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ABSTRACT

The Southern Great Plains are characterized by a fine-scale mixture of different land-cover types, predominantly winter-wheat and grazed pasture, with relatively small areas of other crops, native prairie, and switchgrass. Recent droughts and predictions of increased drought in the Southern Great Plains, especially during the summer months, raise concern for these ecosystems. We measured ecosystem carbon and water fluxes with eddy-covariance systems over cultivated cropland for 10 years, and over lightly grazed prairie and new switchgrass fields for 2 years each. Growing-season precipitation showed the strongest control over net carbon uptake for all ecosystems, but with a variable effect: grasses (prairie and switchgrass) needed at least 350 mm of precipitation during the growing season to become net carbon sinks, while crops needed only 100 mm. In summer, high temperatures enhanced evaporation and led to higher likelihood of dry soil conditions. Therefore, summer-growing native prairie species and switchgrass experienced more seasonal droughts than spring-growing crops. For wheat, the net reduction in carbon uptake resulted mostly from a decrease in gross primary production rather than an increase in respiration. Flux measurements suggested that management practices for crops were effective in suppressing evapotranspiration and decomposition (by harvesting and removing secondary growth), and in increasing carbon uptake (by fertilizing and conserving summer soil water). In light of future projections for wetter springs and drier and warmer summers in the Southern Great Plains, our study indicates an increased vulnerability in native ecosystems and summer crops over time.

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1. Introduction

The Great Plains covers a large area of the central United States. The native vegetation includes prairie grasses and forbs (Sala et al., 1988), with C₄ grasses dominating the warmer and drier regions of the Central and Southern Great Plains (Lauenroth et al., 1999). Since the late 18th century, this region has undergone large scale land-use change, owing to the abundance of available flat terrain, paucity of trees, and year-round precipitation (Cunfer, 2005). Today, the landscape is a fine-scale mix of crops, pasture, and prairie. Wheat is the dominant crop in the southern region, accounting for almost 50% of the total U.S. wheat production

(Vocke and Ali, 2013), and controlling the seasonality of regional carbon fluxes (Torn et al., 2011).

The precipitation regime in this region allows crops to be rain-fed, but the lack of irrigation exposes crops, and natural ecosystems generally, to occasional droughts. Trends in climate change for the Southern Great Plains are distinct from those of other North American regions: 20th century records and model projections indicate increased precipitation and soil-moisture trends over the contiguous U.S., except for the Southwest and Central regions (Andreadis and Lettenmaier, 2006; Seager et al., 2009; Mishra and Singh, 2010; Hoerling et al., 2012; Patricola and Cook, 2012). The combination of warming (similar to the global trend) with lower precipitation (opposed to the overall North American trend) explains the increase in drought duration and severity over the last century in this region (Andreadis and Lettenmaier, 2006; Cook et al., 2007). Mid-21st century climate predictions for the Great Plains indicate a 2.6–2.9 °C increase in

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August temperatures in comparison to 1981–2000 temperatures (Patricola and Cook, 2012), and low-to-moderate soil drying (Hoerling et al., 2012).

Droughts are associated with decreased precipitation and increased temperatures, resulting in decreased soil and atmospheric moisture. Drying and warming affect productivity differently (Bates et al., 2006; Naithani et al., 2012), and it is often unclear which climatic driver – drying or warming, or a combination of both – is responsible for the decrease in productivity during droughts (Reichstein et al., 2002; Aubinet et al., 2009; Zhou et al., 2013). Moreover, not only the overall change in precipitation or temperature is critical for vegetation growth, but also the change in their seasonal pattern (Gillespie and Loik, 2004; Bates et al., 2006; Fischer et al., 2007; Ma et al., 2007; Béziat et al., 2009; Zha et al., 2010; Hussain et al., 2011; Raz-Yaseef et al., 2012). To improve prediction of ecosystem productivity, we need a better understanding of vegetation sensitivity to changes in both the amplitude and timing of precipitation and temperature.

In this study, our aim was to understand the consequences of drought for terrestrial ecosystems in the Southern Great Plains. We have been measuring fluxes of carbon, water, and energy in three different sites in Oklahoma (over 14 site years in total), which represent the most widespread ecosystems of the Southern Great Plains region: (1) cultivated cropland, (2) lightly grazed native prairie, and (3) a planted switchgrass field. Switchgrass is of interest because it is a proposed feedstock for biofuel production (Zenone et al., 2008; Skinner and Adler, 2010). For the crop site, a unique combination of flux measurements alongside a dataset of management practices – such as tillage, planting dates and varieties, herbicide and fertilizer application – suggests insight on how management, in addition to climate, affected ecosystem fluxes. This study provides novel information on vegetation sensitivity to climate change in the Southern Great Plains, and can help improve preparedness for future droughts.

2. Methods

2.1. Site descriptions

The study was conducted in Oklahoma, U.S.A. The climate in this region is continental humid to semi-arid, with a large southeast-to-northwest precipitation gradient (Fig. 1). Precipitation occurs during all months of the year, with less than 25% of it falling as snow, between December and February (Fig. 2(A)).

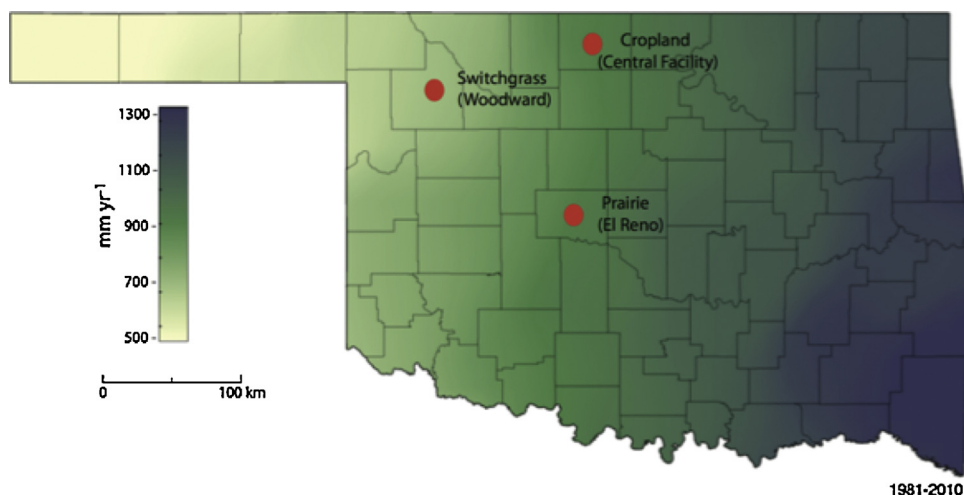


Fig. 1. Location of the research sites on a map of average annual precipitation for Oklahoma (1981–2010). Source: Oklahoma Climatological Survey.

