AGU PUBLICATIONS
JGR
Journal of Geophysical Research: Biogeosciences

RESEARCH ARTICLE
10.1002/2015JG003205

Key Points:
- Carbon exchanges in eastern and western Great Plains grasslands differ
- Eastern and western grasslands differ in the timescales over which they respond to P
- C exchanges are likely to become more heterogeneous as a result of P change

Correspondence to:
M. D. Petrie,
mpetrie@usgs.gov

Citation:
Petrie, M. D., N. A. Brunsell, R. Vargas, S. L. Collins, L. B. Flanagan, N. P. Hanan, M. E. Litvak, and A. E. Suyker (2016), The sensitivity of carbon exchanges in Great Plains grasslands to precipitation variability, *J. Geophys. Res. Biogeosci.*, *121*, 280–294, doi:10.1002/2015JG003205.

Received 1 SEP 2015
Accepted 6 JAN 2016
Accepted article online 14 JAN 2016
Published online 2 FEB 2016

The sensitivity of carbon exchanges in Great Plains grasslands to precipitation variability

M. D. Petrie[1,2], N. A. Brunsell[3], R. Vargas[4], S. L. Collins[5], L. B. Flanagan[6], N. P. Hanan[7], M. E. Litvak[5], and A. E. Suyker[8]

[1]Department of Botany, University of Wyoming, Laramie, Wyoming, USA, [2]USGS Colorado Plateau Research Station, Flagstaff, Arizona, USA, [3]Department of Geography and Atmospheric Science, University of Kansas, Lawrence, Kansas, USA, [4]Department of Plant and Soil Sciences, University of Delaware, Newark, Delaware, USA, [5]Department of Biology, University of New Mexico, Albuquerque, New Mexico, USA, [6]Department of Biological Sciences, University of Lethbridge, Lethbridge, Alberta, Canada, [7]Geospatial Sciences Center of Excellence, SDSU, Brookings, South Dakota, USA, [8]School of Natural Resources, University of Nebraska, Lincoln, Nebraska, USA

Abstract In the Great Plains, grassland carbon dynamics differ across broad gradients of precipitation and temperature, yet finer-scale variation in these variables may also affect grassland processes. Despite the importance of grasslands, there is little information on how fine-scale relationships compare between them regionally. We compared grassland C exchanges, energy partitioning and precipitation variability in eight sites in the eastern and western Great Plains using eddy covariance and meteorological data. During our study, both eastern and western grasslands varied between an average net carbon sink and a net source. Eastern grasslands had a moderate vapor pressure deficit (VPD = 0.95 kPa) and high growing season gross primary productivity (GPP = 1010 ± 218 g C m^{-2} yr^{-1}). Western grasslands had a growing season with higher VPD (1.43 kPa) and lower GPP (360 ± 127 g C m^{-2} yr^{-1}). Western grasslands were sensitive to precipitation at daily timescales, whereas eastern grasslands were sensitive at monthly and seasonal timescales. Our results support the expectation that C exchanges in these grasslands differ as a result of varying precipitation regimes. Because eastern grasslands are less influenced by short-term variability in rainfall than western grasslands, the effects of precipitation change are likely to be more predictable in eastern grasslands because the timescales of variability that must be resolved are relatively longer. We postulate increasing regional heterogeneity in grassland C exchanges in the Great Plains in coming decades.

1. Introduction

The Great Plains of North America encompasses approximately 2.9 million km^2 in the central United States and Canada and is one of the most productive regions of rangeland globally [*Derner et al.*, 2006]. Precipitation and temperature gradients across the Great Plains produce a range of ecosystem types, with higher productivity, C$_3$-dominated grasslands in the north and east and lower productivity, C$_4$-dominated grasslands in the south and west [*Sala et al.*, 1988; *Tieszen et al.*, 1997; *Bachelet et al.*, 2001; *Derner et al.*, 2006]. Grasslands play a major role in the global C budget and in terrestrial C storage, sequestering approximately 0.5 Pg C yr^{-1} [*Scurlock and Hall*, 1998] and accounting for as much as 10% of aboveground and 10–30% of below-ground terrestrial carbon storage [*Olson et al.*, 1985; *Schlesinger*, 1997; *Scurlock and Hall*, 1998]. Globally, mesic and semiarid grasslands may have a large positive or negative effect on annual terrestrial carbon sequestration [*Poulter et al.*, 2014; *Ahlstrom et al.*, 2015], and C storage as vegetation biomass and soil organic matter may be as high as ∼0.3–0.9 kg C m^{-2} in the Great Plains [*Derner et al.*, 2006].

Because many ecosystem processes in grasslands are driven by precipitation, the ecological viability of Great Plains grasslands and the C sequestration services they provide may be impacted by global climate change [*Bachelet et al.*, 2001; *Ahlstrom et al.*, 2015]. Global Climate Model (GCM) projections for central and western North America call for increasing temperatures and change in total annual precipitation in the 21st century [*Brunsell et al.*, 2010; *Cook and Seager*, 2013; *IPCC*, 2013; *Cook et al.*, 2015], and significant warming and drying trends, as well as associated changes in land surface hydrology and vegetation phenology, have already been observed across the region [*Gan*, 1998; *Cutforth et al.*, 2004; *Julien and Sobrino*, 2009]. Even small changes in temperature and precipitation may alter grassland processes including carbon assimilation and nutrient cycling [*Fierer and Schimel*, 2002; *Niu et al.*, 2005; *Nippert et al.*, 2007; *McCulley et al.*, 2009;

Reichmann et al., 2013], yet the timescales over which grasslands respond most strongly to climate variability are difficult to determine. Therefore, it is important to characterize grasslands across the Great Plains by investigating the differing timescales over which they respond to climate variability.

There is growing scientific consensus on the importance of understanding how variability in temperature and precipitation regimes affects grassland ecosystem functioning, yet the majority of available information addresses different, often site-specific processes, limiting the generalizability of this information. For example, eastern Great Plains grasslands may often experience winter soil moisture recharge and a decoupling of photosynthesis from rainfall in spring, which promotes greater vegetation productivity [*Tieszen et al.*, 1997], and also higher productivity in an average rainfall year with more frequent, relatively small rainfall events [*Petrie and Brunsell*, 2012; *Byrne et al.*, 2013]. Western grasslands, which often have a longer spring growing season, may be water-limited and highly coupled to precipitation in all but the wettest years [*Wever et al.*, 2002; *Suyker et al.*, 2003; *Kurc and Small*, 2007; *Collins et al.*, 2014; *Petrie et al.*, 2015b] and may have higher productivity in an average rainfall year with less frequent events of greater magnitude [*Heisler-White et al.*, 2008; *Thomey et al.*, 2011]. This suggests that the timescales of grassland responses to precipitation may differ between eastern and western locations, especially in cases where soil moisture availability differs strongly between them. Yet semiarid grasslands may also upregulate photosynthesis in response to very small (~5 mm) rainfall events [*Sala and Lauenroth*, 1982; *Thomey et al.*, 2011; *Lauenroth and Bradford*, 2012; *Petrie et al.*, 2015a], and important processes such as nutrient mobilization may respond differently to precipitation patterns between wetter and drier sites [*McCulley et al.*, 2009]. The high degree of variability in grassland responses to precipitation illustrates the need to better characterize similarities and differences in grassland processes in the Great Plains, and to investigate the spatial and temporal scales over which these characterizations may be applied.

Arguably, the different scales over which climate and grassland processes interact and feed back on each other makes it difficult to attribute ongoing ecosystem processes to specific climate forcings [*Laio et al.*, 2002; *Austin et al.*, 2004; *Teuling et al.*, 2006; *Brunsell and Gillies*, 2003; *Brunsell and Wilson*, 2013]. For example, total annual precipitation may correlate to grassland vegetation productivity over long time periods and across large spatial areas [*Sala et al.*, 1988; *Epstein et al.*, 1996; *Tieszen et al.*, 1997], yet variability in precipitation forcings at shorter timescales and at local (<10 km^2) spatial scales has a large influence on grassland productivity as well [*Harper et al.*, 2005; *Vermeire et al.*, 2009; *Brunsell and Wilson*, 2013; *Byrne et al.*, 2013]. In these grasslands, ecosystem C dynamics are a valuable way to investigate how climate forcings influence grassland processes because they approximate the combined magnitude of ecosystem processes as a single variable [*Zhang et al.*, 2010, 2011]. Using eddy covariance and enhanced vegetation index (EVI) data, *Wagle et al.* [2015] found a high degree of coupling between ecosystem C fluxes, water fluxes, and climatic variables including precipitation and air temperature for grassland sites in the central and southwestern United States,and also that changes in these relationships may be closely related to ecosystem C uptake and loss during wet and dry years. Yet the way that these variables interact to shape grassland C dynamics at shorter timescales (daily to seasonally) is less understood. By understanding how and at what timescales precipitation influences grassland C dynamics, especially between grasslands that experience differing average temperature and moisture regimes, we can better understand longer-term regional patterns in C exchanges in these grasslands and provide information on how grasslands in different Great Plains ecoregions could respond to future climate change.

