NET ECOSYSTEM EXCHANGE OF CARBON DIOXIDE AND WATER VAPOR FLUXES IN SWITCHGRASS AND HIGH BIOMASS SORGHUM

By

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Abstract: Understanding carbon and water dynamics of switchgrass (*Panicum virgatum* L.) and high biomass sorghum (*Sorghum bicolor* L. Moench) ecosystems is crucial as the acreage of these feedstocks is expanding for cellulosic biofuels. Net ecosystem exchange (NEE) of CO_2 and H_2O was measured using eddy covariance system over co-located switchgrass and sorghum fields in south central Oklahoma, USA. The major objectives of this study were to quantify and examine seasonal variations in NEE, evapotranspiration (ET), and ecosystem water use efficiency (EWUE) over switchgrass and sorghum ecosystems in response to controlling factors, and to explore the underlying mechanisms. The results revealed photosynthetic photon flux density (PPFD) as the most significant environmental factor for variation in NEE under optimal weather conditions. However, warm air temperature and high vapor pressure deficit (VPD) obscured the NEE-PPFD relationship. Larger VPD (>3 kPa) limited photosynthesis and asymmetrical diurnal NEE cycles were observed in both ecosystems. Consequently, rectangular hyperbolic light-response curve (NEE partitioning algorithm) consistently failed to provide good fits at high VPD. Modified rectangular hyperbolic light-VPD response model accounted for the limitation of VPD on photosynthesis and improved the model performance significantly. The magnitudes of CO_2 and H_2O fluxes were similar in both ecosystems during the active growing periods and the differences in carbon sink potential and seasonal water demand were primarily driven by the length of the growing season. Monthly ensemble averaged NEE of switchgrass and sorghum reached seasonal peak values of -33.02 ± 1.96 and -35.86 ± 2.32 $\mu mol\ m^{-2}\ s^{-1}$, respectively. Similarly, weekly average of daily integrated NEE reached seasonal peaks of -8.5 $g\ C\ m^{-2}\ day^{-1}$ in switchgrass and -10.3 $g\ C\ m^{-2}\ day^{-1}$ in sorghum. During peak growth, daily ET reached up to 6.2 $mm\ day^{-1}$ for switchgrass and 6.7 $mm\ day^{-1}$ for sorghum. The EWUE was about 12 $g\ CO_2\ mm^{-1}$ ET in switchgrass and about 10 $g\ CO_2\ mm^{-1}$ ET in sorghum. This research showed strong seasonal carbon sink potential and high water use efficiency of both ecosystems in this region. However, evaluation over a longer term would be more valuable.

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INTRODUCTION

Biofuels

America consumes about 25% of the world's oil as one-third of the automobiles (230 million) are in America (National Biofuels Action Plan, http://www1.eere.energy.gov/biomass/pdfs/nbap.pdf, verified April 11, 2013). According to the projection of the U.S. Energy Information Administration (EIA), the reliance on foreign producers for oil will increase 30% by 2030 and the transport sector's greenhouse gas emissions will rise by 40% (Annual Energy Outlook, 2007, ftp://ftp.eia.doe.gov/forecasting/0383(2007).pdf, verified April 11, 2013). The demand and cost of energy are increasing, and oil and gas reserves are declining. Current ethanol production from sugar/starch is non-sustainable because of direct competition with food and feed sources. In addition, corn (*Zea mays* L.) based ethanol is reaching the mandated blending wall limit of 15 million gallons (56 megaliters) per year in the U.S. Even if the total U.S. corn crop is used for ethanol production, it can supply only less than 25% of the total U.S. fuel consumption. Moreover, CO_2 concentration is increasing in the atmosphere since Industrial Revolution of the mid-nineteenth century and most of the released CO_2 into the atmosphere is a result of burning fossil fuels (Revelle and Suess, 1957). Due to these reasons, it is an essential to supplement the current energy consumption by alternative sources. There are numerous efforts worldwide to produce biofuels from biomass. Substituting fossil fuels with biofuels is one of the major avenues for reducing CO_2 emissions as well (Pacala and Socolow, 2004). This is because bioenergy crops convert atmospheric CO_2 to organic carbon in crop biomass and soil which ultimately could help offset CO_2 emissions (Adler et al., 2007).

The Biomass Research and Development (R&D) Advisory Committee, a panel established by the Congress, has set a vision to supplement 30% of the current U.S. petroleum consumption with biofuels by 2030. Biomass is the America's largest domestic source of renewable energy and the only current renewable source of liquid transportation fuel. To displace 30% of the county's present petroleum consumption, one billion dry tons of biomass feedstock is required each year. The United States Department of Agriculture (USDA) estimated that the annual biomass potential of U.S. from forestland and agricultural land, two largest biomass sources, is over 1.3 billion dry tons (368 million dry tons from forestlands and 998 million dry tons from agricultural lands) (Perlack et al., 2005).

Currently much emphasis has been given to efficiently and sustainably produce liquid transportation fuels from cellulosic feedstocks. As part of the U.S. Energy Independence and Security Act (EISA), the Renewable Fuel Standard mandates 16 billion gallons (60 billion liters) of biofuels from cellulosic feedstock out of total 36 billion gallons (136 billion liters) of biofuel production by 2022. This 2022 biofuel goal requires developing alternative feedstock sources to traditional feedstock like maize for food security and to meet increasing biofuel feedstock demand. Although the use of crop and forest residues can be one potential source of biomass, switchgrass (*Panicum virgatum* L.) which is a highly productive C_4 perennial warm-season grass native to North America has been chosen as a model cellulosic feedstock by the U.S. Department of Energy (DOE) through a decade long, multi-location (31 sites) and multi-species (34 species) trials due to its potential for high yields, deep rooting characteristics, and potential value in carbon sequestration (Wright, 2007). Other species identified as potential bioenergy crops include corn, Miscanthus (*Miscanthus giganteus*), sugarcane (*Saccharum officinarum*), and the tree species poplar (*Populus trichocarpa*). Although it has not been widely reported, high biomass sorghum (*Sorghum bicolor* L. Moench) is also another very promising bioenergy crop because of its potential for high production and drought tolerant (Rooney et al., 2007).

Ethanol production capacity has increased exponentially from 0.66 billion liters in 1980 to more than 49 billion litters in recent years (RFA 2012, http://www.ethanolrfa.org/pages/statistics, verified May 1, 2013). This increased deployment of dedicated biomass crops has sparked numerous environmental concerns. To maximize the environmental and economic benefits of biofuels is a key goal of the National Biofuels Action Plan (NBAP). Biofuel production should be sustainable without adverse impact to the environment or natural resources. Thus, it is an essential to assess the environmental implications such as the effect of feedstock production from major dedicated energy crops on soil, water, and air quality. Fewer environmental impacts are predicted from advanced cellulosic fuel production compared with grain-based ethanol production (Heaton et al., 2004). It is more likely that cellulosic crops provide positive effects on soil properties, biodiversity, energy balance, greenhouse gas mitigation, and carbon footprint (Rowe et al., 2009). However, environmental impacts and ecosystem services of biofuel production should not be neglected (Rowe et al., 2009). Therefore, we have to consider several factors when selecting environmentally and economically viable bioenergy feedstocks (Hill et al., 2006).

Ecosystem level CO_2, H_2O, and heat energy exchange measurements

Exchanges of heat, water vapor, trace gases, and momentum occur between land surfaces and the atmosphere (overlying air). Several aspects of weather and climate are influenced through interactions between terrestrial ecosystems and the atmosphere (Pielke et al., 1998). Thus, a growing interest has recently emerged on the carbon and water dynamics of all kinds of ecosystems. Several methods can be used to measure CO_2 and H_2O fluxes over terrestrial surfaces. However, fluxes are generally measured using measurements of atmospheric elements in micrometeorological methods. Unlike several other methods, they do not modify the surface conditions and provide a spatially and temporally integrated measurement. Recently eddy covariance (EC) system has been considered as one of the most accurate micrometeorological methods which can measure net ecosystem exchange (NEE, the exchange of fluxes between an ecosystem and the atmosphere) at a scale of a few hectares to several kilometers (Baldocchi, 2003). Moreover, EC is the most viable method to measure NEE over short time scales, thus providing elucidation of the climatic controls on NEE (Baldocchi et al., 2001). Long term data sets from EC measurements are important to identify and characterize key physiological processes in the terrestrial carbon and water cycles (Goulden et al., 1998;Black et al., 2000). In addition, EC measurements are the prime source of data for developing and testing ecosystem process models (Baldocchi and Meyers, 1998;Grant et al., 2005) and validating model parameterizations at the stand level (Law et al., 2000;Wilson et al., 2001). Due to these reasons, direct measurements of NEE by the EC technique have increased in recent years in order to determine the roles of different ecosystems in the global carbon and water cycles. FLUXNET, an international network of micrometeorological tower sites, coordinates regional and global analyses of continuous observations of exchanges of CO_2, H_2O, and energy between terrestrial ecosystems and the atmosphere from over 500 tower sites using the EC method (http://fluxnet.ornl.gov/, verified December 18, 2012). The North American Carbon Program Science Plan (Wofsy and Harriss, 2002) laid emphasis to quantify carbon sink of the North America. It requires NEE measurements in a variety of ecosystems. Understanding the response of all ecosystems to different environmental conditions is helpful for better understanding of the exchange of CO_2 and H_2O between biosphere and the atmosphere. Unfortunately, very few studies of NEE measurements are reported in switchgrass (Skinner and Adler, 2010;Zeri et al., 2011). There is no information on carbon status of switchgrass ecosystems for the southern Great Plains of the United States, which will be the home to large stands of switchgrass in the near future (U.S. Department of Energy, 2011). Furthermore, earlier studies lacked thorough investigation of seasonal carbon dynamics in response to controlling factors. To our understanding there is no NEE study reported in high biomass sorghum (hereafter referred to as sorghum) yet. In addition, there is a scarcity of comparative NEE studies from co-located switchgrass and sorghum ecosystems. Better understanding of the seasonality of NEE with respect to controlling factors will be helpful for assessing climate change mitigation potential of these cellulosic feedstocks.

Understanding the efficiency of bioenergy crops in using available water to produce biomass and store carbon in soil is an important metric of bioenergy crop performance (Zeri et al., 2013). Quantifying and understanding of evapotranspiration (ET, the loss of water vapor from the ecosystem) and ecosystem water use efficiency (EWUE, net carbon uptake by the ecosystem per amount of water use) of bioenergy crops is very critical to assess the impact of increased deployment of dedicated biomass crops on local and regional hydrology. In most cases, ET is the second largest term after precipitation in the hydrological balance (Ford et al., 2007), indicating a major component of water balance in terrestrial ecosystems. The associated flux of latent heat, a major component of energy balance, has a major role on the planetary boundary layer dynamics (Baldocchi et al., 2000). Moreover, several hydrological and biological processes in an ecosystem are tightly linked via ET (McNulty et al., 1994;Wilson and Baldocchi, 2000). The study of ET is, therefore, fundamental for better understanding of terrestrial ecosystems. The EWUE, a key component of the hydrologic cycle which relates biomass production or carbon gain to water use, is intricately linked to biogeochemical cycles (Sellers et al., 1997). In recent years, EWUE has been considered as an important characteristic of vegetation productivity (Kuglitsch et al., 2008). The EWUE can be considered as a determinant of the sustainability of newly introduced crop species (Wallace, 2000). Emmerich (2007) suggested that EWUE would be an appropriate tool to compare different plant communities. Thus, the study of ET and EWUE in a variety of terrestrial ecosystems is an essential for the assessment of local, regional, and global water balances. But there is still a dearth of information on ET and EWUE of switchgrass and sorghum. This study takes advantage of recent technological advancements and used the EC technique for continuous half-hourly measurements of CO_2, H_2O, and energy fluxes from two dedicated energy crop species, switchgrass and sorghum. This study will be highly useful to assess the sustainability and environmental benefits of large-scale expansions of these two major dedicated energy crops.

Review of Literature

The eddy covariance method and theory

Measurement of heat, mass, and momentum exchanges between a homogenously flat surface and the overlying atmosphere using the EC method was proposed in the 1950s (Montgomery, 1948;Swinbank, 1951). However, it took several decades for full implementation due to instrumental limitations. The continuous eddy flux measurements became possible only in the 1990s after the development of new generation sonic anemometers and infrared gas analyzers, and the first comprehensive EC software packages (McMillen, 1988). The EC measurements are made in the surface boundary layer. In the surface layer, measured fluxes which are approximately constant with height represent the fluxes from the underlying surfaces. However, atmospheric turbulent is the dominant transport mechanism for eddy flux measurements.

The eddy flux (F) is approximately equal to the mean air density (ρ_a) multiplied by the mean covariance between deviations in instantaneous vertical wind speed (w) and mixing ratio (s), which is expressed as follows:

$$F \approx \overline{\rho_a \; w' s'} \qquad (1)$$

here over bar denotes temporal averaging (30-min) and the primes denote the deviation from the mean. Mixing ratio of a substance ‘c’ is defined as the ratio of density of the substance

(ρ_c) to the density of air (ρ_a). Open path LI-7500 analyzer does not measure mixing ratio, so there is an assumption that

$$\overline{\rho_a w' s'} = \overline{w' \rho_c'} \qquad (2)$$

Carbon dioxide flux (F_c) is presented as the mean covariance between deviations in instantaneous vertical wind speed and density of CO_2 (ρ_c), which is expressed as:

$$F_c = \overline{w' \rho_c'} \qquad (3)$$

Sensible heat flux (H) is equal to the mean air density multiplied by the covariance between deviations in instantaneous vertical wind speed and temperature (T). Inclusion of specific heat (C_p) term coverts it to energy units.

$$H = \rho_a C_p \overline{w' T'} \qquad (4)$$

Latent heat flux (LE) is calculated in a similar manner using water vapor (q) and later converted to energy units as follows:

$$LE = \lambda \rho_a \overline{w' q'} \qquad (5)$$

where λ is latent heat of vaporization.

NEE measurements and partitioning

Eddy covariance measures NEE of matter and energy. The NEE of CO_2 is the balance between two larger CO_2 fluxes: gross ecosystem production (GEP, carbon uptake via photosynthesis) and ecosystem respiration (ER, carbon release from autotrophic and heterotrophic respiratory activities).

$$NEE = ER - GEP \qquad (6)$$

In this equation, ER is always positive and GEP is positive during daytime and zero at nighttime as no photosynthesis occurs during nighttime. In equation 6, during nighttime NEE is equivalent to ER as GEP is zero, resulting in positive values of NEE. But larger values of GEP than ER during daytime yields negative values of NEE. Thus, the sign convention of NEE in this study is that CO_2 uptake by the ecosystem is negative, whereas a net CO_2 release to the atmosphere is positive.

The EC system does not measure ER and GEP individually. Instead, it provides the balance between these two terms. Thus, flux partitioning algorithms are necessary to estimate these component fluxes from measured NEE. One of the most widely used methods to partition NEE into GEP and ER is using the commonly used rectangular hyperbolic light-response curve (Falge et al., 2001).

$$NEE = \frac{\alpha \times GP_{\max} \times PPFD}{\alpha \times PPFD + GP_{\max}} + ER \qquad (7)$$

where α is the apparent quantum yield (i.e., the initial slope of the light-response curve [mol CO_2 mol^{-1} of photons)], PPFD is measured photosynthetic photon flux density (μmol m^{-2} s^{-1}), GP_{max} is the maximum canopy CO_2 uptake rate (μmol m^{-2} s^{-1}) at light saturation, and ER is respiration rate. However, the relationship between NEE and PPFD is influenced by several other factors such as temperature, VPD, and moisture stress. The CO_2 flux of canopy saturates less rapidly than that of a single leaf because lower leaves in plant canopies may be PPFD limited when the upper leaves are PPFD saturated (Ruimy et al., 1995). The failure of rectangular hyperbolic light-response function to describe daytime NEE only as a function of PPFD has been observed in several ecosystems (Li et al., 2005;Pingintha et al., 2010;Wang et al., 2008). It was because of the fact that the light-response function failed to account for the reduction in NEE at high VPD in the afternoon. Lasslop et al. (2010) calculated GP_{max} as the exponential decreasing function at high VPD to include the effect of VPD on photosynthesis as shown below:

$GP_{max} = GP_0 \exp [-k (VPD-VPD_0)]$, if $VPD > VPD_0$ (8)

$GP_{max} = GP_0$, if $VPD < VPD_0$ (9)

where k indicates the response of GP_{max} to VPD. Lasslop et al. (2010) set VPD_0 threshold as 1 kPa.

Daytime and nighttime ER

Ecosystem respiration is the CO_2 efflux from ecosystem to the atmosphere due to autotrophic (vegetation respiration) and heterotrophic (soil respiration) activities. Respiration is the second most important flux in the global carbon cycle after photosynthesis (Davidson et al., 2006). Soil respiration includes release of CO_2 from roots, soil microorganisms, and oxidation of carbon compounds (Lloyd and Taylor, 1994). During nighttime, NEE is equivalent to ER because photosynthesis does not occur at night. But during daytime, we do have both photosynthesis and respiration. Researchers have used different approaches to calculate ER: for example, the use of same ER during night and daytime (Lalrammawia and Paliwal, 2010), extrapolation of functional relationships between nighttime NEE and temperature to daytime conditions to estimate daytime ER (Xu et al., 2001). However, Villar et al. (1994) noted a reduction in dark respiration of leaves of two woody species (*Heteromeles arbutifolia* Ait. and *Lepechinia fragans* Greene) by 55% in light relative to darkness due to light inhibition of dark respiration. Similarly, Falge et al. (1996) modeled daytime respiration as half the rate of night time respiration at any temperature to account for the light inhibition of respiration. The relationship between NEE and PPFD is linear at low levels of light intensities, but the linear relationship breaks and slope changes abruptly as a result of reduction in CO_2 assimilation and higher respiration rates due to a lack of light induced inhibition of dark respiration. Thus, extrapolation of the linear relation of light curve to zero PPFD before the change in slope provides correct estimates of respiration for daytime (Villar et al., 1994;Bruhn et al., 2011). However, majority of the studies have used the intercept value of a hyperbolic light-response curve fit to determine ER using all daytime data.

Energy balance closure

The plausibility of EC measurements is assessed from energy balance closure (EBC) test. The EBC is determined by comparing turbulent heat fluxes (H + LE) with the available energy fluxes (R_n – G) as given below:

$$R_n - G = H + LE \qquad (10)$$

where R_n is net radiation, G is soil heat flux, H is sensible heat flux, and LE is latent heat flux.

