

Extreme Drought Effects on Carbon Dynamics of a Semiarid Pasture

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ABSTRACT

Environmental and management factors are critical in determining the C source or sink status of agroecosystems. Information on the C dynamics of an ecosystem from source to sink and vice versa are critical in determining the role of that ecosystem in regional and global C balances. We investigated the impact of the 2011 mega-drought on seasonal changes in net CO₂ exchange of a WW-B. Dahl Old World bluestem [*Bothriochloa bladhii* (Retz) S.T. Blake] pasture in the Texas High Plains and compared the results with those from 2010, a hydrologically wet year. Carbon dioxide flux between the vegetation and atmosphere was measured using an eddy covariance flux tower. Our results indicate that net ecosystem exchange, ecosystem respiration, and gross primary production for this agroecosystem were strongly affected by environmental variables and grazing. During the period of measurement in 2010 (Days of the Year 152–365), the pasture accumulated 164 g C m⁻² and was a net C sink. During the same period in 2011, the severe drought changed the dynamics of the pasture from a C sink to a source, with a net cumulative loss of 142 g C m⁻². Ecosystem respiration was an exponential function of soil temperature in both years. When extreme water-limiting days were excluded, the exponential model explained 90% of the variation in ecosystem respiration in 2011 and 92% of the variation in ecosystem respiration in 2010. Incorporating the results from our study with ecosystem models can improve our understanding of the contributions of managed pastures to regional C balances.

THE SOUTHERN HIGH Plains of Texas was once a vast native grassland dominated by short-grass prairie and, in some regions, tall-grass prairie (Gould, 1975; Allen et al., 2007). The discovery of the vast underground Ogallala aquifer in the early 20th century and its subsequent exploitation for irrigation transformed this semiarid region into one of the most intensively cultivated regions in the United States (Allen et al., 2008). The Texas High Plains is the largest producer of cotton (*Gossypium hirsutum* L.) in the United States (National Agricultural Statistics Service, 2007). Other crops that significantly contribute to the region's economy are grain sorghum [*Sorghum bicolor* (L.) Moench], corn (*Zea mays* L.), and winter wheat (*Triticum aestivum* L.). More than 90% of the water pumped from the Ogallala aquifer is currently used for irrigated crop production in the region (Nair et al., 2013). However, the groundwater level is declining in many portions of the region due to excess water withdrawal and slow recharge. In areas where irrigation water is limited, producers are adopting dryland agriculture or planting pasture for biomass and grazing (Texas Alliance for Water Conservation, 2011). WW-B. Dahl Old World bluestem is a warm-season perennial grass adapted to limited irrigation while capable of producing

high-quality forage (Philipp et al., 2005; Allen et al., 2012). In a study conducted by Sanderson et al. (1999) in central Texas, WW-B. Dahl had the highest biomass yield compared with several other forage grasses. WW-B. Dahl is gaining popularity with producers in the Texas High Plains region because of high nutritional quality and biomass production (Duch-Carvalho, 2005; Philipp et al., 2007).

A change in land use from traditional row crops such as cotton, grain sorghum, and corn to pasture-based agroecosystems has several environment-related implications. Grasslands are known to play a major role in global C dynamics (Scurlock and Hall, 1998; Frank and Dugas, 2001; Vleeshouwers and Verhagen, 2002). Temperate grasslands usually act as C sinks. For example, Ciais et al. (2005) estimated that European grasslands are net C sinks and sequester approximately 74 g C m⁻² yr⁻¹. Researchers have also reported grasslands acting as net C sources (Flanagan et al., 2002; Jongen et al., 2011). Variations in climate such as drought impact soil moisture conditions, increase temperatures, and reduce the length of the growing season in many regions and can lead to net C losses. Disturbances such as fire can also alter soil and vegetation functions and can affect C source–sink dynamics (Michelsen et al., 2004; Henry et al., 2005). Grazing of grasslands involves additional management-related factors that can affect the cumulative C balance (Conant et al., 2001; Jones and Donnelly, 2004). Several studies have reported grasslands acting as C sources due to overgrazing, leading to excess removal of green vegetation and reduced primary production (Xianglin, 2009; Vetter et al., 2010).

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Abbreviations: DOY, Day of the Year; GPP, gross primary production; NEE, net ecosystem exchange; PPF, photosynthetic photon flux density; VPD, vapor pressure deficit; VWC, volumetric water content.

The exchange of CO₂ between the vegetation surface and atmosphere can be measured directly using the eddy covariance method. Using eddy covariance, the CO₂ flux is determined as the covariance between vertical wind velocity and CO₂ concentration (Goulden et al., 1996; Ham and Heilman, 2003). Measurements of wind velocity and CO₂ concentration are made using fast-response instruments. Eddy covariance has been widely used around the world for studying the C and hydrologic cycles of different ecosystems (Yamamoto et al., 2001; Baldocchi, 2003; Dolman et al., 2006; Yu et al., 2006). During the daytime, the net ecosystem exchange (NEE) measured using eddy covariance represents the balance between CO₂ that is absorbed by the plant canopy through photosynthesis (gross primary production, GPP) and CO₂ that is released through a combination of autotrophic and heterotrophic respiration from the ecosystem (ecosystem respiration, R_{eco}). At night, the eddy covariance measurements of NEE represent R_{eco} .

Because daily NEE represents the balance between C uptake and release, it can effectively be used to study the source–sink status of an ecosystem and its evolution across seasonal, annual, and decadal time scales (Wharton et al., 2012). AmeriFlux is a network of experimental sites established primarily in North and Central America that uses the eddy covariance method for measuring CO₂ and energy exchange in key ecosystems (<http://ameriflux.lbl.gov/SitePages/Home.aspx>). Some of these sites have been functional since the early 1990s and have provided continuous, ecosystem-level measurements of CO₂ flux (Baldocchi et al., 2001). Data from these sites have been integrated into modeling frameworks along with other data (such as remote sensing) for deriving estimates of the C balance at regional and continental scales (Friend et al., 2007; Dang et al., 2011; Xiao et al., 2011).

Eddy covariance measurements are responsive to environmental factors that affect plant growth, such as drought. As soil moisture becomes limiting, plants experience both physiological changes (immediate effects) and longer term structural changes (van der Molen et al., 2011). Plants initially respond to drought by reducing the leaf expansion rate, increasing the leaf senescence rate, and decreasing stomatal conductance (Rosenthal et al., 1987). This produces an immediate decline in photosynthesis, although leaf dark respiration is generally not affected (Meir et al., 2008). As conditions progress from short-term drought to long-term drought, both photosynthesis and respiration become inhibited through reduced substrate availability, leading to significant reductions in GPP and R_{eco} (Reichstein et al., 2002; Zhao et al., 2010). The sensitivity of the R_{eco} to temperature, indicated by Q_{10} (the factor by which respiration increases in response to a 10°C rise in temperature), also decreases under drought conditions. Drought reduces substrate availability due to slow diffusive transport of soluble organic C substrates and intercellular enzymes (Davidson and Janssens, 2006). A large-scale drought event across North America in 2002 was estimated to have reduced regional C uptake by half compared with other non-drought years (Peters et al., 2007). In 2011, the Texas High Plains was impacted by a drought event which was classified as “exceptional” (D4) in the U.S. Drought Monitor Report (<http://droughtmonitor.unl.edu/>). This exceptional drought

was considered to be the worst drought event experienced by the region since the mid-1950s (LeCompte, 2012).

