019

Teuling A, Seneviratne S, Williams C, Troch P (2006b) Observed timescales of evapotranspiration response to soil moisture. Geophys Res Lett 33:1–5

Vermeire L, Heitschmidt R, Rinella M (2009) Primary productivity and precipitation-use efficiency in mixed-grass prairie: a comparison of northern and southern US sites. Rangeland Ecol Manag 62:230–239

Vico G, Porporato A (2008) Modelling C_3 and C_4 photosynthesis under water-stressed conditions. Plant Soil 313:187–203

Williams Jr C, Vose R, Easterling D, Menne M (2006) United states historical climatology network daily temperature, precipitation, and snow data. Tech rep ornl/cdiac-118, ndp-070, carbon dioxide information analysis center, Oak Ridge National Laboratory, Oak Ridge, Tennessee

Woodhouse C, Overpeck J (1998) 2000 years of drought variability in the central United States. Bulletin of the American Meterological Society 12(79):2693–2714