The EC system under-estimates H and LE fluxes, and the sum of turbulent fluxes (H + LE) measured is always less than the available energy (R_n - G) (Twine et al., 2000). The available energy (R_n - G) is found to be larger than the sum of turbulent fluxes (H + LE) in all kinds of ecosystems across the world. Currently the EBC for many field-experiments and for the CO_2 flux networks is about 80% (Aubinet et al., 1999;Wilson et al., 2002). Now it became obvious that experimental data could not close the energy balance at the Earth's surface. However, the cause of underestimation is not well understood.

Initially the EC system was assumed to underestimate turbulent fluxes systematically. Improvements in the sensors and the flux correction methods helped to improve EBC over the past decade (Foken et al., 2005). Errors in available energy measurements or from neglecting heat storage in biomass could be another possible reason for the lack of EBC (Cook et al., 2004;Desai et al., 2005). Various locations of the footprints for the measurements of R_n and G, which are close to the EC tower, and H and LE, which are larger and upwind of the tower, may induce some discrepancy in EBC (Flanagan et al., 2002). However, even a careful application of all corrections of the turbulent fluxes reduced the residual only slightly (Mauder and Foken, 2006). Recently it is reported that the time-averaged fluxes (Finnigan et al., 2003) or spatially averaged fluxes including turbulent-organized structures (Kanda et al., 2004) can close the energy balance. These findings indicate that the unclosed EBC problem is not related to errors involve in the EC system. Instead, it is related to the atmospheric phenomena which EC systems fail to measure. These evidences suggest that it is not simple to correct this problem.

Based on previous investigations, it can be concluded that the correction of the lack of EBC in the surface layer cannot be a part of the EC method or its correction procedures. Missing flux is not a missing flux at the measuring point. Instead, it is related to the heterogeneous terrain and its influence on the turbulent exchange. At a first guess, the energy exchange between the atmosphere and the underlying surface on larger scales (> 1 km) can be corrected with Bowen ratio under the assumption that the scalar similarity is fulfilled (Foken, 2008).

Friction velocity threshold

There is a consensus that the EC system underestimates NEE under stable nighttime conditions due to drainage loss of respired CO_2 to low-lying areas because mixing is weak during weak turbulence conditions. These measurements should be replaced by empirically established values from respiration and temperature relationship during turbulent periods. Several authors have used different methods to determine the friction velocity (u*) threshold. Many researchers have visually examined the scatter plot of night time fluxes versus u* (Flanagan et al., 2002). But this method is subjective and can introduce lots of discrepancies. Use of a single threshold all the time will also introduce biases since u* shows diurnal and seasonal cycles, and meteorological and plant phenological characteristics influence u* threshold (Gu et al., 2005). Potential correlative in-phase relationship at the diurnal scale and out-of-phase relationship of seasonal time scale between ER and u* must be removed before determining u* threshold to make nighttime NEE independent of turbulent regimes (Gu et al., 2005). The critical μ* that produces correct nocturnal CO_2 fluxes is not constant and it is site and vegetation specifics (Veenendaal et al., 2004). Threshold u* at different sites ranges from 0 to 0.6 m s^{-1} (Massman and Lee, 2002). Lalrammawia and Paliwal (2010) observed an underestimation of CO_2 flux of *Cenchrus ciliaris* L. grassland ecosystem at $\mu^* < 0.05$ m s^{-1}. Flanagan et al. (2002) noticed an underestimation of CO_2 fluxes of northern temperate grassland at $\mu^* < 0.25$ m s^{-1}. Hutyra et al. (2008) rejected data at $\mu^* < 0.22$ m s^{-1} in a tropical forest biome.

Desai et al. (2005) compared normalized nighttime NEE to u* to determine u* cutoff. They considered u* cutoff where the deviations from normalized NEE (averaged over 0.05 m

s^{-1} friction velocity bins) remained consistently below zero. Deviations from mean normalized NEE was calculated by subtracting mean monthly nighttime NEE from observed NEE and then dividing the residual by the standard deviation of nighttime NEE for the month.

Nighttime fluxes increase with u* at both high and low ends of u* but independent at intermediate ranges of u* so that this range should be determined for filtering process. Fluxes were underestimated at lower u* threshold and were subject to potential pressure pumping effects at higher u* threshold (Gu et al., 2005). Gu et al. (2005) suggested reproducible and site independent statistical approach called moving point test (MPT) to process large datasets of wide ranges of observed night time flux versus u* relationships.

Flux corrections

Lack of EBC (Twine et al., 2000) and underestimate of night time CO_2 fluxes (Aubinet et al., 1999) are two systematic biases in EC measurements. Eddy covariance underestimated the CO_2 flux by the same factor as it underestimated the turbulent fluxes when EBC was not achieved (underestimation ranged from 10-30%) (Twine et al., 2000). Some authors have added EBC adjustment factors to the measured NEE values to account for underestimation (Twine et al., 2000; Barr et al., 2002). Barr et al. (2002) corrected CO_2 flux for underestimation by EC by applying 12.5% EBC adjustment to high wind speed fluxes ($\mu^* \geq \mu^{*TH}$, where μ^{*TH} is the threshold below which measured night time fluxes are rejected) at night and replacing low wind speed fluxes ($\mu^* \leq \mu^{*TH}$) with values estimated from empirical relationship between the closure-adjusted high wind speed fluxes and soil temperature at 5 cm. Some studies did not apply EBC adjustment factors to correct CO_2 fluxes (Cook et al., 2004; Desai et al., 2005) since these energy imbalances could be from errors in available energy measurements or from neglecting heat storage in biomass.

Data screening

Requirement of turbulent atmospheric conditions is a major limitation of the EC technique otherwise flux is underestimated because of inability of flux sensors to record them. Thus, data screening for weak turbulence based on μ* at night is the most common among eddy flux communities. Another screening criterion is removal of sample from non-representative footprints, for example data for the period when wind is blowing right behind the tower. Turbulent fluxes were filtered to keep in the range of -200 to 800 Wm^{-2} (Wolf et al., 2011). Abnormal values were removed (Flanagan et al., 2002). Sun et al. (2010) removed distinct outliers and kept LE fluxes in a range of -200 to 800 W m^{-2} and H fluxes in a range of -200 to 500 W m^{-2}. Physically unreasonable CO_2 fluxes beyond -50 to 50 µmol $m^{-2}s^{-1}$ were removed (Kochendorfer et al., 2011;Zeeman et al., 2010). Flux values for u'w' < 0 m s^{-1} were removed (Zeeman et al., 2010). Statistical outliers beyond ±3 STD range from a 14 day running mean window were excluded (Wolf et al., 2011).

Gap filling

It is impossible to obtain continuous NEE measurements. Missing data occurs due to system failures and data rejection when wind is blowing through undesirable wind direction or through a tower or when sensors are wet or if the measurements fail to meet acceptance criteria (Baldocchi, 2003). The average data coverage during a year was 65% across 19 sites (Falge et al., 2001) and 65-75% (Law et al., 2002). Thus, gap filling is required to get a cumulative sum over a period.

Several gap-filling methods have been proposed in scientific literature such as mean diurnal variation method (MDV- an interpolation technique based on the temporal auto-correlation of the fluxes), look-up tables (missing values are gap filled with the average of valid measurements under similar meteorological conditions), artificial neural networks (ANNs, an empirical nonlinear regression models), and nonlinear regression relationships between the flux and environmental drivers. A majority of the studies have employed empirical models based on dominant physiological processes for daytime and nighttime to fill data gaps. Respiration is greatly influenced by temperature. Exponential relationship between nighttime NEE and soil temperature can be created to fill gaps during nighttime and in the winter when ER is the only flux. During daytime in the growing season, photosynthesis is mainly driven by light so that hyperbolic relation between GEP and PPFD is commonly used to fill daytime gaps during the growing season (Flanagan et al., 2002).

Linear interpolation between the values adjacent to the missing values is especially used to fill small gaps (2-3 half hourly missing values) for meteorological variables (sunlight, temperature and relative humidity) (Falge et al., 2001). Half-hourly gaps were filled with an average value of immediate before and after the gap (Wever et al., 2002). Two hour or fewer gaps were filled using interpolated values (Flanagan et al., 2002). Linear interpolation can be used if there is a linear relationship between CO_2 flux and other some variables. In many cases, a linear relationship between PPFD and H_2O flux can be used. Gaps in H_2O flux data were filled using diurnal values derived for each time stamp of the day based on 14 day means (Kochendorfer et al., 2011). Established monthly ET – ET_0 regression models were used to fill gaps in a 30-min ET data set, and regression relationships between ET and R_n by month were used in case of unavailability of ET_0 (Sun et al., 2010). They employed a linear interpolation method during lack of all meteorological variables.

In the absence of empirical relationships due to missing meteorological data, mean diurnal variations (replacement of missing observations by the mean for that period on adjacent days) were used to estimate missing data (Falge et al., 2001;Flanagan et al., 2002). The size of data set used to develop these relationships depends on size of data gap. To fill gaps of 5 days or less, data for 3 days before and after the gap can be used. In case of a month data gap, 4 weeks of data before and after can be used. Law et al. (2002) used look-up table method to fill data gaps. For the look-up table method, tables are created for each site so that missing values can be "looked-up" based on the environmental conditions associated with the missing data. Falge et al. (2001) reported that several gap filling methods produced similar results and none of them introduced methodological bias.

Estimates of ET and EWUE

Total ET for 30-min period (mm 30-min^{-1}) is calculated from EC measured H_2O fluxes (mmol m^{-2} s^{-1}) as follows:

$ET = (H_2O \text{ flux}*18.01528*1800)/10^6$

Several methods of EWUE calculations are reported in literature. Emmerich (2007) determined EWUE from the ratio of daily daytime NEE of CO_2 to daily daytime ET (g CO_2

per mm H_2O) summed for the growing season. The EWUE was computed from the ratio of seasonal sums of daily daytime NEE or GEP to daily daytime ET (Tubiello et al., 1999). The EWUE was determined from the slope of daytime NEP vs ET and GEP vs ET using half hourly measurements of a single day (Kuglitsch et al., 2008). Kuglitsch et al. (2008) noticed that GEP and ET were tightly correlated than NEP and ET since respiration is not strongly coupled to ET and NEP relies on respiration. Day times with maximum CO_2 uptake with minimum ET were selected to maximize regression equations and EWUE were compared between plant communities using slopes for the maximum EWUE (Emmerich, 2007). Baldocchi et al. (2001) proposed an instantaneous method of EWUE estimation from the slope of regression of daily day time NEE or GEP vs. ET on seasonal scale. Daily or monthly EWUE can be computed from the ratios of daily or monthly integrals of GEP or NEE to ET.

Objectives

The objectives of these studies were to 1) quantify seasonal variations in ET, EWUE, and seasonal distributions of energy partitioning in switchgrass in response to controlling factors, 2) determine the seasonality of NEE in switchgrass with respect to controlling factors, 3) characterize the effects of key environmental factors on daytime NEE in switchgrass and to explore the underlying mechanisms, 4) quantify and contrast the magnitude of CO_2 flux exchange between switchgrass and sorghum ecosystems under the same growing condition, and 5) compare differences in water use between switchgrass and high biomass sorghum.

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CHAPTER II

GROWING SEASON VARIABILITY IN EVAPOTRANSPIRATION, ECOSYSTEM WATER USE EFFICIENCY, AND ENERGY PARTITIONING IN SWITCHGRASS

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ABSTRACT. Evapotranspiration (ET), ecosystem water use efficiency (EWUE), and energy partitioning in switchgrass (*Panicum virgatum* L.) ecosystems are crucial to understand its water and energy balances since switchgrass acreage is expanding for cellulosic biofuels. We measured CO_2, H_2O, and energy fluxes over a switchgrass field in Chickasha, OK, USA, using eddy covariance method. The objective of this study was to quantify seasonal variations in ET, EWUE, and seasonal distributions of energy partitioning in response to controlling factors. Seasonal (May to mid-November) cumulative ET (450 mm) was similar to cumulative rainfall (432 mm). During June to September, ET was 1.92 times of rainfall indicating that the crop experienced severe drought during the mid-growing season. Evapotranspiration showed a clear seasonality

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with 3 – 4 mm day^{-1} during the active growing season (late May and June) to low rates of about 0.5 mm day^{-1} during the late growing season (November). The ET rate decreased during dry periods. On seasonal scale, more energy was partitioned to sensible heat flux (H) than latent heat (LE) due to drought. Estimation of EWUE by dividing time integrals of gross ecosystem production (GEP) by respective H_2O fluxes (ET) at monthly time scale provided EWUE from 10.46 (August) to 14.08 (October) g CO_2 mm^{-1} ET with a seasonal average of 12.01 g CO_2 mm^{-1} ET. Seasonal patterns in EWUE were observed with smaller values during drought due to more rapid reduction in carbon assimilation (GEP) than ET. These findings confirm the major role of precipitation in determining water and energy balances in switchgrass.

Key words: Ecosystem water use efficiency, Eddy covariance, Energy partition, Latent heat flux, Switchgrass.

Introduction

Increasing impact of greenhouse gas emissions on climate, increasing oil prices, and growing concern on energy security are raising an interest in renewable bioenergy production. In the United States, as corn (*Zea mays* L.) is reaching the mandated blending wall limit of 15 million gallons (56 megaliters) per year, extensive efforts are on to efficiently and sustainably produce liquid transportation fuels from lignocellulosic feedstocks. The lignocellulosic feedstocks vary from woodchips to dedicated energy crops such as switchgrass (NBAP; http://www1.eere.energy.gov/biomass/ pdfs/nbap.pdf;

verified June 10, 2012). Switchgrass, a native C_4 perennial warm-season grass, has been considered as one of the most suitable cellulosic feedstock crops (McLaughlin and Adams Kszos, 2005). Large-scale expansion of switchgrass production in near future may considerably influence regional hydrologic and energy balances (Le et al., 2011). The hydrologic balance of terrestrial ecosystems is gaining interest in recent years (Aubinet et al., 1999) because drought affected geographic areas and drought intensity has increased globally in the last five decades (Dai et al., 2004) and drought is expected to influence the terrestrial hydrologic cycle in the near future.

In the hydrological balance, ET (evapotranspiration or latent heat flux) is the second largest term after precipitation in most cases, consuming about 50 – 90% of precipitation (Ford et al., 2007). Moreover, ET (latent heat flux) is a major component of energy balances in an ecosystem (Burba and Verma, 2005). Evapotranspiration from dedicated energy crops has become a topic of interest due to expanding production of biofuels. Several aspects of weather and climate are greatly influenced by partitioning of energy (net radiation, R_n) into ET and H fluxes (Pielke et al., 1998). An in-depth study of ET and energy partitioning in an ecosystem is of great importance because energy, water, and carbon cycles are tightly linked via ET processes (Wilson and Baldocchi, 2000). Furthermore, ET directly links hydrologic and biological processes in an ecosystem (McNulty et al., 1994).

Field measurement of EWUE (net carbon uptake by the ecosystem per amount of water loss as ET from the ecosystem) has recently been recognized as an important characteristic of vegetation productivity (Kuglitsch et al., 2008). Scaling up of leaf level measurements to the ecosystem level induces additional complications which affect

EWUE measurements (Ponton et al., 2006). Direct and continuous measurements of CO_2 and H_2O exchanges by eddy covariance (EC) system provide the opportunity to determine EWUE (Law et al., 2002). However, EWUE estimations are available for only few ecosystems and are yet to be determined in switchgrass. Even though net ecosystem exchanges of CO_2 and H_2O are studied globally in a number of ecosystems using EC system, there is a dearth of EC studies in switchgrass, especially in the southern great plains of the United States. This study took advantage of recent technological advancements and used EC system for continuous half-hourly measurements of CO_2, H_2O, and energy fluxes in a switchgrass ecosystem to address those knowledge gaps. A study from a northeastern USA switchgrass field reported carbon dioxide and water fluxes (Skinner and Adler, 2010). However, the study lacked detailed analysis of EWUE, ET, and energy partitioning which is crucial to understand the links between ET and other switchgrass ecosystem processes. The major objectives of this study were to quantify ET, EWUE, and seasonal distribution of energy partitioning in switchgrass, and to determine the role of environmental controls over them. These findings will also be helpful to understand the effect of future climate change on water cycle and energy partitioning in a switchgrass ecosystem.

Materials and Methods

Site description

Eddy covariance measurements were collected from a well-established switchgrass (cv. Alamo) field at South Central Research Station, Chickasha, OK (35.04° N latitude, 97.95°

W longitude, and 330 m above sea level altitude) during the 2011 growing season. Eddy covariance system had been set up at the North end of a flat eight hectare field facing towards the South as prevalent wind direction at the site was South to North. The field has 275 m fetch in the direction of prevailing winds and fetch in the East-West direction is 275 m. The surrounding field to the west was sorghum and the fields to the south and east were wheat fallows. The site was established in spring 2010 which was in energy sorghum for the previous two years. The crop was sown under no till condition at 38 cm row spacing in McLain silt loam soil (fine, mixed, superactive, thermic Pachic Argiustolls) and the experiment was rainfed. No fertilizer was applied in the establishment year and ammonium nitrate was broadcast applied in April 2011, the second year, at 75 Kg ha^{-1}.

Description of weather data

Mean monthly maximum and minimum temperatures, and monthly total rainfall in 2011 in comparison with a 30-year mean for the study site are presented in Table 1. Total annual precipitation in 2011 for the site was 525 mm while 30-year average was 896 mm. Table 1 shows that the growing season in 2011 was relatively warmer and drier than 30-year average. Rainfall was not well distributed during the growing season. No rainfall was received in April. The site received very low amounts of rainfall (48% less than that of 30-year mean) during June to September in 2011. In July 2011 (the hottest month with mean monthly maximum temperature = 40.36 ^{0}C), only 9% of 30-year average rainfall was recorded. The daily weather data for the study location was downloaded from the Oklahoma Mesonet website (www.mesonet.org; verified February 10, 2012).

