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Differential responses of native and managed prairie pastures to environmental variability and management practices

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ABSTRACT

Future weather and climates, especially rainfall, are expected to have larger variability in the Southern Plains of the United States. However, the degree and timing of environmental variability that affect productivity of pastures managed differently have not been well studied. We examined the impacts of environmental variability on grassland productivity using 17 years of gross primary productivity (GPP) data for co-located native and managed prairie pastures in Oklahoma. We also considered the interactive effects of management factors and environmental variability into the regression models and identified the critical temporal windows of environmental variables (CWE) that influence annual variability in GPP. Managed pasture (MP) showed greater variability of GPP than did native pasture (NP), particularly with reduced GPP in drought years. The resilience of native prairies under unfavorable climate extremes was evident by lower GPP anomalies in NP than MP during the 2011–2012 drought. Although both pastures experienced the same degree of environmental variability, the CWE affecting GPP was significantly different between NP and MP due to the modulating impact of management practices on the responses of GPP. Not only the range but also the timings of the CWE were different between NP and MP as MP was more responsive to the spring temperature and fall rainfall. Our findings warrant the incorporation of MP as a different commodity from NP when accounting for the ecosystem responses to environmental variability in global climate models.

1. Introduction

Beef cattle production is the main economic activity in agriculture in the Southern Great Plains (SGP) of the United States. Grasslands that are primarily used as grazing pastures constitute about 45% of land area in the SGP (Coppedge et al., 2001; Ji and Peters, 2003) and are also one of the most sensitive and important ecosystems of North America. The pasture productivity is closely linked with the variability in environmental factors and management practices, and it is vital to deal with the challenges posed by uncertain climate conditions including variability and change. Environmental variability and management practices in isolation or in combination influence the properties of ecosystems and the flows of energy and materials through them. The SGP is a dynamic region with respect to climatic variability, particularly rainfall (Flanagan et al., 2018; Hoerling et al., 2012; Patricola and Cook, 2013; Qin et al., 2007; Weaver et al., 2016). The ecosystems of this region have responded enormously to the dynamics of dry and wet periods including long-term drought, flash drought, and rapid transitions between dry and wet conditions (Bajgain et al., 2015; Basara and Christian, 2018; Basara et al., 2013; Christian et al., 2015). The ecosystems' feedback in terms of productivity is generally positive in abundant rainfall periods and is negative when impacted by droughts. Modeling results show large uncertainty in the estimates of plant productivity changes with the changes in temperature, available soil moisture, and rainfall that interactively influence plant growth (Heinsch et al., 2006; Hilker et al., 2008). The effects of environmental variability are likely to be exacerbated in ecosystems that are altered by anthropogenic interventions (Cramer et al., 1999; Huntzinger et al.,

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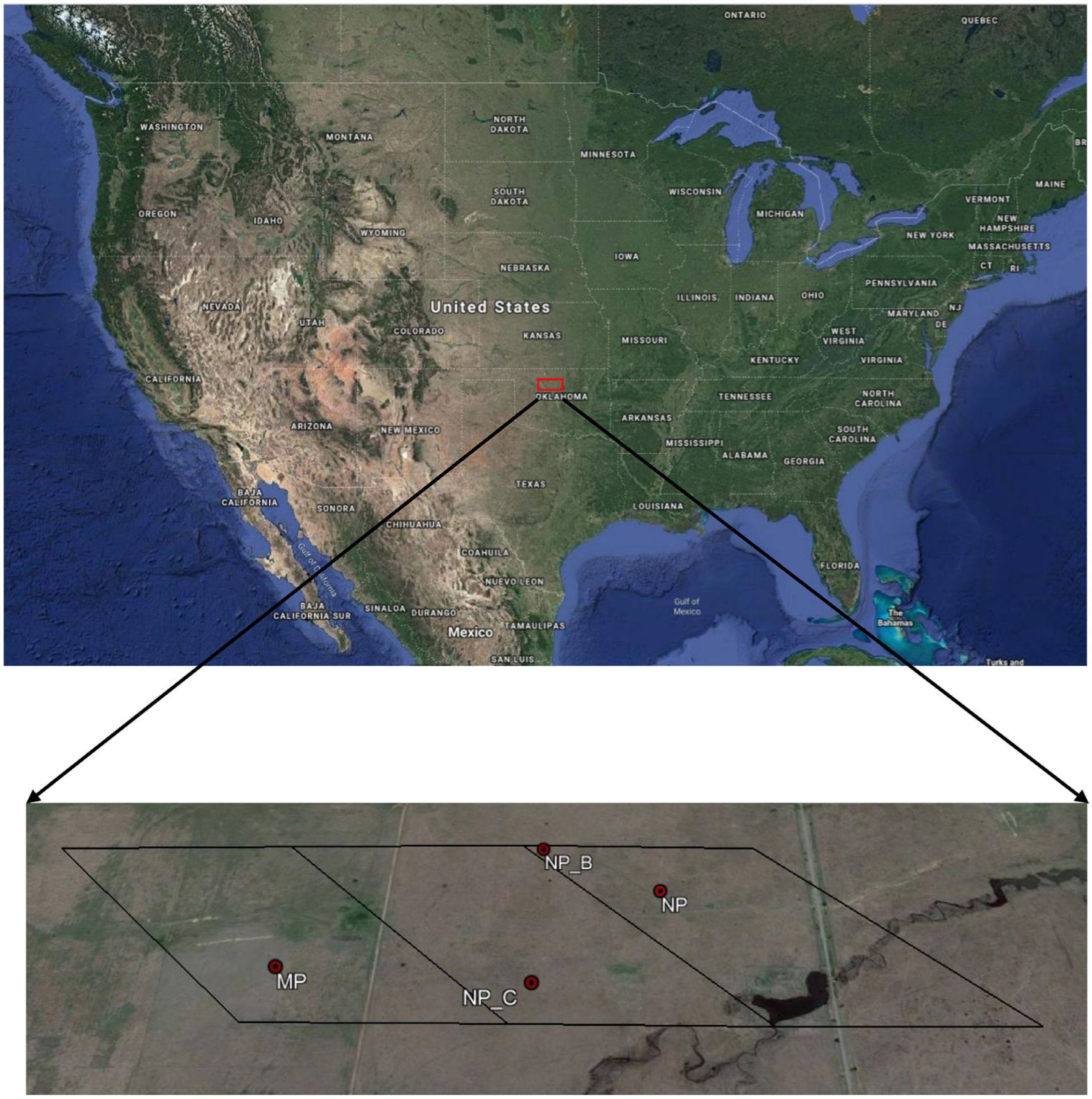

Fig. 1. Location and biophysical features of the study sites. The white boundary line of the rectangle represents the size of MODIS pixel and the red dots inside the rectangle indicate the flux tower location (NP_B: Native pasture burned; NP_C: Native pasture Control, NP: Native Pasture and MP: Managed Pasture). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2012; Thebault et al., 2014). With the US population expected to increase from 319 million to 417 million between 2014 and 2060 (US Census, 2014), the demand for beef is also expected to grow annually. Thus, growing demand imparts pressure on grasslands to produce more beef by grazing at higher stocking densities or achieved by converting native pastures into managed pastures.

Native pastures are converted into managed pastures with the aim of enhancing plant production potential. Activities like fertilizer application, deposition of manure by livestock, burning, and harvesting biomass can substantially influence the fundamental biophysical processes such as mineralization and decomposition because these management effects change the soil carbon (C) and nitrogen (N) pools (Egan et al., 2018; Zhou et al., 2017a). Managed pastures undergo various changes in quick succession compared to natural pastures caused by management intervention (Aguiar et al., 2017). The frequency of biomass removal either in the form of harvesting biomass or grazing affects the pasture productivity as well as the carbon and water budgets of the whole ecosystem (Herrero et al., 2016; Soussana et al., 2004). Process-based models have been increasingly used for simulating the inter-annual and seasonal variations of grassland production (Graux et al., 2011; Riedo et al., 1998). However, most of the existing models simulate managed grasslands either as natural grasslands or as intensively managed croplands (Chang et al., 2017; Drewniak et al., 2015; Reick et al., 2013; Rolinski et al., 2018). Interactions of multiple factors such as water availability, temperature, and management intensity add complexity to the response of grasslands to climate change. Therefore, to make the model predictions more realistic, the impacts from both environmental variables and management need to be sufficiently assessed. The dry-wet episodes during the study period and different management practices between two adjacent pastures provided the opportunity of examining variations in gross primary production (GPP) and the potential impacts of both environmental variability and management practices.