By exploring the sensitivity of grassland C exchanges in the eastern and western Great Plains to current variability in precipitation, we can elucidate how these grasslands could respond to future changes in precipitation amount and seasonality. This information would strengthen our understanding of how precipitation could interact with additional drivers of temperature and atmospheric CO_2 concentration, as change in both of these variables may also strongly influence the structure and function of grasslands in coming decades [*Cardon et al.*, 1995; *Collatz et al.*, 1998; *Buis et al.*, 2009; *Morgan et al.*, 2011]. We also investigate if grasslands across the Great Plains have similar responses to precipitation variability, especially in the context of differing temperature regimes. We explored these relationships using meteorological data and eddy covariance measurements of energy and C exchanges in eight Great Plains grasslands. Our main questions were as follows: (1) Are there generalizable differences in C exchanges and grassland sensitivity to precipitation between and within western and eastern Great Plains ecoregions? (2) To what degree do wet and dry periods influence carbon uptake and loss in these grasslands? (3) How does the timescale and magnitude of grassland responses to precipitation differ between the western and the eastern Great Plains? and (4) Do sites at the ecological boundaries of the Great Plains differ from eastern and western grasslands? We hypothesized that wetter, eastern grasslands would have higher rates of C exchange, higher average annual net C uptake, and lower

Table 1. Sites, Location, Data Range (Study Period), and Approximate Percentage of Values That Required Gapfilling

Abbreviation	Site Name	State or Province	Latitude (°N)	Longitude (°W)	Data Range	Gapfilled (%)
FER	Fermi Prairie	IL	41.84	88.24	2007–2011	22.8
FTP	Fort Peck	MT	48.31	105.10	2004–2007	28.4
KFS	KS Field Station	KS	39.06	95.19	Jun 2007–2011	19.8
KON	Konza Prairie	KS	39.08	96.56	2007–2011	17.4
LTH	Lethbridge	AB	49.71	112.94	2006–2007; 2010–2011	5.6
SEV	Sevilleta	NM	34.36	106.70	2007–2011	23.9
SGS	Shortgrass Steppe	CO	40.83	104.72	Nov 2004 to May 2007	34.9
SHD	Schidler Prairie	OK	36.93	96.68	Sep 1997 to Apr 2000	14.8

normalized variation in C exchanges in response to precipitation variability compared to drier western grasslands. In contrast, drier western grasslands would have lower rates of C exchange, lower net C uptake or C loss, and higher normalized variation in C exchanges in response to precipitation variability. Our primary goal was to compare responses by eastern and western Great Plains grasslands to precipitation variability. In doing so, we evaluated whether or not there were similar patterns of ecosystem sensitivity to precipitation between these grasslands and explored the potential for general characterizations of ecosystem responses to climate to be applied across the Great Plains.

2. Site Description

The Great Plains region is dominated by continental air masses and contains a precipitation gradient from higher annual precipitation in the east to lower annual precipitation in the west (~1200 mm yr^{-1} compared to ~300 mm) [*Sala et al.*, 1988; *Tieszen et al.*, 1997; *Peters et al.*, 2008]. Annual temperature in the region ranges from ~3 to 22°C, and temperature generally increases from north to south [*Peters et al.*, 2008]. Higher elevations in the western Great Plains amplify differences in temperature between western (high elevation; ~1500 m) and eastern (low elevation; ~500 m) locations [*United States Department of Agriculture*, 2013]. Soils in the west tend to be sandy and aridic, with a low (<1000 mm) active depth, and eastern soils tend to be clayey and mollic, with a high active depth (>1000 mm) and higher organic matter content [*United States Department of Agriculture*, 2013]. Vegetation in the eastern Great Plains is dominated by C_3 and C_4 herbaceous and woody species and has higher annual net primary productivity than western Great Plains grasslands, which often have a higher proportion of C_4 grass species [*Sala et al.*, 1988; *Epstein et al.*, 1996; *Tieszen et al.*, 1997].

Grasslands across the Great Plains experience high annual and seasonal variation in temperature and precipitation. In addition to climatic events that are driven by precipitation (such as drought) and temperature (such as extreme freezing periods), Great Plains grasslands experience disturbances including desertification

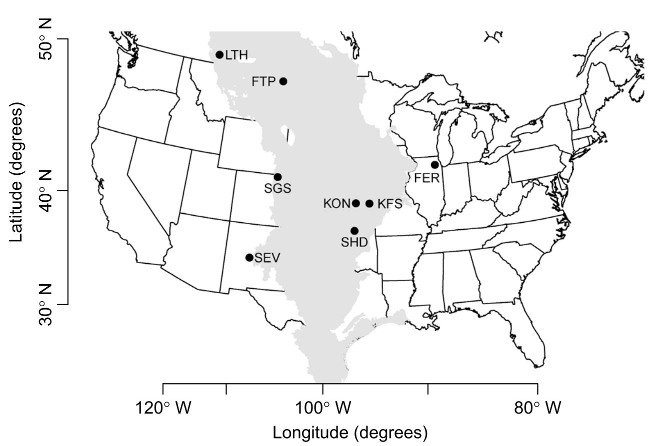

Figure 1. Map of grassland sites in the United States and Canada. The U.S. EPA Great Plains ecoregion is shown in grey.

Table 2. Environmental Characteristics of Each Site[a]

Site	$\bar{P}$ 1980–2012 (mm)	$\bar{P}$ (mm)	$\bar{T}$ (°C)	λ (events d^{-1})	α (mm event^{-1})	EF ($\frac{LE}{LE+H}$)	Classification (Study Period)
FER	913 ± 150	1050	8.6	0.377	7.75	0.70 ± 0.25	Normal
FTP	329 ± 78	422	5.1	0.251	4.61	0.43 ± 0.16	Wetter
KFS	1015 ± 227	978	14.2	0.176	12.80	0.62 ± 0.17	Normal
KON	880 ± 190	792	14.1	0.254	8.58	0.58 ± 0.23	Normal
LTH	385 ± 106	412	6.3	0.364	2.45	0.46 ± 0.26	Normal
SEV	277 ± 75	213	13.2	0.147	3.95	0.25 ± 0.09	Drier
SGS	387 ± 87	306	8.5	0.206	3.53	0.55 ± 0.19	Drier
SHD	1040 ± 244	1082	15.7	0.269	10.40	0.57 ± 0.23	Normal

[a]Classification refers to the overall wetness or dryness of the study period compared to the 1980–2012 average. *P* and *T* data during the study period are from Ameriflux, whereas 1980–2012 data are from the United States Historical Climatology Network.

[*Schlesinger et al.*, 1990; *Reynolds et al.*, 2007; *D'Odorico et al.*, 2013], episodic fire [*Buis et al.*, 2009; *Vargas et al.*, 2012; *Koerner and Collins*, 2014], and ecological state transitions of one vegetation type to another [*Knapp et al.*, 2008; *Jackson et al.*, 2002; *D'Odorico et al.*, 2012; *Ratajczak et al.*, 2012], all of which may fundamentally and irreversibly alter the way these grasslands function. Because changes in ecosystem functioning are often influenced by precipitation and temperature variability, understanding the way that existing grasslands respond to these variables may help predict how climate variability may drive future ecological disturbances in the Great Plains.

In this study we compared and contrasted grasslands in the eastern and western Great Plains (Table 1 and Figure 1). Our analysis included eight grassland sites: three sites in the east (KFS, KON, and SHD; average precipitation (P) = 978 mm; average air temperature (T_a) = 14.7°C), three sites in the west (FTP, LTH, and SGS; average P = 367 mm; average T_a = 6.6°C), and two ecological boundary sites: one in a northeastern location (FER; average P = 913 mm; average T_a = 8.6°C) and one in a southwestern location (SEV; average P = 277 mm; average T_a = 13.2°C) (Figure 1 and Tables 1 and 2). These ecological boundary sites are located just outside the geographic boundary of the Great Plains ecoregion. During our study, grassland sites received differing amounts of precipitation from their 1980–2012 long-term mean. The eastern (KFS, KON, and SHD) grasslands all had close to normal average precipitation, the western grasslands were wetter (FTP), drier (SGS) and normal (LTH), and outlying sites were normal (FER) and drier (SEV) than average (Table 2).

3. Methods

We compiled precipitation data from 1980 to 2012 for each site using United States Historical Climatology Network daily data, using data from stations within 0.75°latitude and longitude of each site [*Williams et al.*, 2006]. Daily precipitation and temperature data were obtained from the Ameriflux data for each site except for KFS and LTH. KFS precipitation data were obtained from a nearby precipitation sensor (<1 km) maintained by the Kansas Biological Survey (http://biosurvey.ku.edu/), and LTH precipitation and temperature data were obtained from an Environment Canada, World Meteorological Organization sensor at the Lethbridge, AB airport (http://climate.weather.gc.ca/). To capture the average length of the growing season at each site, we used daily GPP to estimate growing season onset and vegetation senescence, where onset was the first day of 10 consecutive days where GPP was greater than the average daily GPP in winter (December–February) plus two standard deviations of the winter mean (i.e., $> \bar{x} + 2\sigma_{\bar{x}}$). We defined senescence as the first day of 10 consecutive days in fall or winter where GPP was lesser than the average daily GPP in winter (December–February) plus two standard deviations of the winter mean (i.e., $< \bar{x} + 2\sigma_{\bar{x}}$). This basic threshold technique is sensitive to the abrupt changes in GPP that occur in grassland systems, and *Petrie et al.* [2015b] previously used a similar technique to define grassland and shrubland growing season length. We report the mean and standard deviation of all values ($\bar{x} \pm \sigma_{\bar{x}}$). We used the R project statistical computing software [*R Development Core Team*, 2011] to produce all figures.