Eddy covariance and other supplementary measurements

Fluxes were measured using EC system: CSAT3 sonic anemometer (Campbell Scientific Inc., Logan, UT, USA) and LI-7500 open-path infrared gas analyzer (IRGA, LI-COR Inc., Lincoln, NE, USA) mounted on top of a 2.2 m tall tower from the ground. Data was collected at 10 Hz frequency (10 samples sec^{-1}) and fluxes were calculated for a 30-min averaging period. Fluxes in this study were only the measured CO_2 and H_2O eddy fluxes. Storage fluxes were considered negligible because the tower height was only 2.2 m. Quantum sensor (LI-190, LI-COR Inc., Lincoln, NE, USA) was used to measure photosynthetic photon flux density (PPFD). Net radiation above crop canopy was measured using net radiometer (NR-Lite, Kipp and Zonen, Delft, The Netherlands). Temperature and relative humidity were measured using temperature and relative humidity probe (HMP45C, Vaisala, Helsinki, Finland). Soil heat flux (G) was measured using self-calibrating heat flux sensors (HFP01SC, Hukseflux Thermal Sensors B.V., Netherlands) at 5 cm depth. Near surface soil temperature and moisture were measured using water content reflectometers (CS616, Campbell Scientific Inc., Logan, UT, USA) and averaging soil temperature probes (TCAV-L, Campbell Scientific Inc., Logan, UT, USA). Soil heat storage term (ΔS), stored energy in the soil above heat flux plates, was calculated using temporal changes in soil temperature and soil water content as shown in equation below:

$$\Delta S = \frac{\Delta T_s C_s d}{t} \qquad (1)$$

where C_s is the heat capacity of moist soil, ΔT_s is the change in surface soil temperature (K), d is the depth of soil (m) above heat flux plates, and t is time (sec). The heat capacity of the moist soil (C_s) was calculated as below

$$C_s = \rho_b C_d + \theta_v \rho_w C_w \qquad (2)$$

where ρ_b is soil bulk density (1300 kg m^{-3}), C_d is heat capacity of dry soil (840 J kg^{-1} K^{-1}), θ_v is volumetric soil water content (m^3 m^{-3}), ρ_w is density of water (1000 kg m^{-3}), and C_w is heat capacity of water (4180 J kg^{-1} K^{-1}). Measured G and ΔS were added to obtain G at the surface. Data was collected at 10 Hz frequency and 30-min average values were calculated on-line using a datalogger (CR3000, Campbell Scientific Inc., Logan, UT, USA). The working condition of the flux tower and components, and data quality were continuously monitored through a dedicated online data display (http://energycrops.okstate.edu/eddy-flux-data).

Biometric measurements

Leaf area index (LAI), canopy height, and dry biomass (3 - 5 samples from 1 m^2 area) were measured at two week intervals beginning on 9 May (DOY 129) to October for the better interpretation of flux measurements. Leaf area index was measured using a plant canopy analyzer (LAI-2000, LI-COR Inc., Lincoln, NE, USA).

Data screening and gap filling

It is widely acknowledged that EC system underestimates flux during low turbulent conditions. Hence, we avoided all CO_2 and H_2O flux data during low turbulence periods, below a friction velocity (u*) threshold of 0.20 m s^{-1}. Samples from non-representative footprints, for example data for the period when wind was blowing behind the tower, were excluded. Turbulent fluxes were filtered to keep in the range of -200 to 500 W m^{-2} for H and -200 to 800 W m^{-2} for LE (Sun et al., 2010). Unreliable CO_2 fluxes beyond -50 to 50 µmol $m^{-2}s^{-1}$ were removed (Zeeman et al., 2010; Kochendorfer et al., 2011; Wolf et al., 2011). Statistical outliers beyond ±3.5 STD range from a 14 day running mean window were excluded for CO_2 and H_2O fluxes.

Half-hourly gaps in fluxes were filled with an average value immediately before and after the gap (Wever et al., 2002). Two hour or shorter gaps were filled using linear interpolated values (Flanagan et al., 2002). Linear or multiple linear regressions and exponential relationships between nighttime net ecosystem CO_2 exchange (NEE) values and soil temperature, air temperature, and soil moisture were evaluated for a week to account for seasonal variability in parameters, and finally the relationships with the highest level of significance were used to fill larger gaps in nighttime CO_2 flux. Daytime NEE (PPFD > 1 µmol $m^{-2}s^{-1}$) was partitioned into its two main components, GEP (gross ecosystem production) and ER (ecosystem respiration), and was modeled using commonly used rectangular hyperbolic light-response curve (Falge et al., 2001). Daytime ER was determined from the intercept of the ordinate while fitting the light-response curve. Larger gaps in H_2O flux were filled using linear relationship between PPFD and H_2O flux for a week. The linear relationship described the variability in H_2O fluxes very well for most of the time periods ($R^2 > 0.80$). Examples of selected models and comparison of measured and modeled diurnal trends of H_2O fluxes are provided in Fig. 1. Mean diurnal variations were used to fill gaps if there were no significant relationships between PPFD and H_2O fluxes (Falge et al., 2001). These estimates were used to fill gaps and replace H_2O fluxes during low turbulent periods ($u^* < 0.20$ m s^{-1}). Only measured half hourly values (not gap-filled) were used for the optimization of the model parameters.

Energy balance closure

The plausibility of EC measurements was assessed from energy balance closure (EBC) test. The EBC was determined on seasonal scale comparing turbulent heat fluxes (H + LE) with the available energy fluxes (R_n – G) for May to November. Canopy storage energy and the energy used in photosynthesis were not accounted in EBC calculation. Energy balance closure was calculated only if all four terms of EBC were available.

Estimates of evapotranspiration and ecosystem water use efficiency

Total ET for 30-min period (mm 30-min^{-1}) was calculated from EC measured H_2O fluxes (mmol m^{-2} s^{-1}) as follows:

$$ET = (H_2O \text{ flux} \times 18.01528 \times 1800)/10^6 \qquad (3)$$

We calculated EWUE during the daytime when there was carbon uptake into the ecosystem to relate EWUE to carbon sequestration (Tubiello et al., 1999). Nighttime measurements were not used in calculations because there were no carbon uptake by the ecosystem during the nighttime (Ohmura, 1982). We quantified EWUE using following five methods:

A) Ratio of seasonal sums (DOY 121 - 304) of daily daytime NEE or GEP to daily daytime ET (Tubiello et al., 1999).
B) Ratio of monthly totals of daily daytime NEE or GEP to daily daytime ET.
C) Estimation of EWUE from the slope of monthly amounts of GEP or NEE and ET.
D) Instantaneous method of EWUE estimation from the slope of regression of daily day time NEE or GEP vs. ET on seasonal scale (Baldocchi et al., 2001).
E) Estimation of daily EWUE from the ratios of daily integrals of GEP or NEE to ET

Results and Discussion

Energy balance closure

The sum of half hourly values of turbulent fluxes (H + LE) was strongly correlated with available energy ($R_n – G$) ($R^2 = 0.93$, $P < 0.0001$). Fitting the data points of the scatter plot in Fig. 2 yielded the slope of 0.77 for a linear regression which corresponds to EBC which is 23% less than the theoretical value (slope = 1). Such kind of underestimation of the EBC is very common for EC studies in all measured vegetation types (Aubinet et al., 1999; Wilson et al., 2002). However, the cause of underestimation is not well understood. Twine et al. (2000) reviewed the observation results over grasslands and reported an average EBC of 70 – 80%. The mean EBC based on comprehensive evaluation of 22 sites and 50 site-years of data at FLUXNET sites was 80% (Wilson et al., 2002). In comparison with these findings, our EBC value indicated the typical outcome for our data. It is reliable to examine energy partitioning among all energy fluxes.

Leaf area index, above ground biomass, and canopy height

Maximum LAI was only 3.8 $m^2 m^{-2}$ (mid-August) and the highest dry biomass was just 6.52 t ha^{-1} (early September) due to severe drought. A strong relationship between LAI and dry plant biomass (t ha^{-1}) was achieved (Biomass = 1.493 * LAI – 1.0, $R^2 = 0.86$, $P = 0.0008$). Both started to decline in late October due to the crop senescence. The crop reached a maximum height of 1.2 m in mid-September.

Rainfall and evapotranspiration patterns

Cumulative ET for the growing season (May to mid-November) in this study was 450 mm while cumulative rainfall for the period was 432 mm. Similarly, Skinner and Adler (2010) reported that cumulative average annual ET from a switchgrass field in the northeastern USA was 474 mm with seasonal ET (May to September) ranging from 331 to 358 mm. Monthly sums of rainfall and ET in Table 2 show that rainfall was higher than ET in May and October, but during the mid-season of active growing periods from June to September ET loss exceeded rainfall for each month. Cumulative water loss from ecosystem to the atmosphere via ET during June to September was 1.92 times higher than rainfall (cumulative ET was 321 mm and rainfall was 167 mm). Seasonal cumulative ET and rainfall patterns are shown in Fig. 3a. The figure shows that cumulative ET was consistently higher than the cumulative rainfall from DOY 166 (June 15) to DOY 330 (November 26). This result pointed out that the crop experienced severe drought during the mid-growing season. However, it depends on how much water the soil was able to supply. The initial profile water content and seepage were not measured and must have contributed to the total ET. Stored soil water during the non-growing season influenced ET and the yield during the growing season (Sun et al., 2011).

Seasonal and diurnal variations in evapotranspiration

Evapotranspiration showed clear seasonal pattern (Fig. 3b). The ET rate was 3 – 4 mm day^{-1} in late May and June, and it dropped to about 2 mm day^{-1} or less in July due to severe drought, and again slightly increased in August after some rainfall events. Lower ET rates of about 0.5 mm day^{-1} were observed during late growing season in November. Similar ET rates (3 - 3.75 mm day^{-1} during active growing periods and 0.5 mm day^{-1} in winter) from a switchgrass field in the northeastern USA were observed by Skinner and Adler (2010). We observed some spikes of ET (> 5–6 mm day^{-1}) after big rainfall events during active growing season, but not after the crop senescence (November). The result signified that plant transpiration was the dominant component of measured ET over soil and plant evaporations. During the growing season, the daily ET in switchgrass in our study ranged from 0.5 - 4.8 mm while excluding ET spikes for rainfall recorded days and the day after a rainfall event of 5 mm or greater. Comparison of our results and the results from Skinner and Adler (2010) in switchgrass with reported values of ET for other crops available in the literature indicated the lower water consumption characteristic of switchgrass. The daily ET was 3.5 – 5 mm in native tall grass prairie and 2.5 – 7 mm in wheat (*Triticum aestivum* L.) in north-central Oklahoma (Burba and Verma, 2005). The daily ET ranged from 1 - 7.8 mm in wheat and 1 - 5.1 mm in maize in the North China Plain, which in near similar latitudes of North America (Lei and Yang, 2010). It is important to mention here that severe drought during the growing season resulted in complete failure of forage sorghum [*Sorghum bicolor* (L.) Moench] in an adjacent plot but switchgrass still provided good biomass (> 6 t ha^{-1}). This finding illustrates the possibility of switchgrass production under environments that experience regular drought.

Great variation was observed for the maximum rates of ET among months during the growing season. Typical diurnal trends of ET (mm 30-min^{-1}) for active growing periods (May to October) are provided in Fig. 4. Daytime ET was high, starting at around 8 AM and reached a maximum at around 2 – 3 PM. The average peak daytime ET rates were 0.16, 0.18, 0.11, 0.15, 0.10, and 0.06 mm 30-min^{-1} in May, June, July, August, September, and October, respectively. The highest ET rates were observed in June due to active crop growth and the lowest in October due to crop senescence and lower solar radiation. The ET rate decreased in July due to drought, and it increased again in August due to increased availability of water. Our result supported the finding of Burba and Verma (2005) that distribution of precipitation played a major role in determining ET. However, it was evident only during the active growing season, but not after crop senescence indicating that the crop phenology strongly influences the precipitation - ET relationship.

Variability in energy partitioning

Typical diurnal trends of energy fluxes and vapor pressure deficit (VPD) during active growing periods (May to October) are presented in Fig. 5. The figure shows great variations in VPD and energy partitioning among months during the growing season. Higher values of VPD (peak ranged from 5.2 to 6.2 kPa) were observed from June to August. Diurnal trends of VPD show that the minimum VPD was at around 7 AM and it reached a maximum at around 5 PM. The peak values of energy fluxes were observed at around 2 PM. Mean monthly peak values of R_n during the growing season ranged from 524 – 590 W m^{-2}. Mean monthly maximum values of H were from 176 W m^{-2} (August) to 246 W m^{-2} (July). Mean monthly peak values of LE ranged from 83 W m^{-2} (October) to 240 W m^{-2} (June). Monthly maximum values of G ranged from 27 W m^{-2} in October to 122 W m^{-2} in May. The maximum values of G showed declining trends over the growing season due to more coverage of land by the plant canopies. Due to this reason, a strong negative relationship between monthly peak values of G and LAI was observed (G = -30.94 x LAI + 172.11, $R^2 = 0.73$, $P = 0.03$). However, variability in LAI failed to describe variations in monthly peak values of H and LE due to drought effect.

Figure 5 shows that LE was the dominant turbulent flux in May, June, and August, but H dominated in July, September, and October. Table 2 also shows the seasonal variation in energy partitioning. The monthly mean values of H, LE, G, and R_n during the growing season ranged from 54 to 100, 49 to 112, -5 to 32, and 195 to 262 W m^{-2}, respectively (Table 2). Even though Table 2 provides monthly mean values of energy components and Fig. 5 provides half-hourly binned diurnal courses of energy fluxes for months, both yielded similar results regarding energy partitioning. Interestingly, more energy was partitioned towards H during dry periods even during the mid-growing season (July, the hottest and the driest month). Similarly, H was greater than LE even in wet periods during the late growing season due to crop senescence. The results suggested that energy partitioning is sensitive to both biological and climatic factors. Sun et al. (2010) found smaller H than LE during the growing season, but H was greater than LE during dormant period in a pine (*Pinus taeda*) forest. On an annual basis, more energy (59%) was partitioned into LE in an irrigated cropland in China (Lei and Yang, 2010). Greater H than LE during the mid-growing season (July) in our study illustrated the effect of drought on partitioning of R_n and suggested that H can dominate over LE even during the growing season under water limited environment. Veenendaal et al. (2004) reported similar results that almost all available energy was consumed by H in water limited African woodland. The fraction of R_n used in ET (LE) was significantly reduced in drought year (59% during a year with no moisture stress vs. 49% during severe moisture stress) in native tallgrass prairie (Burba and Verma, 2005). It indicated that precipitation variation is a major control factor for partitioning of R_n into turbulent fluxes (H and LE). We observed the following scenarios of energy partitioning over switchgrass field on seasonal scale:

$H = 0.3919 \times R_n – 16.12$ ($R^2 = 0.80$, $P < 0.0001$)

$LE = 0.2777 \times R_n + 39.37$ ($R^2 = 0.62$, $P < 0.0001$)

$G = 0.1444 \times R_n – 6.0998$ ($R^2 = 0.66$, $P < 0.0001$)

H, LE, and G were significantly correlated with R_n ($P < 0.0001$). These regression models indicated that 39.19, 27.77, and 14.44 % of R_n were converted to H, LE, and G, respectively. The result showed that H was the dominant turbulent flux on seasonal scale under a drought stressed switchgrass ecosystem and G contributed less in energy partitioning.

Different calculations of ecosystem water use efficiency and seasonal variations

We observed similar relationships between GEP and ET ($R^2 = 0.63$, $P < 0.0001$), and NEE and ET ($R^2 = 0.61$, $P < 0.0001$) at the seasonal time scale. However, monthly amounts of GEP (g CO_2) and ET (mm) showed higher correspondence (GEP = 9.89 x ET – 2.1737, $R^2 = 0.86$, $P = 0.007$) than monthly amounts of net ecosystem productivity (NEP =-NEE) and ET (NEP = 5.4 x ET – 206.89, $R^2 = 0.53$, $P = 0.10$). This result indicated that variability in GEP and ET were more strongly linked than NEP and ET because NEP is the balance between GEP and ER, and ER is not tightly coupled with ET. Similar results were reported by Kuglitsch et al. (2008). Due to this reason, EWUE calculation based on GEP and ET are only described hereafter.

Estimation of EWUE by dividing time integrals of GEP by respective H_2O fluxes (ET) provided similar results at seasonal and monthly time scales. Ratio of seasonal sums of daily daytime GEP to daily daytime ET estimated daytime growing season EWUE of 11.74 g CO_2 mm^{-1} ET. Ratio of monthly totals of daytime GEP to daytime ET provided EWUE from 10.46 (August) to 14.08 (October) g CO_2 mm^{-1} ET with a seasonal average of 12.01 g CO_2 mm^{-1} ET (Table 3). The highest EWUE was observed in October due to smaller ET. These results were similar to the WUE of 12 – 15 g CO_2 mm^{-1} ET observed by Skinner and Adler (2010) in a switchgrass field in the northeastern USA and of about

12 g CO_2 mm^{-1} ET reported by Eggemeyer et al. (2006) in the sandhill grassland of Nebraska. We observed smaller values of EWUE during drought periods due to more rapid reduction in GEP than ET, similar to results reported by Kuglitsch et al. (2008) and Dong et al. (2011).

Regression of monthly amounts of GEP and ET provided EWUE (regression slope) of 9.89 g CO_2 mm^{-1} ET ($R^2 = 0.86$, $P = 0.007$). More instantaneous method of EWUE calculation from regression slope of daily day time GEP to ET on seasonal scale yielded EWUE of 7.55 g CO_2 mm^{-1} ET ($R^2 = 0.63$, $P < 0.0001$). Removal of rainfall recorded days and the day after a rainfall event of 5 mm or greater produced slightly larger values of EWUE 8.64 g CO_2 mm^{-1} ET ($R^2 = 0.66$, $P < 0.0001$). Exclusion of rainy periods from the calculation helped to minimize the contribution of evaporation (not linked to GEP) on ET and slightly improved the regression model. Kuglitsch et al. (2008) also reported very minor changes in EWUE when rainy periods were excluded from the analysis.

Ratios of daily values of GEP to ET (daily EWUE) ranged from 3.96 to 26.95 g CO_2 mm^{-1} ET. The great variations in EWUE indicated that it is not a constant property (Emmerich, 2007) and greatly influenced by variability in CO_2 and ET fluxes in response to environmental and physiological factors. However, variability in LAI did not explain variations in EWUE, GEP, and ET. Under normal conditions, the highest values of GEP and ET are observed during the period of maximum LAI. Declining trends of GEP and ET were seen at higher values of LAI in our study most likely due to dry and warm growing periods (Table 3). Timing and amounts of precipitation pulses affect CO_2 and water fluxes (Huxman et al., 2004), which greatly influences EWUE. Lower EWUE was observed at high VPD under hot and dry conditions. Thus, relationships between half hourly values of daytime EWUE and VPD were investigated for July (the driest and hottest month). The regression analysis showed that EWUE was negatively related to VPD (EWUE = 24.39 – 2.45 x VPD, $R^2 = 0.42$, $P < 0.0001$). Strong negative relationship between EWUE and VPD was also reported by Testi et al. (2008). Water use efficiency is inversely related to VPD primarily because as VPD increases, the gradient driving water vapor transport increases, but the CO_2 gradient is largely unchanged. The VPD effect was higher on GEP than ET (Kuglitsch et al., 2008). This leads to reduction in EWUE during daytime (high VPD).