Although native and managed grasslands in the semiarid Texas High Plains are unique ecosystems adapted to this region, their role in regional C exchange processes has not been adequately studied and they are not adequately represented in the current estimates of regional- or continental-scale C balance. Currently, there are no active AmeriFlux sites in this region; however, we have obtained eddy covariance flux measurements of the type made at AmeriFlux sites from an improved WW-B. Dahl pasture in the Texas High Plains region since mid-2010. These measurements are contributing to our understanding of how grasslands in the region respond to the semiarid Texas High Plains environment. Fortunately, the measurement period for this site contains the mega-drought event of 2011. This offers us a special opportunity to investigate the impact of an extreme drought event on key C exchange processes in this agroecosystem. The main objectives of this study were to assess the impact of the mega-drought event of 2011 on daily and seasonal NEE of this pasture and compare the results to those obtained in 2010, which was a year with above-normal rainfall. We also examined the relationship between GPP, R_{eco} , and light use efficiency as affected by temperature and grazing.

MATERIALS AND METHODS

Study Site

The study was conducted in an irrigated improved pasture located approximately 3.5 km northwest of Lockney, TX (34°8'17" N and 101°28'45" W, 1100 m elevation). This field is part of the Texas Alliance for Water Conservation (TAWC) Demonstration Project being conducted in the Texas High Plains region to promote water conservation. The field was irrigated using a mid-elevation spray application center-pivot irrigation system. The total area of the center-pivot field was 88 ha, with the north half of the pivot in pasture (44 ha) and the rest in row crops. The pasture was seeded to WW-B. Dahl Old World bluestem in May 2007 at a seeding rate of 2.8 kg h⁻¹. WW-B. Dahl is a warm-season C₄ perennial bunch grass with peak growth generally occurring in mid- to late July. Unlike other Old World bluestems, WW-B. Dahl remains vegetative for much of the growing season, with flowering starting in September and seed shedding in October. The field is normally grazed two to three times per year during late spring and summer, with seeds harvested in October or November. In 2010, the field was grazed in May (before establishing the eddy covariance flux tower), July, and August. No grazing or harvesting of seeds was done in 2011 due to extreme drought conditions throughout the year. The soil type is a Pullman clay loam (a fine, mixed, superactive, thermic Torrertic Paleustoll) with 0 to 1% slope. The climate of this region is semiarid, with a mean long-term annual precipitation of 450 mm. About two-thirds of the precipitation is normally received during the growing season (Fig. 1).

Data Collection

An eddy covariance flux tower was established in the center of the field in mid-June of 2010 for making continuous measurements of NEE. A rectangular area (3 by 10 m) was

fenced off around the flux tower to prevent grazing livestock from interfering with the site instrumentation. Wind velocity was measured using a three-dimensional sonic anemometer (Model CSAT-3, Campbell Scientific). An open-path infrared gas analyzer (IRGA, Model LI-7500, LI-COR) was used for measuring the CO₂ concentration in the ambient atmosphere. The IRGA was calibrated annually. These instruments were set up facing southwest (into the prevailing wind direction) at a height of 1.5 m above the top of the vegetation. The sonic anemometer was leveled after installation. The IRGA was installed next to the sonic anemometer and was tilted 20° from the vertical. Other environmental variables measured included air temperature and relative humidity (HMP50, Campbell Scientific), net radiation (Kipp & Zonen NR-Lite net radiometer), global irradiance (LI-190SB pyranometer, LI-COR), precipitation (TE525 rain gauge, Campbell Scientific), soil temperature at 4 cm below the surface (TCAV averaging soil thermocouples, Campbell Scientific), soil volumetric water content at 4 cm below the surface (CS-616 water content reflectometer, Campbell Scientific), and soil heat flux at 8 cm below the surface (Hukseflux self-calibrating soil heat flux plate, Campbell Scientific). The soil heat flux at the surface was calculated using soil heat flux plate data at the 8-cm depth, and the change in heat storage above the heat flux plates calculated from soil temperature and moisture data. The IRGA and radiometer surfaces were cleaned periodically to avoid accumulation of dust according to the manufacturers' guidelines. Data from all sensors were measured at a 10-Hz sampling rate using a CR3000 datalogger (Campbell Scientific). The datalogger was programmed to calculate and save 30-min average values of all environmental variables. The raw 10-Hz wind velocity and IRGA data were saved for later analysis of CO₂ exchange.

Data Analysis

The 10-Hz wind velocity and IRGA data were analyzed using EddyPro 4.0 software (LI-COR). This software has built-in functions for performing eddy covariance data processing as described by Rajan et al. (2010). The final output from the software included 30-min average values of NEE. By convention, a positive flux represents a net ecosystem loss or flux from the ecosystem to the atmosphere, while a negative flux represents a net ecosystem gain or flux from the atmosphere to the ecosystem. The theoretical assumptions involved in eddy covariance flux estimates of CO₂ require turbulent mixing in the boundary layer. Hence, data were omitted when the friction velocity was <0.10 m s⁻¹. Data collected during precipitation events and equipment maintenance were also excluded from analysis. All missing data were replaced using the CarboEurope and Fluxnet eddy covariance gap-filling tool (Elbers et al., 2011; Zona et al., 2013). This on-line tool (<http://www.bgc-jena.mpg.de/~MDIwork/eddyproc/>) is based on methods similar to those described in Falge et al. (2001) and Reichstein et al. (2005). The NEE data were gap-filled using meteorological data available during the time period when these values were missing or unusable. The missing values were calculated by averaging data under similar meteorological conditions using a moving look-up table with flexible window sizes (Bell et al.,

2012). Meteorological conditions were considered similar when the air temperature (T_{air}), vapor pressure deficit (VPD), and irradiance did not deviate by more than 2.5°C, 0.5 kPa, and 50 W m⁻², respectively. Linear interpolation was used to fill small gaps in the data set.

Seasonal variables were calculated for three growth periods: peak growth (June–August), flowering (September–October), and dormant (November–December) seasons. Daily NEE was calculated by integrating half-hourly measurements. In the absence of photosynthesis at night, NEE values represent R_{eco} , which includes soil and plant respiration. Daytime R_{eco} was evaluated using an exponential regression model developed between nighttime NEE measurements averaged across 1°C-wide bins and corresponding soil temperature (T_{soil}) measurements made at the 4-cm depth. Soil volumetric water content (VWC) <0.15 (1.5 MPa) was considered moisture limiting in the current study. Regression models were developed for moisture-limiting (VWC < 0.15) and nonlimiting (VWC > 0.15) conditions. The general form of the model is

$$R_{\text{eco}} = A \exp(BT_{\text{soil}}) \quad [1]$$

where A and B are constants evaluated with least squares regression.

This model was applied to compute daytime R_{eco} using T_{soil} measurements. Daily R_{eco} was calculated by integrating daytime and nighttime measurements. Daily GPP was calculated as

$$\text{GPP} = R_{\text{eco}} - \text{NEE} \quad [2]$$

To understand the impact of environmental conditions and grazing on the photosynthetic response of the pasture, a rectangular hyperbola model was used (Flanagan et al., 2002; Hussain et al., 2011). This model is a modified form of the Michaelis–Menten equation originally developed for describing enzyme kinetics but frequently applied to photosynthesis. The hyperbolic model has the general form

$$\text{NEE} = \frac{\text{NEE}_{\text{max}} \text{PPFD}}{\text{PPFD} + (\text{NEE}_{\text{max}}/\alpha)} + R \quad [3]$$

where NEE_{max} is the maximum NEE rate ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), PPFD is the photosynthetic photon flux density ($\mu\text{mol photon m}^{-2} \text{ s}^{-1}$), α is the initial slope of the light response curve ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}/\mu\text{mol photon m}^{-2} \text{ s}^{-1}$), $\text{NEE}_{\text{max}}/\alpha$ is the PPFD associated with half of the maximum NEE rate, and R is the intercept term, which is the average daytime R_{eco} ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). The term $(\text{NEE}_{\text{max}} + R)$ is the theoretical maximum C uptake. Several studies have found the rectangular hyperbola saturating slowly with increasing PPFD yielding high NEE_{max} . Hence, in the present study, we evaluated Eq. [4] at PPFD of 2000 $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$, and the term $(\text{NEE}_{\text{max}} + R)_{2000}$ represents the average maximum uptake rate, as described by Owen et al. (2007).