We compared grasslands using 30 min eddy covariance data from the AmeriFlux network (FER, FTP, KFS, KON, SEV, and SHD; http://ameriflux.lbl.gov/) or directly from site investigators (LTH and SGS). Because these sites

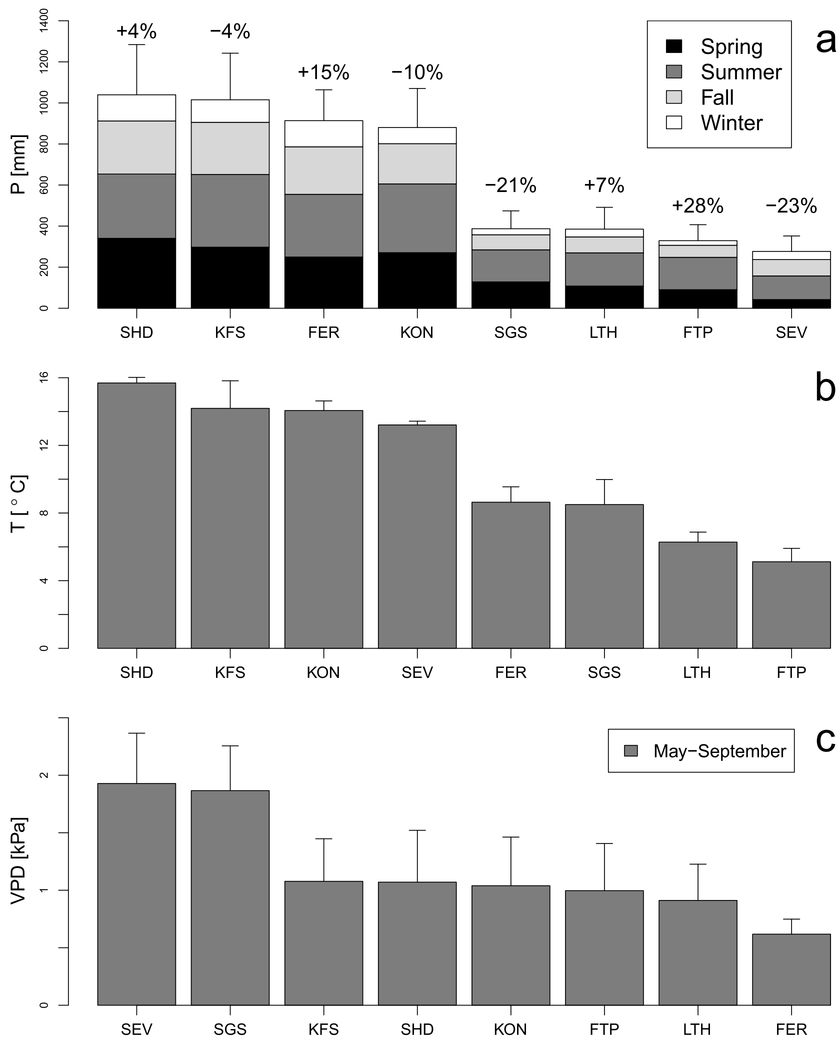

Figure 2. (a) Seasonal average total precipitation (mm) from 1980 to 2012, (b) mean annual air temperature (*T*: °C; 1–3 m height) during the study period, and (c) mean daily vapor pressure deficit (VPD: kPa) from May to September for each site. The percentage value corresponds to lower or higher annual precipitation during each site's study period compared to the 1980–2012 average.

were instrumented differently, we limited our analysis to available variables. Data availability at each site ranged from 2.5 to 5 years (Table 1), and we used gapfilled data provided by site investigators in cases where site investigators felt their methodology was preferable to that of the following gapfilling procedure. For FER, FTP, KFS, KON, SHD, and SGS, we gapfilled net ecosystem exchange (NEE), latent and sensible heat fluxes, vapor pressure deficit and air temperature, and estimated ecosystem respiration (RE) using the Max Planck Institute (Open MPI) procedure [*Falge et al.*, 2001; *Reichstein et al.*, 2005] (http://www.bgc-jena.mpg.de/~MDIwork/eddyproc/index.php). We calculated gross primary production (GPP) as NEE + RE. Site managers for SEV and LTH preferred a different gapfilling and partitioning methodology, which produces better partitioning results at their sites. Meteorological and C flux data at SEV were gapfilled using the methods described in *Reichstein et al.* [2005], which uses a similar methodology to the Open MPI procedure, and the C flux at SEV was partitioned into GPP and RE using the methodology described by *Lasslop et al.* [2010]. LTH data were provided by L.B. Flanagan and gapfilled and partitioned using the Fluxnet-Canada Research Network moving-window methodology, outlined in *Barr et al.* [2004]. Thus, the uncertainty in gapfilled C exchanges differs between LTH, SEV, and the other grassland sites, due to the gapfilling and partitioning methods used. Yet these gapfilled data also capture the most accurate flux estimates for SEV and LTH. Across all sites, approximately 21 ± 9% of 30 min measurements were gapfilled (Table 1). For SGS and FTP, we conducted an additional filtering of NEE to remove spikes prior to the gapfilling and partitioning process.

Table 3. Carbon Exchanges and Growing Season Length at the Grassland Sites[a]

Class	Sites	$\overline{GPP}$	$\overline{RE}$ (g C m^{-2} yr^{-1})	$\overline{NEE}$	Growing Season Length (DOY)	GPP (%) Growing Season	RE (%) Growing Season
Eastern	KON	1407.3	1472.6	65.3	122–295	97	81
Eastern	KFS	906.0	824.1	−81.9	103–319	82	85
Eastern	SHD	1209.7	1179.3	−30.4	108–307	100	87
Northeastern	FER	1170.0	968.0	−202.0	96–308	98	87
Western	FTP	288.7	429.6	140.9	108–247	74	64
Western	LTH	215.6	185.4	−30.2	99–260	95	61
Western	SGS	636.8	622.9	−13.9	82–299	95	71
Southwestern	SEV	171.0	217.0	46.0	92–295	82	76

[a] $\overline{GPP}$, $\overline{RE}$, and $\overline{NEE}$ are mean annual values. Growing season GPP and RE are percentages of annual GPP and RE that occurred during each site's active growing season.

4. Results

The grasslands in our study experienced high variation in annual precipitation compared to their average values from 1980 to 2012 (Table 2). Thus, our study investigates the functioning of these grasslands in the context of year to year variability in precipitation, which often deviates from mean annual values. The eastern grassland sites (SHD, KFS, KON, and FER) received higher annual precipitation compared to the four western sites (SGS, FTP, LTH, and SEV; Figure 2a). The four southern and lower elevation grasslands (SHD, KFS, KON, and SEV) were warmer on average (14.3°C) than the four northern and higher elevation grasslands (7.1°C; SGS, FTP, LTH, and FER; Figure 2b). SEV was the driest and fourth warmest site, and FER was the second wettest and fourth coolest (Table 2). From May to September, vapor pressure deficit (VPD) was highest at SGS (1.93 kPa) and SEV (1.87 kPa), lowest at FER (0.62 kPa), and similar at the other sites (1.02 ± 0.07 kPa on average; Figure 2c).

Carbon exchanges differed between eastern and western grasslands. Eastern grasslands had higher average annual GPP and higher percentage of annual GPP that occurred from May to September compared to western grasslands (Table 3), and eastern grasslands also had higher average annual RE and a higher percentage of annual RE that occurred from May to September (Table 3). Annually, both eastern and western grasslands varied between an average net carbon sink and a net source, and western grasslands (FTP, LTH, and SGS) had annual C dynamics that were slightly more variable compared to those of eastern grasslands (KON, KFS, and SHD; Table 3). In contrast to other regional grasslands, FER had 0.3% lower GPP and 17% lower RE compared to the average for eastern grasslands, yet had 1347% greater C uptake. SEV had 55% lower GPP than the average GPP of western grasslands and was a net C source (Figure 3 and Table 3). Every grassland site was a net source of C from October to April, yet only FTP (+95 g C m^{-2}) and SEV (+16 g C m^{-2}) were a source of C from May to September on average (Figure 3c).

As an illustration of the pattern of C uptake during the growing season, daily GPP was higher in eastern grasslands (5.7 ± 1.8 g C m^{-2} d^{-1}; FER, KFS, KON, and SHD) compared to western grasslands (1.6 ± 0.9 g C m^{-2} d^{-1}; FTP, LTH, SEV, and SGS; Figure 4). Compared to the 1:1 line of cumulative daily GPP, western grasslands (FTP, LTH, SEV, and SGS) had lower seasonality in GPP throughout the year (76 ± 7% similarity to the 1:1 line) compared to eastern grasslands, which had higher seasonality (FER, KFS, KON, and SHD; 70 ± 3% similarity to 1:1) (Figure 4). Both eastern and western grasslands experienced growing season onset and vegetation senescence on similar dates (DOY (day of year) ~100 and DOY ~300, respectively; Table 3), with the exception of the northernmost grasslands, LTH and FTP, which experienced vegetation senescence on DOY ~254 (Table 3). Thus, the active growing season was ~45–50 days shorter at LTH and FTP compared to that of other grasslands (Figure 4).