A multiple regression analysis was performed using half hourly daytime values for May to October to examine the combined effects of environmental factors (VPD, soil moisture, and PPFD) on EWUE. The regression analysis showed negative relationship between EWUE and environmental factors (EWUE = 29.31 – 1.72 x VPD – 25.78 x soil moisture – 0.004 x PPFD, $R^2 = 0.39$, $P < 0.0001$, N=4016). The decline in EWUE during daytime is also attributed to increase in solar radiation because of a shift between the earlier maximum GEP and the later maximum ET (Kuglitsch et al., 2008). The GEP reached maximum at or before noon while ET reached a peak at 2-3 PM in our study. The higher the solar radiation, the more is the energy available to ET. Linear relationship between PPFD and H_2O fluxes was observed in this study. Due to these reasons, EWUE was the highest in the early morning and then decreased to a more stable level during daytime with increasing VPD and radiation, and again rose in the evening after VPD and radiation dropped (Fig. 6a). Soil water content is also an important determinant of ET. In particular, an insufficient supply of water reduces ET rates. The multiple regression analysis showed that EWUE decreased with increasing soil moisture. Furthermore, we calculated mean EWUE for four soil moisture classes (0.11 – 0.20, 0.20 – 0.30, 0.30 – 0.40, and > 0.40 m^3 m^{-3}) for the growing season to investigate the influence of soil moisture on EWUE. Mean EWUE rates were 14.3, 13.29, 12.12, and 11.4 g CO_2 mm^{-1} ET, respectively. This showed that increased soil moisture causes a decrease in EWUE most likely due to more increase in ET than GEP with increased rate of water supply. Large variability in diurnal patterns of EWUE for three selected periods (June 8 to 15, July 8 to 15, and October 8 to 15) during the growing season showed how the pattern varied seasonally (Fig. 6b). July had the lowest daytime EWUE due to more rapid reduction in carbon assimilation than water loss. The GEP was reduced by 35%, but ET decreased by 21% in July as compared to June. Stronger decline in GEP than ET is also reported by Kuglitsch et al. (2008). The EWUE of gross carbon uptake declined during drought (Reichstein et al., 2002). Daytime EWUE was higher in October when ET demand was lower due to beginning of crop senescence and smaller VPD (the peak VPD was 5.2 kPa in June, 6.22 kPa in July, and 3.27 kPa in October).

Law *et al*. (2002) evaluated EWUE of croplands, grasslands, forests, and tundra across international network “FLUXNET” sites, and reported that the slope of relationship between monthly GEP and ET (EWUE) was 3.4 g CO_2 kg^{-1} H_2O for grasslands, 3.2 g CO_2 kg^{-1} H_2O for deciduous broadleaf forests, 2.4 g CO_2 kg^{-1} H_2O for evergreen conifers, 3.1 g CO_2 kg^{-1} H_2O for crops, and 1.5 g CO_2 kg^{-1} H_2O for tundra vegetation. In comparison, our result in switchgrass yielded the slope of 9.89 g CO_2 kg^{-1} H_2O. The results demonstrate higher water use efficiency of switchgrass ecosystems and the great potential of switchgrass production in drought prone regions.

Conclusions

Seasonal patterns of ET, EWUE, and energy partitioning in switchgrass were analyzed from EC measurements. Partitioning of more energy towards H rather than LE in drought-stressed ecosystem on the seasonal scale and the observed lower values of ET and EWUE during dry periods indicated that precipitation patterns play a major role in determining ET, EWUE, and energy partitioning in switchgrass. The EWUE declined during drought periods due to more rapid reduction in carbon assimilation (GEP) rather than water loss (ET). Our results demonstrated lower ET and higher EWUE of switchgrass when compared with ET and EWUE values of other ecosystems. The results illustrated the great potential of switchgrass production in drought prone regions. However, evaluation over a longer term is required to understand seasonal variability of switchgrass EWUE and ET.

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Table 1. Monthly mean maximum and minimum temperatures, and monthly total rainfall in 2011 in comparison with 30-year mean for Chickasha, Oklahoma, USA.

	2011			30-year mean		
Month	Max T (^{o}C)	Min T (^{o}C)	Rain (mm)	Max T (^{o}C)	Min T (^{o}C)	Rain (mm)
Jan	10.03	-7.49	1.0	10.06	-3.44	33.5
Feb	12.70	-2.65	12.2	14.00	-0.78	45.2
Mar	19.42	4.36	1.3	18.83	4.06	71.9
Apr	25.82	9.01	0	24.06	9.06	91.9
May	27.51	13.79	105	28.06	14.72	133.1
Jun	37.43	21.73	56	32.39	19.50	104.6
Jul	40.36	24.19	5	35.28	21.56	53.6
Aug	39.78	24.11	74	34.56	20.61	69.3
Sep	30.55	13.1	32	30.61	16.22	91.4
Oct	24.25	9.01	104	24.89	9.83	98.6
Nov	16.35	3.21	94.2	17.06	3.22	54.4
Dec	10.22	-1.42	39.9	11.50	-1.72	48.5

Table 2. Monthly mean values of sensible heat flux (H), latent heat flux (LE), soil heat flux (G), and net radiation (R_n), and monthly sums of rainfall and evapotranspiration (ET) in a switchgrass field during the 2011 growing season.

Month	H (Wm^{-2})	LE (Wm^{-2})	G (Wm^{-2})	R_n (Wm^{-2})	Rainfall (mm)	ET (mm)
May	54	93	31	195	105	81
June	59	112	23	203	56	100
July	100	93	32	262	5	75
Aug	62	106	20	219	74	86
Sep	94	68	15	215	32	60
Oct	70	49	-5	-	104	36

Table 3. Monthly sums of gross ecosystem production (GEP) and daytime evapotranspiration (ET), and leaf area index (LAI) in a switchgrass field during the 2011 growing season. Monthly values of ecosystem water use efficiency (EWUE) were determined by dividing monthly sums of daytime GEP by respective daytime ET.

Month	LAI	GEP (g CO_2/m^2)	ET (mm)	EWUE_GEP (g CO_2 mm^{-1} ET)
May	1.65	900	70	12.86
June	1.97	1007	88	11.44
July	2.91	650	62	10.48
August	3.78	711	68	10.46
September	3.80	547	43	12.72
October	3.70	366	26	14.08

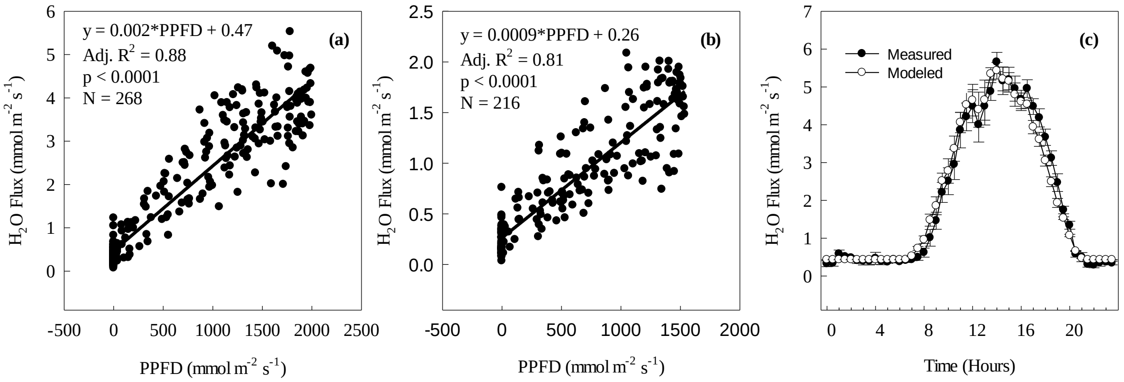

Fig. 1. Linear relationship between photosynthetic photon flux density (PPFD) and H_2O fluxes in a switchgrass field for selected time periods: June 20 to 29 (a) and October 1 to 8, 2011 (b). The solid lines in Fig. 1a and 1b are the best fit lines for linear regressions. Total independent data points are represented by N. Comparison of measured and modeled mean diurnal trends of H_2O fluxes from May 28 to June 3, 2011 (c). Bars in Fig. 1c represent standard errors of the means.

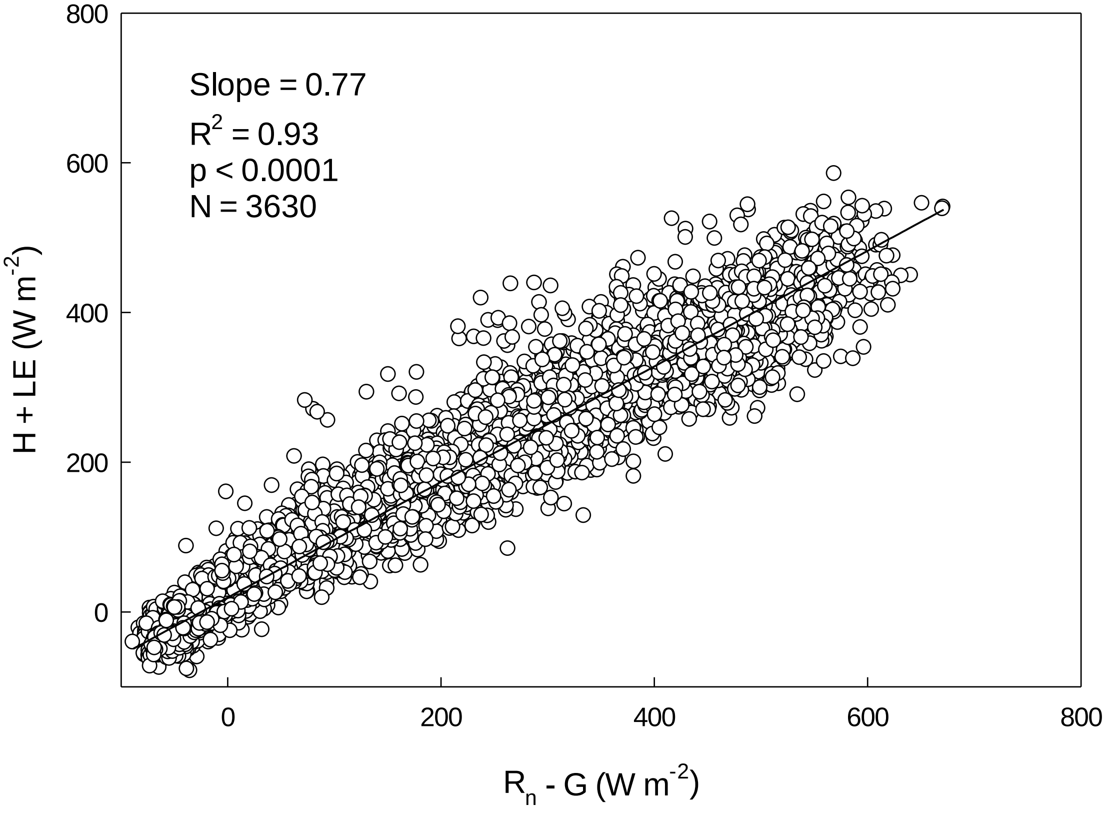

Fig. 2. Relation between half hourly values of the available energy (net radiation (R_n) - soil heat flux (G)) and the sum of the turbulent fluxes (sensible heat (H) + latent heat (LE)) in a switchgrass field during the 2011 growing season (May to November). The solid line is the best fit line for linear regression (R^2 =0.93, *P* < 0.0001). Total number of independent data points are represented by N (=3630). The regression slope of 0.77 with R^2 value of 0.93 indicated the good energy balance closure.

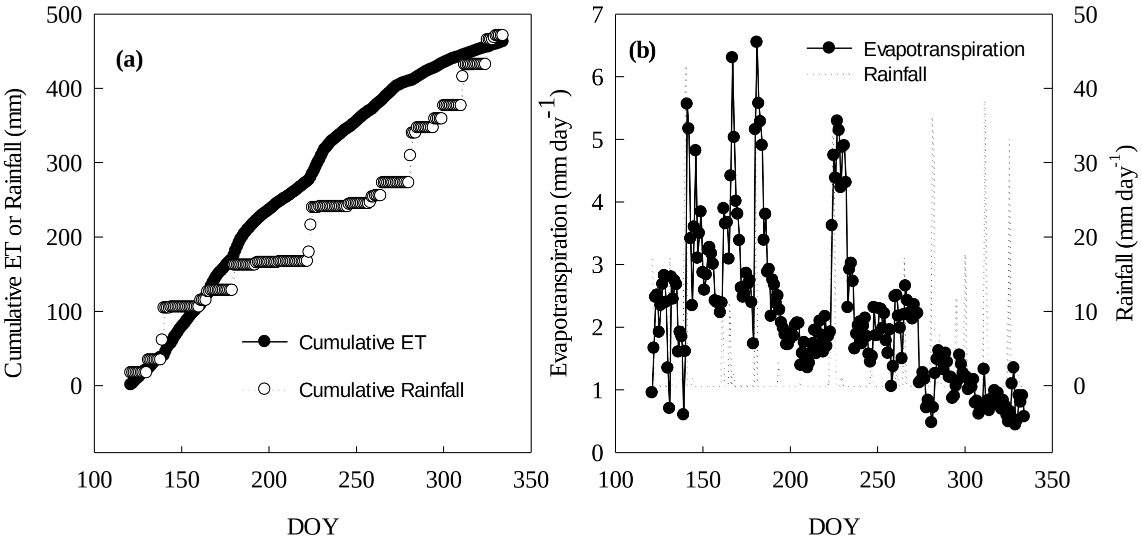

Fig. 3. Comparison of cumulative evapotranspiration (ET) and rainfall (a), and daily trends of ET and rainfall in a switchgrass field during the growing season (b).

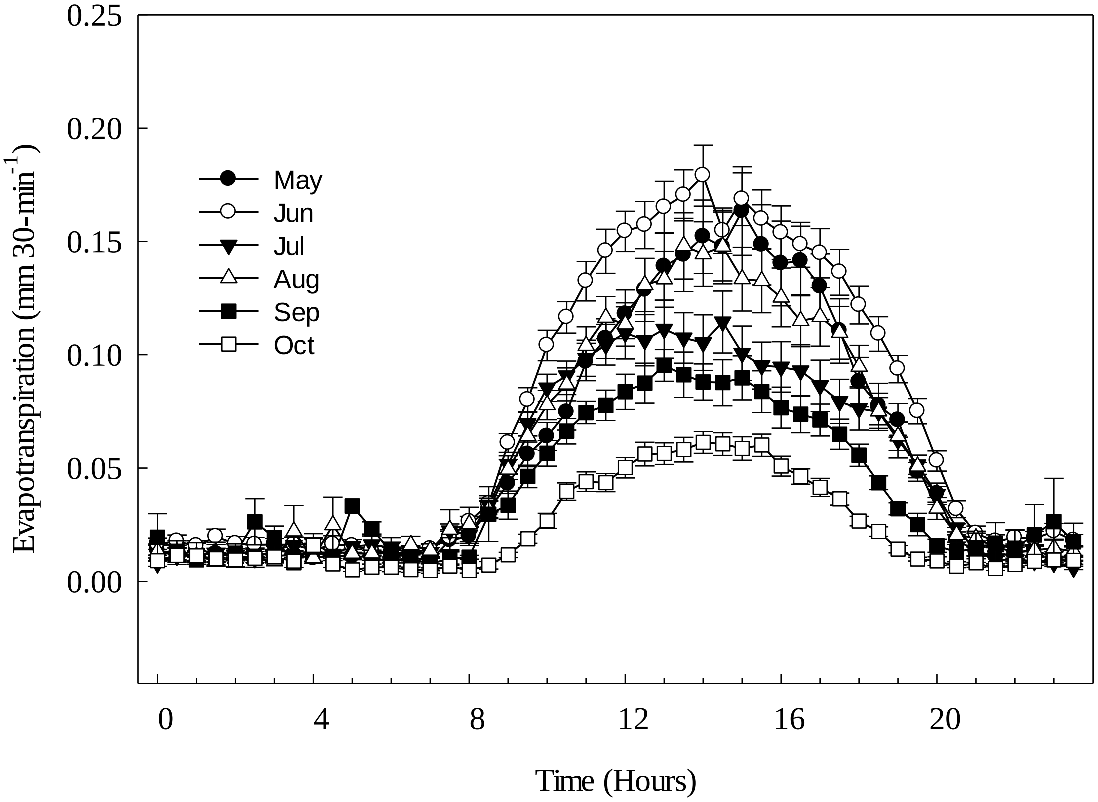

Fig. 4. Diurnal trends of evapotranspiration for different months of the growing season. Bars represent standard errors of the means.