The temperature sensitivity of ecosystem respiration describes the increase in R_{eco} with every 10°C increase in soil temperature. Exponential regression models were developed

Table 1. Seasonal averages of precipitation (P), air temperature (T_{air}), soil temperature (T_{soil}), relative humidity (RH), and vapor pressure deficit (VPD) at the pasture eddy covariance flux site near Lockney, TX.

Parameter	2010			2011		
	Peak growth (June–Aug.)	Flowering (Sept.–Oct.)	Dormant season (Nov.–Dec.)	Peak growth (June–Aug.)	Flowering (Sept.–Oct.)	Dormant season (Nov.–Dec.)
P , mm	278	47.2	12.7	12	44.5	31.5
T_{air} , °C	24.7	18.4	6.4	28.0	20.0	7.3
T_{soil} , °C	24.9	19.7	9.3	24.8	17.1	8.5
RH, %	62.0	59.2	50.6	38.0	54.3	59.0
VPD, kPa	1.6	1.1	0.7	2.9	1.2	0.5
Irrigation, cm	0.0	0.0	0.0	1.4	2.2	0.0

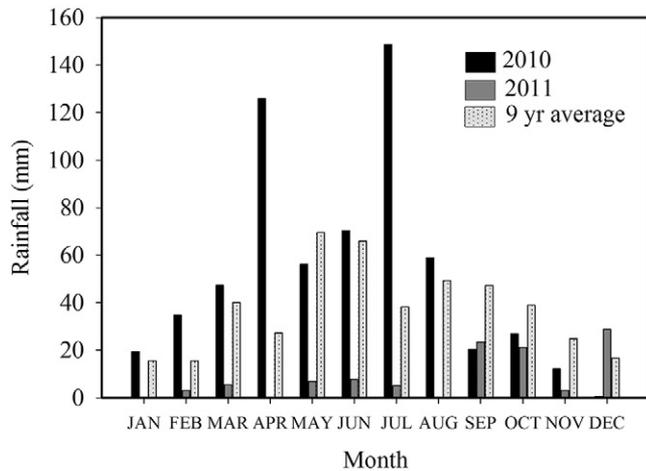


Fig. 1. Monthly precipitation during 2010 and 2011 and 9-yr average (2000–2009) at the study site.

between daily R_{eco} and T_{soil} measurements as shown in Eq. [1] for both years. The Q_{10} function was then computed as

$$Q_{10} = \exp(10B) \quad [4]$$

where B is the constant fitted using Eq. [1].

The evaluation of regression models and statistical analyses were performed using SigmaPlot version 11.0 software (Systat Software).

RESULTS

Weather

Meteorological differences between the 2 yr were evident in the observations of precipitation (P), T_{air} , T_{soil} , relative humidity (RH), and VPD. The cumulative precipitation and seasonal distribution were noticeably different between 2010 and 2011 (Table 1; Fig. 1). The precipitation received during the 2010 peak growing season (June–August) was 278 mm, which was much greater than the 9-yr average precipitation of 153 mm recorded by the TAWC weather station located near the site (Fig. 1). In contrast, the growing season precipitation received in 2011 was only 12 mm, or 8% of the 9-yr average precipitation. As shown in Fig. 2a, the exceptionally dry 2011 summer was coupled with a higher average T_{air} than 2010 during the period of peak growth in the summer months. Significant differences between the 2 yr were also observed in T_{air} during June to September. The average T_{air} in June to August 2011 was 3.3°C higher than the corresponding value from 2010, while the average T_{air} during the flowering

period in 2010 was 1.8°C higher than in 2011. There were no significant differences between the average T_{air} values during the dormant seasons for the 2 yr.

The T_{soil} values recorded during the peak growth months were similar in both years; however, the T_{soil} values recorded in the flowering and dormant seasons in 2010 were higher than those recorded in 2011 ($P < 0.05$). Average RH values recorded for all growing season periods were significantly different between the 2 yr. The dry, warm 2011 summer caused the VPD to peak above 3.0 kPa on several days, and VPD values generally stayed above 2.0 kPa on most days during the summer. During the 2010 peak growth months, the VPD stayed below 2.0 kPa on most days (Fig. 2c). The VPD values were similar in both years for the flowering and dormant seasons.

Daily and Seasonal Net Ecosystem Exchange

Summer

Figure 3 presents daily accumulated C uptake of the pasture in 2010 and 2011, respectively. Daily NEE observed during the summer months of 2010 showed a net CO_2 uptake by the pasture (negative NEE) on most days. Daytime NEE showed a steady decrease following the establishment of the eddy flux tower on Day of the Year (DOY) 167 until DOY 179. This decrease was due to gradual soil drying. Above-average rainfall received after DOY 179 (a total of six rain events) caused a rapid increase in green biomass in late July (DOY193–207). The peak C uptake of 27.9 $\text{g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$ was measured on DOY 202. Grazing started in the pasture on DOY 199. As grazing progressed, the removal of vegetation in the flux footprint area had a direct effect on NEE, with daily NEE values showing a rapid decrease and approaching zero at the end of grazing on DOY 227. The short-term C release occurring on 14 d (DOY 179, 182–184, 217–221, and 226–230) during the summer was primarily triggered by precipitation events (also termed *precipitation pulses*). The CO_2 released on those days ranged from near zero to as high as 13.2 $\text{g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$ (DOY 218).

Unlike the rainy 2010 summer, the summer in 2011 was characterized by extreme drought, which significantly impacted the CO_2 exchange of the pasture. Daily NEE in the summer of 2011 showed a net CO_2 release by the pasture (positive NEE). Figure 4 presents examples of diurnal variations in NEE in the summers of 2010 and 2011. Diurnal variations in NEE in 2010 (DOY 195) showed daytime CO_2 uptake and nighttime CO_2 release, as would be expected during the peak growth period of the pasture; however, the diurnal variations in NEE in 2011 on the same day showed