Environmental factors generally impact grassland productivity through changes in different weather elements such as temperature and rainfall, and the responses vary when environmental variability interacts with management practices (Craine et al., 2012; Xu et al., 2018). Most studies analyzed annual or seasonal mean of environmental variables for explaining the variability in GPP (Brookshire and Weaver, 2015; Chou et al., 2008; McCulley et al., 2005; Nippert et al., 2006). Few studies refined the time window for a higher temporal resolution required for understanding variability within the season which is more related to critical ecological processes than annual variability (Craine et al., 2012; Dukes et al., 2005; Robertson et al., 2009).

Although narrower windows (weekly or monthly) for environmental variables have been used in these studies, the windows are fixed, and the relationship of environmental variables from those selected windows and either monthly or annual productivity had been investigated. This study analyzes the relationship of environmental variables (rainfall and temperature) at the daily temporal scale with the growing season GPP. We used the climwin R package (Bailey and van de Pol, 2016; Pol et al., 2016) to identify the critical temporal window of environmental variables (CWE) during the growing season, which may cause large variability in GPP. Thus, (1) tracking interannual variability in GPP (and GPP anomalies) due to different weather conditions and (2) identifying the CWE in differently managed pastures will help to answer the following research questions:

a) How did the productivity of native and managed pastures change during the 17 years (2000–2016) in response to a wide range of variability in environmental conditions?
b) Does CWE for GPP variability, based on anomalies, differ for native and managed prairie pastures?
c) Do management practices change the CWE?
d) Does interaction of management practices such as harvesting biomass, burning, and fertilizer application with environmental variability play an active role in explaining the anomalies of GPP?

2. Methods

2.1. Study site

Four grassland sites: three native pasture sites [(i) NP (35.54865 N, 98.03759 W) (ii) NP_B (35.5497 N, 980,402 W, (iii) NP_C (35.5497 N, 98.0401 W)]; and one managed pasture site (MP) (35.54679 N, 98.04529 W) were used in this study. The sites are located at the United States Department of Agriculture-Agricultural Research Service (USDA-ARS), Grazinglands Research Laboratory (GRL), El Reno, Oklahoma, USA (Fig. 1). The 30-year (1980–2010) average daily maximum and minimum temperature of the study sites were 23 $^{\circ}C \pm 8.7$ °C and 8.9 $^{\circ}C \pm 6.4$ °C. The long-term (1980–2010) average total annual rainfall was 855 mm ± 44.7 mm. The eddy covariance data from NP_B and NP_C (2005–2006), NP and MP (2015–2016) sites were used to validate the GPP values simulated from the satellite model (described later) for long term (2000–2016) productivity analysis at the NP and MP sites. The details of the two sites along with the management history over time are described below:

Native pasture (NP): Tallgrass prairie is predominantly warm season vegetation representing the native, mixed species grassland of Oklahoma. The site has big bluestem (*Andropogon gerardi* Vitman) and little bluestem (*Schizachyrium halapense* (Michx.) Nash.) as dominant species. The soil is classified as Norge loamy prairie (Fine, mixed, thermic Udertic Paleustalf) with a depth greater than 1 m, high water holding capacity, and slope averaging about 1%.

Historical management of the NP has varied over time. This pasture did not receive a prescribed spring burn from 1990 to 2005 but was sprayed with a broad-leaf herbicide occasionally to control weeds, and grazed at moderate stocking rates through 2003. The pasture was not grazed from 2004 through 2006 to support a flux experiment comparing burned and unburned prairie (Fisher et al., 2012). On March 9 (DOY 68), 2005 the northern half of the pasture received a prescribed spring burn in the form of a cool, slow-moving fire, while the remaining half was left unburnt. The litter layer at the time of burn was moist, and the winds were not strong (<5 m s^{-1}). Therefore, a large portion of litter remained on the soil surface post-fire. Grazing at moderate stocking rates resumed in 2007 and continued through 2011. From 2012 through to the present, the NP was combined with three other pastures of similar sizes into a year-round system of rotational grazing with a 50-head herd of mature cows with calves. Pastures were grazed for about 30-day periods, alternating with 90-day rest periods, with individual pastures receiving prescribed spring burns on a 4-year rotation; the NP was burned on 3/6/2013 as part of the normal assigned management.

The 2013 prescribed burn was a hot, fast moving fire (~6 m s^{-1}, the rate at which the fire covers the ground) with a large fuel load (estimated around 6 Mg ha^{-1}, including standing dead and surface litter) which had built up since the last burn in 2005. The resulting fire consumed all standing biomass and surface litter; remnant materials were essentially a fly ash. Grazing at the site is represented by black doubled head arrows in Fig. S1. The study site was grazed for nine months (Jan-Feb, Jun-Dec) in 2015 and for six months in 2016 (Jan, May-Jun, Aug-Oct) at different grazing intensities.

Managed pasture (MP): The pasture is an introduced warm-season, pasture and was planted with old world bluestem in 1998 (*Bothriochloa caucasica* C. E. Hubb.) (Coleman et al., 2001).The soil is classified as Norge silt loam characterized by fine, mixed, active, thermic Udic Paleustolls (Fischer et al., 2012; Zhou et al., 2017b). The average land slope is about 2% within the flux tower footprint of about 300 m.The MP has received long-term management practices including burning, baling, fertilizer, herbicide, and cattle grazing (Northup and Rao, 2015; Zhou et al., 2017b). The MP was burned four times (2001, 2009, 2010 and 2014) in the 17-year study period. The site was periodically sprayed with broad-leaf herbicide to control weeds. The pasture was under rotational grazing, except from 2004 to2007 because of flux-experiment. With the resumption of grazing in 2007 the pasture was fertilized periodically (67.25 N kg ha^{-1} in 2007 and 2009 and 44 kg N ha^{-1} in 2014). Significant biomass was removed from the pasture by harvesting biomass every year from 2008 to 2011 and in 2014. More details on the management practices are presented in Appendix S1and Figure S1.

2.2. Data

Eddy Covariance data in 2005/2006 in native tallgrass prairie sites (NP_B and NP_C)

Two years (2005 and 2006) of GPP data for NP_B and NP_C were acquired from the AmeriFlux website (http://ameriflux.ornl.gov/ and was used to validate the GPP simulated from the model for the study sites.

Eddy Covariance data in 2015–2016 from NP and MP

Net Ecosystem Exchange (NEE) from the NP and MP were continuously measured from Jan 2015 to Dec 2016 using eddy covariance (EC) systems consisting of a three-dimensional sonic anemometer (CSAT3, Campbell Scientific Inc., Logan, UT, USA) and an open path infrared gas analyzer (LI-7500, LI-COR Inc., Lincoln, NE, USA). The raw data, collected at 10 Hz frequency (10 samples sec^{-1}), were processed using the EddyPro processing software (LI-COR Inc., Lincoln, NE, USA). The sensors were mounted at the height of 2.5 m and the fetch of the fluxes measured by the tower was within 500 m radius. The software employed several corrections, and the final output of 30-min fluxes (NEE) were obtained. The measured NEE was gap-filled and then partitioned into GPP and ecosystem respiration (ER) based on the short-term temperature sensitivity of ER (Lloyd and Taylor, 1994; Reichstein et al., 2005). Daily GPP was obtained by summing of each 30-min partitioned GPP values. The daily values were then aggregated into 8-day averaged daily GPP to match the temporal resolution of GPP (GPP_{VPM}) derived from Vegetation Photosynthesis Model (VPM). The details on the instruments set up and data processing are described in previous publications (Bajgain et al., 2018; Zhou et al., 2017b)