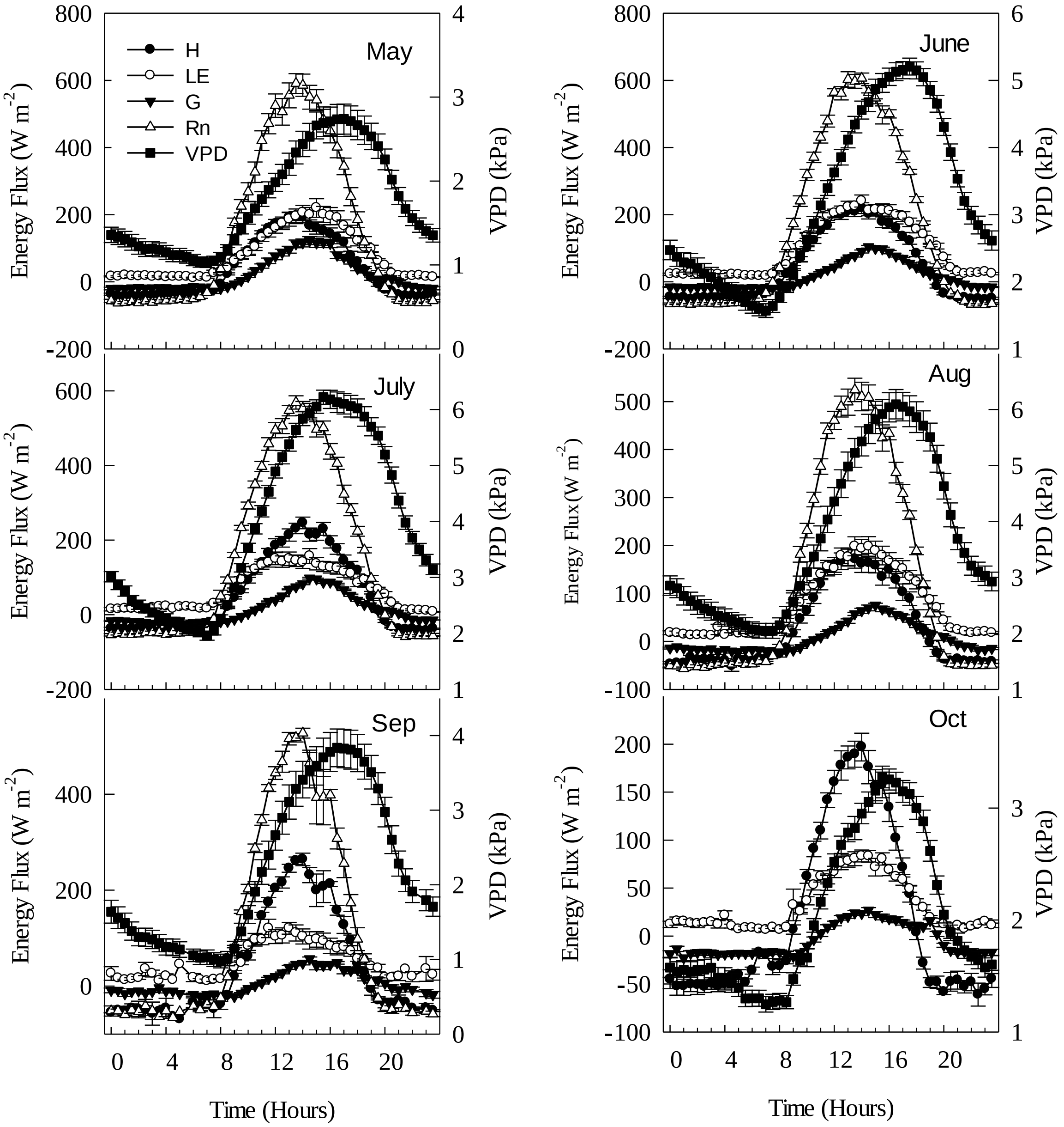

Fig. 5. Half-hourly binned diurnal courses of energy fluxes for different months of the growing season. Diurnal courses of vapor pressure deficit (VPD in kPa) are also shown in separate y-axis. Bars represent standard errors of the means.

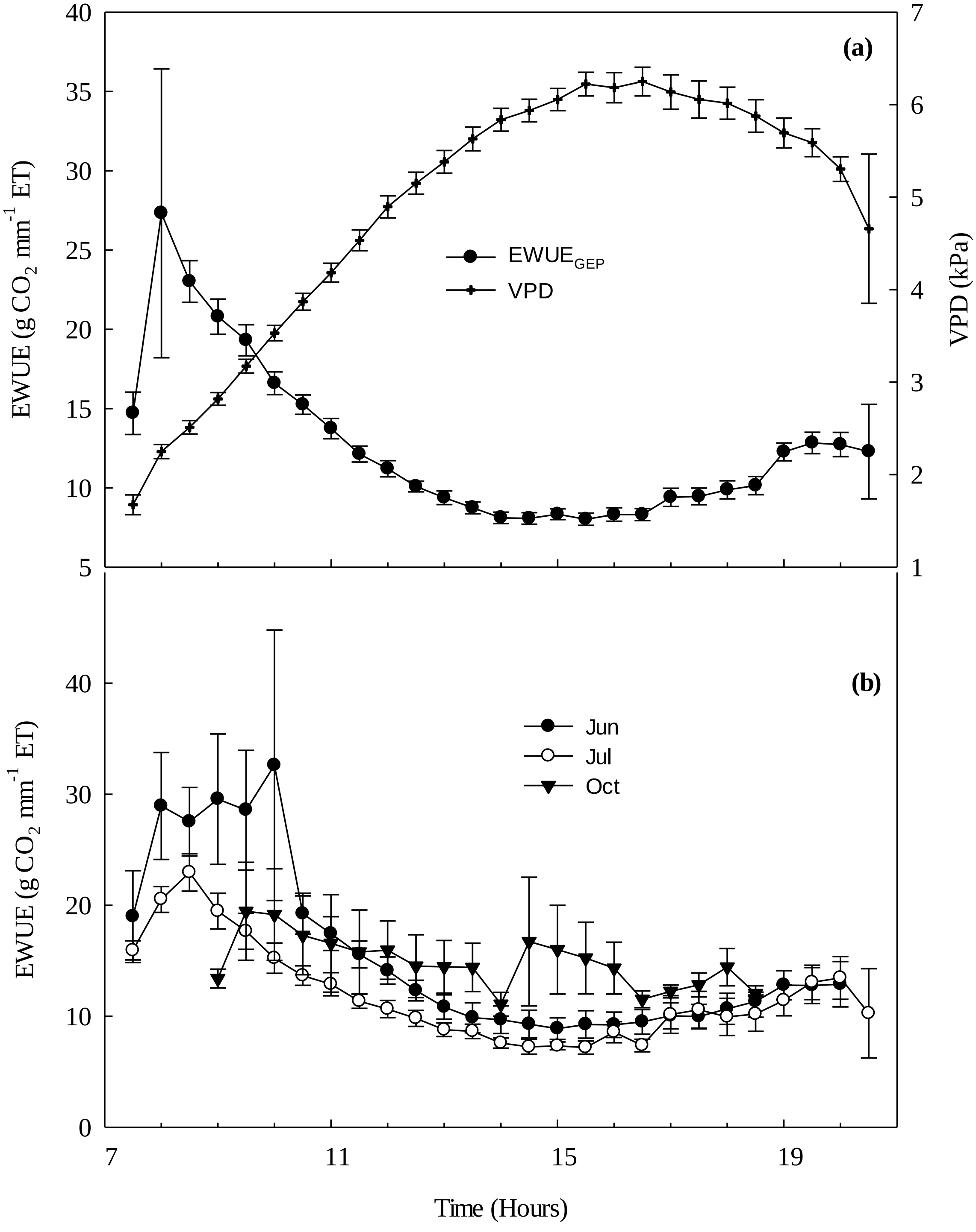

Fig. 6. Diurnal trends of ecosystem water use efficiency (EWUE) and vapor pressure deficit (VPD) in July (a), and variability in diurnal patterns of EWUE for three selected periods (June 8 to 15, July 8 to 15, and October 8 to 15) during the growing season (b).

CHAPTER III

SEASONAL VARIABILITY IN NET ECOSYSTEM CARBON DIOXIDE EXCHANGE OVER A YOUNG SWITCHGRASS STAND

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ABSTRACT. Understanding carbon dynamics of switchgrass ecosystems is crucial as switchgrass (*Panicum virgatum* L.) acreage is expanding for cellulosic biofuels. We used eddy covariance system and examined seasonal changes in net ecosystem CO_2 exchange (NEE) and its components – gross ecosystem production (GEP) and ecosystem respiration (ER) in response to controlling factors during the second (2011) and third (2012) years of stand establishment in the southern Great Plains of the United States (Chickasha, OK). Larger vapor pressure deficit (VPD > 3 kPa) limited photosynthesis and asymmetrical diurnal NEE cycles (substantially higher NEE in the morning hours than in the afternoon at equal light levels). Consequently, rectangular hyperbolic light-response curve (NEE partitioning algorithm) consistently failed to provide good fits at

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high VPD. Modified rectangular hyperbolic light-VPD response model accounted for the limitation of VPD on photosynthesis and improved the model performance significantly. The maximum monthly average NEE reached up to -33.02 ± 1.96 μmol CO_2 m^{-2} s^{-1} and the highest daily integrated NEE was -35.89 g CO_2 m^{-2} during peak growth. Although large differences in cumulative seasonal GEP and ER were observed between two seasons, total seasonal ER accounted for about 75% of GEP regardless of the growing season lengths and differences in aboveground biomass production. It suggests that net ecosystem carbon uptake increases with increasing GEP. The ecosystem was a net sink of CO_2 during 5 to 6 months and total seasonal uptakes were -1128 ± 130 and -1796 ± 217 g CO_2 m^{-2} in 2011 and 2012, respectively. In conclusion, our findings suggest that the annual carbon status of a switchgrass ecosystem can be a small sink to small source in this region if carbon loss from biomass harvesting is considered. However, year-round measurements over several years are required to assess a long-term source-sink status of the ecosystem.

Introduction

Carbon dioxide (CO_2) concentration is increasing in the atmosphere since Industrial Revolution of the mid-nineteenth century. Most of the released CO_2 into the atmosphere is a result of burning fossil fuels (Revelle and Suess, 1957). One of the major avenues for reducing CO_2 emissions is by substituting fossil fuels with biofuels (Pacala and Socolow, 2004). Bioenergy crops convert atmospheric CO_2 to organic carbon in crop biomass and soil which ultimately could help offset CO_2 emissions (Adler et al. 2007). As part of the

US Energy Independence and Security Act (EISA, an Act concerning the energy policy of the United States), the Renewable Fuel Standard mandates 36 billion gallons (136 billion liters) of biofuel production by 2022, of which 16 billion gallons (60 billion liters) is mandated from cellulosic feedstock. Switchgrass (*Panicum virgatum* L.), a highly productive C_4 perennial warm-season grass native to North America, has been chosen as a model cellulosic feedstock by the U.S. Department of Energy through a decade long, multi-location (31 sites) and multi-species (34 species) trials due to its potential for high yields, deep rooting characteristics, and potential value in carbon sequestration (Wright, 2007). Thus, a growing interest has recently emerged on the carbon dynamics of switchgrass.

Several studies have investigated carbon sequestration potential of switchgrass and reported that switchgrass has a great potential for storing significant quantity of soil carbon (Frank et al. 2004; McLaughlin and Walsh, 1998; Liebig et al. 2005). The deep and dense rooting system of switchgrass is an added advantage for soil carbon sequestration (Monti et al. 2012). Although switchgrass has a great potential to increase soil organic carbon, more information on measurements of net ecosystem CO_2 exchange (NEE, the exchange of CO_2 between an ecosystem and the atmosphere) is needed to determine the source-sink status, and the magnitude and seasonal dynamics of carbon in switchgrass ecosystems. Unfortunately, NEE measurements in switchgrass are limited. A study in switchgrass from northeastern USA (southwestern Pennsylvania) by Skinner and Adler (2010) and another study from central Illinois by Zeri et al. (2011) reported that switchgrass ecosystems were sinks of carbon for at least the first few years of establishment in those regions. However, information is not available on carbon status of switchgrass ecosystems for the southern Great Plains of the United States, which will be the home to large stands of switchgrass in the near future (U.S. Department of Energy, 2011). Thus, this study has great importance at a regional level since measured ecosystem level CO_2 flux can be extrapolated to estimate the regional carbon balance (Wofsy et al. 1993).

Switchgrass has been classified into lowland and upland types based on its morphology and habitat (Porter, 1966). Lowland ecotypes have higher biomass yield potential and longer retention of photosynthetically active tissues in southern locations of the United States (Casler et al. 2004). The previous eddy covariance studies with switchgrass (Skinner and Adler, 2010; Zeri et al. 2011) have employed upland ecotypes of switchgrass while our study is with a lowland ecotype ‘Alamo’. Furthermore, earlier studies lacked thorough investigation of seasonal carbon dynamics. Better understanding of the seasonal NEE changes, with respect to controlling factors, will be helpful for assessing climate change mitigation potential of switchgrass.

Our study analyzed eddy covariance measurements of CO_2 fluxes during two growing seasons in 2011 and 2012. These two growing seasons represent diverse arrays of climatic conditions including severe droughts experienced by the crops in 2011, which provided us a unique opportunity to quantify the carbon dynamics of a switchgrass ecosystem under different environmental conditions. This study also examined the direct effects of drought on NEE and its components – gross ecosystem production (GEP, total amount of carbon fixed by photosynthesis in an ecosystem) and ecosystem respiration (ER, total amount of carbon loss from an ecosystem due to autotrophic and heterotrophic respiratory activities). This information will be of great importance as drought-affected geographic areas and drought intensity has increased globally in the last five decades (Dai et al. 2004), and drought is expected to influence the terrestrial carbon cycle in the near future. Thus, a major objective of this study was to determine the seasonality of NEE in response to controlling factors. Analysis of two seasons of eddy covariance data can help determine the length of active growing period and seasonal patterns of photosynthetic and respiratory activities in switchgrass. This study also evaluates rectangular hyperbolic light-response curve and modified rectangular hyperbolic light-VPD response model to fit daytime NEE across different vapor pressure deficit (VPD) ranges.

Materials and Methods

Site description and weather conditions

Eddy covariance measurements were conducted over a switchgrass (cv. Alamo) field at South Central Research Station, Chickasha, OK (35.04° N latitude, 97.95°W longitude, and 330 m above sea level altitude) during the 2011 and 2012 growing seasons (the second and third years of establishment, respectively). The crop was sown at 38 cm row spacing under no till conditions. The soil type was McLain silt loam (fine, mixed, superactive, thermic Pachic Argiustolls). Fertilizer was not applied in the establishment year, and ammonium nitrate was broadcast applied in April in the second and third years at 75 Kg ha^{-1}. The experiment was rainfed and the site received 525 and 673 mm total annual rainfall in 2011 and 2012, respectively while the 30-year average (1981 to 2010) annual rainfall for the site was 896 mm (Table 4). The crop experienced mid-growing season drought in 2011. As compared with the 30-year mean, spring was relatively warmer and wetter in 2012, and cooler and drier in 2011. Summer 2011 was exceptionally warm and dry, and summer 2012 was slightly warmer and drier as compared with the 30-year mean. Mesonet data for the area was downloaded from the Oklahoma Mesonet website (www.mesonet.org, verified January 2, 2013).

Eddy covariance and other supplementary measurements, and sign convention

Continuous CO_2 fluxes measured from April 25 to October 31 (DOY 115-304) in 2011 and from March 1 to October 31 (DOY 61-305) in 2012 using an eddy covariance system equipped with CSAT3 sonic anemometer (Campbell Scientific Inc., Logan, UT, USA) and LI-7500 open-path infrared gas analyzer (IRGA, LI-COR Inc., Lincoln, NE, USA) are presented in this study. The sensors were mounted at 2.2 m height from the ground in 2011, but increased to 3 m on May 31, 2012, and again raised to 3.4 m on September 2, 2012 due to increasing canopy height and to avoid measurement in the roughness sub-layer. The switchgrass field (with energy sorghum in 2008 and 2009) was 8 ha and adjacent to the sorghum field to the west, mixed grass field to the north, and wheat fallows to the south and east. The EC system was set up at the north end of the plot facing towards the south, the prevalent wind direction. The fetch in the direction of prevailing wind and in the east-west direction was 275 m. Data were collected at 10 Hz frequency (10 samples sec^{-1}) and NEE was calculated for a 30-min averaging period. The CO_2 storage was considered negligible. Thus, NEE presented in this study is the measured CO_2 eddy flux only. Sign convention in this paper is that CO_2 uptake by the ecosystem is negative, whereas a net CO_2 release to the atmosphere is positive. Supplementary measurements include photosynthetic photon flux density (PPFD), net radiation (R_n), soil heat flux (G), soil temperature and moisture, air temperature, and relative humidity. Details on these measurements as well as calculation of soil heat storage term for energy balance closure are provided in a previous publication (Wagle and Kakani, 2012). Periodic biometric measurements (mostly biweekly) of leaf area index (LAI), canopy height, and dry biomass (3-5 samples from 1 m^2 area at randomly located positions) were taken throughout the entire growing season for better understanding of flux measurements. Leaf area index was measured with a plant canopy analyzer (LAI-2000, LI-COR Inc., Lincoln, NE, USA). Canopy height was measured from soil surface to the top most ligule. Harvested biomass samples were dried in an oven at 70° C for a week and weighed.

Data screening

There is consensus that eddy covariance system underestimates NEE under stable nighttime conditions. We also observed underestimation of flux during low turbulence periods, below a friction velocity (u*) threshold of 0.20 m s^{-1}. Hence, unreliable flux data during calm periods (u*< 0.20 ms^{-1}) were excluded. However, the use of a single u* threshold at all times may induce some uncertainties because u* shows diurnal and seasonal cycles, and meteorological and plant phenological characteristics influence u* threshold (Gu et al. 2005). Negative nighttime NEE (as no photosynthesis occurs during night) during low wind velocity (< 1.5 m s^{-1}) were removed. Samples from non-representative footprints (e.g., data for the period when wind was blowing from behind the tower) were avoided. Sensible heat (H) and latent heat (LE) fluxes were filtered to keep in the range of -200 to 500 Wm^{-2} and -200 to 800 Wm^{-2}, respectively (Sun et al. 2010). Physically unreasonable CO_2 fluxes beyond -50 and 50 $\mu mol\ m^{-2}s^{-1}$ were removed (Zeeman et al. 2010; Kochendorfer et al. 2011; Wolf et al. 2011). In addition, we removed statistical outliers beyond ±3.5 STD range from a 14 day running mean window.

Gap filling and partitioning of net ecosystem exchange

An average value immediately before and after the gap was used to fill half-hourly gaps (Wever et al. 2002). Linear interpolated values were used for 2 h or fewer gaps (Flanagan et al. 2002). Larger gaps were filled using empirical models based on dominant physiological processes for daytime and nighttime. During nighttime, NEE is equivalent to ER whereas GEP is zero as photosynthesis does not occur at night (Barr et al. 2002). Only 6 h (22:00-04:00 h) of nighttime data during high turbulence ($u^* > 0.20\ ms^{-1}$) were used to model ER to avoid the period of formation and breakup of the air temperature inversion (Black et al. 1996). Linear and multiple linear regressions between nighttime NEE and soil temperature, air temperature, and soil moisture were evaluated during a 7-day period (sometimes 4 – 14 days) to account for seasonal variability in parameters. The exponential relationship between NEE values and the most significant variable was also investigated. Finally, the relationships with the highest level of significance were chosen (Flanagan et al. 2002). Mean respiration rates were calculated if no significant relationships of the variables were observed (Flanagan et al. 2002). These estimates of

ER were used to fill gaps and replace NEE values under low turbulent conditions ($u^* < 0.20$ m s^{-1}) during nighttime. Daytime NEE (PPFD > 1 µmol m^{-2} s^{-1}) was modeled and partitioned into its two components (GEP and ER) using the commonly used rectangular hyperbolic light-response curve (Falge et al. 2001).

$$NEE = \frac{\alpha \times GP_{\max} \times PPFD}{\alpha \times PPFD + GP_{\max}} + ER \qquad (1)$$

where α is the apparent quantum yield (i.e., the initial slope of the light-response curve [mol CO$_2$ mol^{-1} of photons)], PPFD is measured photosynthetic photon flux density (µmol m^{-2} s^{-1}), GP$_{max}$ is the maximum canopy CO$_2$ uptake rate (µmol m^{-2} s^{-1}) at light saturation, and ER is respiration rate. Here, GP$_{max}$ was calculated as the exponential decreasing function at high VPD to include the effect of VPD on photosynthesis as suggested by Lasslop et al. (2010):

$$GP_{max} = GP_0 \exp\left[-k\left(VPD - VPD_0\right)\right], \text{ if } VPD > VPD_0 \qquad (2)$$

$$GP_{max} = GP_{0,} \text{ if } VPD < VPD_0 \qquad (3)$$

where VPD$_0$ threshold was set to 1 kPa (Lasslop et al. 2010). All the fitted parameters were estimated using nonlinear least squares regression in SAS software (SAS Institute Inc. 2009, Cary, NC, USA) using short time period data (mostly a week and sometimes up to 14 days in case of insufficient data points or lack of good fits) to account for climatic variability. Daytime ER was estimated from the intercept of the ordinate while fitting light-response curves. Only measured half hourly values (not gap-filled) were used for the optimization of model parameters. These empirical functions were used to fill gaps during daytime. The gap filled time series of CO$_2$ flux was summed to calculate seasonal NEE values. The sampling uncertainty (gap filling) errors with in seasonal estimates of CO_2 fluxes were determined as the standard error of the gap filling models as in Black et al. (2007).