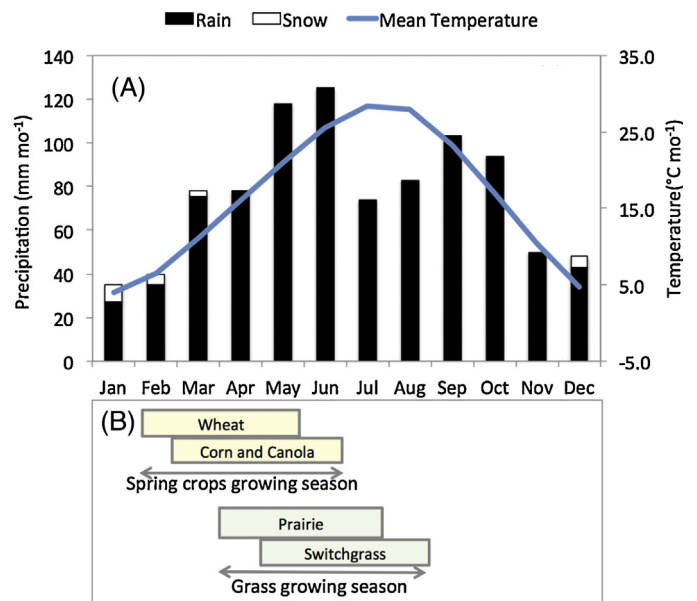


Fig. 2. (A) Long-term average monthly precipitation (rain and snow), and temperature (monthly average) for Oklahoma City (1981–2010; Oklahoma Climatological Survey). (B) The four-month growing season for spring crops (February–May for wheat, March–June for corn and canola), and for grasses (April–July for prairie, May–August for switchgrass).

Winters are relatively mild and summers experience high temperatures, leading to warm and humid summers. This region often experiences tornados, and Oklahoma City is one of the most tornado-prone cities in the U.S. (Brooks et al., 2003).

Measurements took place at three different sites (Fig. 1):

- (1) *Crop field* (U.S. Department of Energy Atmospheric Radiation Measurement [DOE-ARM] Climate Research Central Facility near Billings, Oklahoma, 36.61°N, 97.49°W, 300 m asl). Measurements of ecosystem fluxes and meteorological variables were conducted between December 2002 and December 2012 over a managed crop field. Long-term average annual precipitation for this site is 857 mm, and the average annual temperature is 15.6 °C (1981–2010; Oklahoma Climatological Survey). Soils in the area are well-drained Kirkland loams (Fischer et al., 2007). *Field history*. The main crop grown in this field is hard red winter wheat (“common wheat,” *Triticum*

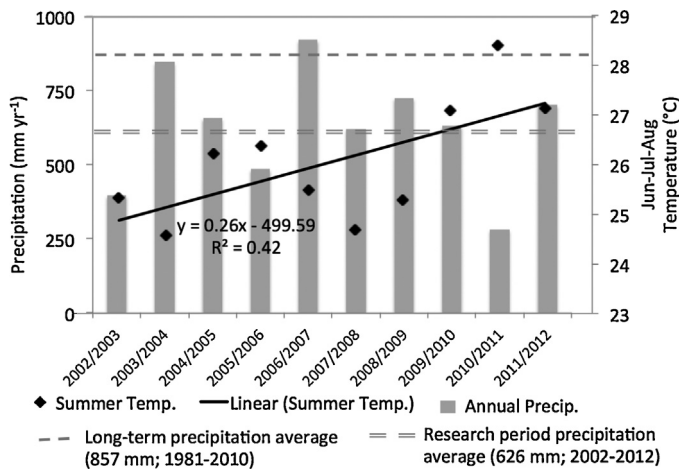


Fig. 3. Annual precipitation and summer temperatures during the research period measured at the Central Facility crop site. The linear regression and coefficient (R^2) for the decadal trend in summer temperatures is shown. The long-term (1981–2010) and the research period (2002–2012) precipitation averages are also shown.

aestivum L., main var. Jaeger, Jagalene, and Fuller) with infrequent crop rotations (seven seasons of wheat, two seasons of corn, and one season of canola). Between these spring-growing crops, summer crops were grown twice: soybeans in 2006 and cowpeas in 2012. The field was never irrigated, but was treated with various levels of tillage, fertilizers, herbicides, and pesticides (Fig. 4(E)). As typical for the region, management practices were designed to minimize intervention and reduce costs.

(2) *Prairie* (USDA-ARS Grazinglands Research Laboratory near El Reno, Oklahoma, 35°33'N, 98°02'W, 423 m asl). Measurements of ecosystem fluxes and meteorological variables were conducted between March 2005 and March 2007 over a pasture. Dominant species include big bluestem (*Andropogon gerardii* Vitman), little bluestem (*Schizachyrium halapense* (Michx.) Nash.), and others common to tallgrass prairie ecosystems (Lauenroth et al., 1999). Long-term average annual precipitation for this site is 920 mm, and average annual temperature is 15.1 °C (1981–2010; Oklahoma Climatological Survey). The soil is classified as Norge loamy prairie, with a depth greater than 1 m, high water-holding capacity, and slope averaging about 1% (Fischer et al., 2012). *Field history.* The 33 ha field had not been burned since 1990. Grazing at moderate