GPP data from GPP_{VPM}

The VPM (Xiao et al., 2004) was employed to simulate gross primary production (GPP_{VPM}) from 2000 to 2016 at 500 m spatial resolution. The model estimates daily GPP (g C/m^2/day) as a product of photosynthetically active radiation absorbed by chlorophyll of plants ($APAR_{chl}$) and the efficiency of plants to convert absorbed PAR into carbon (ε_g):

$$GPP = APAR_{chl} * \varepsilon_g \quad (1)$$

where, APAR $_{chl}$ is a product of PAR and, $fPAR_{chl}$ which is estimated as a linear function of the enhanced vegetation index (EVI)

$$fPAR_{Chl} = (EVI - 0.1) * 1.25 \quad (2)$$

$$\epsilon_g = \varepsilon 0 * T_{scalar} * W_{scalar} \quad (3)$$

$$T_{scalar} = \frac{(T - T_{max})*(T - T_{min})}{(T - T_{max})*(T - T_{min}) - (T - T_{opt})^2} \quad (4)$$

$$W_{scalar} = \frac{1 + LSWI}{1 + LSWI_{max}} \quad (5)$$

where fPARchl value was calculated from EVI, obtained from the spectral reflectance data measured by the MODIS platform (Zhang et al., 2016, 2017). Because the ratio of C_3 to C_4 plants affects primary production at any given location (Epstein et al., 1997), the model adjusted this factor by deriving maximum light-use efficiencies of C_3 (0.035 mol CO_2 mol^{-1} PAR) and C_4 (0.0525 mol CO_2 mol^{-1} PAR) and the area of C_3 and C_4 at each 500 m MODIS pixel, calculated from the Cropland Data Layer (CDL) (Zhang et al., 2017). Annual GPP_{VPM} was calculated by summing the 8-day dataset for each year and the GPP_{VPM} anomalies for each 8-day was calculated from the mean 8-day values from 2000 to 2016.The global GPP_{VPM} dataset is available at https://doi.org/10.1594/PANGAEA.879560

Mesonet dataset

Daily rainfall and daily average air temperature data from 2000 to 2016 at the Oklahoma Mesonet El Reno station were downloaded from the Oklahoma Mesonet website (http://www.mesonet.org/index.php/weather/daily_data_retrieval).

The Oklahoma Mesonet consists of instruments mounted on or near a 10-meter-tall tower which continuously record measurements and aggregate into five minute observations (McPherson et al., 2007). For the anomaly calculation, we used 30-year climatic normal data estimated by the Mesonet. The drought and wet years were identified based on the standard deviations (± 2.5) from the 30-year rainfall data.

2.3. Methods

i) Validation of GPP_{VPM} dataset by using a linear correlation with EC datasets

The GPP_{VPM} values were compared with EC-derived GPP (GPP_{EC}) to assess the validity of the model simulations. We used three statistics parameters: RMSE (root mean squared error), MAE (mean absolute error), and R^2 (coefficient of determination), to evaluate the model performance. The 8-day composite GPP_{EC} and GPP_{VPM} values were linearly regressed against each year and site for determining R^2, RMSE and MAE values. The RMSE and MAE values were calculated using the following equations:

$$RMSE = \sqrt{\frac{\sum_j^i (GPP_{EC} - GPP_{VPM})^2}{j}} \quad (6)$$

$$MAE = \left[\frac{\left(\sum_j^i |GPP_{EC} - GPP_{VPM}| \right)}{j} \right] \quad (7)$$

where j is the total number of observations.

ii) Identification of critical temporal window of environmental variables (CWE) based on regression models

The critical period of temperature and rainfall during the growing season sensitive to GPP_{VPM} anomalies was identified for better understanding how the timing of environmental variability affected grassland productivity. The critical temporal window was identified based on a sliding window method, a window of specified length (one day in our study) was moved over the dependent variables (i.e., temperature and rainfall) separately. Then average temperature or sum of rainfall on each specified window of each year was regressed against the nearest 8-day GPP_{VPM} anomalies. The steps were repeated by moving across by one day to create a series of regression models. The approach is based on the "climwin R package" (Bailey and van de Pol, 2016; Pol et al., 2016) . Firstly, a baseline model (baseline= lm (gpp~1) for both pastures was determined, which is basically a linear model with null effects of environmental variables. Secondly, candidate models were created by selecting weather variables. In this study, we chose average temperature and sum of rainfall as environmental variables and used the linear functional relationship describing GPP_{VPM} anomalies (8-day) to different windows. Finally, best regression models based on the least values of Akaike Information Criteria (AIC, (Akaike, 1973)) values as calculated using the Eq. (8) were selected

$$\Delta AICc_{model\ i} = AICc_{model\ i} - AICc_{baseline\ model} \quad (8)$$

where, i represents the candidate model

Regression models based on temperature or rainfall of the critical temporal period that determines the GPP_{VPM} anomalies were selected for both pastures separately. For example, if the best regression model which was built on the average temperature of May1 to May 10 showed the least AIC values for the MP, then this period was considered CWE of temperature for MP. This calculation was done for temperature, rainfall, and the interaction between them for both pastures. (See Appendix S1: Identification of critical temporal window of environmental variables (CWE) and Hypothesis testing and Fig S2 for more details).

3. Results

3.1. Seasonal dynamics and inter-annual variations of GPP_{EC} (2015–2016) at NP and MP

At the study site, varying rainfall between 2015 and 2016 (Fig. 2a) impacted the magnitudes of GPP_{EC} rates at NP and MP differently. During 2015, the sites received approximately 1140 mm of rainfall during the growing season (March-September), and 1273 mm annually, which were nearly double the seasonal (532 mm) and annual (635 mm) rainfall in 2016. The MP exhibited higher GPP_{EC} rates (half hour), especially during the months of May-August in 2015 and in fall (August-October) in 2016. The usual dry period (June -August) of Oklahoma was different in 2015 due to anomalous rainfall and the MP showed strong responses to the rainfall with higher GPP_{EC} rates as compared to NP during summer months in 2015 (Fig 2b). Similarly, the productivity of MP during the fall of 2016 was higher in response to the normal fall rainfall with higher rates of GPP_{EC}.

The differences in carbon fluxes (NEE, GPP and ER) between years and sites at daily scales are presented in (Fig. 3). The results showed large differences in daily and annual values of carbon fluxes between NP and MP at both years. Both pastures had larger cumulative annual values of GPP_{EC} in 2015 (NP= 1735 and MP= 1789 g C m^{-2}) than 2016 (NP= 1128 and MP=1372 g C m^{-2}), most likely due to higher and evenly distributed rainfall in 2015 (Fig. 2a, Table 1). Despite seasonal variations, GPP_{EC} and ER in both years were higher in MP than NP (Fig. 3). However, the carbon uptake (negative NEE, the balance between GPP_{EC} and ER) by MP was similar in both years.

3.2. Seasonal dynamics and inter-annual variation of GPP_{EC} and GPP_{VPM} in NP_B and NP_C (2005–2006) and NP and MP (2015–2016)

A comparison of the seasonal dynamics of GPP_{VPM} and GPP_{EC} for 8 site-years are presented in Fig. 4. The seasonal peaks of GPP_{VPM} matched the seasonal peaks of GPP_{EC} in all site-years. The model showed strong performance during the peak growth period with some discrepancies in 2005 at the NP_ site, where the VPM slightly overestimated GPP_{EC} in both 2005 and 2006. When linear regression was applied to GPP_{VPM} and GPP_{EC}, the results showed varied R^2 and slope values (Table 2). However, GPP_{VPM} explained most of the variation in