Results

Energy balance closure

Energy balance closure (EBC) above the switchgrass field was used to evaluate the accuracy of eddy covariance measurements. Only high quality fluxes of H and LE were used and EBC was calculated only when all four measurements (H, LE, R_n, and G) were available. Strong correlations were observed between the sum of half-hourly values of turbulent fluxes (H + LE) and available energy (R_n – G) on seasonal scale with R^2 value of 0.93 for both years (Fig. 7). The slopes of regression lines which correspond to EBC were 0.77 and 0.83 for 2011 and 2012, respectively. The result indicated the typical outcome for our data as compared with EBC values reported in literature. An average EBC is 70 – 80% over grasslands across the globe at 30-min intervals (Twine et al. 2000). We did not apply the EBC adjustment factor to correct underestimation of CO_2 fluxes since these energy imbalances could be from errors in available energy measurements or from neglecting heat storage in biomass (Cook et al. 2004; Desai et al. 2005).

Variations in leaf area index, biomass, and canopy height

Switchgrass growth started earlier in 2012 due to a warmer and wetter spring (Table 1). Thus, we initiated biometric measurements on May 9 (DOY 129) in 2011 but on March

28 (DOY 88) in 2012. Evolution of LAI and dry biomass during the 2011 and 2012 growing seasons is presented in Figure 8. Leaf area index, canopy height, and biomass were higher in 2012 than they were in 2011 due to better growing conditions (mild winter and greater precipitation) and increased maturity of the switchgrass stand. Canopy height reached a maximum of 1.2 m in mid-September in 2011 and 1.8 m in mid-July in 2012. Maximum LAI was 3.8 m^2 m^{-2} (mid-August) in 2011, while it reached a maximum of 5.9 m^2 m^{-2} (mid-July) in 2012. The highest recorded aboveground dry biomass was 6.52 t ha^{-1} in early September in 2011 as compared to 16.95 t ha^{-1} in mid-July in 2012. Strong relationships between LAI and dry plant biomass (t ha^{-1}) were obtained in both years (in 2011: Biomass = 1.49 x LAI – 1.0, $R^2 = 0.86$; in 2012: Biomass = 4.51 x LAI – 7.72, $R^2 = 0.82$). Plant canopy height explained 85% and 97% of variability in aboveground biomass in 2011 and 2012, respectively.

Flux Partitioning: ecosystem respiration and gross ecosystem production

Development of specific relationships between nighttime ER and its controlling factors (soil temperature, air temperature, and soil moisture) for short windows (a week, sometimes 4 to 15 days to account for climatic variability) showed different responses of ER to environmental factors throughout the entire study period. For example, the exponential function of soil temperature provided a better fit for the period June 1 to 7, 2012 ($\text{ER} = 0.11\, e^{0.19 \text{ x soil temperature}}$, $P < 0.0001$, $R^2 = 0.90$) while the exponential function of air temperature explained more variability in ER during May 16 to 19, 2011 ($\text{ER} = 0.098\, e^{0.17 \text{ x air temperature}}$, $P < 0.0001$, $R^2 = 0.81$). Multiple regression of ER with air temperature and soil moisture provided a better fit to the data during June 16 to 23, 2011 (ER = 175 x soil moisture + 0.25 x air temperature – 26.46, $P < 0.0001$, $R^2 = 0.61$). Linear regression of ER with soil moisture explained 54% of the variability in ER during July 16 to 23, 2012. Improved model fits were observed using only 6 h (22:00-04:00 h) of nighttime data than the use of whole nighttime data because of the removal of underestimated and overestimated ER values during formation and breakup of the air temperature inversion.

To fit rectangular hyperbolic light-response curve for the daytime NEE measurements is a well-established method in eddy covariance communities in order to determine parameters for the light-response curve to estimate GEP and also to determine daytime respiration from the intercept of the ordinate (Zhao et al. 2010; Pilegaard et al. 2001; Falge et al. 2001). Our study showed that the rectangular hyperbolic light-response curve failed to provide good fits for the periods with higher VPD (> 3 kPa) most probably due to the limitation of VPD on photosynthesis. Instead, modified rectangular hyperbolic light-VPD response model, which included the limitation of VPD on photosynthesis, provided better estimates of GEP and daytime ER, and improved the model performance significantly (Table 5, Fig. 9). Both models yielded similar results for the periods with smaller VPD (< 3 kPa). Comparison of diurnal trends of measured and modeled NEE using the original light-response curve and the modified light-VPD response model along with diurnal trends of PPFD and VPD for two selected periods: July 16-23, 2012 (diurnal mean of VPD ranged from 0.73 to 5.17 kPa) and May 24-31, 2011 (diurnal mean of VPD ranged from 1.22 to 2.94 kPa) is provided in Figure 10. During dry period with high VPD, NEE increased rapidly after sunrise following the trend of PPFD and then decreased suddenly at higher VPD before noon which resulted in asymmetrical diurnal cycles of measured NEE (Fig. 10a). In Figure 10b, symmetrical diurnal NEE cycle following the same pattern of PPFD was observed when the maximum VPD was smaller than 3 kPa. The magnitude and timing of peak NEE for the modified light-VPD response model were in good agreement with measured NEE, but the original light-response curve underestimated the daily peak of NEE before noon and overestimated NEE in the afternoon when VPD was more than 3 kPa. In contrast, modeled NEE from both models were in good agreement with measured NEE at smaller VPD (< 3 kPa).

Diurnal and seasonal trends of net ecosystem exchange

Typical daily trends of NEE for both growing seasons (May to October) are provided in Figure 11. Large differences were observed for NEE rates among months within and between growing seasons. Higher rates of carbon uptake and release were observed in 2012 till July and then similar rates and patterns were observed in both seasons. The peak monthly average daytime and nighttime NEE rates during the 2011 and 2012 growing seasons are provided in Table 6. In 2011, the magnitude of daytime monthly average NEE rates ranged from -9.0 ± 0.74 µmol CO_2 m^{-2} s^{-1} (October) to -17.92 ± 0.67 µmol CO_2 m^{-2} s^{-1} (June) while in 2012 it ranged from -8.84 ± 0.99 µmol CO_2 m^{-2} s^{-1} (September) to -33.02 ± 1.96 µmol CO_2 m^{-2} s^{-1} (May). The magnitude of nighttime monthly average NEE rates in 2011 ranged from 3.82 ± 0.54 µmol CO_2 m^{-2} s^{-1} in October to 6.48 ± 1.60 µmol CO_2 m^{-2} s^{-1} in July. Similarly, in 2012 it ranged from 5.61 ± 0.98 µmol CO_2 m^{-2} s^{-1} in October to 11.55 ± 0.74 µmol CO_2 m^{-2} s^{-1} in May.

The seasonal courses of daily NEE, GEP, ER, VPD, and top-surface soil moisture (5 cm depth) changes are shown in Figure 12. During the beginning of the growing season, values of CO_2 fluxes were small. Both GEP and ER started to increase with the beginning of the growing season. However, more rapid increments in photosynthesis than respiration, as a result of emergence and rapid growth of green leaves, caused a sharp increase in NEE in the beginning of the growing season. The remarkable differences in NEE between two seasons were its magnitude and the timing. Photosynthesis started dominating ER in the last week of March in 2012 with a NEE rate of -3.55 g CO_2 m^{-2} d^{-1}. The ecosystem began to absorb -2.23 g CO_2 m^{-2} d^{-1} in the end of April in 2011. The maximum rate of net carbon uptake reached -21.5 g CO_2 m^{-2} d^{-1} during May 24 to 31 in 2011. In 2012, the maximum daily NEE reached a magnitude of -35.89 g CO_2 m^{-2} d^{-1} during June 8 to 15. Both GEP and ER decreased during late growing seasons. In both years, GEP rates were similar in late growing seasons, but ER rates were consistently higher for the 2012 growing season which altered the status of the ecosystem from sink to source of carbon from the beginning of September in 2012. In contrast, the ecosystem was a sink of carbon till the third week of October in 2011.

Figure 12 shows that the magnitude of CO_2 fluxes decreased during warm and dry periods and increased immediately after rainfall events. Both GEP and ER followed similar patterns of increasing and decreasing trends (signs are opposite: GEP is negative and ER is positive) over time (Fig. 12b). It indicates the similarity in responses of GEP and ER to environmental variables. The higher values of VPD were closely associated with warm and dry periods (Fig. 12c). Top-surface soil moisture was highly variable during growing seasons. Volumetric soil water content was consistently lower during the 2011 growing season, reaching the lowest value up to 0.11 m^3 m^{-3}. Soil moisture at 5 cm depth was over 0.20 m^3 m^{-3} for most of the periods during the 2012 growing season due to timely rainfall.

In 2011, cumulative seasonal (DOY 115-304) GEP and ER were -4370 ± 466 and 3242 ±340 g CO_2 m^{-2}, respectively. Cumulative seasonal (DOY 61-305) GEP and ER were -7390 ± 1083 and 5594 ± 865 g CO_2 m^{-2}, respectively in 2012. These results show that total seasonal ER accounted for about 75% of cumulative seasonal GEP in both years, suggesting the great coupling between GEP and ER. However, GEP was reduced more rapidly than ER during drought and crop senescence period. In this study, ER was about 60% of GEP or less until June (peak growing period), increased to about 70-80% in July, and reached 90% or more after that. Weekly ecosystem carbon use efficiency (CUE) was calculated as the ratio of weekly average of daily net ecosystem productivity (NEP = -NEE, the sign changed NEE) to GEP. The greatest CUE was 52% (mid-May) in 2012 and 51% (early June) in 2011. In other words, ER loss was about 48-49% of GEP during peak growth, indicating that 51-52% of GEP was the net uptake by the ecosystem during active growing periods.

Discussion

We found that the response of ER to the environmental factors (soil and air temperatures, and soil moisture) was different throughout the entire study period. No single controlling factor explained variability in ER over the whole season. Exponential functions of soil or air temperature provided good fits at adequate soil moisture (> 0.20 m^3 m^{-3}). Volumetric water content below 0.20 m^3 m^{-3} started to limit ER in this site. For most of the cases when soil moisture ranged from 0.17 to 0.22 m^3 m^{-3}, multiple regressions explained more variability than the simple linear regression or exponential function. The simple linear regression of soil water content was occasionally found to work when ER rates linearly declined as soil moisture gradually depleted from 0.20 m^3 m^{-3}. No significant relationships of the variables were observed during severe drought periods. The results suggest that the response of ER to environmental factors should be evaluated for short time periods (preferably a week) to account for the climatic variability.

Asymmetrical diurnal NEE cycles were observed during periods with higher VPD due to substantially higher rates of NEE in the morning hours than in the afternoon at equal light levels (Fig 10a). Reduction in carbon uptake via stomatal limitation of GEP due to higher VPD and larger rate of respiration in the afternoon causes asymmetric shapes of diurnal NEE cycles (Körner, 1995; Lasslop et al. 2010). The original light-response curve failed to reproduce asymmetrical diurnal NEE cycles even during dry periods with high VPD (Fig. 10a). It demonstrates that the model is unable to account for the decrease in NEE due to higher VPD in the afternoon. Consequently, the model underestimated NEE in the morning hours and overestimated in the afternoon hours, which is similar to the results reported by a previous study (Lasslop et al. 2010). However, the modified light-VPD model was able to reproduce asymmetrical diurnal NEE cycles due to better estimates of the parameters. At higher VPD, the original light-response curve consistently overestimated α and daytime ER, but underestimated GP_{max}

(Table 5). This indicated that underestimation of GP_{max} was attributed to overestimation of daytime ER. The biases in the parameter estimates by the original light-response curve were larger at higher values of VPD, but the estimates were similar at smaller VPD (< 3 kPa). These results illustrated that VPD > 3 kPa started to limit photosynthesis in switchgrass. Suyker and Verma (2001) also reported that VPD > 3.5 kPa constrained photosynthesis in prairie grasses and the ecosystem behaved as a source of carbon even during the daytime in north-central Oklahoma.

The ecosystem was a net sink from the end of April through the third week of October in 2011 and from the end of March through the end of August in 2012 in this study. Reduction in photosynthetic capacity due to early senescence of crop (most likely due to a month earlier growth in the spring) and more respiratory CO_2 loss due to bigger crops caused a net loss of CO_2 to the atmosphere earlier in 2012. The results suggested that the ecosystem was a net sink of CO_2 for 5 to 6 months (160-180 days). The switchgrass ecosystem was a sink for 98 days (late May through early September) in southwestern Pennsylvania (Skinner and Adler, 2010). Net carbon uptake by perennial grasses (miscanthus, switchgrass, and prairie) began around June and lasted until November in central Illinois (Zeri et al. 2011). Native prairies were sinks for about 125 days in Texas (Dugas et al. 1999) and 150 days in north-central Oklahoma (Suyker and Verma, 2001). These results indicate a longer growing season of grasses in the southern Great Plains. Perennial grasses start growing earlier in southern regions due to mild winter and early spring. Moreover, lowland switchgrass ecotypes (commonly grown in sourthern regions) retain photosynthetically active tissues for longer periods than their upland counterparts (Casler et al. 2004).

Skinner and Adler (2010) observed stable amounts of annual GEP, ranging from -3355 to -3451 g CO_2 m^{-2} over four years, and declining trends of ER during the first three years, ranging from 3339 to 2487g CO_2 m^{-2} yr^{-1} in a switchgrass field. The study also reported that increase in biomass was not related to GEP. But we observed significantly much higher GEP and ER in 2012 than in 2011, which can be explained by earlier crop growth, higher aboveground biomass due to more favorable climatic conditions, and increased maturity of switchgrass stand. Total seasonal GEP and ER in our study were -4370 ± 466 and 3242 ± 340 g CO_2 m^{-2} in 2011 and -7390 ± 1083 and 5594 ± 865 g CO_2 m^{-2} in 2012, respectively. The big differences in cumulative GEP and ER between our study and Skinner and Adler (2010) study are attibuted to different ecotypes of switchgrass, different climatic conditions, and different lengths of the growing season. Lowland ecotypes grown in southern regions are generally taller, thicker, and produce higher yields as compared to their upland counterparts grown in northern regions (Porter, 1966). Higher ER rates in southern regions are associated with bigger crop size of lowland ecotypes and higher temperature in this region. The maximum daily intergrated NEE of -35.89 g CO_2 m^{-2} d^{-1} in our study was greater than -30 g CO_2 m^{-2} d^{-1} observed by Skinner and Adler (2010) in northeastern USA where photosynthesis is limited by both suboptimal light and temperature. The maximum diurnal carbon uptake rate of -33 ± 1.96 µmol CO_2 m^{-2} s^{-1} in our study was of magnitude as reported in prairie grasslands by previous studies for this region. The maximum rates of NEE during the growing season was -32 µmol CO_2 m^{-2} s^{-1} in north-central Oklahoma (Suyker and Verma, 2001), -30 µmol CO_2 m^{-2} s^{-1} in northeastern Kansas (Kim and Verma, 1990), and -27.2 µmol CO_2 m^{-2} s^{-1} at the Blackland Research Center, Temple, Texas (Dugas et al. 1999).

In this study, cumulative GEP in 2011 was 41% less than that of 2012. The large portion of this difference came during the early growing season (before the canopy fully developed) while similar rates were observed later due to reduction in carbon assimilation capacity of plants (Fig. 11). Actively growing leaves, relatively longer days, and optimal temperature for photosynthesis in the spring favored more carbon uptake. Because of more rapid increase in GEP than ER carbon use efficiency of the ecosystem was about 40% or more (up to 52%) until June. A gradual decline in net carbon uptake started from July because GEP started to decline rapidly due to reduction in photosynthetic area, but ER did not decrease greatly (Fig. 12), most likely due to respiration from dead and senescence tissues (Dufranne et al. 2011). As a result, the ratio of ER to GEP increased and ultimately the ecosystem was a source of carbon. Although different ratios of ER to GEP were observed over time during growing seasons, total seasonal ER accounted for about 75% of cumulative seasonal GEP in both years regardless of the length of growing seasons and differences in aboveground biomass production. However, due to differences in seasonal sums of GEP the ecosystem was able to gain -1128 ± 130 g CO_2 m^{-2} and -1796 ± 217 g CO_2 m^{-2} during the 2011 and 2012 growing seasons, respectively. If loss of carbon from harvesting biomass needs to be included, assuming 40% carbon in biomass the carbon loss is estimated to be 586 g CO_2 m^{-2} (removing 4 t dry biomass ha^{-1}) and 2051 g CO_2 m^{-2} (removing 14 t dry biomass ha^{-1}) during 2011 and 2012, respectively. In addition, the ecosystem releases small amounts of CO_2 even during the dormant period via soil respiration. Accounting all these carbon losses and uncertainties in the measurements, our results suggest that the annual carbon status of a switchgrass ecosystem can be a small sink to small source in this region based on removal of annually harvested biomass yields. This result is consistent with some previous studies (Skinner and Adler, 2010; Suyker et al. 2003; Zeri et al. 2011). When the loss of carbon during the burning was added in annual NEE, carbon source or sink strength of non-harvested prairie grassland in north-central Oklahoma was negligible in normal years and the ecosystem was a source in a year with severe soil moisture stress (Suyker et al. 2003). The switchgrass ecosystem in southwestern Pennsylvania was a small sink of carbon at no harvest or smaller biomass yields (< 4 t ha^{-1}) but a small source at removal of about 6 t ha^{-1} dry biomass in its fourth year of establishment (Skinner and Adler, 2010). Switchgrass was a small sink at the end of 2.5 years of establishment in central Illinois, but higher amount of harvested biomass could exceed the net carbon balance uptake (Zeri et al. 2011). Year round measurements over several years are required to assess the long-term source-sink status of this important ecosystem in this region. Our findings provide some guidance on seasonal carbon dynamics in switchgrass and also for regional estimates of carbon sequestration potential of switchgrass.