The relationship between seasonal evaporative fraction $\left[\mathrm{EF}:\frac{\mathrm{LE}}{H+\mathrm{LE}}\right]$, the ratio of latent energy partitioning of available energy, and daily average NEE showed that the majority of C uptake in all grasslands occurred during the active growing season and on days with relatively high EF (>~0.7; Figure 5). Generally, eastern grasslands showed a prominent difference between negative NEE during the growing season and positive NEE during the rest of the year, and KON (R^2 = 0.66), SHD (R^2 = 0.47), FER (R^2 = 0.26), and LTH (R^2 = 0.52) showed a strong negative correlation between daily EF and NEE during the growing season (Figure 5). KFS and SGS had

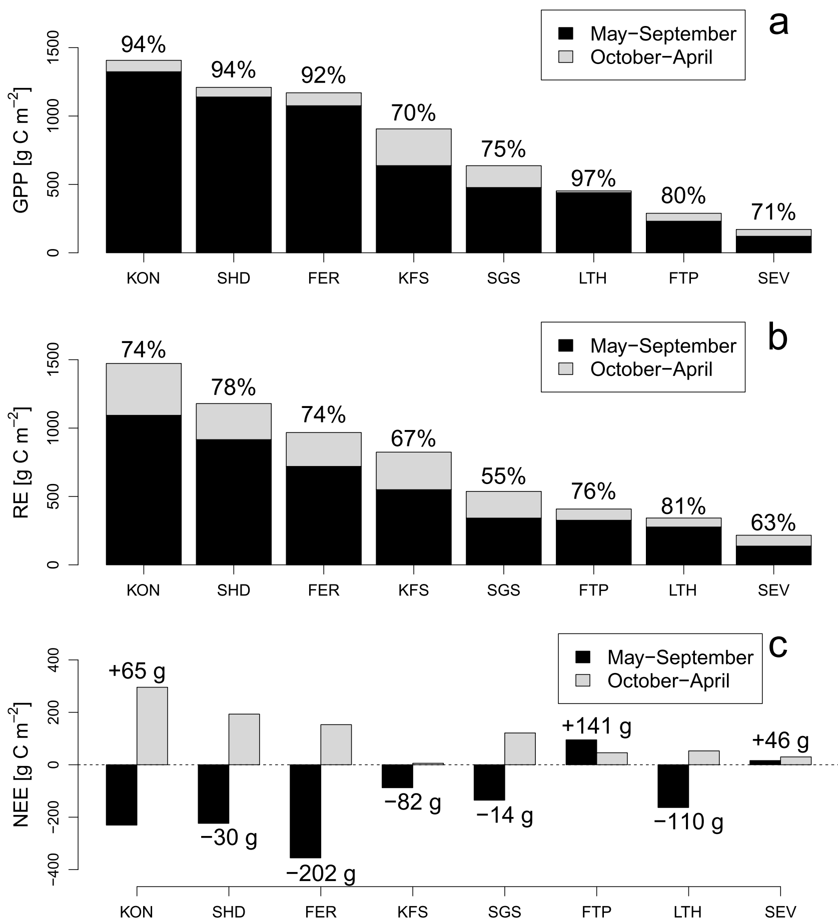

Figure 3. (a) Mean annual gross primary production (GPP: g C m^{-2} yr^{-1}), (b) ecosystem respiration (RE), and (c) net ecosystem exchange (NEE). For GPP and RE, the contribution of June–September fluxes to annual averages is shown as a percentage, and the total average C sink or source (as NEE) is shown in Figure 3c.

significant but slightly lower correlations between NEE and EF (Figure 5). Average daily EF was 0.62 at eastern sites compared to 0.43 at western sites, and FER had the highest daily average EF of 0.70 (Table 2).

Based on the slope of the regression line, eastern and western grasslands had differing sensitivity of monthly ecosystem rain use efficiency $\left[\mathrm{RUE}: \frac{\mathrm{GPP}}{P}\right]$ to monthly total precipitation and the monthly precipitation anomaly $\left[\frac{P-\bar{x}}{\sigma^2}\right]$ (Figure 6). During the growing season, only eastern grasslands showed correlations between RUE and monthly P and P anomaly (Figure 6), which suggests that western grasslands often do not respond to precipitation at monthly timescales, whereas eastern grasslands do respond at monthly timescales. Conversely, at daily timescales, both western and eastern grasslands showed similar normalized increases in GPP after isolated rainfall pulses occurred (+6.3% in western grasslands, +7.1% in eastern; Figure 7), although western grasslands were seemingly more sensitive due to the smaller pulses that they experienced (5.3 ± 0.5 mm versus 13.3 ± 3.0 mm). For both eastern and western grasslands, these isolated rainfall pulses constituted only a small proportion of total annual rainfall. Of all grasslands, only FTP, SEV, and SHD showed a maximum increase in GPP of >10% after a pulse event (+12%, +43%, and +15%, respectively; Figure 7). The response of RE to precipitation pulses was highly variable, which suggests that the efflux of C is controlled by different processes and/or at different timescales among these grasslands (Figure 7).

5. Discussion

5.1. The Eastern and Western Great Plains

We used eddy covariance data to characterize differences in C exchange dynamics between eastern and western Great Plains grasslands and to investigate how these dynamics were influenced by precipitation

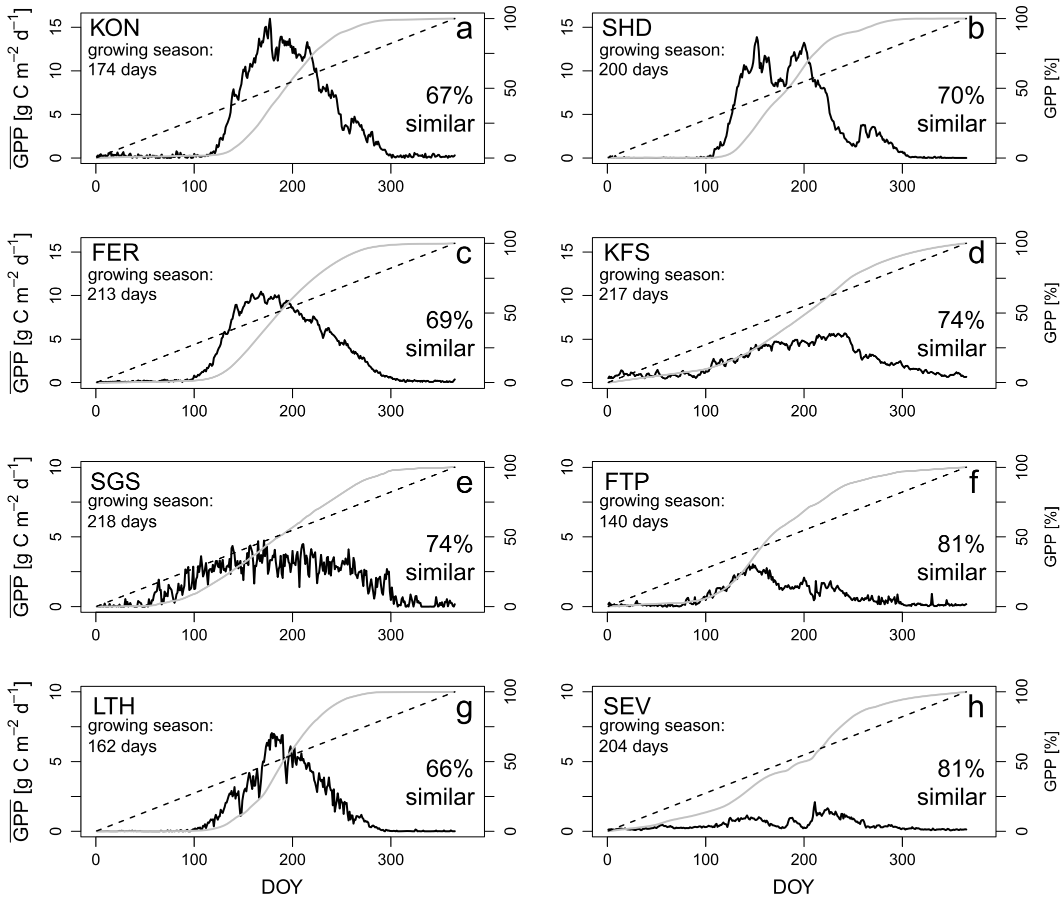

Figure 4. Mean daily gross primary production (GPP: g C m^{-2} d^{-1}) illustrating variation in within-year GPP variability. The length of the average growing season is shown for each site in days. Cumulative GPP (%) is also compared to the 1:1 line to evaluate high seasonality in GPP (low % similarity to 1:1) and low seasonality in GPP (high %). The *y* axis scale differs between Figures 4a–4d and 4e–4h.

variability. The Great Plains region may often be an annual net C sink [*Zhang et al.*, 2011], yet there is high variability in local C exchanges. Generally, eastern grasslands have greater productivity and C storage than western grasslands as a result of higher precipitation [*Derner et al.*, 2006; *Zhang et al.*, 2011]. Our results support prior studies demonstrating that eastern Great Plains grasslands have higher net primary production compared to western grasslands [*Sala et al.*, 1988; *Derner et al.*, 2006; *Zhang et al.*, 2011] and, over this time period of flux measurements, eastern grasslands were a net C sink on average (Table 3). Yet we found eastern and western grasslands to be a net sink in wet years and a net source in others, and many grasslands in this region remain C neutral on the order of years to decades [*Ham and Knapp*, 1998; *Dugas et al.*, 1999; *Sims and Bradford*, 2001; *Suyker et al.*, 2003; *Flanagan et al.*, 2002; *Zhang et al.*, 2010, 2011; *Petrie et al.*, 2015b]. Indeed, *Frank and Dugas* [2001] found that productivity in northern and southern Great Plains grasslands may actually be similar under the same annual precipitation forcing. Therefore, fluctuations in precipitation around the annual means are likely the dominant control on C exchanges throughout the Great Plains, not just in the more arid west.