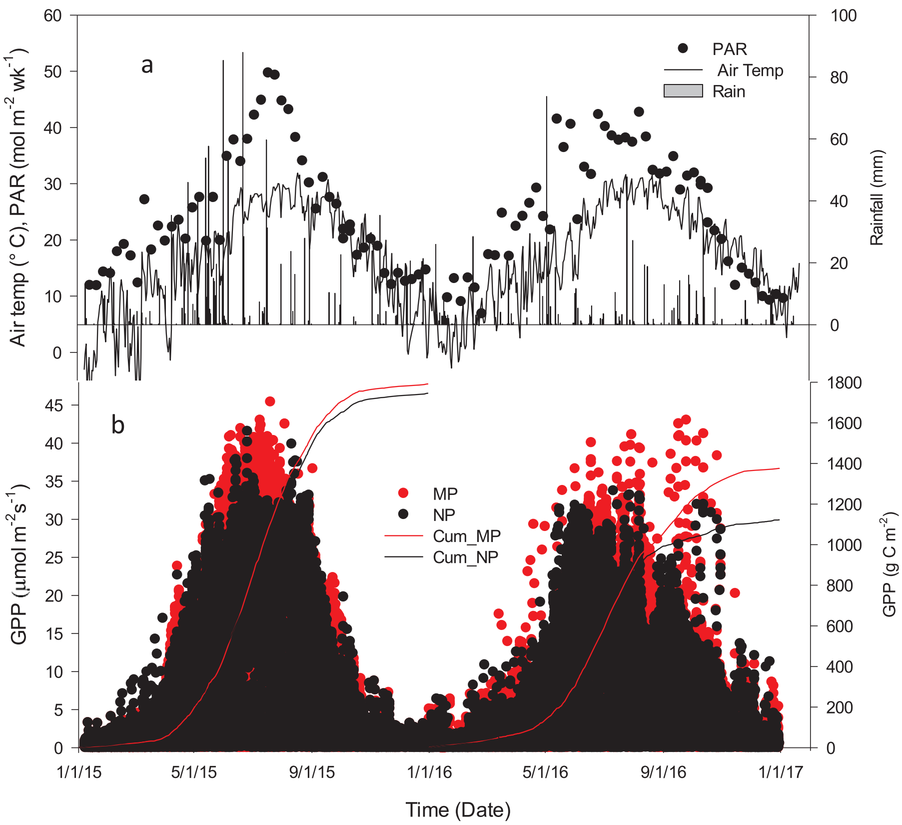

Fig. 2. Daily average air temperature, rainfall and weekly photosynthetically active radiation (PAR) at the study sites in 2015 and 2016 (a). Half-hourly gross primary productivity (GPP) values obtained from eddy covariance measurements from two pasture sites in 2015 and 2016 (b). The line is the representation of the cumulative values.

GPP_{EC} and the overall R^2 and slope values across sites and years were 0.88 (range = 0.81–0.94) and 0.85 (range = 0.7–0.99), respectively, suggesting slight underestimation of GPP_{EC} by the VPM which mostly resulted from NP_C site. Both RMSE and MAE statistics applied to the linear regrssion models yielded small values, indicating the GPP_{VPM} values were consistent with GPP_{EC}(Table 2).

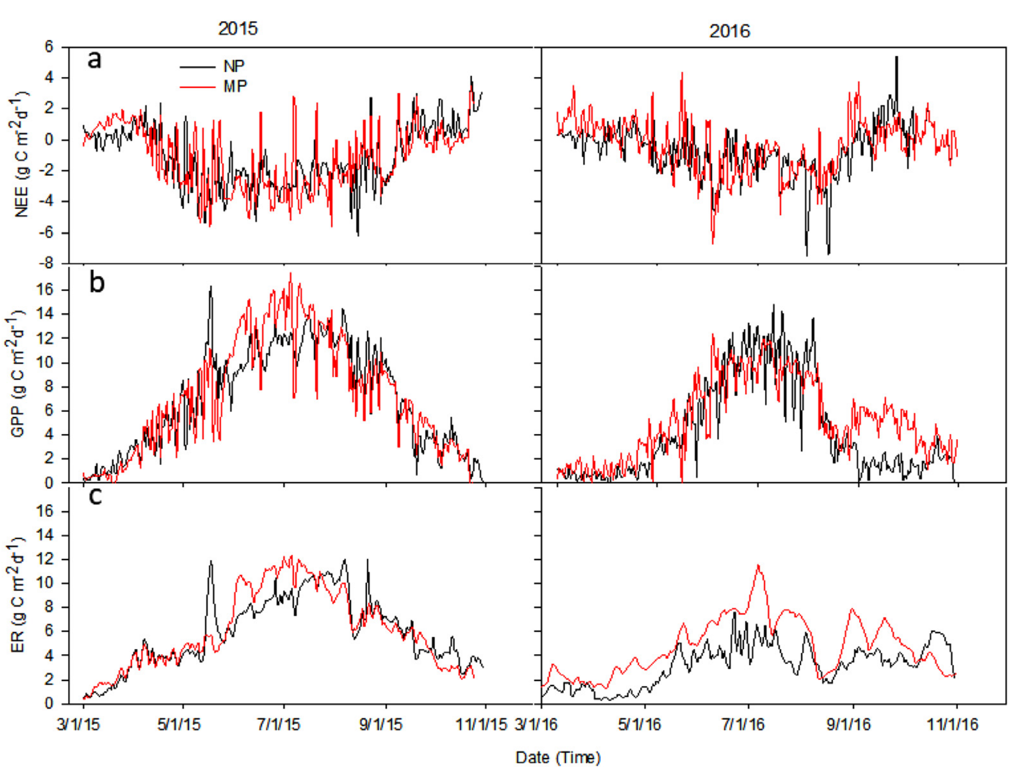

Fig. 3. The comparison of daily carbon fluxes: (a) net ecosystem exchange (NEE), (b) gross primary productivity (GPP), and (c) ecosystem respiration (ER in Managed Pasture (MP) and Native Pasture (NP) during growing seasons of 2015 and 2016.

Table 1
Seasonal mean temperature (T_mean) and seasonal total rainfall in 2000–2016 in comparison with study year average (2000–2016) and 30 –year mean (1981–2010) for El Reno OK, USA.

year	winter		spring		summer		fall		annual	
	Rain	T_mean	Rain	T_mean	Rain	T_mean	Rain	T_mean	Rain	T_mean
2000	193.8	7.12	307.85	19.28	250.19	26.15	257.3	6.73	1009.14	14.83
2001	141.73	4.12	214.63	20.46	134.62	25.8	116.08	9.56	607.06	15.26
2002	133.6	5.11	194.56	19.28	151.13	25.35	311.91	7.86	791.21	14.45
2003	50.29	4.3	147.83	19.21	171.7	25.52	104.9	9.82	474.73	14.76
2004	87.63	5.82	129.79	19.72	318.52	23.64	347.98	9.86	883.92	14.48
2005	127.76	6.2	104.65	19.67	353.82	24.79	123.44	9.38	709.68	15.02
2006	76.71	7.66	211.07	21.62	214.38	25.52	126.49	9.45	628.65	16.17
2007	63.5	5.83	488.95	18.31	654.81	24.66	152.15	9.34	1359.41	14.6
2008	110.24	5.38	366.01	19.65	356.11	24.09	109.73	8.8	942.09	14.5
2009	41.66	6.54	267.46	19.31	259.84	24.14	225.81	7.5	794.77	14.4
2010	87.38	3.49	159.51	20.39	313.69	25.71	195.83	9.28	756.41	14.72
2011	62.99	4.89	146.81	21.84	152.65	27.55	279.65	9.36	642.11	15.9
2012	86.61	8.08	237.74	21.17	101.6	26.54	140.97	9.86	566.93	16.48
2013	139.19	5.16	423.16	18.21	433.58	24.55	161.54	7.48	1157.48	13.9
2014	28.45	3.38	141.73	19.86	278.89	24.63	161.04	9.33	610.11	14.37
2015	117.35	4.88	603.25	19.54	353.06	25.19	199.64	10.46	1273.3	15.09
2016	88.39	7.4	222.76	20.01	206.25	25.51	118.11	11.05	635.51	16.02
2000–2016	96.31	5.61	256.93	19.86	276.76	25.26	184.27	9.13	814.26	15
1981–2010	103.63	5.42	268.99	18.93	280.42	25.01	218.44	9.24	871.47	14.54

3.3. Effects of environmental variables on seasonal dynamics and inter-annual variation of GPP_{VPM} (2000–2016)

The degree in variation of GPP_{VPM} is discussed with reference to the variation in environmental conditions. The mean annual rainfall of the study site was 872 mm (30-year average, 1980–2010) and 814 mm (study period), with a standard deviation of 253 mm and coefficient of variation (CV) of 326% (SD). Further, the minimum and maximum annual recorded rainfall were 474 mm (in 2003) and 1273 mm (in 2015), respectively (Table 1). Based on the 30-year record, the drier years (2006, 2011 and 2012) had overall warmer summer temperature conditions whereas the wetter years (2007 and 2013) had cooler summer temperatures.