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Table 4. Monthly mean maximum and minimum temperatures, and monthly total rainfall in 2011 and 2012 in comparison with the 30-year mean (1981 to 2010) for Chickasha, Oklahoma, USA.

	2011			2012			30-year mean		
Month	Max T (^{o}C)	Min T (^{o}C)	Rain (mm)	Max T (^{o}C)	Min T (^{o}C)	Rain (mm)	Max T (^{o}C)	Min T (^{o}C)	Rain (mm)
Jan	10.03	-7.49	1	13.56	-2.57	49.78	10.06	-3.44	33.5
Feb	12.7	-2.65	12.2	13.00	0.25	16.26	14	-0.78	45.2
Mar	19.42	4.36	1.3	21.66	8.35	112.52	18.83	4.06	71.9
Apr	25.82	9.01	0	24.11	12.03	78.74	24.06	9.06	91.9
May	27.51	13.79	105	29.48	15.88	150.37	28.06	14.72	133.1
Jun	37.43	21.73	56	33.51	19.33	71.37	32.39	19.5	104.6
Jul	40.36	24.19	5	37.98	22.59	48.01	35.28	21.56	53.6
Aug	39.78	24.11	74	36.04	20.61	42.67	34.56	20.61	69.3
Sep	30.55	13.1	32	31.56	16.16	117.35	30.61	16.22	91.4
Oct	24.25	9.01	104	22.61	9.02	13.72	24.89	9.83	98.6
Nov	16.35	3.21	94.2	20.3	3.0	21.84	17.06	3.22	54.4
Dec	10.22	-1.42	39.9	12.19	-2.19	21.84	11.5	-1.72	48.5

Table 5. Comparison of rectangular hyperbolic light-response curve fitting with or without using vapor pressure deficit (VPD) for selected time periods during growing seasons.

	Model fit parameters		
Time periods	Without VPD	VPD included	VPD range (kPa)
May 24 – 31, 2011	α = 0.043 GP_{max} = 50 R = 6.43 R^2 = 0.96	α = 0.043 GP_{max} = 51 R = 6.41 R^2 = 0.96	1.22 to 2.94
April 16 – 23, 2012	α = 0.0448 GP_{max} = 70 R = 7.67 R^2 = 0.90	α = 0.0447 GP_{max} = 71 R = 7.64 R^2 = 0.90	0.50 to 1.42
July 16 – 23, 2011	α = 0.111 GP_{max} = 12 R = 5.14 R^2 = 0.24	α = 0.029 GP_{max} = 16 R = 2.9 R^2 = 0.82	1.97 to 6.1
July 16 – 23, 2012	α = 0.0925 GP_{max} = 23 R = 8.45 R^2 = 0.36	α = 0.0377 GP_{max} = 41 R = 6.30 R^2 = 0.87	0.73 to 5.17

The VPD range is the diurnal mean of VPD for the week. α is the apparent quantum yield (the initial slope of the light response curve (mol CO_2 mol^{-1} of photons)), GP_{max} is the maximum canopy CO_2 uptake rate (μmol m^{-2} s^{-1}) at light saturation, R is respiration (μmol m^{-2} s^{-1}) during daytime, and R^2 is the coefficient of determination. The *P* values were < 0.0001 in all conditions.

Table 6. The peak monthly average daytime and nighttime net CO_2 ecosystem exchange (NEE) rates with standard errors (in brackets) during the 2011 and 2012 growing seasons.

	2011		2012	
Month	Daytime NEE (μmol CO_2 m^{-2} s^{-1})	Nighttime NEE (μmol CO_2 m^{-2} s^{-1})	Daytime NEE (μmol CO_2 m^{-2} s^{-1})	Nighttime NEE (μmol CO_2 m^{-2} s^{-1})
Apr			-26.39 (± 1.77)	7.51 (± 0.71)
May	-16.0 (± 1.34)	6.23 (± 0.57)	-33.02 (± 1.96)	11.55 (± 0.74)
Jun	-17.92 (± 0.67)	6.20 (± 0.42)	-23.80 (± 2.30)	9.52 (± 2.21)
Jul	-12.17 (± 0.53)	6.48 (± 1.60)	-13.46 (± 0.91)	7.89 (± 1.59)
Aug	-11.74 (± 1.03)	6.39 (± 1.10)	-11.72 (± 1.05)	7.88 (± 2.46)
Sep	-9.25 (± 0.75)	5.82 (± 1.31)	-8.84 (± 0.99)	6.13 (± 0.55)
Oct	-9.0 (± 0.74)	3.82 (± 0.54)	-10.23 (± 1.08)	5.61 (± 0.98)

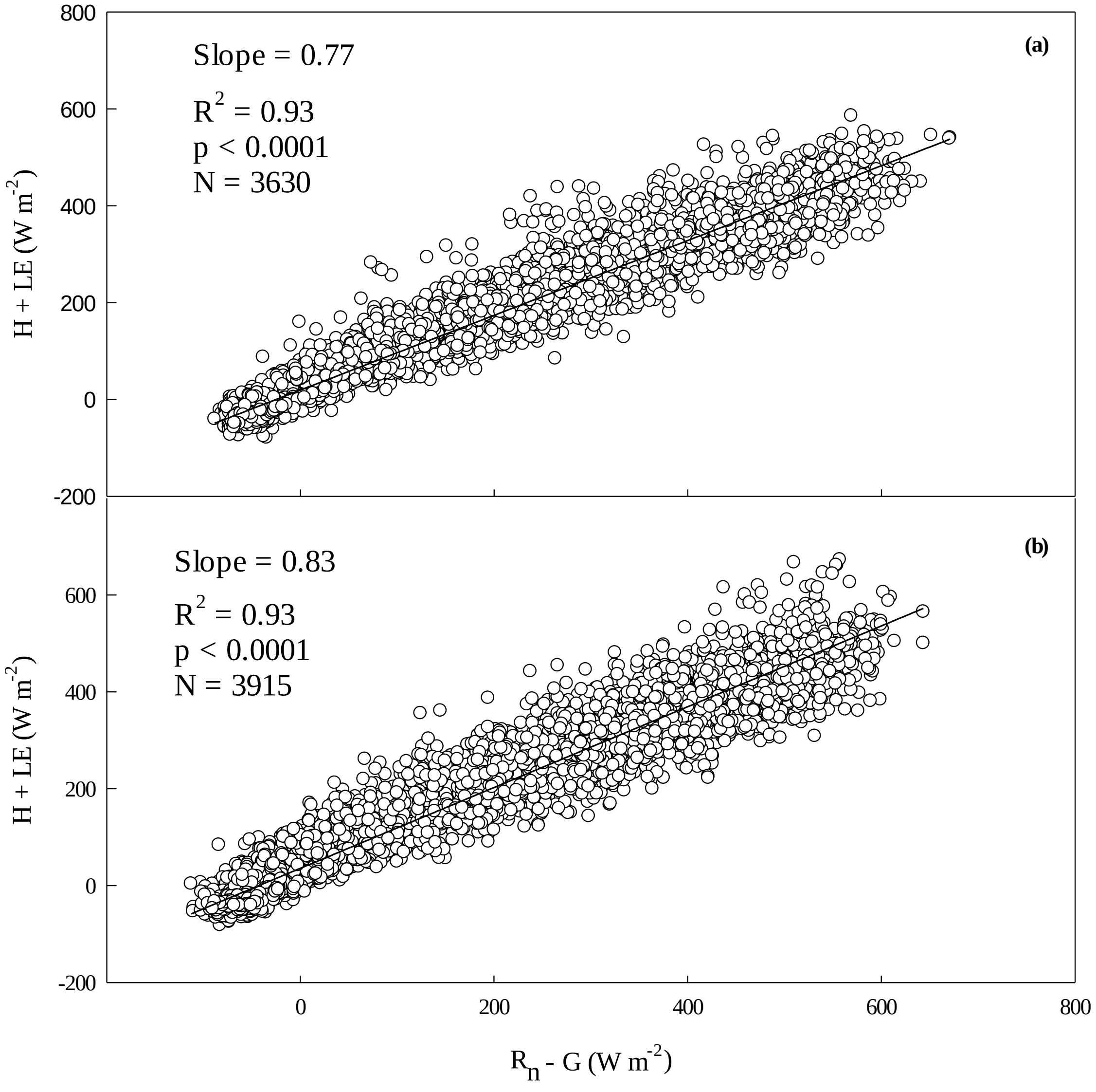

Fig. 7. Energy balance closure for 2011 (DOY 121 to 304) and 2012 (DOY 61 to 305) growing seasons (a and b, respectively). Turbulent fluxes were measured by eddy covariance and the available energy was measured independent of eddy covariance. The black line is the best fit line for linear regression ($P < 0.0001$). Total numbers of independent data points were represented by N. The regression slopes of 0.77 and 0.83 indicate the good closure of the energy balance ($R^2 = 0.93$).

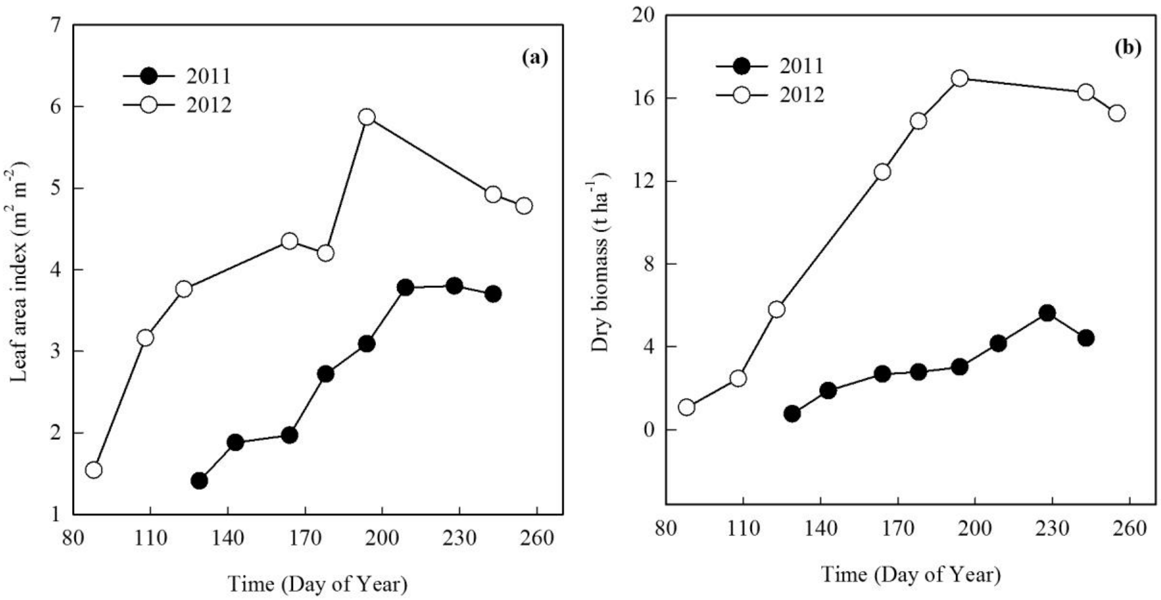

Fig. 8. Evolution of leaf area index (a) and dry biomass (b) of switchgrass during the 2011 and 2012 growing seasons. Higher leaf area index and dry biomass were observed during the 2012 growing season.

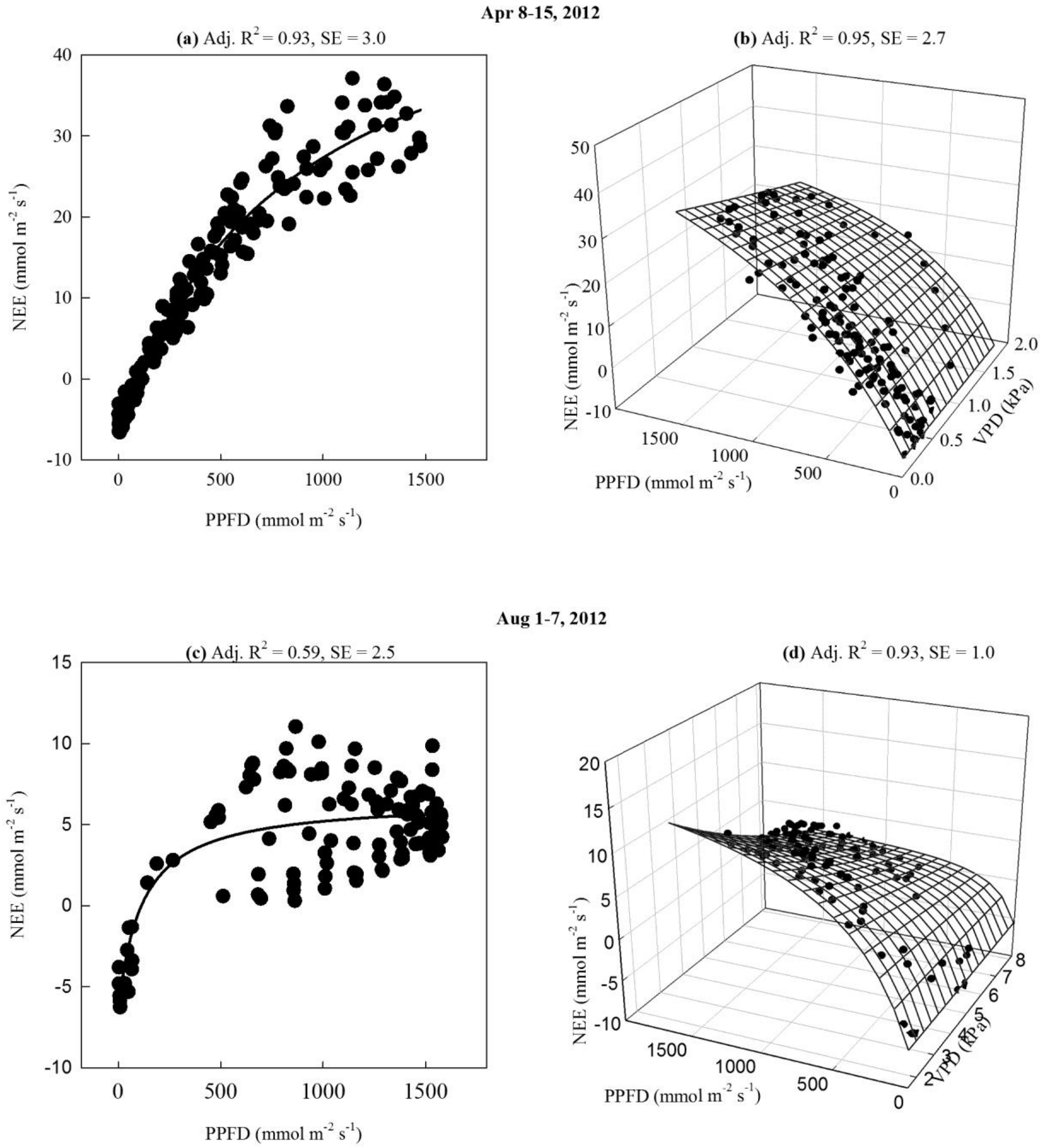

Fig. 9. Light-response curve functions with or without using vapor pressure deficit (VPD) in the model for selected time periods: dots, 30-minute daytime net ecosystem CO_2 exchange (NEE) data from tower measurements; PPFD, photosynthetic photon flux density; SE, standard error of the estimate.

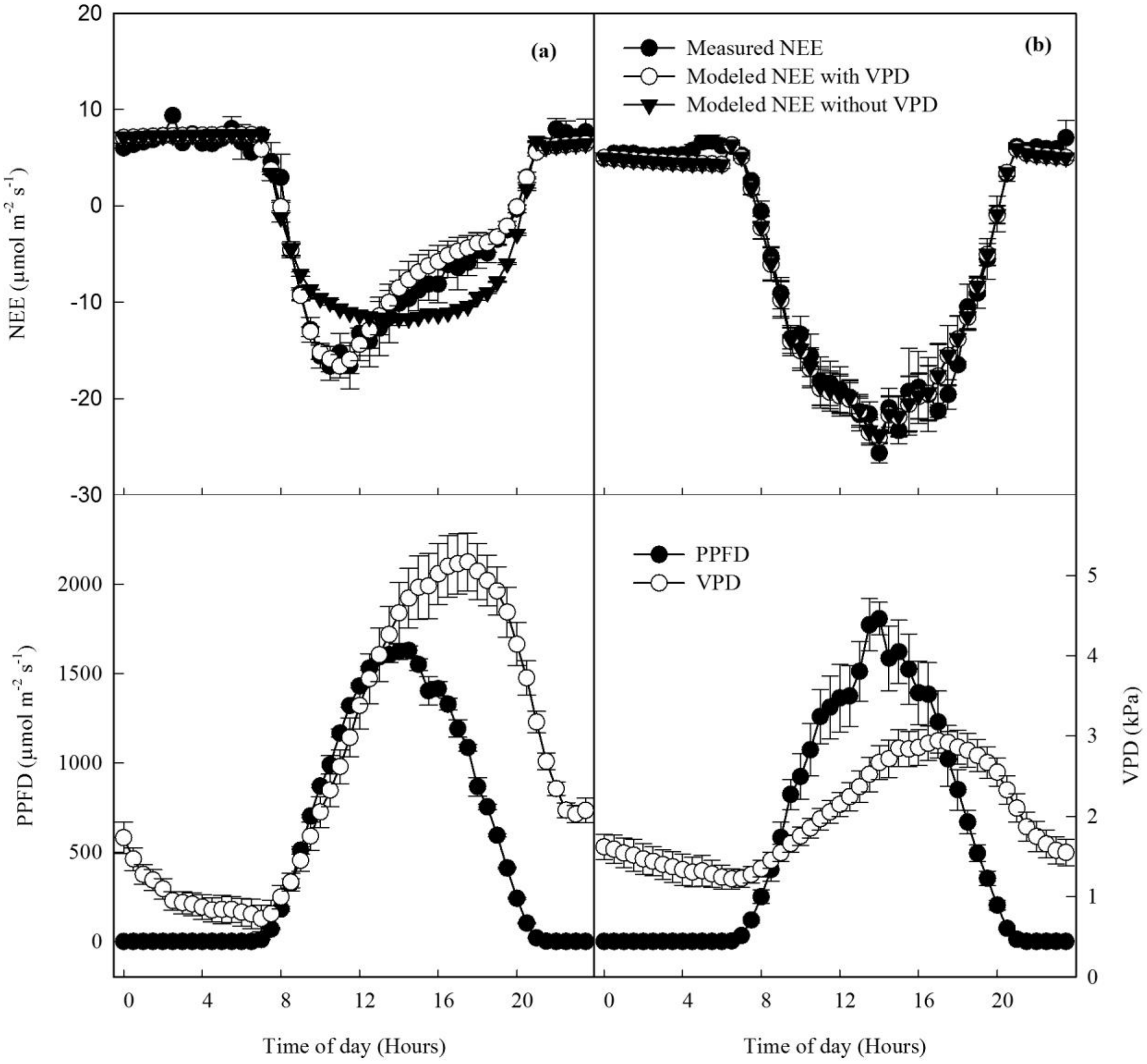

Fig. 10. Comparison of diurnal trends of measured and modeled net ecosystem exchange (NEE) using the original rectangular hyperbolic light-response curve and the modified light-VPD (vapor pressured deficit) response model along with diurnal trends of photosynthetic photon flux density (PPFD) and VPD for selected time periods: July 16-23, 2012 (a), and May 24-31, 2011 (b). Bars represent standard errors of the means.