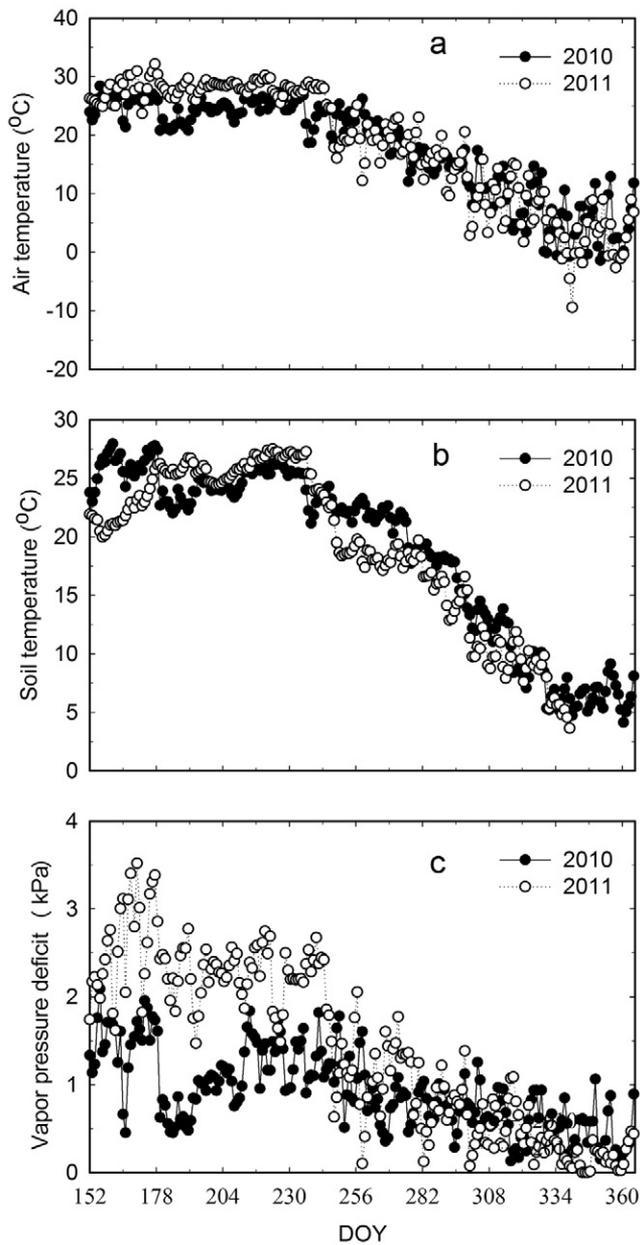


Fig. 2. Daily average values of meteorological variables recorded at the pasture eddy covariance flux site near Lockney, TX, for Days of the Year (DOY) 152–360: (a) air temperature, (b) soil temperature at 4 cm below the surface, and (c) vapor pressure deficit.

daytime CO_2 uptake near zero. Similar characteristics of diurnal variations were observed for most days during the 2011 summer. The CO_2 release peaked above $15 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$ on 6 d (DOY 170, 172, 197, 198, 238, and 239) during the 2011 summer. Two small rain events in June and July of 2011 caused short-term periods of CO_2 uptake, but the pasture rapidly reverted to a dormant state as the soil dried.

Autumn and Winter

September through October was the blooming period for the pasture in 2010. Daily NEE stayed relatively constant on most days during the blooming period. Similar to the summer months, precipitation triggered short-term pulse events on several days (Fig. 3a). The NEE gradually decreased

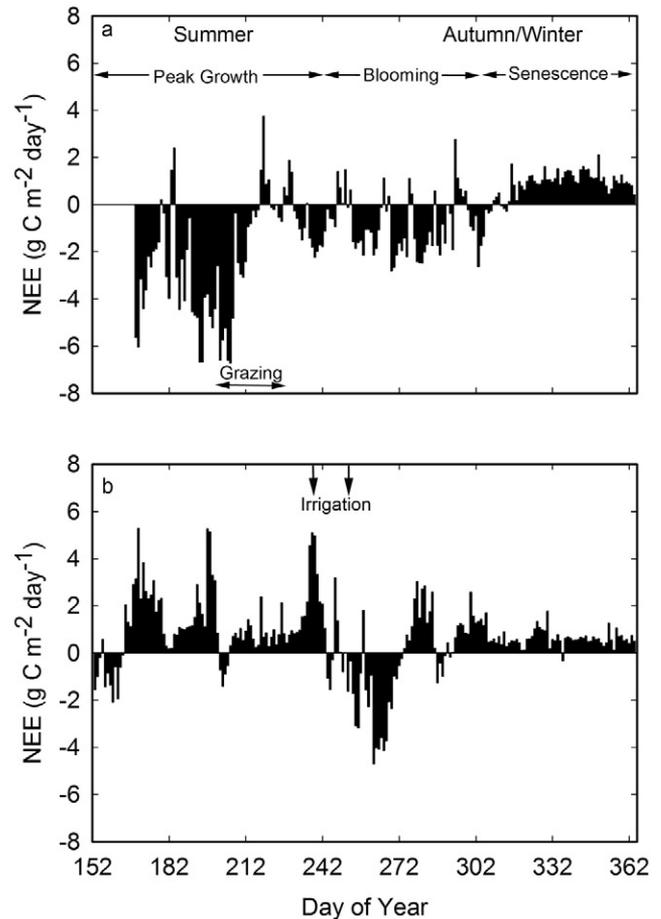


Fig. 3. Daily accumulated net ecosystem exchange (NEE) of CO_2 during the measurement period in (a) 2010 and (b) 2011. Negative values indicate a gain of C by the ecosystem and positive values indicate ecosystem loss of C.

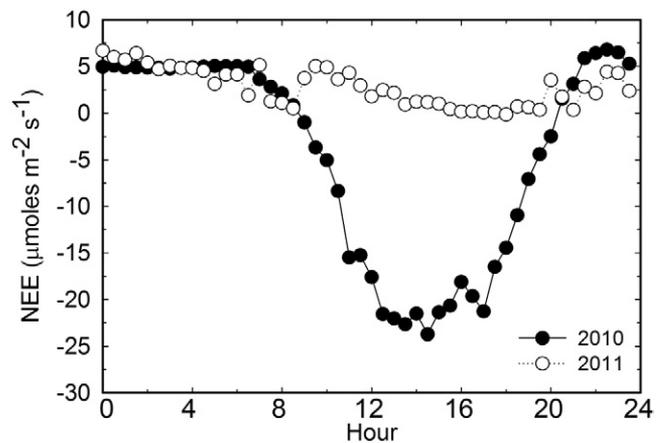


Fig. 4. Diurnal variations in half-hourly net ecosystem exchange (NEE) of CO_2 on Day of the Year 195 in 2010 and 2011.

following DOY 302. The pasture remained dormant from November through December, becoming a CO_2 source. The severe drought and poor growth during the summer months in 2011 caused the pasture to be in the dormant stage, with no blooming occurred during September through October. The pasture was irrigated in late August and early September (DOY 237 and 250), which caused a brief greening of the pasture and

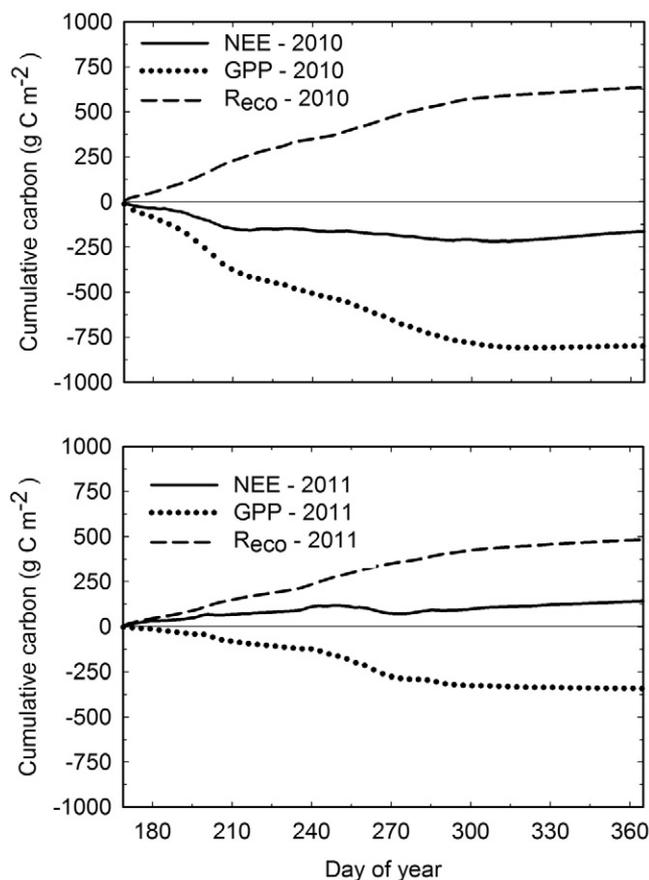


Fig. 5. The cumulative gross primary production (GPP), net ecosystem exchange (NEE), and ecosystem respiration (R_{eco}) since Day of the Year 169 for 2010 and 2011. Negative values indicate a gain of C by the ecosystem and positive values indicate ecosystem loss of C.