The Great Plains region will likely become much more arid in the 21st century [*Cook et al.*, 2015], and one way to sharpen predictions of future grassland functioning in this region is to better understand how these grasslands function under current, less arid, climate conditions. During our study, eastern grasslands (FER, KFS, KON, and SHD) experienced different total annual precipitation, GPP, RE, and NEE (Table 2, Figure 3), yet they had similar patterns of cumulative GPP and NEE during summer (Figures 4 and 5) and displayed similar sensitivities to monthly precipitation (Figure 6). Eastern grasslands exhibited a strong pattern of greater C uptake when moisture was available (Figure 5) and were all responsive to rainfall at monthly timescales (Figure 6). We postulate that moderate climate change is likely to alter the functioning of eastern grasslands

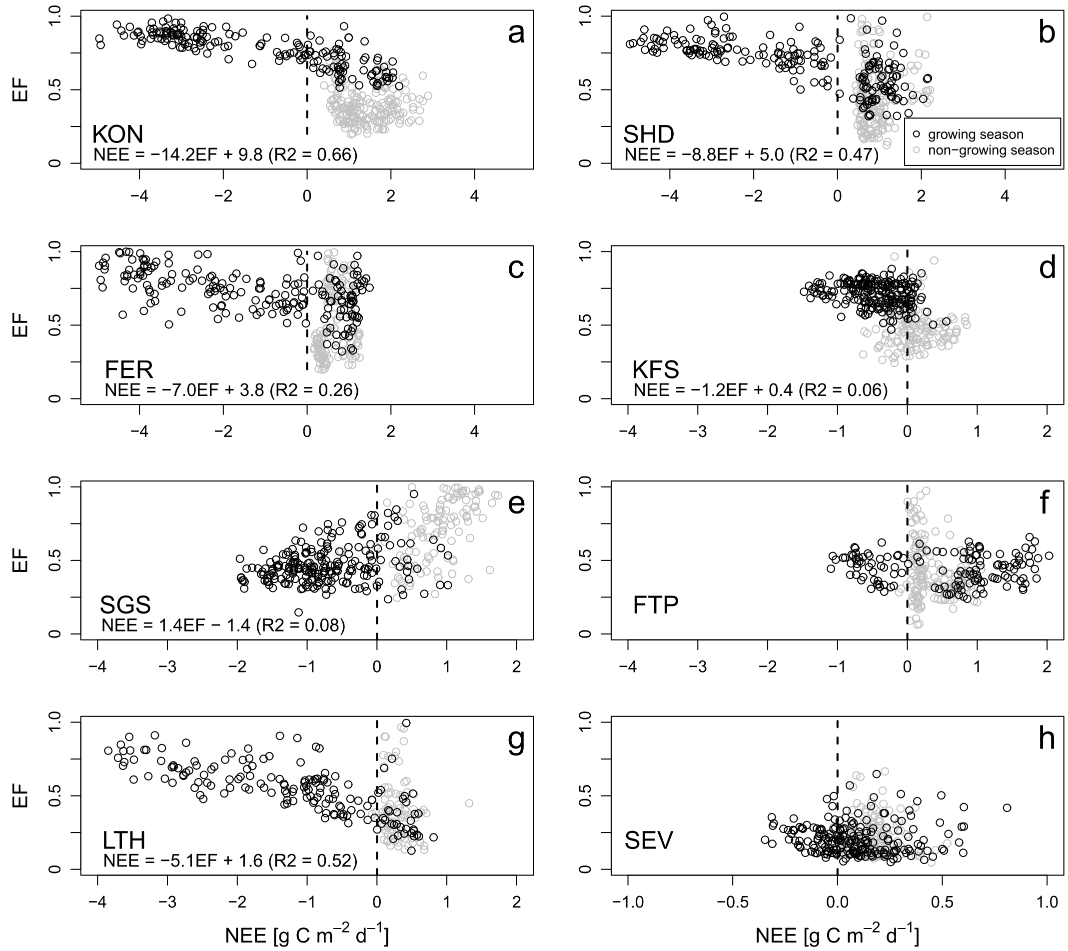

Figure 5. Relationship between daily mean net ecosystem exchange (NEE: g C m^{-2} d^{-1}) and daily mean evaporative fraction (EF: $\frac{LE}{H+LE}$). Points are divided between those days occurring within and outside each site's active growing season. Regression equations correspond to values during each site's active growing season. The R^2 statistic is provided in parenthesis, and all values are significant at $p < 0.05$. The x axis scale differs between panels.

in ways that are already observed under current variability in precipitation, and the timescales at which these grasslands respond to precipitation (monthly to annual) could mean that climate change predictions for the eastern Great Plains may be applied at these relatively coarse temporal resolutions.

Conversely, western grasslands were not sensitive to precipitation at monthly timescales (Figure 6), did not always have strong responses to pulses of rainfall (Figure 7), and had greater normalized variability in annual C exchange dynamics compared to eastern grasslands (Table 3). Precipitation change in the Great Plains is predicted to impact western grasslands to a greater degree than eastern grasslands [*Zhang et al.*, 2011], and our results suggest that one reason for this is the shorter and perhaps less uniform timescales at which these grasslands respond to precipitation. For example, *Williams et al.* [2009] found that semiarid grasslands in southern Africa displayed a lagged response of photosynthesis (GPP) to precipitation events, such that the more rapid response of RE to these events resulted in a pulse of C efflux that occurred prior to C uptake. Among western grasslands, only FTP and SEV experienced a characteristic pulse response of GPP to isolated precipitation events, and only SEV displayed characteristic pulse responses of both GPP and RE (Figure 7). *Williams et al.* [2009] reported that varying levels of prior and incident moisture availability altered the timing of GPP pulses, and we hypothesize that the western grasslands of our study are not likely to exhibit similar responses to precipitation change because existing precipitation patterns already differ between them (Figure 2a), and because even a slight deviation in local precipitation may result in drastically lower vegetation productivity in these systems [*Fay et al.*, 2008; *Heisler-White et al.*, 2009; *Thomey et al.*, 2011]. That is, the size, frequency, and seasonality of rain events must be considered along with total amounts of precipitation in investigations of

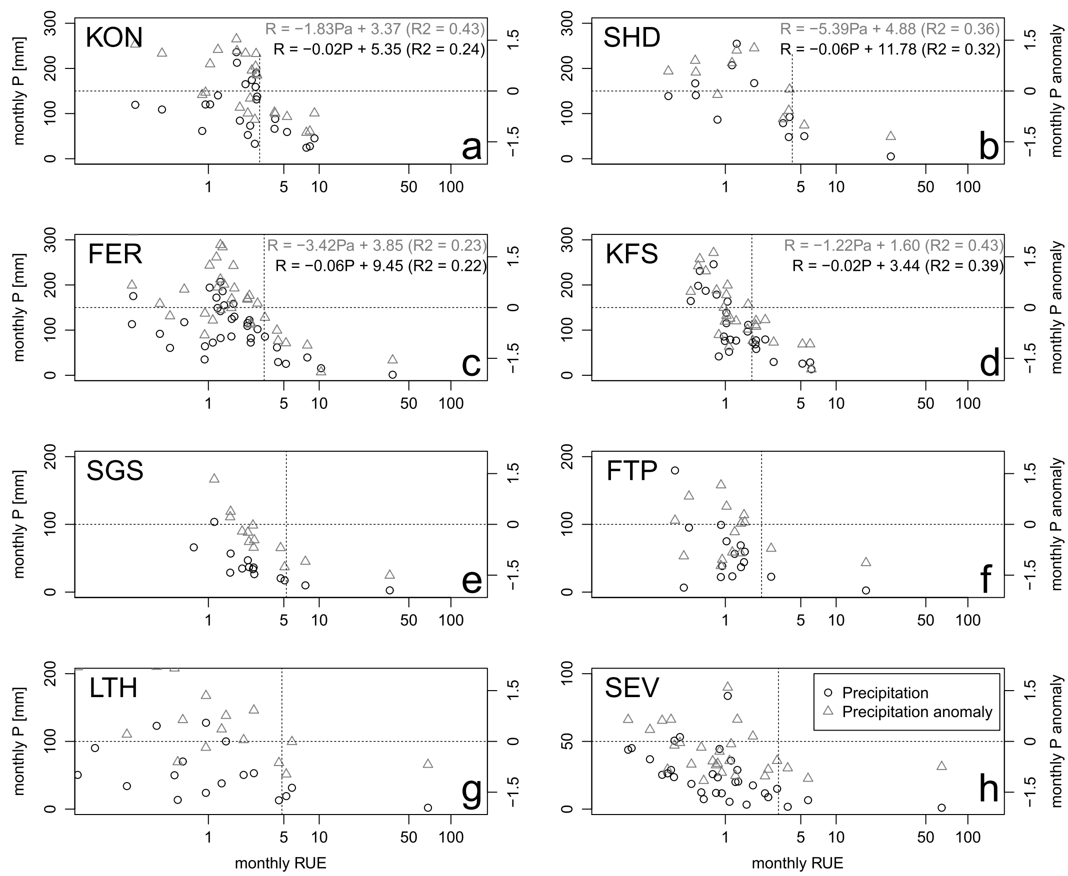

Figure 6. Relationship between an estimate of monthly mean ecosystem rain-use efficiency (RUE: $\frac{GPP}{P}$) and monthly mean precipitation (mm) (black circles), and the relationship between RUE and the monthly precipitation anomaly (grey triangles) during each site's active growing season. The regression line equation and R^2 statistic (in parenthesis) are shown in each panel, and all values are significant at $p < 0.05$. Average RUE is illustrated by the vertical line in each panel. The *y* axis scale differs between panels.

grassland responses to precipitation variability. As a result, accurate predictions of future grassland functioning in the western Great Plains will likely require a good deal of detailed climate, ecological, and vegetation demographic information at a relatively fine temporal resolution.

5.2. Contrasting Grassland Dynamics at Ecological Boundaries

Ecosystems at ecological boundaries are hypothesized to be highly sensitive to climate variability [*Gosz*, 1993], and we hypothesized that SEV and FER would respond to precipitation differently from other western and eastern grassland sites, respectively. During our study, SEV received 30% lower annual precipitation than the next driest grassland site (SGS), EF at SEV was 42% lower than the next lowest site (FTP; Table 2), and SEV had the highest VPD and lowest growing season GPP of all grasslands (Figure 2). As a result, SEV was an average C source at all timescales that we analyzed (Figures 3 and 5). SEV experiences vegetation processes and nutrient cycles that are pulse driven and thus respond to infrequent periods of resource availability [*Collins et al.*, 2008; *Williams et al.*, 2009; *Collins et al.*, 2014], and this high degree of water limitation likely means that SEV responds to rainfall differently than other Great Plains grasslands.