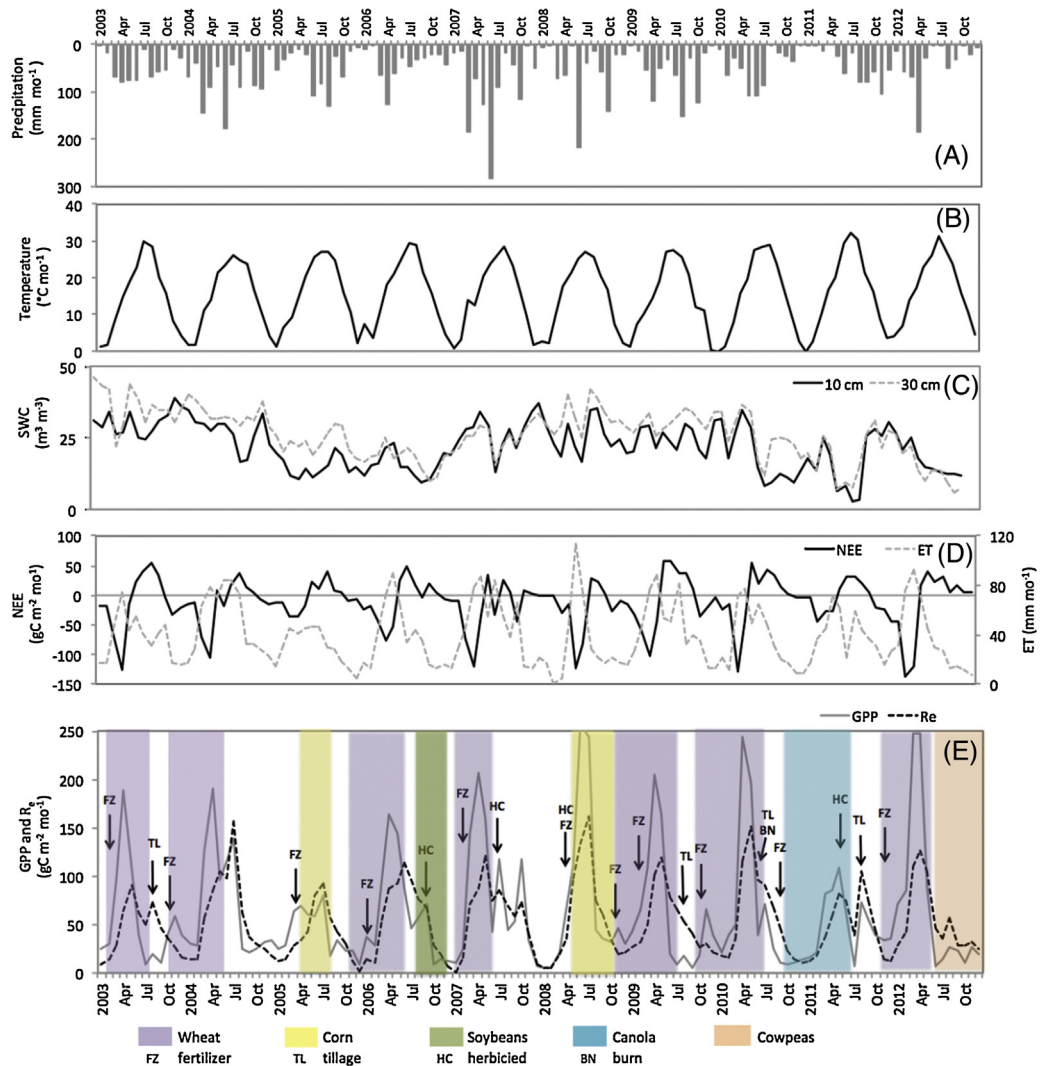


Fig. 4. Monthly climate variables and fluxes measured at the Central Facility cropland site: (A) precipitation, (B) temperature, (C) soil water content at depth 10 and 30 cm, (D) fluxes of net ecosystem exchange (NEE) and evapotranspiration (ET), and (E) fluxes of gross primary production (GPP) and ecosystem respiration (R_e). Growing season length (planting to harvest), crop type, and treatment are presented in (E).

stocking rates and occasional herbicide spraying were conducted during the year 2000 growing season (Fischer et al., 2012).

- (3) *Switchgrass* (USDA-ARS Southern Plains Range Research Station near Woodward, Oklahoma, 36°25'N, 99°25'W, 614 m asl). Measurements of ecosystem fluxes and meteorological variables were conducted between May 2009 and November 2012 over a cultivated switchgrass field (*Panicum virgatum*, var. Alamo). Long-term average annual precipitation for this site is 657 mm, and average annual temperature is 14.4 °C (1981–2010; Oklahoma Climatological Survey). Soils in the area are shallow, well-drained coarse loams (Sharpley et al., 1987). *Field history*. The previous prairie vegetation was burnt, overgrazed, and sprayed with herbicide between April 2009 and March 2010. Switchgrass was seeded in April 2010. No additional treatments were made after seeding. The crop was cut and baled after the first growing season, in December 2010. Drought conditions during 2011 killed the young seedlings, which did not recover in the following year. A tornado touchdown near the flux tower in March 2012 compromised eddy covariance measurements, and the system returned to full operation in September 2012.

2.2. Environmental and micrometeorological measurements

Carbon and water fluxes were measured with nearly identical eddy-covariance systems at each of the three field sites. The systems included a sonic anemometer (Gill-Solent WindMaster Pro) and an open-path infrared gas analyzer (IRGA LiCor LI-7500) located 4 m above the ground, allowing a minimum of ~3 m between the top of the canopy and the instruments for all vegetation types in this study. Turbulent vertical fluxes of CO₂, water, and heat were calculated every half hour using algorithms for spike removal, coordinate rotation to zero mean vertical and cross wind speed, and block averaging of scalar quantities (Billesbach et al., 2004). A threshold to u^* was applied, and flux values measured when friction velocity was smaller than 0.1 m s⁻¹ were discarded. Density corrections were applied to the covariances of vertical wind, using CO₂ and H₂O densities obtained with the open-path IRGA. Random uncertainties in measured fluxes, obtained from averaging turbulence measurements, were estimated to be approximately 10% (Billesbach, 2011). Missing segments of flux data were gap-filled using the method of Falge et al. (2001). Briefly, individual missing points in small gaps

(1–4 consecutive points) were filled with linearly interpolated values between neighboring good points. Larger gaps were filled with a mean diurnal cycle determined from a two-week window surrounding the missing data. Nighttime data were replaced when the hour averaged friction velocity was insufficient to insure adequate turbulence. The total percentage of gap-filled values was approximately 35% for NEE and 15% for ET. At the ARM Central Facility crop field site, NEE was partitioned into gross primary production (GPP) and ecosystem respiration (R_e). R_e was calculated using an exponential temperature relation with nighttime NEE (Lloyd and Taylor, 1994). GPP was estimated using a simple rectangular hyperbolic function fit of light intensity and daytime NEE, as described in Gilmanov et al. (2003) and Fischer et al. (2007).