gradual increase in NEE until DOY 262. As the soil dried out, the NEE again rapidly declined. This was followed by another short-lived increase in NEE after two small rainfall events on DOY 251 and 281. The pasture continued as a CO_2 source for the rest of the year.

Cumulative Net Ecosystem Exchange, Ecosystem Respiration, and Gross Primary Production

Figure 5 presents the cumulative NEE, GPP, and R_{eco} of the pasture. At the beginning of the measurement period in 2010, the increase in cumulative NEE and GPP reflected the intensive growth period of the pasture. The pasture continued to sequester C until the end of the flowering period, when the GPP curve reached a peak. The NEE curve started declining at the onset of senescence because of the continued increase in R_{eco} . The pasture remained a C sink for the rest of the year. The total accumulated C for 2010 was 164 g C m^{-2} . In 2011, the total R_{eco} was greater than the gross photosynthetic production, which resulted in positive NEE throughout the measurement period. The occurrences of short-lived negative NEE events (see Fig. 3) did not alter the general nature of the pasture as a C source during 2011. The net cumulative loss of C from the pasture for 2011 was 142 g C m^{-2} .

Ecosystem Respiration and Temperature Sensitivity

Exponential functions described by Eq. [1] were developed using daily R_{eco} and T_{soil} (Fig. 6). In both years, the magnitude of R_{eco} increased with increasing temperature. The computed value of Q_{10} , which indicates the temperature sensitivity of R_{eco} , was $2.1 \text{ g C m}^{-2} \text{ s}^{-1}$ in 2010. Under the drought conditions of 2011, the corresponding value of Q_{10} was $1.5 \text{ g C m}^{-2} \text{ s}^{-1}$. When we excluded days when the VWC was < 0.15 , the fit of the exponential relationships improved significantly. In 2010, when days with VWC < 0.15 were excluded, the coefficient of determination (r^2) increased from 0.66 to 0.92 and Q_{10} increased from 2.1 to $3.0 \text{ g C m}^{-2} \text{ s}^{-1}$ (Fig. 6b). Similarly, excluding the extreme dry conditions in 2011 increased the r^2 significantly from 0.35 to 0.90 and Q_{10} from 1.5 to $2.4 \text{ g C m}^{-2} \text{ s}^{-1}$ (Fig. 6d).

Ecosystem Respiration and Gross Primary Production

Figure 7a shows GPP plotted vs. R_{eco} for 2010 and 2011. In 2010, most of the data points fell below the 1:1 line, indicating that GPP exceeded R_{eco} and the ecosystem was acting as a net C sink on those days. The effect of grazing on GPP was high. As grazing progressed, GPP decreased from 14.7 to $2.7 \text{ g C m}^{-2} \text{ d}^{-1}$ at the end of grazing. The GPP in 2010 was also strongly correlated to ecosystem respiration (Fig. 7b, $r^2 = 0.81$). In 2011, the majority of points were above the 1:1 line, indicating that R_{eco} exceeded GPP and the ecosystem was acting as a net C source. The small number of points below the 1:1 line were associated with the infrequent rain events that occurred that year. Poor correlation was found between GPP and R_{eco} in 2011, in part because most of the points were concentrated near the origin (Fig. 7c, $r^2 = 0.35$).

Light Response Curves

The responses of daytime NEE to PPFD are presented in Fig. 8. These light response curves were developed for 8- to 10-d periods during the major growing seasons in 2010 and 2011. Light response curves were also developed for the beginning and end of the grazing period in 2010. Light saturation was not apparent during the peak growth and beginning of grazing periods in 2010 (Fig. 8a and 8b). Values of NEE_{max} at the peak growth stage (DOY 190–199) and initial grazing period (DOY 200–209) were similar in magnitude; however, the average daytime ecosystem respiration during the grazing period ($8.5 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) was approximately double that for the period before grazing ($4.3 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). This resulted in a higher $(NEE_{\text{max}} + R)_{2000}$ value during the grazing period ($-26.7 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) compared with the period before grazing ($-23.9 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). The NEE_{max} fell to $-14.1 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and $(NEE_{\text{max}} + R)_{2000}$ decreased to $-5.8 \mu\text{mol}$ at the end of the grazing period (DOY 218–227). The average daytime ecosystem respiration at the end of the grazing period was $6.1 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. The NEE_{max} during the flowering period in 2010 (DOY 244–254) was $-13.3 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (Fig. 8d). Higher NEE_{max} ($-21.8 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) was observed for the same period in 2011 due to the growth of the pasture during that time following irrigation (Fig. 8f). During the period before irrigation