In contrast, FER benefited from 15% higher than average precipitation (Figure 2). FER experienced the highest average EF of all sites (Table 2), and also had the lowest VPD (Figure 2c). FER also experienced lower average temperatures than other eastern grasslands (Figure 2b). These conditions maximized C uptake at FER, especially during summer, yet the patterns of C exchanges were similar between FER and other eastern grasslands (Figures 3 and 5). Thus, grasslands at the eastern ecological boundary of the Great Plains may often respond to precipitation in ways that are similar to other eastern grasslands. These findings further emphasize that eastern Great Plains grasslands will likely have more predictable responses to climate change, whereas western grassland responses will be more localized.

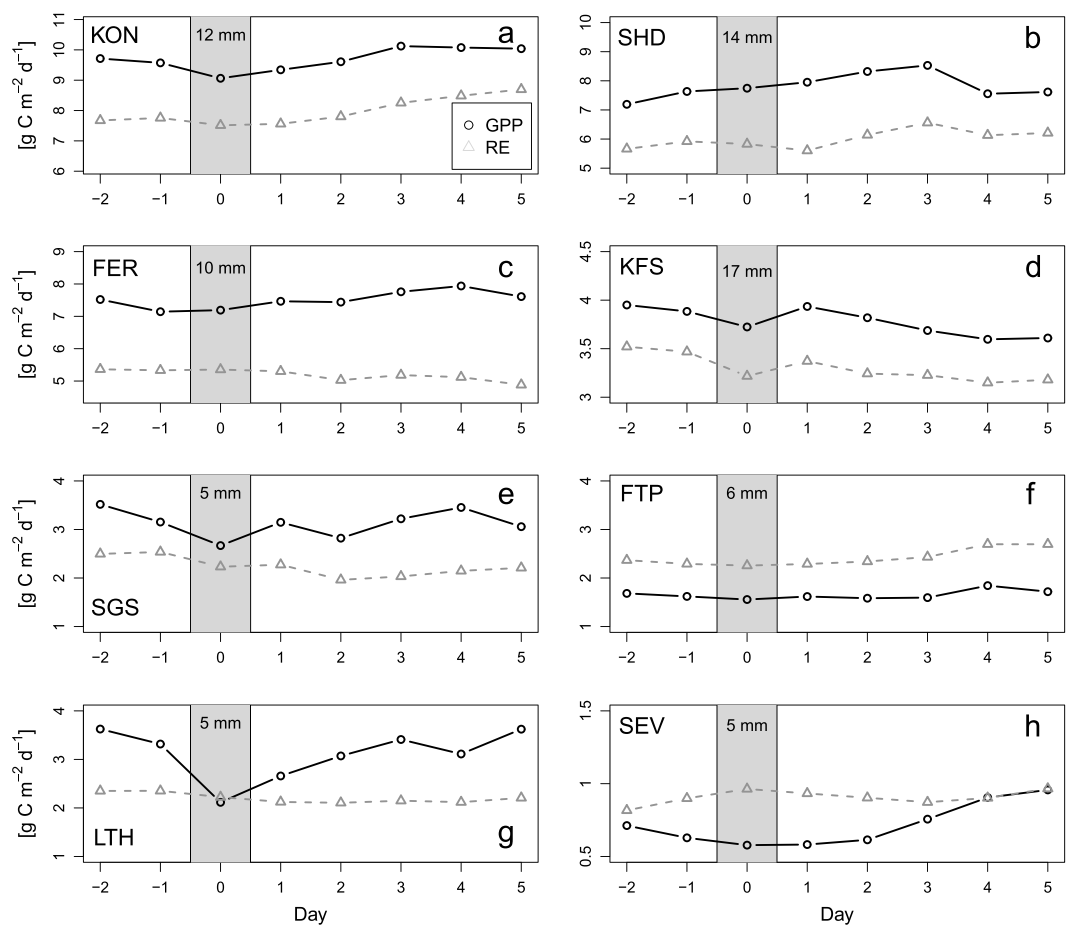

Figure 7. Response of daily gross primary production (GPP: g C m^{-2} d^{-1}) and ecosystem respiration (RE: g C m^{-2} d^{-1}) to isolated rainfall pulses occurring during each site's active growing season. Values correspond to rainfall events between the $\bar{x}$ and $\bar{x} \pm \frac{1}{2}\sigma^2$ of average precipitation event magnitude for each site. On the *x* axis, values correspond to days prior to (negative) or after (positive) the rainfall pulse. The *y* axis scale differs between panels.

5.3. Additional Site Characteristics

Patterns of C exchanges at LTH resembled those of eastern grasslands more so than those of western grasslands. LTH experienced the third lowest average annual *P* and EF of all sites (Table 3), yet experienced the highest percentage of annual GPP that occurred during the growing season and was a strong net C sink (Figure 3). Patterns of GPP, NEE, and EF at LTH were similar to that of eastern sites (Figures 4 and 5). Despite these similarities, RUE at LTH was not strongly correlated to precipitation (Figure 6), and LTH did show a strong pulse response of GPP to precipitation during summer (Figure 7g). This suggests that LTH experienced short, relatively high-productivity growing seasons on average, and was sensitive to precipitation later in the growing season when moisture availability was likely lower (Figure 7g). *Flanagan and Adkinson* [2011] found that soil moisture recharge may amplify growing season productivity in this grassland, and productivity may be especially high in years with high summer precipitation associated with El Niño conditions. Based on these patterns, we hypothesize that northern grasslands such as LTH may be sensitive to increasing spring temperature and changing large-scale precipitation patterns, which could lengthen the growing season and increase moisture deficit during summer.

Vegetation community characteristics may also affect C exchanges in these grasslands. SGS experienced lower than average precipitation and high VPD during our study (Figure 2), yet was an annual net C sink on average (Figure 3c). At SGS, cool-season C_3 grass productivity may be very high and constitute a large proportion of annual aboveground net primary productivity [*Blumenthal et al.*, 2013; *Prevey et al.*, 2014]. We found that spring productivity drove SGS to be a net C sink—SGS had the earliest growing season onset of all grasslands (Figure 4e), and was actually a net C sink on average despite having low EF during much of the growing season

(Figure 5e). The degree to which cool-season productivity may drive C exchanges in Great Plains grasslands is not well understood, although grazing and higher atmospheric CO_2 concentrations may support spring forb emergence and C_3 grass productivity in western grasslands [*Blumenthal et al.*, 2013; *Prevey et al.*, 2014]. Our results emphasize the need to better explore demographic patterns in western grasslands as a potential ecosystem-scale response to climate variability.

Ecological disturbances may also dampen or amplify the effects of climate forcings on grassland C exchanges [*Huenneke et al.*, 2002; *Knapp et al.*, 2008; *Koerner and Collins*, 2014]. KON experiences annual burning and was a small annual C loss on average (Figure 3) [*Logan and Brunsell*, 2015]. This average net loss was dominated by a low-precipitation year in 2011 of 234 mm (73.4% lower than average), and a loss of 242.4 g C m^{-2} y^{-1}. In 2011, transpiration at KON was significantly lower than average from March to August [*Logan and Brunsell*, 2015]. Thus, the carbon budget of KON over a 5 year period from 2007 to 2011 was dominated by a single year where drought amplified the effects of burning by reducing grassland GPP relative to RE (2011 GPP = 552 g C m^{-2}, 2011 RE = 795 g C m^{-2}). Values of RE do not account for C losses during burning, and the net C loss we observed at KON is therefore in addition to C losses that occurred during burning events. Our findings support other studies that report net C losses as a result of burning in both eastern and western Great Plains grasslands [*Zhang et al.*, 2011; *Vargas et al.*, 2012; *Logan and Brunsell*, 2015] and additional studies that show that many Great Plains grasslands may be a net C source during dry years [*Flanagan et al.*, 2002; *Zhang et al.*, 2010, 2011; *Petrie et al.*, 2015b]. As a disturbance, periodic fire may amplify the effects of drier than average conditions and reduce ecosystem C uptake on the order of multiple years.

Despite these findings, it remains unclear why FTP was a net source of C during our study, even though *Derner et al.* [2006] observed a similar pattern at this site in years prior to our study. The net C loss that we observed at FTP occurred in spite of 28% higher than average annual precipitation (Figure 2) and similar EF, VPD, and sensitivity to precipitation compared to other western grasslands (Table 2 and Figures 3 and 6). We hypothesize that some form of disturbance such as grazing resulted in net C loss, as annual C losses on the order of 200 g C m^{-2} are likely not sustainable in grassland systems. Grazing may increase soil C losses, thus decreasing GPP relative to RE even in a year of high grassland productivity [*Derner et al.*, 2006]. Although we cannot say for sure if this was the case at FTP, the C uptake dynamics that we observed at this site, KON, LTH, and SGS demonstrate the importance that local processes have in shaping longer-term grassland dynamics, especially when these conditions may amplify or mute the effects of climate variability.

6. Conclusions

We explored C exchanges in Great Plains grasslands in response to local precipitation variability, with a specific focus on the differences between wetter eastern and drier western Great Plains grasslands. We found generalizable differences in how western and eastern grasslands responded to precipitation, yet these differences may be muted locally by precipitation and temperature regimes, especially at ecotones. In a changing climate and under existing weather variability, we hypothesize that the similarity in C exchange dynamics between eastern grasslands facilitates more predictable responses to future variation in precipitation across this subregion, and the heterogeneity in C exchanges that we observed in western Great Plains grasslands suggests that this subregion will have less predictable responses. Our results strengthen understanding of precipitation variability as a local driver of year to year variation in grassland processes and C sequestration and as a regional driver that, over longer timescales, interacts with temperature to shape differences in functioning between the eastern and western Great Plains.