At each of these sites, identical slow-response data systems were installed adjacent to the flux tower. Soil moisture was measured at 10 and 30 cm below the soil surface (ML-2, Delta-T Devices Ltd., Cambridge, England, two replicas at each depth). Soil temperature was measured at 5, 15, and 25 cm depth (type E soil temperature thermocouples, two replicas at each depth). Radiation was measured at 2.5 m above the soil surface (R_n ; NR-lite, Kipp & Zonen B.V., Delft, The Netherlands; PAR: LI-190, LiCor Biosciences, Lincoln, NE; SWR: LiCor LI-200 shortwave pyranometer). Soil heat flux was measured at 4–5 cm depth (HFT3, Radiation and Energy Balance Systems, Bellevue, WA, four replicas). Air temperature and relative humidity were measured at 2.5 and 3.8 m above ground (50-Y Humitter, Vaisala Oyj., Helsinki, Finland housed in REBS 6-plate, non-aspirated radiation shields), and air pressure was measured (Vaisala PT-101B barometer) at a height of 2.5 m above the surface. Precipitation was measured with an unheated tipping bucket rain gauge (model 52 mm, Texas Electronics, Dallas, TX). For further details about these data systems, refer to Billesbach et al. (2004).

2.3. General definitions

We defined the *main growing season* as a four-month period when, based on our measurements, carbon uptake was strongest (most negative NEE): February–May for wheat, March–June for corn and canola, April–July for prairie, and May–August for switchgrass (Fig. 2(B)). Although the main growing season for wheat species at our field site was spring, these varieties are commonly referred to as *winter wheat* because they are sown in late fall. The term *hydrological year* was used to describe a time period of 12 months for which precipitation and flux totals were

Table 1

Annual precipitation (PPT), evapotranspiration (ET), net carbon ecosystem exchange (NEE), and gross primary production (GPP; Central Facility only).

Site	Year	Vegetation	PPT (mm year ⁻¹)	ET (mm year ⁻¹)	NEE (gC m ⁻² year ⁻¹)	GPP (gC m ⁻² year ⁻¹)
Cropland ^a (Central Facility)	2002/2003	Wheat	396	327	-125	
	2003/2004	Wheat	845	621	-179	899
	2004/2005	Corn	657	417	-45	517
	2005/2006	Wheat and Soybean	485	440	-120	713
	2006/2007	Wheat	920	527	-205	854
	2007/2008	Corn	621	439	-253	968
	2008/2009	Wheat	725	518	-115	776
	2009/2010	Wheat	630	477	-102	814
	2010/2011	Canola	281	399	17	502
	2011/2012	Wheat and Cowpea	701	527	-254	953
Prairie ^b (El Reno)	2005/2006	Prairie	627	897	-200	
	2006/2007	Prairie	679	764	11	
Switchgrass ^c (Woodward)	2010	Switchgrass	666	742	-85	
	2011	Switchgrass	330	360	187	

^a Hydrological year starts at September.

^b Hydrological year starts at March.

^c Hydrological year starts at January.

measured. The span of the hydrological years varied between sites, based on the difference in the main growing season, and the date at which measurement started (Table 1: January at the crop site, March at the prairie site, and May at the switchgrass site). We define *drought years* as hydrological years with annual precipitation below 50% of the long-term average. We defined seasons as follows: *winter* – December, January, and February; *summer* – June, July, and August, and *spring* and *autumn* for the months between them. By *grasses*, we mean the native prairie species (both C₃ and C₄) measured at the prairie site near El Reno, as well as the engineered hybrid species measured at the switchgrass site near Woodward.

3. Results

3.1. Climate

3.1.1. Crop field site

Average annual precipitation during the research decade 2002–2012 was 626 ± 185 mm (10-year average \pm SD), which was lower than the long-term average of 857 mm for this site (1981–2010; Oklahoma Climatological Survey, Fig. 3). Summer temperatures showed a gradual rise, with an average increase of 0.26°C per year ($R^2=0.42$) for the measured decade (Fig. 3). This climatic trend of precipitation decrease and temperature increase confirms other reports of increase in heat waves, and serves as a good analog for future climate scenarios for in this region (Andreadis and Lettenmaier, 2006; Patricola and Cook, 2012). Interannual variability in precipitation was large (Table 1 and Fig. 3), and included three drought years (2002–2003, 2005–2006, and 2010–2011; having 46%, 57%, and 33% of the long-term average precipitation, respectively), and two wet years (2003–2004 and 2006–2007; having 99% and 107%, of the long-term average precipitation, respectively). An overall decrease in soil moisture was observed between 2004 and 2007 (Fig. 4(C)), more apparent at depth of 30 cm than at 10 cm, because periodical moderate rain events replenished the topsoil. Extreme soil dryness was measured in September 2011, with soil moisture content as low as 3% at a depth of 10 cm.

3.1.2. Prairie site

Annual precipitation for the two years measured at the El Reno prairie site was similar (626 and 681 mm; Table 1 and Fig. 5(A)),

but well below the long-term average of 920 mm for this region (1981–2010; Oklahoma Climatological Survey). The seasonal rain distribution during these two years was different: summer precipitation accounted for 63% of annual precipitation in the first year, but only 32% in the second: frequent summer storms in the first year led to lower summer temperatures, lower VPD, and higher soil-moisture content throughout the summer (Fig. 5). Hence, despite similar total precipitation amounts in the two measured years, climatic and environmental conditions during the growing season were very different, and were associated with a distinct contrast in ecosystem response. Accordingly, we considered 2005–2006 a wet year, and 2006–2007 a dry year.