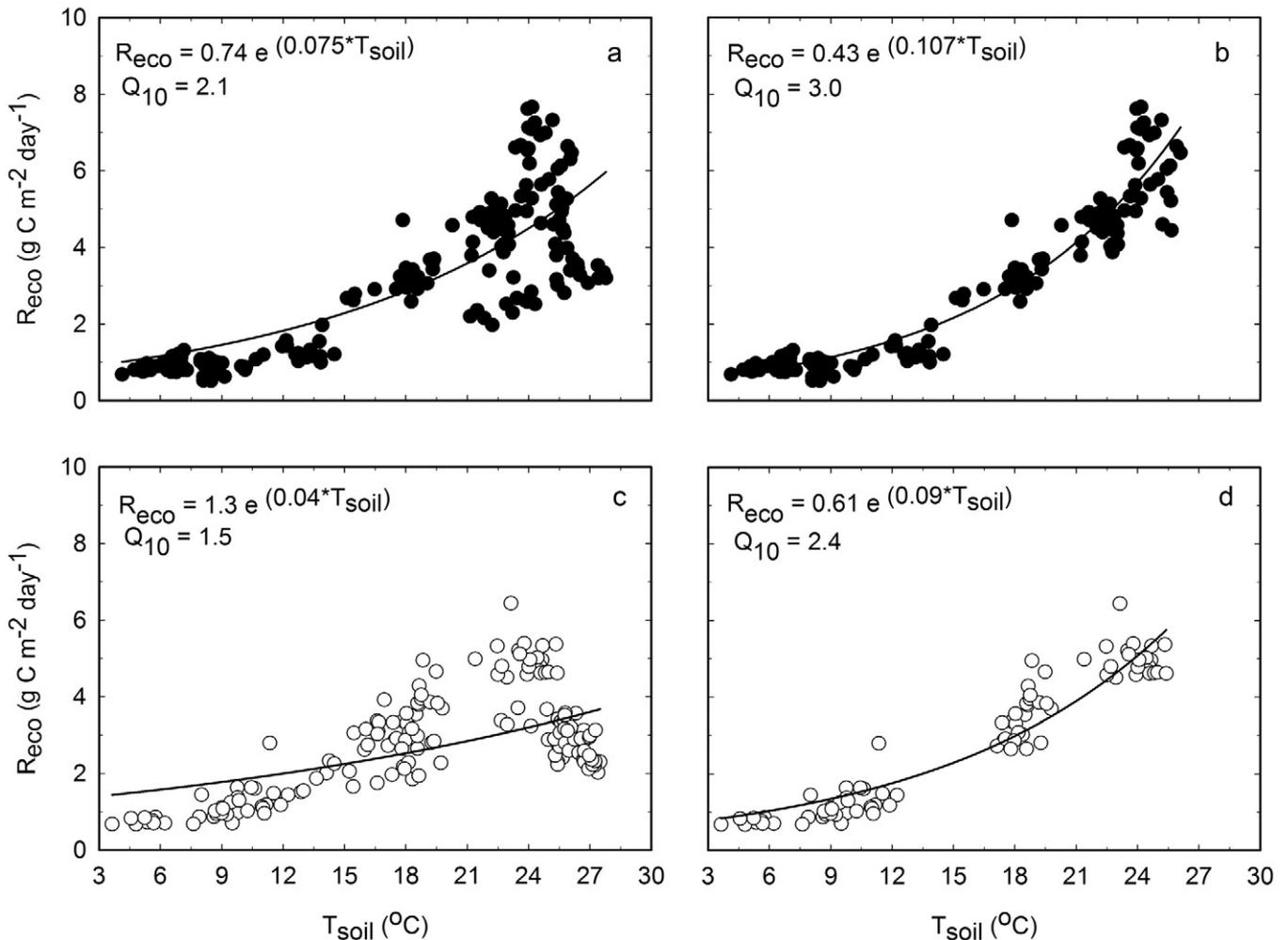


Fig. 6. Response of ecosystem respiration (R_{eco}) to soil temperature measurements (T_{soil}) at the 4-cm depth in 2010 for (a) all days ($r^2 = 0.66$, $n = 197$, $P < 0.001$) and (b) all days except days when volumetric water content was $< 0.15 \text{ m}^3 \text{ m}^{-3}$ ($r^2 = 0.92$, $n = 156$, $P < 0.001$) and in 2011 for (c) all days ($r^2 = 0.35$, $n = 171$, $P < 0.001$) and (d) all days except days when volumetric water content was $< 0.15 \text{ m}^3 \text{ m}^{-3}$ ($r^2 = 0.90$, $n = 86$, $P < 0.001$). The solid lines represent the regression functions.

(DOY190–199) in that year, however, NEE values showed no response to PPFD because the canopy was dormant with no photosynthetic activity. The initial slope of the light response curve representing apparent quantum efficiency (α) was 0.024 at the beginning of the peak growth stage in 2010 (DOY 190–199). The apparent quantum efficiency reached maximum values of 0.036 and 0.038 during DOY 200 to 209 and DOY 218 to 227 (Fig. 8b and 8c). Alpha declined to 0.019 during the flowering period in 2010 (Fig. 8d). During the same period in 2011, the estimated value of α was 0.013 (Fig. 8f).

DISCUSSION

In semiarid natural and managed grasslands, water is the most limiting factor for plant growth (Yang et al., 2011). The timing and amount of precipitation play major roles in the C balances of these agroecosystems. We normally think of grasslands and pastures as C sinks, but extreme climate events such as drought can change the ecosystem from a C sink to a C source (Ciais et al., 2005; Zhang et al., 2011). The timing and duration of the drought with respect to the growing stage of the grasses are important in determining the source–sink relationships (Kim et al., 1992; Novick et al., 2004; Scott et

al., 2009; Zhang et al., 2011). Annual precipitation in 2011 was 343 mm less (77% reduction) than the 9-yr (2001–2010) average precipitation. Normally, the dryland and deficit-irrigated cropping systems in the region depend on soil moisture accumulated during the winter and early spring to support early growth; however, the limited precipitation following the 2010 growing season resulted in little soil moisture reserves for the start of the 2011 growing season. Additionally, the summer of 2011 also exhibited extremely high temperatures (see Table 1). Although the pasture was irrigated a few times in 2011, the paucity of growing season precipitation and high temperatures (see Fig. 1) resulted in little growth of the WW-B. Dahl grass in this field during 2011, as evidenced by the daily and cumulative net ecosystem C exchange (Fig. 3 and 5). The pasture was a CO_2 source during the summer months (June–August) of 2011, with a net C release of 116 g C m^{-2} . During the same period in 2010, the pasture was a strong CO_2 sink, with a net C uptake of 164 g C m^{-2} . Flanagan et al. (2002) reported for a northern temperate grassland that the ecosystem became a source of C in a dry year due to slightly higher respiration compared with a year with average precipitation. A number of other studies have

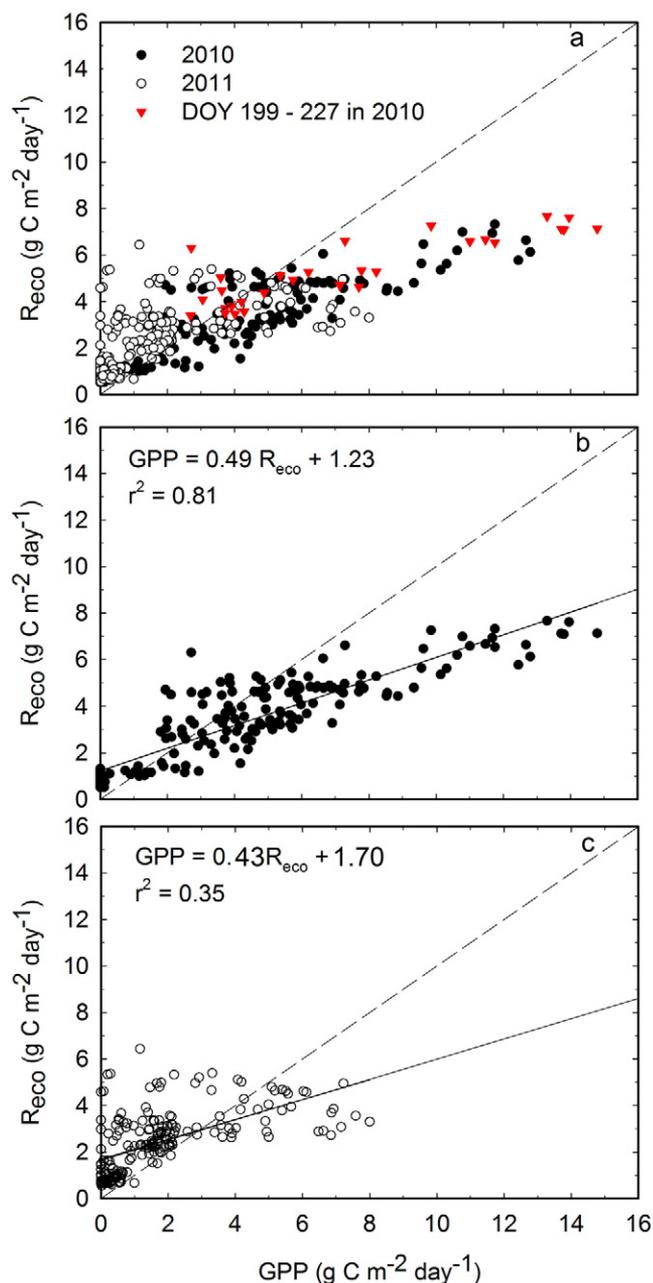


Fig. 7. Daily gross primary production (GPP) plotted against corresponding daily ecosystem respiration (R_{eco}): (a) data for the whole study period and the grazing period in 2010 (Days of the Year [DOY] 199–227); (b,c) data for 2010 and 2011 ($n = 197$, $P < 0.001$). Solid lines represent the regression line and dashed lines represent the 1:1 line.

also reported grasslands and pastures changing from a C sink to a C source due to severe drought conditions experienced during the growing season (Nagy et al., 2007; Hussain et al., 2011; Jongen et al., 2011; Mudge et al., 2011).