Acknowledgments
We thank site data managers for their data and for feedback on the manuscript. This work is part of the North American Carbon Program. N.A.B. acknowledges support from the LTER program at the Konza Prairie Biological Station (DEB-0823341). In addition, the US-KON and US-KFS Ameriflux sites are sponsored as a portion of the Konza Core Ameriflux Site by the U.S. Department of Energy under a subcontract from DE-AC02-05CH11231. R.V. and N.A.B. acknowledge support from the U.S. Department of Agriculture (2014-67003-22070). N.P.H. acknowledges support from DOE-NIGEC (26-6223-7230-002) for measurements at SGS. L.B.F. acknowledges funding from the Natural Sciences and Engineering Research Council of Canada Discovery grant program (RGPIN-2014-05882). M.L. acknowledges funding from the Sevilleta LTER program, NASA, and support as a Core Ameriflux Site. The data used in this manuscript are available from the AmeriFlux network (http://ameriflux.lbl.gov/) or directly from site investigators.

References

Ahlstrom, A., et al. (2015), The dominant role of semi-arid ecosystems in the trend and variability of the land CO_2 sink, *Science*, *348*, 895–899, doi:10.1126/science.aaa1668.

Austin, A., L. Yahdjian, J. Stark, J. Belnap, A. Porporato, U. Norton, D. Ravetta, and S. Schaeffer (2004), Water pulses and biogeochemical cycles in arid and semiarid ecosystems, *Oecologia*, *141*, 221–235, doi:10.1007/200442-004-1519-1.

Bachelet, D., R. Neilson, J. Lenihan, and R. Drapek (2001), Climate change effects on vegetation distribution and carbon budget in the United States, *Ecosystems*, *4*, 164–185, doi:10.1007/s10021-001-0002-7.

Barr, A., T. Black, E. Hogg, N. Kljun, K. Morgenstern, and Z. Nesic (2004), Inter-annual variability in the leaf area index of a boreal aspen-hazelnut forest in relation to net ecosystem production, *Agric. Forest Meteorol.*, *126*, 237–255, doi:10.1016/j.agrformet.2004.06.011.

Blumenthal, D., V. Resco, J. Morgan, D. Williams, D. LeCain, E. Hardy, E. Pendall, and E. Bladyka (2013), Invasive forb benefits from water savings by native plants and carbon fertilization under elevated CO_2 and warming, *New Phytol.*, *200*, 1156–1165, doi:10.1111/nph.12459.

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

Brunsell, N. A., and C. J. Wilson (2013), Multiscale interactions between water and carbon fluxes and environmental variables in a Central U.S. Grassland, *Entropy*, *15*(4), 1324–1341, doi:10.3390/e15041324.

Brunsell, N. A., A. Jones, T. Jackson, and J. Feddema (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.

Buis, G., J. Blair, D. Burkepile, C. Burns, A. Chamberlain, P. Chapman, S. Collins, R. Fynn, N. Govender, K. Kirkman, M. Smith, and A. Knapp (2009), Controls of aboveground net primary productivity in mesic savanna grasslands: An inter-hemispheric comparison, *Ecosystems*, *12*, 982–995, doi:10.1007/s10021-009-9273-1.

Byrne, K. M., W. K. Lauenroth, and P. B. Adler (2013), Contrasting effects of precipitation manipulations on production in two sites within the Central Grassland region, USA, *Ecosystems*, *16*, 1039–1051, doi:10.1007/s10021-013-9666-z.

Cardon, Z., J. Berry, and I. Woodrow (1995), Fluctuating [CO_2] drives species-specific changes in water use efficiency, *J. Biogeogr.*, *22*, 203–208.

Collatz, G., J. Berry, and J. Clark (1998), Effects of climate and atmospheric CO_2 partial pressure on the global distribution of C-4 grasses: Present, past, and future, *Oecologia*, *114*, 441–454, doi:10.1007/s004420050468.

Collins, S. L., R. L. Sinsabaugh, C. Crenshaw, L. Green, A. Porras-Alfaro, M. Stursova, and L. H. Zeglin (2008), Pulse dynamics and microbial processes in aridland ecosystems, *J. Ecol.*, *96*, 413–420, doi:10.1111/j.1365-2745.2008.01362.x.

Collins, S. L., et al. (2014), A multi-scale, hierarchical model of pulse dynamics in aridland ecosystems, *Annu. Rev. Ecol. Evol. Syst.*, *45*, 397–419, doi:10.1146/annurev-ecolsys-120213-091650.

Cook, B., and R. Seager (2013), The response of the North American Monsoon to increased greenhouse gas forcing, *J. Geophys. Res. Atmos.*, *118*, 1690–1699, doi:10.1002/jgrd.50111.

Cook, B., T. Ault, and J. Smerdon (2015), Unprecedented 21st century drought risk in the American Southwest and Central Plains, *Sci. Adv.*, *1*, e1400082, doi:10.1126/sciadv.1400082.

Cutforth, H., E. O'Brien, J. Tuchelt, and R. Rickwood (2004), Long-term changes in the frost-free season on the Canadian prairies, *Can. J. Plant Sci.*, *84*, 1085–1091, doi:10.4141/P03-169.

Derner, J., T. Boutton, and D. Briske (2006), Grazing and ecosystem carbon storage in the North American Great Plains, *Plant Soil*, *280*, 77–90, doi:10.1007/s11104-005-2554-3.

D'Odorico, P., G. S. Okin, and B. T. Bestelmeyer (2012), A synthetic review of feedbacks and drivers of shrub encroachment in arid grasslands, *Ecohydrology*, *5*, 520–530, doi:10.1002/eco.259.

D'Odorico, P., Y. He, S. L. Collins, S. F. J. de Wekker, V. Engel, and J. D. Fuentes (2013), Vegetation-microclimate feedbacks in correspondence to woodland-grassland ecotones, *Global Ecol. Biogeogr.*, *22*, 364–379, doi:10.1111/geb.12000.

Dugas, W., M. Heuer, and H. Mayeux (1999), Carbon dioxide fluxes over bermudagrass, native prairie, and sorghum, *Agric. Forest Meterol.*, *93*, 121–139.

Epstein, H., W. Lauenroth, I. Burke, and D. Coffin (1996), Ecological responses of dominant grasses along two climatic gradients in the Great Plains of the United States, *J. Vegetation Sci.*, *7*, 777–788, doi:10.2307/3236456.

Falge, E., et al. (2001), Gap filling strategies for long term energy flux data sets, *Agric. Forest Meterol.*, *107*, 71–77, doi:10.1016/S0168-1923(00)00235-5.

Fay, P. A., D. M. Kaufman, J. B. Nippert, J. D. Carlisle, and C. W. Harper (2008), Changes in grassland ecosystem function due to extreme rainfall events: Implications for responses to climate change, *Global Change Biol.*, *14*, 1600–1608.

Fierer, N., and J. Schimel (2002), Effects of drying-rewetting frequency on soil carbon and nitrogen transformations, *Soil Biol. Biochem.*, *34*, 777–787.

Flanagan, L., and A. Adkinson (2011), Interacting controls on productivity in a northern Great Plains grassland and implications for response to ENSO events, *Global Change Biol.*, *17*, 3293–3311, doi:10.1111/j.1365–2486.2011.02461.x.

Flanagan, L., L. Wever, and P. Carlson (2002), Seasonal and interannual variation in carbon dioxide exchange and carbon balance in a northern temperate grassland, *Global Change Biol.*, *8*, 599–615, doi:10.1046/j.1365-2486.2002.00491.x.

Frank, A., and W. Dugas (2001), Carbon dioxide fluxes over a northern, semiarid, mixed-grass prairie, *Agric. Forest Meteorol.*, *108*, 317–326, doi:10.1016/S0168-1923(01)00238-6.

Gan, T. (1998), Hydroclimatic trends and possible climatic warming in the Canadian prairies, *Water Resour. Res.*, *34*, 3009–3015, doi:10.1029/98WR01265.

Gosz, J. R. (1993), Ecotone hierarchies, *Ecol. Appl.*, *3*, 369–376, doi:10.2307/1941905.

Ham, J., and A. Knapp (1998), Fluxes of CO_2, water vapor, and energy from a prairie ecosystem during the seasonal transition from carbon sink to carbon source, *Agric. Forest Meterol.*, *89*, 1–14.

Harper, C., J. Blair, P. Fay, A. Knapp, and J. Carlisle (2005), Increased rainfall variability and reduced rainfall amount decreases soil CO_2 flux in a grassland ecosystem, *Global Change Biol.*, *11*, 322–334, doi:10.1111/j.1365-2486.2005.00899.x.

Heisler-White, J. L., A. K. Knapp, and E. F. Kelly (2008), Increasing precipitation event size increases aboveground net primary productivity in a semi-arid grassland, *Oecologia*, *158*, 129–140, doi:10.1007/s00442-008-1116-9.

Heisler-White, J. L., J. M. Blair, E. F. Kelly, K. Harmoney, and A. K. Knapp (2009), Contingent productivity responses to more extreme rainfall regimes across a grassland biome, *Global Change Biol.*, *15*, 2894–2904, doi:10.1111/j.1365-2486.2009.01961.x.

Huenneke, L., J. Anderson, M. Remmenga, and W. Schlesinger (2002), Desertification alters patterns of aboveground net primary production in Chihuahuan ecosystems, *Global Change Biol.*, *8*, 247–264, doi:10.1046/j.1365-2486.2002.00473.x.

IPCC (2013), *Climate Change 2013: I. The Physical Science Basis*, Cambridge Univ. Press, London.

Jackson, R., J. Banner, E. Jobbagy, W. Pockman, and D. Wall (2002), Ecosystem carbon loss with woody plant invasion of grasslands, *Nature*, *418*, 623–626, doi:10.1038/nature00952.

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

Knapp, A. K., J. M. Briggs, S. L. Collins, S. R. Archer, M. S. Bret-Harte, B. E. Ewers, D. P. Peters, D. L. Young, G. R. Shaver, E. Pendall, and M. B. Cleary (2008), Shrub encroachment in North American grasslands: Shifts in growth from dominance rapidly alters control of ecosystem carbon inputs, *Global Change Biol.*, *14*, 615–623, doi:10.1111/j.1365-2486.2007.01512.x.