3.1.3. Switchgrass site

In 2010, the first year after switchgrass planting, the site received near long-term average precipitation of 666 mm (657 mm for 1981–2010; Oklahoma Climatological Survey). The following year was a drought year, with total precipitation reaching only 50% of the long-term average for this location (Table 1 and Fig. 6(A)).

3.2. Ecosystem fluxes

3.2.1. Crop field site

On average for the research period, the field was a net carbon sink (NEE of $-138 \pm 82 \text{ gC m}^{-2} \text{ year}^{-1}$; 10 year average \pm SD), despite dry conditions during most of this period. The only year with positive (i.e., net loss of) carbon fluxes was 2010–2011, which was an extreme drought year. In most years, GPP peaked in April, when wheat growth was rapid, and R_e peaked later (June–August), when temperatures increased, resulting in a peak NEE flux in April and May (Fig. 4). Monthly ET was better correlated with monthly GPP ($R^2=0.59$; data not shown) than with monthly precipitation ($R^2=0.30$; data not shown). ET was high during the growing season, but low during the noncrop season, even in months with high precipitation and high temperatures.

3.2.2. Prairie site

Although total precipitation amounts were similar between the two measured years, carbon uptake was significantly different, with the system serving as a net carbon sink during the first year, and a near-net-zero flux during the second (Table 1, Fig. 5). ET decreases in 15% between years, and exceeded precipitation in both years.

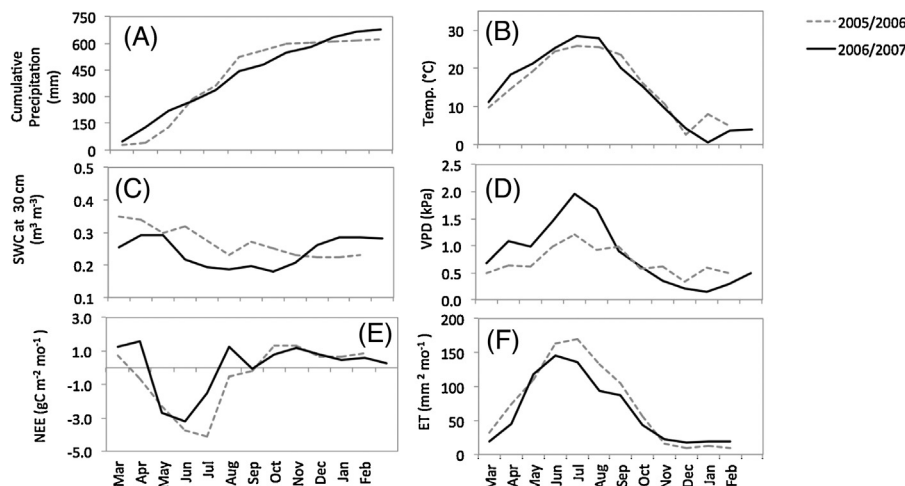


Fig. 5. Monthly climate variables and fluxes measured at the El-Reno prairie site for two consecutive years: (A) precipitation, (B) temperature, (C) soil water content at depth of 30 cm, (D) vapor pressure deficit (VPD), (E) net ecosystem exchange, and (F) evapotranspiration.

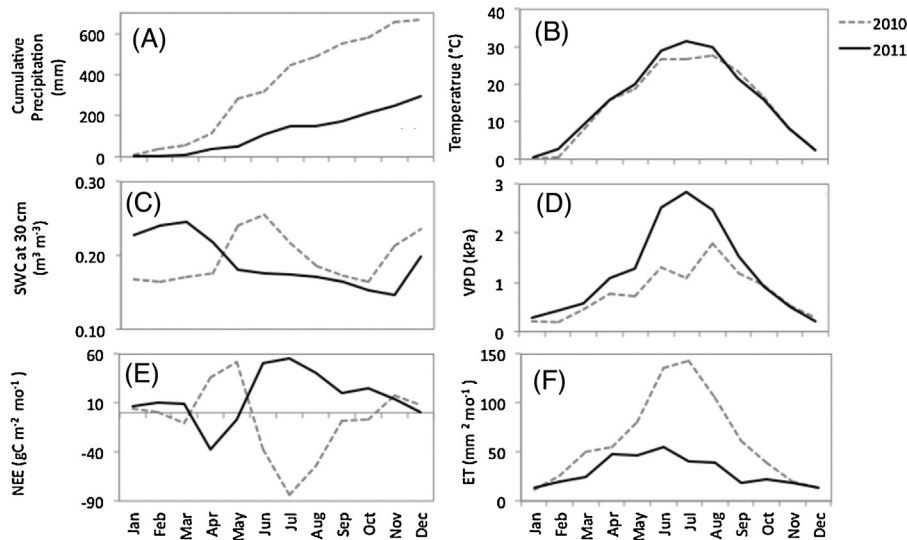


Fig. 6. Monthly climate variables and fluxes measured at the Woodward switchgrass site for two consecutive years: (A) precipitation, (B) temperature, (C) soil water content at depth of 30 cm, (D) vapor pressure deficit, (E) net ecosystem exchange, and (F) evapotranspiration.

3.2.3. Switchgrass site

The field was already a net carbon sink in the first growing season after planting (2010, Table 1). High carbon uptake was facilitated by the abundance of summer rains, which led to lower temperatures, lower VPD, and higher soil-water content throughout the 2010 summer season when compared to the 2011 summer season (Fig. 6). The summer of 2011 saw the onset of drought, and while carbon uptake started early (negative NEE values in April), by June the field had become a net carbon source (positive NEE values). ET was accordingly high in the first year and low in the second, and in both years was 10% higher than precipitation.

3.3. Cross-site synthesis

Annual NEE was weakly correlated with annual precipitation (data not shown), but a clear relationship was observed between annual NEE and growing-season period precipitation (Fig. 7(A)). Carbon uptake (more negative NEE) increased with an increase in growing-season precipitation in all measured ecosystems. The linear relationship between NEE and growing-season precipitation had a higher slope and a larger intercept value for summer grasses (prairie and switchgrass; $n = 4$, $R^2 = 1.00$, slope = -1.13 , intercept = 354 mm, $p < 0.05$) than for spring crops (wheat, corn, and canola; $n = 4$, $R^2 = 0.89$, slope = -0.90 , intercept = 99 mm, $p < 0.05$).