The 8-day average GPP_{VPM} (Fig.S3) illustrated how the magnitude of GPP varied seasonally and annually during 17 years at both sites. The magnitudes of GPP_{VPM} values varied greatly within seasonal scale between two pastures. Overall, the years with the greatest rainfall (2007, 2013, and 2015) showed higher GPP_{VPM} and the years with minimal rainfall (2003, 2006, and 2011) showed lower GPP_{VPM} in both pastures. Additionally, the MP showed relatively larger values of GPP_{VPM}

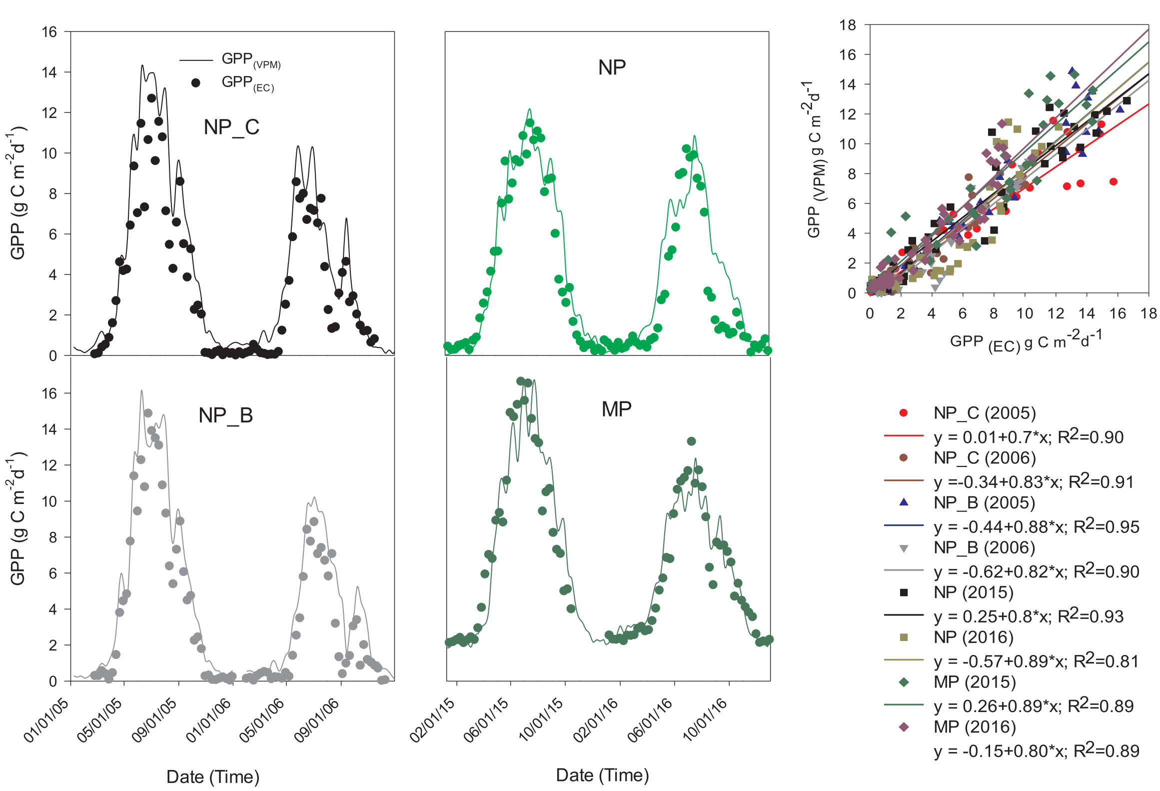

Fig. 4. Comparison of the seasonal dynamics of gross primary productivity (GPP) between VPM simulated and eddy covariance (a, b). The correlation between GPP_{VPM} and GPP_{EC} combined for different years and different sites (c).

Table 2
The performance of the Vegetation Photosynthesis Model (VPM) using simple regression between VPM-modeled GPP (GPP_{VPM}) and eddy covariance tower GPP(GPP_{EC}) based on Coefficient of determination (R^2), mean absolute error (MAE) and root mean squared error (RMSE). The GPP values in parenthesis represent the total annual values.

Site - Year		Mean GPP (g C/m²/day)					
		GPP_{VPM}	GPP_{EC}	Slope	R^2	RMSE	MAE
MP	2015	5.04	6.08	0.92	0.89	1.58	1.21
	2016	3.92	3.73	0.99	0.9	1.08	0.83
NP	2015	4.41	4.74	0.8	0.93	1.82	1.31
	2016	4.06	3.05	0.89	0.81	1.89	1.43
El Reno Burn	2005	5.25	4.86	0.88	0.94	1.59	1.14
	2006	3.2	2.39	0.82	0.9	1.52	1.14
El Reno Control	2005	5.11	4.12	0.7	0.9	2.38	1.55
	2006	3.21	2.78	0.81	0.88	1.27	0.96
Overall		4.28	3.97	0.85	0.89	1.64	1.20

compared to NP, particularly in the normal and wet years. However, the 8-day values of GPP_{VPM} were smaller in MP for the drought years. The MP responded more with greater GPP_{VPM} values to the fall rainfall events in most years. The difference in GPP_{VPM} between two pastures at 8-day temporal scale is presented in Fig.S3(c). The cold spots (small difference in GPP_{VPM}) are the periods when MP had lower values compared to NP and they were substantial in the drought years, more notably during the 2010–2012 extended drought period. The large difference in GPP_{VPM} during DOY 136–200 was observed in 2014 due to a burning event (March) in the MP.

The GPP_{VPM} showed variations between years corresponded with the amount and distribution of rainfall. There was concordance between dry/ wet events and low/high magnitudes of GPP_{VPM} at both sites. In general, the annual GPP_{VPM} of MP was significantly larger in normal and wet years, and significantly lower in drought years (Fig. 5). The paired *t*-test showed GPP_{VPM} were statistically different between NP and MP in some years (Table S1). The normal and high rainfall years (2004, 2014, and 2015) showed higher GPP_{VPM} and the drought years (2006, 2011, and 2012) showed significant lower GPP_{VPM} in MP than NP. The annual GPP_{VPM} values in the MP exhibited large inter-annual variations due to substantially higher values in normal and wet years and lower values in the drought years (Fig. 5). In comparison, the inter-annual variations of GPP_{VPM} were smaller in NP since increase/decrease during wet/drought years remained relatively smaller. The total annual GPP_{VPM} varied from 131.16 to 285.20 g C in NP and 107.87 and 282.21 g C in MP, with 17 years average of 207.21 and 203.69 g C in NP and MP, respectively (Fig. 5).

3.4. Anomalies of GPP_{VPM} in NP and MP during 2000–2016

We analyzed the anomalies from the average 17-year mean of each 8-day GPP_{VPM} and plotted the histogram (Fig 6a, b). For both pastures, the distribution of GPP_{VPM} anomalies were non-Gaussian and was positively skewed. Ninety-five percent of the GPP_{VPM} anomalies in NP ranged between -5 and $+5$ g C $m^{-2}d^{-1}$ as compared to the 95% of G GPP_{VPM} anomalies ranged between -6 and $+8$ g C $m^{-2}d^{-1}$ in MP. The statistics of this distribution of anomalies possessed a skewness equal to 0.49 and 0.80 and a kurtosis equal to 2.45 and 3.41 for NP and MP, respectively. The higher values of skewness and kurtosis in MP suggested higher variability of GPP_{VPM} in MP than NP, which was also reflected in the annual anomalies. The MP had higher negative GPP_{VPM} anomalies in drought years (2006, 2011, and 2012) than NP (Fig. 6c). However, the anomalies in the wet years (2005, 2007, and 2013) did not differ between two pastures. The variability in environmental factors and the management activities had played role in exhibiting the higher anomalies of GPP_{VPM} in MP, which is discussed in the following sections.