Koerner, S., and S. Collins (2014), Interactive effects of grazing, drought, and fire on grassland plant communities in North America and South Africa, *Ecology*, *95*, 98–109, doi:10.1890/13-0526.1.

Kurc, S. A., and E. E. Small (2007), Soil moisture variations and ecosystem-scale fluxes of water and carbon in semiarid grassland and shrubland, *Water Resour. Res.*, *43*, W06416, doi:10.1029/2006WR005011.

Laio, F., A. Porporato, L. Ridolfi, and I. Rodriguez-Iturbe (2002), On the seasonal dynamics of mean soil moisture, *J. Geophys. Res.*, *107*, 4272, doi:10.1029/2001JD001252.

Lasslop, G., M. Reichstein, D. Papale, A. D. Richardson, A. Arneth, A. Barr, P. Stoy, and G. Wohlfahrt (2010), Separation of net ecosystem exchange into assimilation and respiration using a light response curve approach: Critical issues and global evaluation, *Global Change Biol.*, *16*(1), 187–208, doi:10.1111/j.1365-2486.2009.02041.x.

Lauenroth, W. K., and J. B. Bradford (2012), Ecohydrology of dry regions of the United States: Water balance consequences of small precipitation events, *Ecohydrology*, *5*, 46–53, doi:10.1002/eco.195.

Logan, K., and N. Brunsell (2015), Influence of drought on growing season carbon and water cycling with changing land cover, *Agric. Forest Meteorol.*, *213*, 217–225, doi:10.1016/j.agrformet.2015.07.002.

McCulley, R. L., I. C. Burke, and W. K. Lauenroth (2009), Conservation of nitrogen increases with precipitation across a major grassland gradient in the Central Great Plains of North America, *Oecologia*, *159*, 571–581, doi:10.1007/s00442-008-1229-1.

Morgan, J., D. LeCain, E. Pendall, D. Blumenthal, B. Kimball, Y. Carrillo, D. Williams, J. Heisler-White, F. Dijkstra, and M. West (2011), C4 grasses prosper as carbon dioxide eliminates desiccation in warmed semi-arid grassland, *Nature*, *476*, 202–206, doi:10.1038/nature10274.

Nippert, J., P. Fay, and A. Knapp (2007), Photosynthetic traits in C3 and C4 grassland species in mesocosm and field environments, *Environ. Exp. Bot.*, *60*, 412–420.

Niu, S., Z. Yuan, Y. Zhang, W. Liu, L. Zhang, J. Huang, and S. Wan (2005), Photosynthetic responses of C3 and C4 species to seasonal water variability and competition, *J. Exp. Bot.*, *56*(421), 2867–2876.

Olson, K., R. White, and B. Sindelar (1985), Response of vegetation of the northern Great Plains to precipitation amount and grazing intensity, *J. Range Manage.*, *38*, 357–361, doi:10.2307/3899422.

Peters, D., P. Groffman, K. Nadelhoffer, N. Grimm, S. Collins, W. Michener, and M. Huston (2008), Living in an increasingly connected world: A framework for continental-scale environmental science, *Frontiers Ecol. Environ.*, *6*, 229–237, doi:10.1890/070098.

Petrie, M. D., and N. A. Brunsell (2012), The role of precipitation variability on the ecohydrology of grasslands, *Ecohydrology*, *5*, 337–345, doi:10.1002/eco.224.

Petrie, M. D., S. L. Collins, and M. E. Litvak (2015a), The ecological role of small rainfall events in a desert grassland, *Ecohydrology*, *8*, 1614–1622, doi:10.1002/eco.1614.

Petrie, M. D., S. L. Collins, M. E. Litvak, A. L. Swann, and P. L. Ford (2015b), Grassland to shrubland state transitions enhance carbon sequestration in the northern Chihuahuan Desert, *Global Change Biol.*, *21*, 1226–1235, doi:10.1111/gcb.12743.

Poulter, B., et al. (2014), Contribution of semi-arid ecosystems to interannual variability of the global carbon cycle, *Nature*, *509*, 600–603, doi:10.1038/nature13376.

Prevey, J., D. Knochel, and T. Seastedt (2014), Mowing reduces exotic annual grasses but increases exotic forbs in a semiarid grassland, *Restoration Ecol.*, *22*, 774–781, doi:10.1111/rec.12140.

R Development Core Team (2011), R: A language and environment for statistical computing, R Foundation for Statistical Computing, Vienna, Austria. [Available http://www.R–project.org.]

Ratajczak, Z., J. B. Nippert, and S. L. Collins (2012), Woody encroachment decreases diversity across North American grasslands and savannas, *Ecology*, *93*, 697–703.

Reichmann, L. G., O. E. Sala, and D. P. C. Peters (2013), Water controls on nitrogen transformations and stocks in an arid ecosystem, *Ecosphere*, *4*(1), 11, doi:10.1890/ES12-00263.1.

Reichstein, M., et al. (2005), On the separation of net ecosystem exchange into assimilation and ecosystem respiration: Review and improved algorithm, *Global Change Biol.*, *11*, 1424–1439, doi:10.1111/j.1365–2486.2005.001002.x.

Reynolds, J., et al. (2007), Global desertification: Building a science for dryland development, *Science*, *316*, 847–851, doi:10.1126/science.1131634.

Sala, O. E., and W. K. Lauenroth (1982), Small rainfall events: An ecological role in semiarid regions, *Oecologia*, *53*, 301–304.

Sala, O. E., W. Parton, L. Joyce, and W. Lauenroth (1988), Primary production of the central grassland region of the United-States, *Ecology*, *69*, 40–45, doi:10.2307/1943158.

Schlesinger, W. (1997), *Biogeochemistry: An analysis of global change*, Academic Press, San Diego, Calif.

Schlesinger, W. H., J. F. Reynolds, G. L. Cunningham, L. F. Huenneke, W. M. Jarrell, R. A. Virginia, and W. G. Whitford (1990), Biological feedbacks in global desertification, *Science*, *247*, 1043–1048, doi:10.1126/science.247.4946.1043.

Scurlock, J., and D. Hall (1998), The global carbon sink: A grassland perspective, *Global Change Biol.*, *4*, 229–233, doi:10.1046/j.1365-2486.1998.00151.x.

Sims, P. L., and J. Bradford (2001), Carbon dioxide fluxes in a southern plains prairie, *Agric. Forest Meteorol.*, *109*, 117–134, doi:10.1016/S0168-1923(01)00264-7.

Suyker, A., B. Shashi, and G. Burba (2003), Internnual variability in net CO_2 exchange of a native tallgrass prairie, *Global Change Biol.*, *9*, 255–265.

Teuling, A., S. Seneviratne, C. Williams, and P. Troch (2006), Observed timescales of evapotranspiration response to soil moisture, *Geophys. Res. Lett.*, *33*, L23403, doi:10.1029/2006GL028178.

Thomey, M., S. L. Collins, and R. Vargas (2011), Effect of precipitation variability on net primary production and soil respiration in a Chihuahuan Desert grassland, *Global Change Biol.*, *17*, 1505–1515, doi:10.1111/j.1365-2486.2010.02,363.x.

Tieszen, L., B. Reed, N. Bliss, B. Wylie, and D. DeJong (1997), NDVI, C-3 and C-4 production, and distributions in great plains grassland land cover classes, *Ecol. Appl.*, *7*, 59–78, doi:10.2307/2269407.

United States Department of Agriculture, N. R. C. S. (2013), Soil Survey Geographic (SSURGO) database—Hydric rating, U.S. Depart. of Agric., Natural Resour. Conservation Serv., Fort Worth, Tex. [Available at http://websoilsurvey.sc.egov.usda.gov/App/HomePage.htm.]

Vargas, R., S. L. Collins, M. L. Thomey, J. E. Johnson, R. F. Brown, D. O. Natvig, and M. T. Friggens (2012), Precipitation variability and fire influence the temporal dynamics of soil CO_2 efflux in an arid grassland, *Global Change Biol.*, *18*, 1401–1411, doi:10.1111/j.1365-2486.2011.02628.x.

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

Wagle, P., X. Xiao, R. Scott, T. Kolb, D. Cook, N. Brunsell, D. Baldocchi, J. Basara, R. Matamala, Y. Zhou, and R. Bajgain (2015), Biophysical controls on carbon and water vapor fluxes across a grassland climatic gradient in the United States, *Agric. Forest Meteorol.*, *214-215*, 293–305, doi:10.1016/j.agrformet.2015.08.265.

Wever, L., L. Flanagan, and P. Carlson (2002), Seasonal and interannual variation in evapotranspiration, energy balance and surface conductance in a northern temperate grassland, *Agric. Forest Meteorol.*, *112*, 31–49.

Williams, C., Jr., R. Vose, D. Easterling, and M. Menne (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, Tenn.

Williams, C., N. Hanan, R. Scholes, and W. Kutsch (2009), Complexity in water and carbon dioxide fluxes following rain pulses in an African savanna, *Oecologia*, *161*, 469–480.
Zhang, L., B. Wylie, L. Ji, T. Gilmanov, and L. Tieszen (2010), Climate-driven interannual variability in net ecosystem exchange in the northern Great Plains grasslands, *Rangeland Ecol. Manage.*, *63*, 40–50, doi:10.2111/08-232.1.
Zhang, L., B. Wylie, L. Ji, T. Gilmanov, L. Tieszen, and D. Howard (2011), Upscaling carbon fluxes over the Great Plains grasslands: Sinks and sources, *J. Geophys. Res.*, *116*, G00J03, doi:10.1029/2010JG001504.