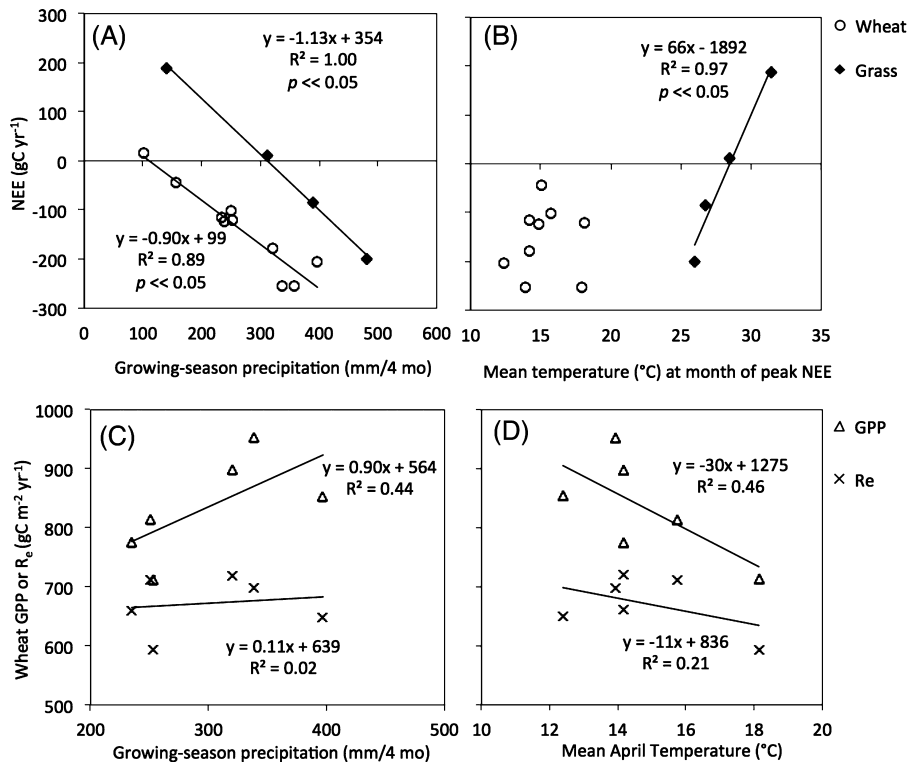


Fig. 7. Relationships between (A) annual NEE and growing-season precipitation, and (B) annual NEE and average temperature for the month of peak NEE, varying between April and May for spring crops (wheat, corn, and canola), and June and July for grasses (prairie and switchgrass). Relationships, for wheat crops only, between GPP or R_e with (C) growing-season precipitation (February–May), and (D) average temperature during the month of peak NEE (April or May).

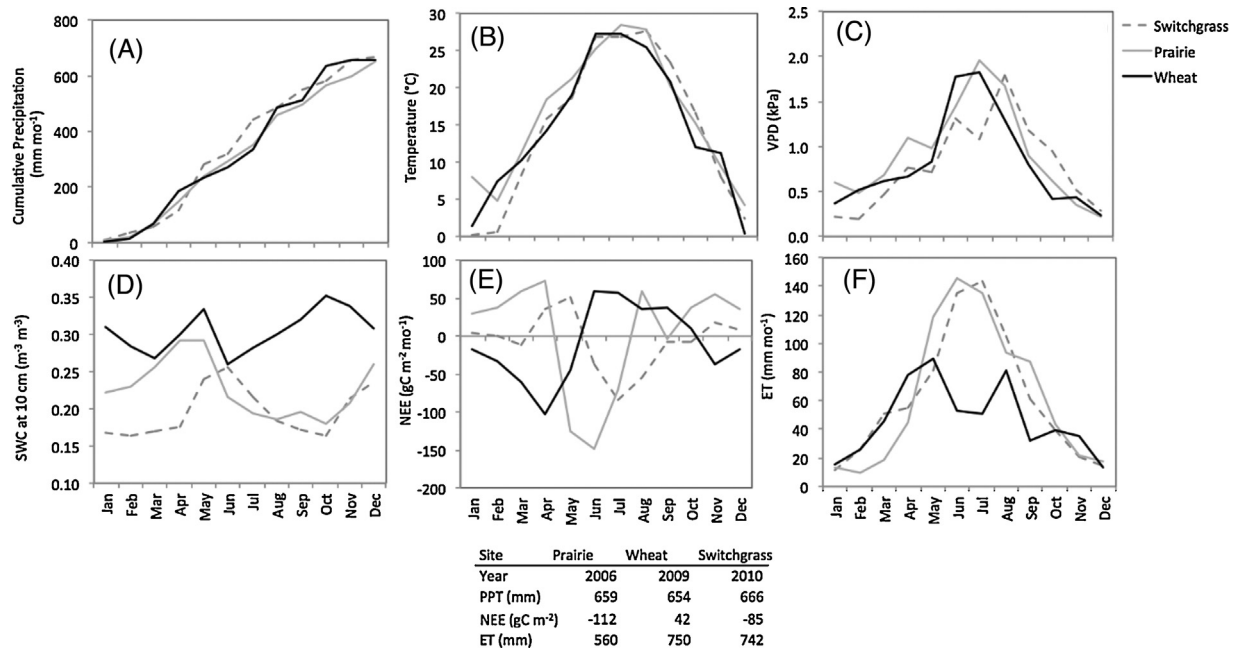


Fig. 8. Climate and fluxes measured at the three research sites in different calendar years that had similar climatic conditions: (A) precipitation, (B) temperature, and (C) vapor pressure deficit. Changes in vegetation between sites led to large variability in net ecosystem exchange (E) and (F) evapotranspiration. Annual totals are noted in the table.

$n = 10$, $R^2 = 0.89$, slope = -0.90 , intercept = 99 mm, $p < 0.05$). A decrease in carbon uptake (more positive NEE) was observed with an increase in temperature during the month of peak NEE for summer grasses, but not for spring crops (Fig. 7(B)). Grasses switched to net carbon sources when monthly averaged temperatures during the month of peak NEE (June or July) exceeded 28.4 °C. We examined which of the carbon fluxes – GPP or R_e – was more sensitive to these climatic drivers. Here we used observations of wheat crops only, to isolate the effect of climate from vegetation type. Although overall relationships were not strong, the linear correlation with growing-season precipitation (Fig. 7(C)) and temperature (Fig. 7(D)) was stronger for GPP ($R^2 \sim 0.45$) than for R_e .