3.4.1. Environmental variables dependence of inter-annual variation in anomalies of GPP_{VPM}

The inter-annual variations in GPP_{VPM} anomalies of both pastures explained by the environmental variables (average temperature, rainfall, and interactions between average temperature and rainfall) are presented in Fig. 7, which showed information of range in the days of which these climatic elements drive the GPP_{VPM} anomalies. We illustrated how ΔAICc (the AICc difference between the candidate and null models) can be used to compare the effects of mean temperature, rainfall, and their interactions on the anomalies of GPP_{VPM} in NP and MP over different time windows (1–365 days). The lower ΔAICc values means (red shades) means, the regression models constructed taking the weather variables in that time window (start time and end time) is the best to determine GPP_{VPM} anomalies. For example, in Fig. 7d, the red shades in between start time from DOY 200 to 280 and end time from DOY 275 to 315 means the sum of rainfall starting from 200 to 315 is critical for GPP_{VPM}. Although both pastures had similar environmental variations due to proximity in location, the CWE based on rainfall,

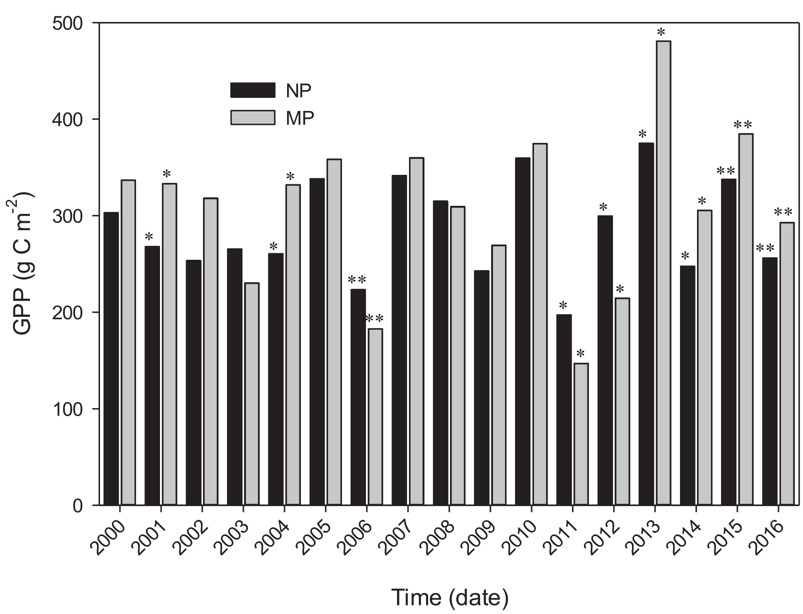

Fig. 5. The inter-annual dynamics of total gross primary productivity from 2000 to 2016 at native pasture (NP) and managed pasture (MP) sites. The total annual GPP_{VPM} was obtained by summing the 8-day GPP_{VPM} values. The paired *t*-test was used to test the significance of difference between the two pastures with 45 degrees of freedom (df). *and ** indicates the statistical significance difference in GPP_{VPM} between NP and MP at 1%, and 5% respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

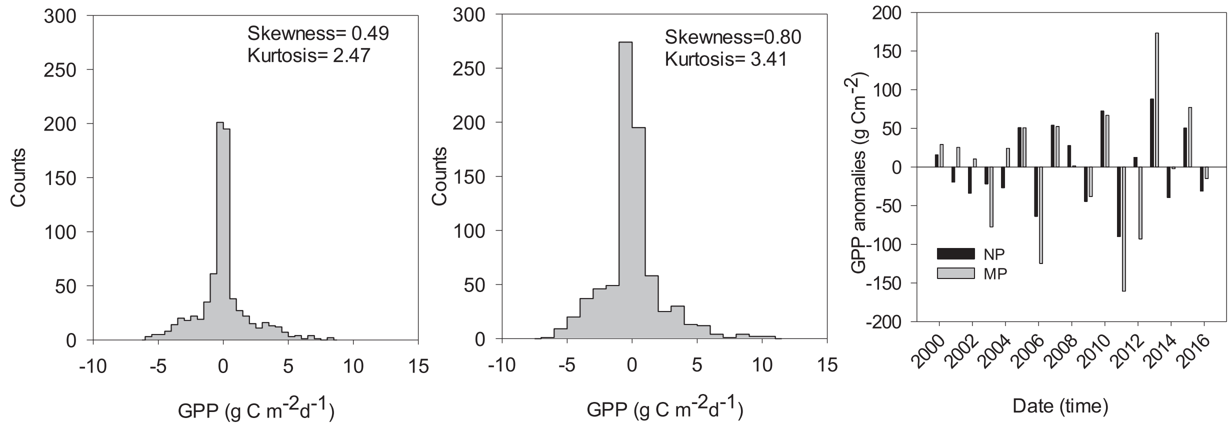

Fig. 6. Histogram of 8-day anomalies in gross primary productivity (GPP_{VPM}): (a) in Native pasture (NP) and (b) Managed pasture (MP). The frequency distribution was calculated from 17-years of 8-day values and anomalies were computed with regards to the mean of each time series from 17-years and (c) Annual anomalies (2000–2016) in total GPP_{VPM} calculated from the average total annual anomalies from 17 years data.

average temperature and their interaction differed between MP and NP. The marked difference in the CWE between NP and MP are represented by black circles in lower plots. Some marked rainfall windows during which the total rainfall controlled the GPP_{VPM} anomalies in MP were during the late growing season (fall). Some differences in CWE for temperature and interaction between rainfall and temperature were observed between NP and MP. The wider CWE of temperature during spring for MP suggested that the variation in spring temperature had contributed more to GPP_{VPM} anomalies of MP than NP. Both pastures had a similar summer temperature window, however, the range of window extended further to fall in MP (Fig. 7d, e black circles). Similarly, the CWE for interaction of rainfall and temperature was observed during spring and fall for MP only.

In Table 3, we presented the top ten models for each weather variable. Both rainfall and temperature CWE were greater in range for MP than NP with the largest CWE range for NP during DOY 150–210 and DOY 246–266, respectively, for rainfall and temperature. In comparison, the rainfall and temperature between DOY 103–235 and DOY

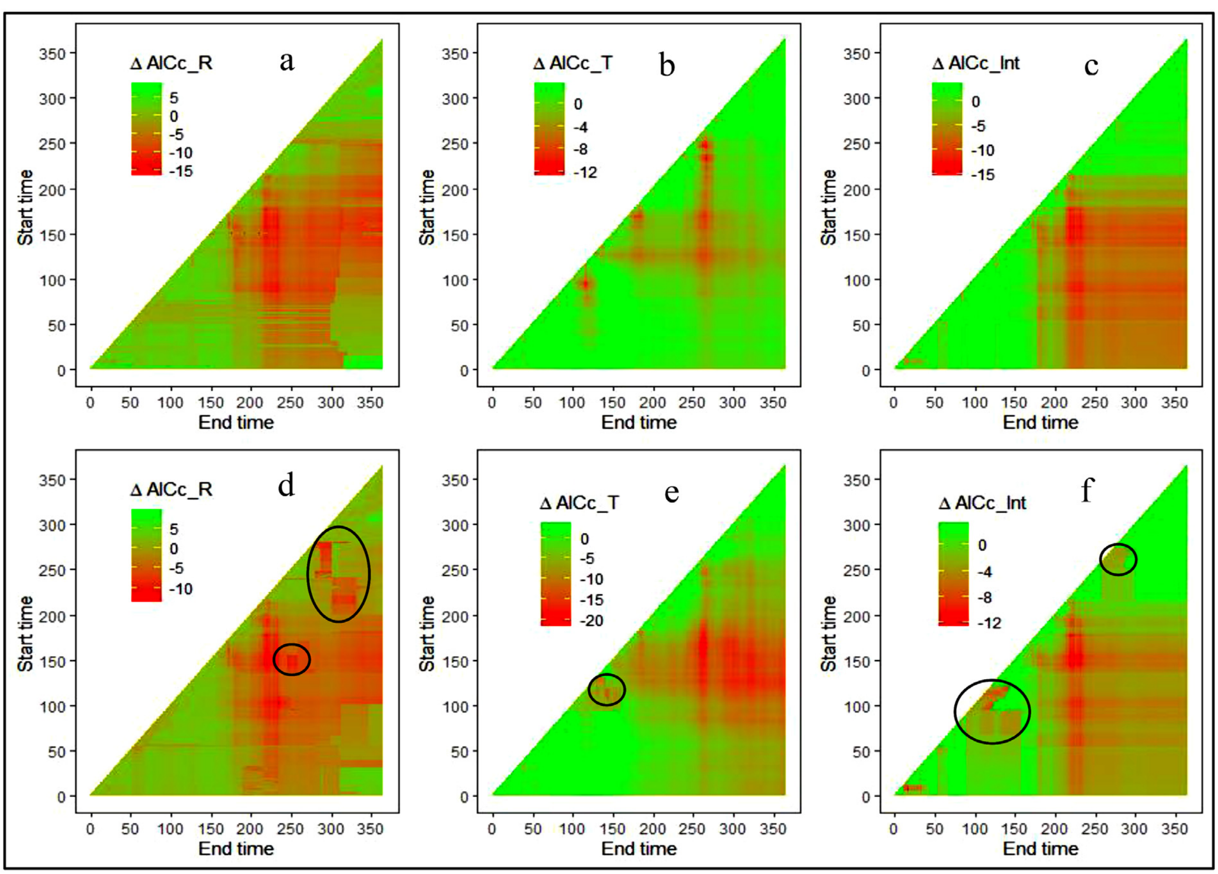

Fig. 7. The difference in the model support (ΔAICc) for the different temporalwindows of an effect of weather variables of rainfall (left), mean temperature (middle), and interaction of and rain(right) and mean temperature) on anomalies of GPP_{VPM} compared to a base model with no weather effect included. The upper panels (a,c) are for native pasture (NP) and lower panels (d,e,f) for managed pasture (MP). The black circle in the lower panels indicates some distinct signals different from NP. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3
Top ten climate windows detected using slidingwin with absolute window approach for NP and MP. The significance in difference of the climate windows is tested based on the fit different windows (**ΔAICc** $_{FDW}$) and fit shared windows (**ΔAICc** $_{FSW}$).