Ecosystem respiration is another major factor in determining the source–sink relationships of terrestrial ecosystems. Annual total R_{eco} primarily results from autotrophic respiration during the growing season (approximately 60%) and heterotrophic respiration during the dormant season. Thus, a number of biotic and abiotic factors are involved in determining the rate and seasonal evolution of R_{eco} . Temperature is the major environmental variable controlling the rate of R_{eco}

in the absence of severe drought (Lloyd and Taylor, 1994; Yvon-Durocher et al., 2012). At our study site, R_{eco} was an exponential function of increasing T_{soil} at the 4-cm depth in both years. The exponential model explained 66% of the variation in R_{eco} during 2010 with a temperature sensitivity index (Q_{10}) of 2.1 during that period. When we excluded the 41 d with limited soil water from the 2010 data, the exponential model explained 92% of the variation in R_{eco} , and Q_{10} increased from 2.1 to 3. These water-limiting days occurred primarily in the peak growing season for the pasture, when R_{eco} should normally be relatively high. We can hypothesize that the reduction in total R_{eco} for these water-limiting days was primarily due to reduced growth respiration as a result of the immediate physiological response of the grass to water stress. Closing of stomata during water stress can lead to reduced gross photosynthesis. Because growth respiration depends on gross photosynthesis, it can also decrease during periods of water stress. The severe drought in 2011 caused the pasture to remain in a dormant state throughout what would normally be the growing season. As van der Molen et al. (2011) pointed out, continued drought can cause structural changes in the vegetation and reduced GPP and R_{eco} . Thus, we can assume that the contribution of autotrophic respiration to total R_{eco} was minimal in that year, and the major contribution to the total cumulative R_{eco} came through heterotrophic respiration. For 2011, Eq. [1] described only 35% of the variation in R_{eco} . When days with water-limiting conditions were excluded, however, the exponential function explained 90% of the total variation in R_{eco} , and Q_{10} increased from 1.5 to 2.4. Xu and Baldocchi (2004) reported Q_{10} values ranging from 2.1 to 2.5 for a Mediterranean annual grassland in California. In their study, the high Q_{10} values occurred during the active growth period of the grass. Several other researchers have reported low Q_{10} values during dry periods (Flanagan and Johnson, 2005; Aires et al., 2008). Carbone et al. (2008) reported Q_{10} values for soil respiration ranging from 1.1 to 1.35 for a semiarid perennial grassland. Researchers have suggested that respiration models developed using multiple factors, such as soil moisture, humidity, and canopy temperature, could be effective in explaining the seasonal and annual variations in R_{eco} (Wang et al., 2010). Such an analysis was outside the scope of this study.

In agroecosystems, the effects of management-related factors such as grazing can be observed in CO_2 flux measurements. Depending on the timing, duration, and intensity of grazing, its effects on C exchange can vary. In the Southern Great Plains, warm-season perennial grasses are primarily grazed during the summer and fall. In our study, the daily NEE in 2010 peaked in July as grazing commenced (see Fig. 3). As grazing progressed, the daily NEE fell precipitously as vegetation was removed from the pasture so that, at around the time that grazing ceased, the daily NEE became positive (indicating a net loss of C to the atmosphere). It has commonly been observed that grazing cattle preferentially remove the leaves of tall grasses while leaving many of the stems intact. As grazing progressed, therefore, the C uptake component of NEE (photosynthesis) was reduced through leaf loss while the C release component (maintenance respiration) remained at substantial levels due to the presence of living stems. The