To examine the control of vegetation type and phenology on fluxes, we compared the three measured ecosystems during years with similar total precipitation amounts (660 ± 6 mm year⁻¹; 3 year average \pm SD; Table in Fig. 8), similar seasonal distribution of rain events (Fig. 8(A)), and similar pattern in temperature (Fig. 8(B)). Despite the similarity in meteorological conditions, the differences between vegetation types led to large differences in fluxes and soil moisture conditions between these ecosystems. Peak NEE (highest uptake) was measured in April at the wheat field, in June at the prairie site, and in July at the switchgrass site (Fig. 8(E)). Although precipitation was evenly distributed throughout the year, soil moisture had a bimodal trend at the prairie and switchgrass sites, with lower summer values, due to enhanced soil drying under high summer temperatures (Fig. 8(D)). Indeed, high ET fluxes were measured between May and August for the prairie and switchgrass sites (Fig. 8(F)). At the crop field site, the lack of summer vegetation after harvest in May decreased ET fluxes, allowing conservation of soil moisture even under high summer temperatures.

3.4. Management practices and fluxes

3.4.1. Crop site only

A marked increase in GPP was observed following fertilizer application (Fig. 4(E)); for example: October 2004, December 2006, October 2009, and October 2010). A decrease in GPP was observed

after herbicide treatment (Fig. 4(E)); for example: September 2006, July 2007, May 2011), which was applied to stop weed growth and minimize noncrop water consumption. Subsequent to tillage, an increase in R_e was observed in some years (Fig. 4(E); July 2003 and July 2011), but not in others (Fig. 4(E); July 2009 and July 2010), implying tillage had a partial affect on R_e , if at all. No difference was observed in total NEE between years with tillage and those without (inline with Anthoni et al., 2004). A decrease in net carbon release (less positive or more negative NEE) was observed in most years in the short period directly following wheat harvest (Fig. 4(D)); for example: March 2004, March 2007, July 2009, June 2010). This increase is related to harvests conducted after the vegetation has already reached senescence (Aubinet et al., 2009). In years with no summer crops and inefficient weed treatment, uptake was still observed (Fig. 4(D and E)); for example: 2004 and 2007), and related to secondary regrowth of crops and weeds (Ammann et al., 2007; Béziat et al., 2009). Although the causal effect was not directly linked, measurements during the severe drought year of 2010–2011 suggest that application of tillage, fertilization, and burning had little or no effect on the NEE, due to strong water limitation.

The effect of management practices on ET fluxes appeared to be even more distinct than those on carbon fluxes. A clear decrease in ET was observed in most years after harvest (Fig. 4(D)); June 2003, July 2005, June 2006, May 2009, May 2011, May 2012). The decrease in summer ET after harvest was most apparent when compared to the two unmanaged sites (Fig. 8). At the prairie and switchgrass sites, the combination of soil evaporation and plant transpiration depleted soil moisture. In the crop field site, without the presence of vegetation, soil moisture was preserved throughout the summer, and created improved conditions for autumn crop establishment.

4. Discussion

Results from this study show that droughts lead to a reduction in NEE at the prairie and switchgrass sites, and to a lesser extent at the crop site. Previous studies presented similar trends for the

Great Plains (Bates et al., 2006; Heitschmidt and Vermeire, 2006; Kwon et al., 2008), and our study was able to quantitatively describe the relationships between NEE and climate: crops became a net carbon sink in all years receiving 100 mm of precipitation or more, during a four-month period synchronized with the growing-season (February–May for wheat, and March–June for corn and canola); grasses (prairie and switchgrass) became net carbon sinks only when receiving 350 mm of precipitation or more during the growing season (April to July for prairie, and May to August for switchgrass; x -intercept, Fig. 7(A)). Although the regression lines for grasses and crops were not significantly different (ANCOVA p -value = 0.14), the higher slope of the NEE versus growing-season precipitation relationship for grasses may indicate that grasses were more sensitive to changes in growing-season precipitation than crops.

We explain these relationships as follows. Although precipitation in the Southern Great Plains is normally higher during the summer season than the spring season, warm summer temperatures enhance evaporation, leading to drier soil conditions in summer. Therefore, crops and grasses experience different climatic conditions during their growing season (Fischer et al., 2007; Hanan et al., 2005). Based on our 10-year dataset, 36% of total precipitation falls on average during the wheat-growing season (February and May), and 44% of total precipitation falls during the growing season of prairie and switchgrass (May–August). Even so, soil moisture was lower during the grass-growing season than the wheat-growing season (Fig. 8(D)). Lower soil moisture may exacerbate the adverse conditions of high temperatures on productivity: the strong negative linear relationship observed between growing-season temperature and annual NEE for grassland, but not for crops (Fig. 7(B)) is explained by the hot temperatures predominant during summer ($28 \pm 2^\circ\text{C}$ monthly average for July, and up to 32°). In contrast, changes in the overall mild temperatures during spring ($16 \pm 2^\circ\text{C}$ monthly average for April) have a smaller negative effect on productivity.

NEE partitioning at the wheat field showed that the decrease in NEE during drought periods was derived from GPP suppression, more than being derived from R_e increase (Fig. 7(C and D)). Indeed, during periods of low soil water content and high temperatures, further decreasing photosynthesis, a clear midday depression in NEE (less uptake) was observed in all measured ecosystems (not shown).

Of special concern are heat waves in spring and early summer, which occur during the grass germination period. Drought conditions that develop in early growth stages often lead to irreversible low productivity, because stomatal closure restricts assimilation and produces smaller flag-leaf sizes (Dufranne et al., 2011; Lund et al., 2012). In the case of the newly planted switchgrass field with juvenile root systems, the dry summer of 2011 killed the immature plants, and the field did not produce biomass even in the following wet year.