	NP			MP				
SN	WO	WC	$NP_{\Delta AICc}$	WO	WC	$MP_{\Delta AICc}$	$FDW_{\Delta AICc}$	FSW $_{\Delta AICc}$
Rain								
1	150	210	−15.95	103	235	−13.18	−29.13	−25.61
2	150	176	−15.77	102	235	−13.14	−28.91	−25.59
3	151	167	−15.77	103	236	−13.06	−28.83	−25.11
4	151	184	−15.59	102	236	−13.01	−28.60	−24.96
5	150	193	−15.59	101	235	−12.95	−28.54	−24.80
6	150	159	−14.92	101	236	−12.81	−27.74	−24.57
7	155	233	−14.91	146	220	−12.76	−27.67	−24.08
8	155	232	−14.85	153	220	−12.72	−27.57	−23.92
9	155	218	−14.77	151	220	−12.60	−27.37	−23.73
10	155	220	−14.47	152	220	−12.59	−27.05	−23.72
Temperature								
1	246	266	−12.49	168	263	−21.12	−33.61	−31.37
2	245	266	−12.48	168	264	−21.10	−33.58	−31.35
3	246	267	−12.24	169	263	−21.05	−33.29	−31.13
4	95	116	−12.16	169	264	−21.02	−33.19	−31.11
5	232	267	−12.08	168	262	−20.76	−32.84	−30.74
6	95	117	−11.97	167	263	−20.74	−32.71	−30.71
7	246	265	−11.72	169	262	−20.73	−32.46	−30.50
8	94	116	−11.64	167	264	−20.71	−32.36	−30.49
9	247	266	−11.55	168	265	−20.57	−32.12	−30.45
10	248	266	−11.54	163	263	−20.52	−32.06	−30.37
Interaction								
1	155	218	−15.07	153	220	−12.18	−27.25	−30.77
2	155	233	−14.91	154	232	−12.15	−27.06	−30.45
3	155	220	−14.90	146	220	−12.14	−27.04	−30.44
4	155	232	−14.86	154	233	−12.12	−26.98	−30.35
5	155	219	−14.76	151	220	−12.07	−26.83	−30.16
6	156	218	−14.46	152	220	−12.06	−26.52	−29.55
7	157	218	−14.34	154	220	−12.04	−26.38	−29.32
8	158	218	−14.34	153	219	−12.00	−26.34	−29.31
9	155	224	−14.33	146	219	−11.94	−26.27	−29.30
10	156	220	−14.23	151	219	−11.89	−26.12	−29.10

168–263were critical for MP. The delta AICc values for fit different window (FDW) was smaller than the fit shared window (FSW) i.e., $FDW_{\Delta AICc} < FSW_{\Delta AICc}$, suggesting the CWE was significantly different between NP and MP.

3.4.2. Interactive effects of environmental variables and management on GPP_{VPM} anomalies

Following the identification of significantly different CWE between NP and MP, we tested for an interaction between the environmental variables and the management factor index (MFI) on GPP_{VPM} anomalies (Table 4). Based on the best ten models of each environmental variables (only top model is presented in Table 3), neither average temperature nor rainfall showed a significant relationship with the GPP_{VPM} anomalies of NP and pooled GPP_{VPM} anomalies of both pastures. In contrast, we found that the effects of rainfall and the combined effects of temperature and rainfall on GPP_{VPM} anomalies of MP were significant. However, temperature effects solely did not impact the GPP_{VPM} of MP. The statistical significance of weather variables with MFI in MP indicated that the management factors interacted with the environmental effects for impacting the variability of GPP_{VPM}. The MFI had significant role in modulating the effects of environmental variables, especially rainfall, on GPP_{VPM} anomalies of MP with different CWE as reflected by the lower AICc values for pooled data model than that for the AICc values obtained for model from each pasture separately.

Table 4
Best regression model tested for interactions between management factor index (MFI) and climate variables (T_avg = average temperature, Rain_sum = total rainfall). The numbers in best window represent the day of the year (start and end) during which the variables were critical. P-values indicate the statistical significance (n.*s* = not significant, * at <1% and ** at <5%).

Pasture	Variables	Best window	delta AICc	T_value	P-value
NP	T_avg*MFI	95:117	−9.82	−1.04	n.s
	Rain_sum*MFI	89:217	−10.93	1.51	n.s
	T_avg*Rain_sum*MFI	155:218	−11.10	0.85	n.s
MP	T_avg*MFI	168:264	−23.72	0.27	n.s
	Rain_sum*MFI	103:232	−13.81	−2.57	*
	T_avg*Rain_sum*MFI	103:229	−12.68	−2.61	**
Both	T_avg*MFI	169:265	−32.92	0.68	n.s
	Rain_sum*MFI	85:233	−28.69	−1.30	n.s
	T_avg*Rain_sum*MFI	155:220	−27.83	−0.31	n.s

4. Discussion

Monitoring grassland productivity using remote sensing models based on eddy covariance observations is important in analyzing the impacts of climatic variability and management practices. Differences in the seasonal and inter-annual variability of GPP_{VPM} in NP and MP reflected the variability of the governing environmental variables and management factors in isolation as well as in interaction (in MP). Management factors such as harvesting biomass, burning, grazing, and fertilizer application modify the photosynthetically active green biomass and alter ecosystem responses to the environmental variability (Rogiers et al., 2005; Schönbach et al., 2011), resulting in the modulation of seasonal and inter-annual variability in GPP_{VPM}. Another potential factor determining the differential responses between NP and MP to environmental variability is the composition of C_3 and C_4 species in the ecosystems. Both change in environmental variables and management factors such as burning and grazing alter species composition in natural grasslands (Hunt Jr et al., 2003; Ricotta et al., 2003; Sage and Kubien, 2007). Because MP is controlled to be mostly a monoculture, the natural ratio of C_3/C_4 species equilibrium has been disturbed and the response of the ecosystem to environmental variability has been altered as exhibited by the higher inter-annual variability of GPP_{VPM}. However, the new drought tolerant grass species might have been induced into the NP making the pasture better adapted to drought conditions. Although C_4 dominant managed pastures theoretically should have advantages in water limiting conditions over the NP with mixed C_3 and C_4 grasses that was not realized in our study. Several other studies (Briggs and Knapp, 2001; Nippert et al., 2007; Taylor et al., 2011; Tieszen et al., 1997) also reported that C_4 species failed to perform with the same higher intrinsic photosynthetic capacity (as measured in laboratory conditions) under field conditions and monoculture C_4 in our MP also showed lower adaptability in dry conditions. Some major differences in productivity of NP and MP in responses to the variability in environmental variables over 17 years are discussed below:

4.1. Identifying weather or management signals

Of the climatic variables tested, sum of daily rainfall was most strongly correlated with the GPP_{VPM} anomalies at both pastures. Both pastures showed sensitivity to the environmental variable signals (hot and dry events) with net negative changes in GPP_{VPM}, the degree of changes being larger in the MP. Seasonal changes in the GPP_{VPM} at MP indicated the effects of the management on the GPP_{VPM}. For example, GPP_{VPM} values were smaller in 2008–2010 during July and August due to harvesting of biomass at the MP (Fig. S3). Similarly, higher magnitudes of GPP_{VPM} were detected for post-burning period at both pasture sites. Analysis of anomalies also showed that grass productivity of NP and MP responded differently to environmental variability at different times of the year and between years, the reason being the modulation of ecosystem responses due to management factors. Similar to other