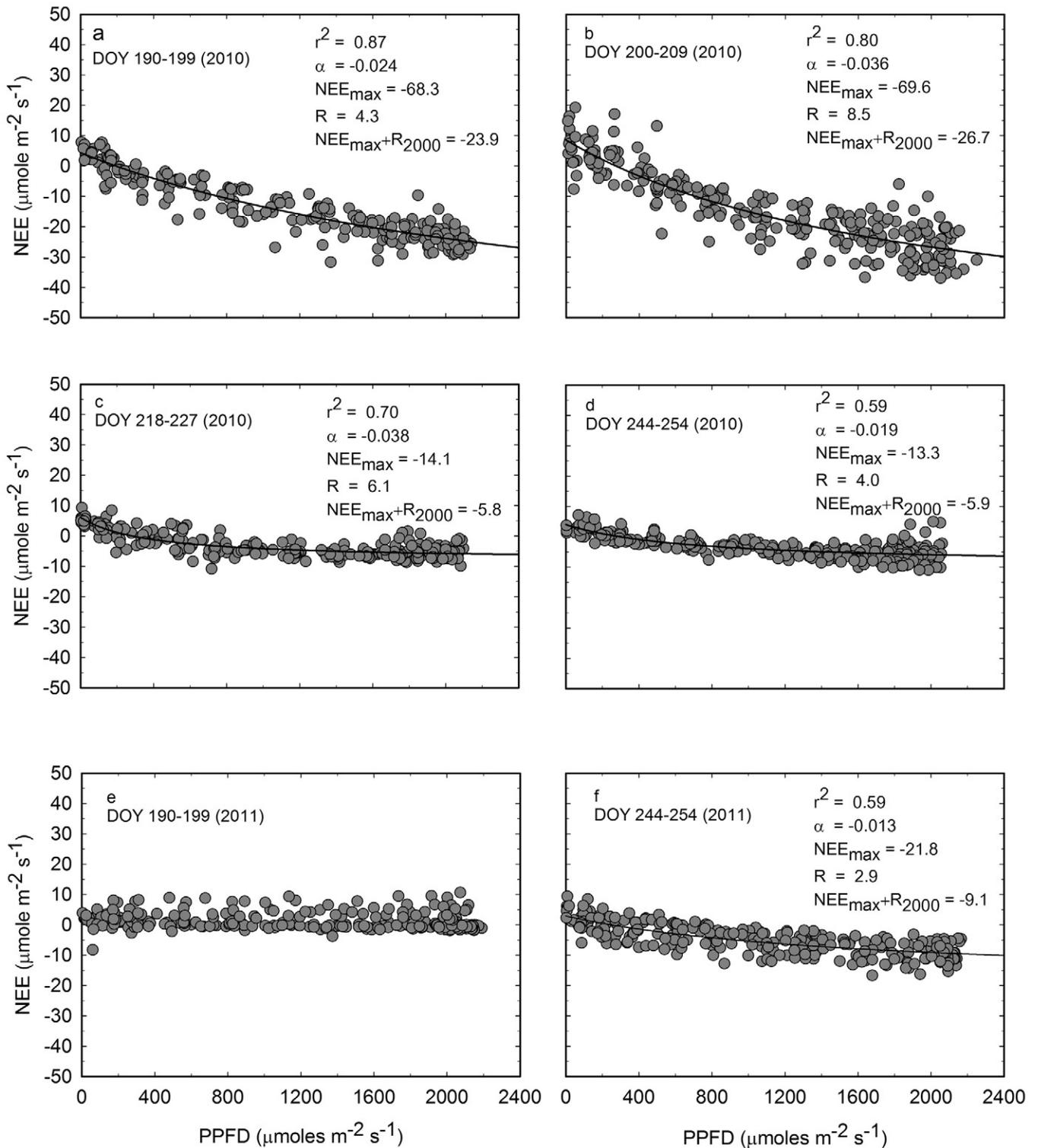


Fig. 8. Light response curves generated by plotting daytime half-hourly net ecosystem exchange (NEE) against corresponding photosynthetic photon flux density (PPFD) for different periods of growth in 2010 and 2011: (a) Days of the Year (DOY) 190 to 198 (peak growth) in 2010, (b) (DOY 200 to 209 (beginning of grazing) in 2010, (c) DOY 218 to 227 (end of grazing) in 2010, (d) DOY 244 to 254 (flowering) in 2010, (e) DOY 190 to 199 in 2011 and (f) DOY 244 to 254 in 2011. The curves (solid lines) were fitted using the modified Michaelis–Menten equation (Eq. [3]) except for (e).

combination of maintenance respiration and the background soil respiration ultimately resulted in the observed positive daily NEE values near the end of the grazing period. Similar declines in NEE have been observed in several other studies involving grazed pastures (Mudge et al., 2011). At our study

site, grazing occurred in the peak growing season, hence the effect of grazing on NEE and GPP was high. Kato et al. (2006) reported that winter grazing during the dormant season had little effect on the CO_2 flux measurements in an alpine meadow. In a similar ecosystem, Cao et al. (2004) found

that the grazing intensity can affect the aboveground and belowground biomass and hence the soil respiration rate even with winter grazing. Understanding grazing effects on the annual C balance of managed grasslands requires investigating a multitude of factors, including environmental, management, and biological variables. Further studies are needed to investigate these factors.

The empirically determined light response parameters similar to those developed in this study are often used in modeling C dynamics at larger spatial scales (Goetz and Prince, 1999; Baldocchi, 2008). Studies have found that NEE–PPFD response curve relationships are affected by vegetation type, phenological stage, and environmental variables such as temperature and soil moisture (Ruimy et al., 1995; Zhang et al., 2012). In our study, light saturation was not observed within the range of measured values during the peak growth stage of the pasture in 2010 (Fig. 8a and 8b). The maximum rates of CO₂ exchange at infinite PPFD (NEE_{max}) calculated from the curves during those periods were higher than those reported in the literature for unmanaged C₄ grasses (Suyker and Verma, 2001). The value of NEE_{max} ($-68.3 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) during DOY190 to 199 exceeded the largest observed daytime NEE flux ($-31.7 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) during that period. Similarly, the value of NEE_{max} ($-69.6 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) during DOY 200 to 209 exceeded the largest observed daytime NEE flux ($-37.0 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) during that period. These high NEE_{max} values are theoretical and could not be achieved at the PPFD levels present in our pasture. Thus, $(NEE_{max} + R)_{2000}$ values (see Fig. 8a and 8b) are more realistic representations of the maximum C uptake that can be achieved under actual field conditions (Reichstein et al., 2012). Lack of light saturation in the NEE–PPFD relationship was also reported by Eamus et al. (2001) for a north Australian savannah dominated by C₄ grasses during the rainy season. Xu and Baldocchi (2004) reported an NEE_{max} value of $-40.2 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ during the active growing stage for a C₃ grass in a Mediterranean climate. In our study, the high NEE_{max} and $(NEE_{max} + R)_{2000}$ values corresponded to the period of lush growth after the above-normal rainfall received in July 2010. Therefore, we propose that these ideal growing conditions during the peak growing season in 2010 were responsible for the higher photosynthesis and net C uptake by this managed C₄ grass pasture. The observed declines in NEE_{max} and $(NEE_{max} + R)_{2000}$ due to grazing, flowering, senescence, and drought were similar to trends reported in previous studies involving grasslands (Suyker and Verma, 2001; Flanagan et al., 2002; San José et al., 2008).

The apparent quantum yield estimated from the NEE–PPFD curve varied during the growing season. The range of α (0.013–0.038) is similar to values reported for C₄ grasses by other researchers (Ruimy et al., 1995). The high NEE_{max} values calculated from the NEE–PPFD curves usually are associated with high α values (Zhang et al., 2011). As seen in our results from the beginning of the grazing period, the estimated NEE_{max} was $-69.6 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and α was 0.036. At the end of grazing period, however, α was slightly higher (0.038) and NEE_{max} had fallen to $-14.1 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. This could be explained by the observation that, at the end of the grazing period, the plants in the pasture were producing new leaves to replace the older leaves removed by the grazing animals.

We can hypothesize that NEE increased at lower light levels due to the presence of these newly formed leaves; however, the amount of vegetation capable of net C uptake was not adequate to utilize the increasing light intensity levels later in the day. This, in conjunction with high dark respiration rates ($6.1 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), resulted in a higher α at the end of the grazing period. Zhang et al. (2011) reported a similar trend for croplands without adequate N fertilization during dry periods. The drought in 2011 also impacted the overall productivity of the pasture, as evidenced by the low apparent quantum yield during the period when the pasture was growing following irrigation (DOY 250–259). Several researchers have reported reduced apparent quantum yields during drought periods in grasslands (Suyker and Verma, 2001; Aires et al., 2008).

The results of this study showed that environmental and management factors can significantly affect the C sink or source status of managed pastures. Accurate measurements of net CO₂ exchange and factors affecting the exchange processes are important in understanding the role of a particular land cover type on feedbacks between the biosphere and the atmosphere at regional, continental, and even global scales. The new restrictions on pumping water from the Ogallala aquifer in the Texas High Plains could accelerate a change in land use in the region from high-water-demand crops to dryland farming and grasslands. The USDA Biofuels Strategic Production Report (USDA, 2010) recognized this region as a potential cellulosic biofuel feedstock production region. In the near future, managed grasslands and pastures could emerge as a dominant land cover type in the region. Integrating results from our study in a modeling framework will help to improve our understanding of the contributions of managed pastures in the regional C balance and the responses of these ecosystems to climate change.

CONCLUSIONS

Carbon flux measurements made on a managed WW-B. Dahl Old World bluestem pasture in the semiarid Texas High Plains demonstrated that the dynamics of NEE, R_{eco} , and GPP for this agroecosystem were strongly affected by environmental variables. In a year with adequate precipitation (2010), the pasture acted as a strong sink for C. In contrast, severe drought conditions in the following year (2011) resulted in the pasture acting as a strong source for C. In the absence of water-stress conditions, temperature was the major driving force for total ecosystem respiration. Although we did not explicitly model the effect of soil moisture on ecosystem respiration in the current study, our analysis showed that low soil moisture levels were the main factor associated with reducing the temperature sensitivity (Q_{10}) of ecosystem respiration. During 2010, grazing reduced the NEE and GPP of the pasture, but the reductions were not sufficient to change the overall C balance of the ecosystem from a sink to a source. The extreme drought of 2011 caused the pasture grass to remain dormant throughout most of the year, and the ecosystem remained an overall C source throughout this period. These results support the need for continued study of pastures in the Southern High Plains to better understand the highly dynamic nature of their C exchange processes and their implications on regional and hemispheric C dynamics.

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