The few studies on crops and grasses rooting patterns in the Great Plains indicate that these plants are mainly shallow-rooted, with >70% of root biomass in the top 30 cm of soil (Weaver, 1958), and extract most of their water from the top 50 cm of the profile (Eggemeier et al., 2009). Results from this study show that ET surpasses precipitation in drought years in all measured sites (Table 1), suggesting that roots tap water from deeper sources during droughts, where moisture has been accumulated in previous, wet years. For example, ET was 142% of precipitation during the extreme drought year of 2010–2011 at the crop field site, and more than 110% during all measured years in the prairie and switchgrass sites. In addition, the variability in soil-moisture content at the beginning of the growing season at all three sites (Figs. 4–6(C)) indicated non-uniform antecedent conditions, and a clear soil-moisture memory effect. This phenomenon,

characteristic of drought conditions (Wagle and Kakani, 2012), is not expected to persist throughout prolonged droughts, after which soil moisture is exploited even at depth.

In the Great Plains grasslands, the relative abundance of warm-season C_4 species versus cool-season C_3 species follow a north-south temperature gradient, with higher abundance of drought-tolerant C_4 species in the drier, southern regions (Luauenroth et al., 1999 Teeri and Stowe, 1976). It is therefore counterintuitive that, based on our study, summer-growing species (which include C_4 switchgrass and most of the grasses in the prairie site) were more sensitive to precipitation changes than C_3 species (winter-wheat). These results indicate that C_3 versus C_4 species distribution may be more sensitive to seasonal water availability than to temperature (Vermeire et al., 2009). Similar conclusions arise from historical evidence, showing a prolonged shift into cool-season grasses during the 1930s droughts (Weaver and Albertson, 1943), and during paleo-drought cycles in the Great Plains (Clark et al., 2002). In both cases, the decrease in summer C_4 grass cover led to a higher extent of bare soil, more erosion, and more frequent dust storms.

Under mid-21st century climate projections for the Southern Great Plains, conditions might be more damaging for native grasses than for spring-growing crops. A 10% increase in precipitation is expected in spring, but a 10–30% decrease in precipitation and a 2.4 – 2.9°C increase in temperature is expected during the summer seasons (in comparison to the 1981–2000 average; Patricola and Cook, 2012; Westcott and Trostle, 2013). Measurements during 2012 may shed some light on the consequences of such climatic conditions on the ecosystems of the Southern Great Plains. This was the most severe and extensive drought in the last 25 years, with devastating impacts on crops, food for livestock, and potential effects on food prices (U.S. Drought 2012: Farm and Food Impacts). Similar to climate projections for the Southern Great Plains, the spring of 2012 was relatively wet, but drought conditions begun in June, and rapidly increased in severity, peaking in September. Although more than 65% of the contiguous United States was under drought conditions in 2012, damaging corn and soybean fields, only a few changes in wheat production of the Midwest were recorded (Elliott et al., 2013). At our field site, 338 mm of rain fell during the wheat-growing season, resulting in high carbon uptake (NEE = $-388\text{ gC m}^{-2}\text{ year}^{-1}$ for the wheat season November 2011–April 2012). After wheat harvest, the field was planted with cowpeas, but because of extreme dry-summer conditions (83 mm; May–August 2012), this crop did not prosper and resulted in a net carbon release (NEE = $144\text{ gC m}^{-2}\text{ year}^{-1}$ for the cowpeas season, May–December 2012).

In addition to the seasonal advantage of the spring-growing wheat over the summer-growing grasses, our study suggested that management practices at the crop field site were effective in decreasing water loss and increasing carbon uptake. We note that the effect of management practices could not be entirely separated from the impacts of climate and phenology on fluxes—the 10-year pattern in NEE and ET fluxes was clearly dominated by climate, but a subtler, shorter-term effect could be attributed to management practices. On annual time scales, management practices seemed to increase carbon uptake and decrease ET losses, when compared to the switchgrass and prairie sites (Table 1, Fig. 8). However, without irrigation, crop management could not overcome the adverse effect of severe droughts, especially during the summer seasons (management practices at the crop field were maintained at a low cost, as typical for the Southern Great Plains, due to moderate and variable year-to-year yield economical income (Vocke and Ali, 2013)). During the summers of 2005 (corn), 2006 (soybean), and 2012 (cowpeas) crops failed, and the field was a net carbon source.

Recurring summer-drought conditions indicate that these regions may become drier over time, and suggest a possible vegetation shift. For native ecosystems, a higher dominance of

cool-season C₃ species may be expected, and for managed ecosystems, stricter limitations on summer-growing crop-type varieties may apply. Indeed, Malcolm et al. (2012) found that, based on agricultural modeling for 2030, wheat and corn prices are expected to be less sensitive to climate change projections in comparison to soybeans. This conclusion calls for a continuing re-evaluation of the current decrease in U.S. wheat-harvested area, which dropped by more than 30% since its peak in 1981 (Vocke and Ali, 2013). While the main reasons for this change were economic (a decline in wheat profitability relative to other crops), it will be important to note whether commodity prices change commensurably under future climate scenarios (Malcolm et al., 2012; Westcott and Trostle, 2013).

5. Conclusions

For three different vegetation types characteristic of the U.S. Southern Great Plains – crops, prairie, and switchgrass – a reduction of approximately 45 gC m⁻² (for crops) and 55 gC m⁻² (for prairie and switchgrass) in net carbon uptake occurred for each 50 mm decrease in precipitation during the growing-season. To become net carbon sinks (negative NEE) grasses needed at least 350 mm of rain during a four-month growing season (May–August), while crops needed only 100 mm for the same length of period but earlier in the year (February–May). Crops were more productive than prairie grass and switchgrass even though more precipitation falls in the summer (the main grass-growing season), because high temperatures caused soil-moisture deficit, with the spring (the main crop-growing season) less likely to have dry soil conditions. In addition, results from this study suggested that management practices were successful in increasing GPP during the growing season (fertilization) and suppressing ET and R_e after senescence (harvest and removal of secondary growth). However, under severe drought conditions, even summer crop rotations at the agricultural field site turned into a net carbon source. In light of future projections for wetter springs and drier summers in the Southern Great Plains region, our study suggests that native C₄ grass ecosystems may be increasingly vulnerable to climate change.

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