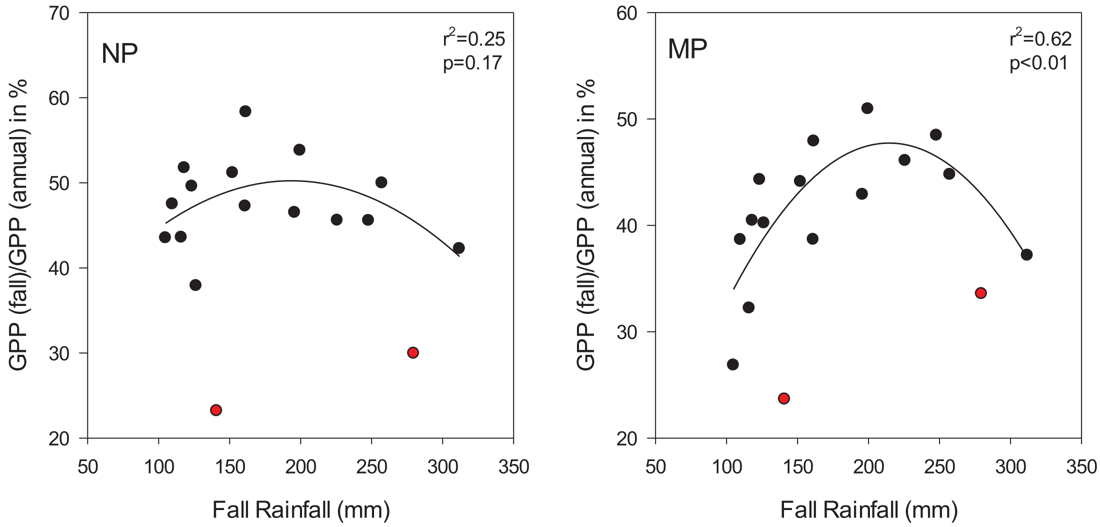

Fig. 8. Relationship between fall rainfall and the ratio between GPP_{VPM} during fall months (September-November) to total annual GPP_{VPM} at native pasture (NP) and managed pasture (MP) site. The two red dots are the values for 2011 and 2012 (exceptional drought years) and not included in the curve fitting. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

studies, grassland ecosystems exhibited profound effects from management factors (Asner et al., 2004; Dangal et al., 2016; Harrison et al., 2003). Our study also found that both the total GPP_{VPM} and GPP_{VPM} anomalies of MP showed larger variation especially in drought years. The differences in GPP_{VPM} (GPP_{VPM} of NP subtracted from GPP_{VPM} of MP) was substantially higher in water limited years, implying the management activities in MP are the driving forces interacting with environmental variables such as rainfall (drought) for the lower GPP_{VPM}. However, some differences in variability in GPP_{VPM} within some years (e.g., 2014) was unclear and cannot be attributed either to management or environmental variables since the management factor role is minimum in NP and the environmental variables were similar for both sites. The possible explanation of lower GPP in NP in 2014 is the infestation of *Helianthus species* based on visual observation.

Generally, insights on how productivity of any ecosystems are influenced by environmental variables, land use management, and pasture types can be explained through the partitioning of NEE into GPP and ER (Flage et al. 2001, Gilmanov et al., 2014).The difference in productivity between two pastures was not simply the function of environmental and management factors. The difference in productivity in between two pastures in this study could have been resulted from the difference in ER at two different sites because the NEE of an ecosystem is the balance between the carbon gain through photosynthesis (GPP) and carbon loss through respiration (ER), which were separately infuenced by the environametal variables and management activities at different degree. The greater amount of biomass removed in the form of harvesting (hays) or grazing by cattle in the MP have showed larger decrease in GPP. The reduction in GPP would reduce the supply of sugar to fuel the respiration by roots and microbes, resulting in reduced ER. Both decreased GPP and ER due to removal of biomass caused the larger net sink of the carbon in MP consistent with the findings of a previous study (Delucia et 2014).

4.2. Higher resistance to drought of NP compared to MP reflected by low GPP_{VPM} anomalies

The debate concerning whether biodiversity ameliorates the effects of environmental extremes on ecosystem functions, but research has shown mixed results (Ives and Carpenter, 2007; Van Ruijven and Berendse, 2010; Wright et al., 2015). Higher diversity moderates the effects of climatic variability, especially drought, by promoting the stability in production (Allan et al., 2011; Isbell et al., 2015; Seabloom, 2007; Tilman, 1996). Both species richness and management played role in determining the resistance of grassland against drought (Vogel et al., 2012). We also observed the higher resillience of NP to the extended drought of 2010–2012 in Oklahoma based on the lower GPP_{VPM} anomalies, yet it did mot recover to the normal levels of productivity. The degree to which MP responded to environmental variables in terms of change in GPP_{VPM} was higher (positive) in average rainfall year, similar in wet year and higher (negative) in drought years as compared to the response of NP to similar environmental conditions. The difference in response to drought was large. Our results suggest that loss of biodiversity through establishing monoculture of MP from well adapted multispecies NP seems likely to decrease the ecosystem stability with low resistance of productivity in drought events. This is mainly beacsuse of two reasons; the first is the acclimatization to the local conditions from a long period and the second is the compensation hypothesis where greater number of species have a wide range of responses to ecosystem disturbance increasing the likelihood of the performance of some species and compensating of the poor performance of some other species under unfavorable conditions (Pfisterer and Schmid, 2002; Yachi and Loreau, 1999).

4.3. Different critical temporal window of environmental variables between two pastures

The wider CWE for MP suggests that expected future climate change, especially the unpredictable nature of rainfall, would increase the vulnerability of managed grasslands. The management such as removal of biomass for hay required rainfall for the recovery. The harvesting of biomass or grazing followed by rainfall events stimulated the growth of vegetation causing higher productivity (Zelikova et al., 2015; Zhou et al., 2017b). However, drought following harvesting of biomass impedes the productivity. For example, the devastating drought of 2011, which occurred after MP was harvested for hay and resulted in the highest anomalies among study years, and the difference in the anomalies of GPP_{VPM} between MP and NP was also the highest.

The CWE analysis also revealed that the fall rainfall window was substantial in controlling the GPP_{VPM} anomalies and inter-annual variability in MP. The significant relationship was observed in MP between the fall rainfall and the ratio of total GPP_{VPM} during fall to the total annual GPP_{VPM} (Fig. 8). The larger slope (NP = 0.24 and MP = 0.49) and R^2 (NP = 0.25and MP = 0.62) in the second degree polynomial equation suggested that MP responded to fall rainfall better than NP, the latter showing stablity in fall GPP_{VPM} contribution to total annual GPP_{VPM} irrespective of low or high fall rainfall amounts. Further, the interaction of rainfall with the fall temperature conditions also had impacts on the GPP_{VPM} anomalies. Consistent with our finding, a study on bluestems in the managed pasture in Oklahoma demonstrated that the MP species were more responsive to late-summer and fall rainfall than were the native grasses (Redfearn, 2013).

Conclusion and perspectives

The NP and MP responded differently to the environmental variability during 2000–2016. The MP showed higher degree of sensitivity to the drought conditions compared to NP, as reflected by the wider range of GPP_{VPM} anomalies distribution. The analysis also showed spring temperature and fall rainfall were critical in controlling GPP_{VPM} variability of MP. The differential responses of NP and MP to environmental variability was caused by the modulation of management activities in the MP. Multiple CWEs were identified for the MP, and those identified CWEs were wider in MP than NP. The difference in CWE between NP and MP was explained by the interaction of management factor and environmental variables. Therefore, adequate inputs of management factors into models are required for the quantitative assessment of the variability of grassland productivityfor maintaining the sustainable pasture productive capacity. Identifying the vulnerabilities of managed pasture and following adaptive management strategies for increasing the resiliency of the pasture system is one of the remedial measures that ranchers should consider under the context of changing climate. Our analyses also suggest to incorporate managed pastures as a different land use type from natutral pastures in the analysis of ecosystem feedback to global change.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2020.108137.

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