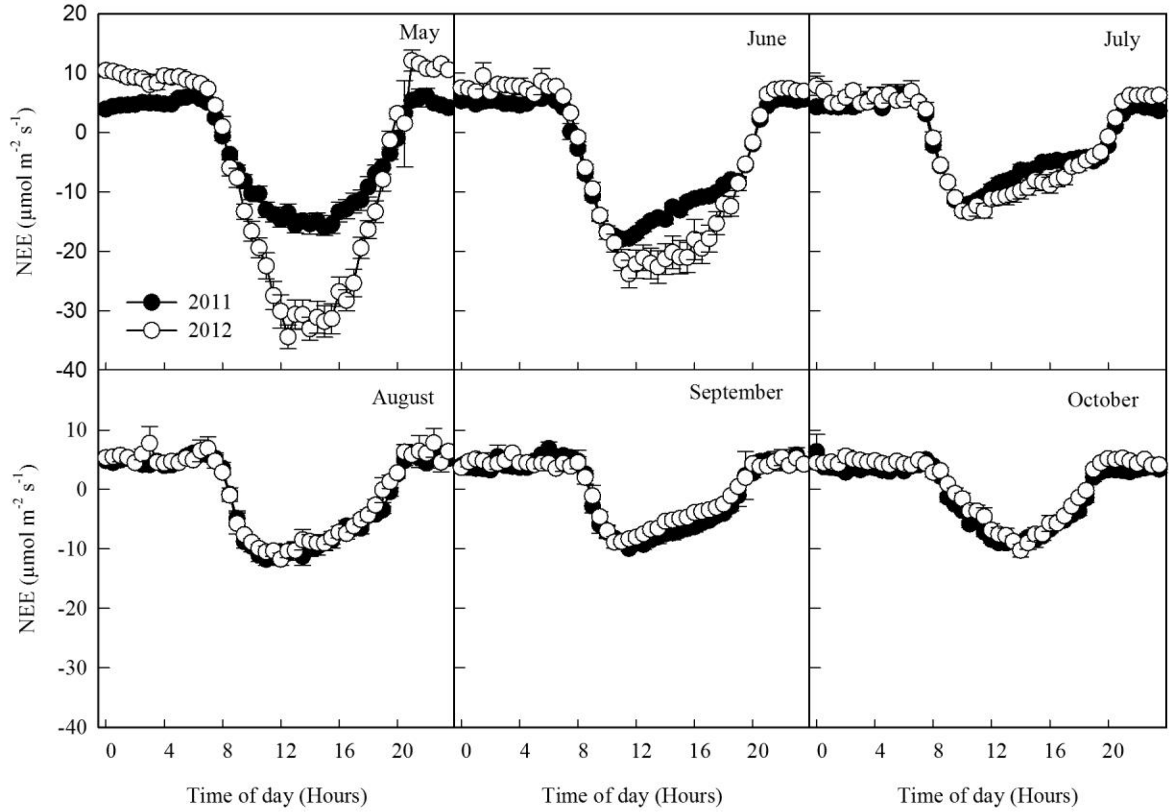

Fig. 11. Half-hourly binned diurnal courses of net ecosystem CO_2 exchange (NEE) rates for different months of the growing seasons (May – October, 2011 and 2012). Each data point is a 30-min average value for the entire month. Negative values of NEE indicate carbon uptake and positive values indicate carbon release by the ecosystem. Bars represent standard errors of the means.

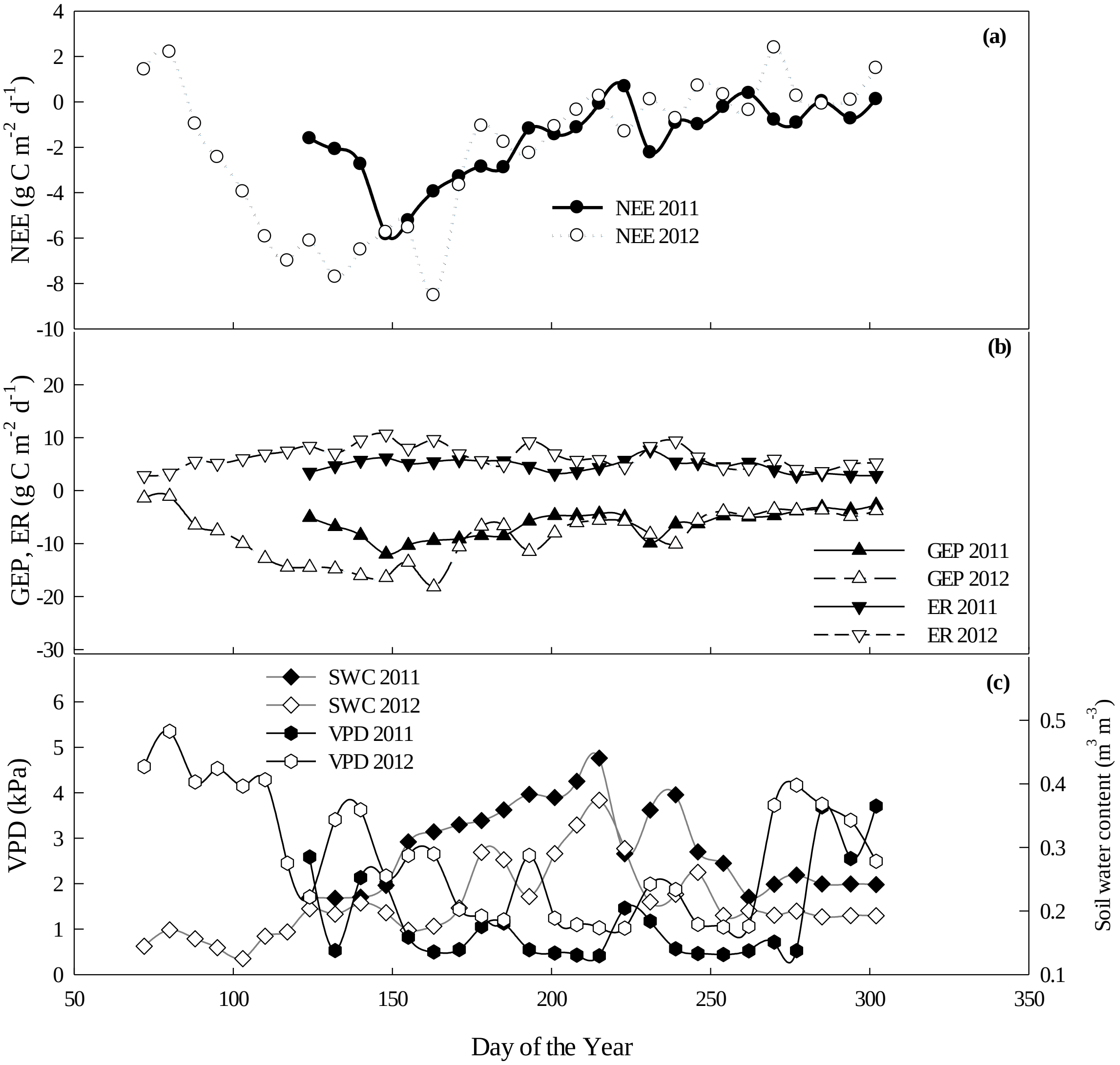

Fig. 12. Comparison of patterns of net ecosystem CO$_2$ exchange (NEE) (a); gross ecosystem production (GEP) and ecosystem respiration (ER) (b); vapor pressure deficit (VPD) and top-surface soil moisture (5 cm depth) (c) during the 2011 and 2012 growing seasons.

CHAPTER IV

ENVIRONMENTAL CONTROLS OF DAYTIME NET ECOSYSTEM EXCHANGE OF CARBON DIOXIDE IN SWITCHGRASS

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ABSTRACT. Net ecosystem CO_2 exchange (NEE) over a young switchgrass (*Panicum virgatum* L.) stand was measured with the eddy covariance technique across two growing seasons in the southern Great Plains of the United States (Chickasha, OK). The objectives of the study were to characterize the effects of environmental factors on daytime NEE and to explore the underlying mechanisms. Photosynthetic photon flux density (PPFD) alone explained over 90% of the NEE variation during optimum environmental conditions. Canopy photosynthesis did not saturate at as high as 2000 μmol $m^{-2}s^{-1}$ PPFD. However, the carbon uptake by the ecosystem decreased up to 62% (monthly average) from morning to afternoon at equal light levels because of the stomatal closure control of photosynthesis at high vapor pressure deficit (VPD). This resultant large hysteresis in NEE led to the failure of the rectangular hyperbolic light-response function in explaining the NEE-PPFD relationship. The NEE exhibited an optimum temperature range of 28-34 °C and decreased markedly beyond 35 °C. Our results demonstrate that warm temperature and high VPD altered the NEE-PPFD relationship and thereby affected the ecosystem light-response parameters (respiration, quantum yield, and light saturated photosynthetic capacity). Thus, it is essential to incorporate the effects of temperature and VPD on ecosystem light-response into both empirical and mechanistic models. This study also suggests including the VPD effect in the NEE flux partitioning technique can account for the systematic presence of NEE hysteresis during non-optimal environmental conditions.

Key words: CO_2 flux, Eddy covariance, Net ecosystem exchange, Switchgrass, Vapor pressure deficit

Introduction

There is a growing interest to understand the influence of environmental factors, such as temperature and precipitation patterns, on net ecosystem CO_2 exchange (NEE, the balance between CO_2 uptake and release by an ecosystem) between terrestrial ecosystems and the atmosphere. Even though the carbon capture process is ultimately regulated at the molecular level, climate greatly affects the way in which terrestrial ecosystems sequester carbon (Jones and Donnelly, 2004). A mechanistic understanding of environmental controls on NEE will be helpful to anticipate the potential impact of climate change scenarios on terrestrial ecosystem carbon cycling (Peters et al., 2007;Pingintha et al., 2010). Temperature response functions, based on leaf level photosynthetic processes and organic matter decomposition, have been used in many ecosystem-level carbon cycle models (Friedlingstein et al., 2006). These models can be improved by better understanding the NEE-temperature relationship. However, thermal optimality of switchgrass NEE has not yet been determined. Direct measurement of NEE between an ecosystem and the atmosphere, and the associated environmental factors by the eddy covariance (EC) technique, provides an elucidation of the climatic controls on NEE (Baldocchi et al., 2001a). Recently EC data are being used to determine ecosystem parameters and to evaluate land surface models for the carbon cycle (Bonan et al., 2011). However, few studies have been reported on NEE measurements in switchgrass (Skinner and Adler, 2010;Zeri et al., 2011;Wagle and Kakani, 2013). Moreover, the previous studies lacked a detail investigation of environmental controls on NEE. A detailed study of physiological processes at the ecosystem scale may improve our ability to parameterize ecosystem models.

A wide variety of different feedstocks would be necessary to produce one billion tons of biomass annually to generate enough biofuel to displace 30% of the United States petroleum usage by the year 2030 (Perlack et al., 2005). Substantial increase in productivity of biomass feedstocks, particularly switchgrass (*Panicum virgatum*), over the next two decades is one of the key assumptions of the ‘Billion Ton Study’ (U.S. Department of Energy, 2011). Biorefineries require efficient and accurate methods of estimating switchgrass biomass supplies (Schmer et al., 2010). Therefore, there is great interest in predicting the productivity of this bioenergy crop spatially and temporally using modeling techniques (Brown et al., 2000;Adler et al., 2007). However, a majority of the models are empirical in nature and fail to provide inference to the underlying mechanisms for differences in productivity (Dohleman et al., 2009). Mechanistic models that employ photosynthetic CO_2 assimilation require comprehensive field data sets across growing seasons at various environmental conditions for validating the models and understanding the physiological basis for observed differences in productivity (Dohleman et al., 2009). However, there is still a lack of information on the effect of environmental variables on ecosystem scale CO_2 fluxes, and the magnitude and seasonality of light-response parameters in switchgrass. Continuous field measurements of NEE and associated environmental factors over two full growing seasons provide a unique dataset for this emerging bioenergy crop.

As NEE is the balance between carbon uptake (GEP, gross ecosystem production) and release (ER, ecosystem respiration), the partitioning of NEE into these two flux components is important for understanding the mechanistic response of NEE to environmental variables. It is common in EC studies to separate NEE into GEP and ER using a rectangular hyperbolic light-response function (LRF) (Falge et al. 2001). Although the response of NEE to photosynthetic photon flux density (PPFD) is described by a rectangular hyperbola, earlier we demonstrated that vapor pressure deficit (VPD) modified the NEE-PPFD relationship at high VPD and the LRF failed to provide good fits to daytime NEE (Wagle and Kakani, 2013). Previous studies have also reported the failure of the LRF to describe daytime NEE in other ecosystems (Li et al., 2005;Lasslop et al., 2010;Pingintha et al., 2010). Temperature and VPD are expected to alter the response of NEE to PPFD. However, the mechanistic understanding of those alterations is still lacking. Investigation of the relationships between light-response parameters and major environmental drivers provides insight into the response of an ecosystem to environmental stresses.

The objectives of this study were to determine the response of switchgrass NEE to major environmental drivers (PPFD, air temperature, and VPD) and to explore the underlying mechanisms. This study also determines the magnitudes and seasonality of light-response parameters in response to controlling factors.

Materials and Methods

Site information

The study site was located at Oklahoma State University South Central Research Station, Chickasha, OK (35.04° N latitude, 97.95°W longitude, and 330 m above sea level altitude). The measurements were conducted in a well established switchgrass (cv. Alamo) field during the 2nd and 3rd years of establishment (2011 and 2012, respectively). The EC system was set up at the North end of a flat eight hectare field with sufficient upwind fetch (275 m) of uniform cover in the prevailing wind direction (South) and the East-West direction. The experiment was rainfed and the crop was sown in 38 cm wide rows. The soil is McLain silt loam soil (fine, mixed, superactive, thermic Pachic Argiustolls). Fertilizer was not applied in the establishment year, but ammonium nitrate was broadcast applied in April 2011 and 2012 at 75 kg N ha^{-1}.

Net ecosystem CO_2 exchange and other auxiliary measurements

Continuous CO_2 fluxes were measured using an EC system: CSAT3 sonic anemometer (Campbell Scientific Inc., Logan, UT, USA) and LI-7500 open-path infrared gas analyzer (IRGA, LI-COR Inc., Lincoln, NE, USA) during the 2011 (DOY 115-304) and 2012 (DOY 61-305) growing seasons. The IRGA was tilted to a 30° angle to minimize dust and water droplet accumulation on the windows. Sensors were fixed at a 2.2 m height from the ground in 2011 due to a smaller canopy height but adjusted according to increasing canopy height in 2012 to avoid measurement in the roughness sub-layer. The post-processing software *EddyPro* (LI-COR Inc., Lincoln, NE, USA) was used to process 10 Hz frequency flux data and fluxes were computed for 30-min averaging periods. A quantum sensor (LI-190, LI-COR Inc., Lincoln, NE, USA) was used to measure PPFD. Net radiation above the crop canopy was measured using a net radiometer (NR-Lite, Kipp and Zonen, Delft, The Netherlands). Temperature and relative humidity were measured using temperature and relative humidity probes (HMP45C, Vaisala, Helsinki, Finland). Top-surface soil temperature and moisture (5 cm depth) were recorded using water content reflectometers (CS616, Campbell Scientific Inc., Logan, UT, USA) and averaging soil temperature probes (TCAV-L, Campbell Scientific Inc., Logan, UT, USA). Soil heat flux (G) was measured using self-calibrating heat flux sensors (HFP01SC, Hukseflux Thermal Sensors B.V., Netherlands) at 5 cm depth. Environmental data collected at 10-Hz frequency were averaged for 30-min periods using a datalogger (CR3000, Campbell Scientific Inc., Logan, UT, USA). Rainfall and air temperature data for the study site was downloaded from the Oklahoma Mesonet website (www.mesonet.org, verified January 2, 2013). Flux data quality was assessed by the degree of energy balance closure [(LE + H)/ (R_n - G)]. The energy balance closures of 0.77 in 2011 and 0.83 in 2012 were typical for EC experiments (Wilson et al., 2002). Data for the period when wind was blowing from behind the tower and data for the period during low turbulence (friction velocity, $u^* < 0.20$ m s^{-1}) were removed. We also excluded unreasonable flux values and statistical outliers beyond ± 3.5 STD range from a 14-day running mean window. The details on these measurements, including data screening and gap filling, have been provided in a previous publication (Wagle and Kakani, 2013). Sign convention in this study is that CO_2 uptake by the ecosystem is negative and a net CO_2 release to the atmosphere is positive.

Analysis of canopy CO_2 fluxes

The data sets used in this study are daytime half-hourly data for the two growing seasons (May-October for the 2011 growing season and March-October for the 2012 growing season). Because of warm spring temperature the 2012 growing season started considerably earlier than in 2011. Simple and multiple regression analyses were performed at a monthly time scale between CO_2 fluxes and major environmental variables (monthly average PPFD and air temperature, and monthly total precipitation) to examine the response of the ecosystem to changes in major environmental drivers.

The light-response of NEE was evaluated using the LRF (Falge et al., 2001) as shown in equation 1 and the modified light-VPD-response model (LVRM) that accounted for an exponential reduction in the light saturated maximum canopy CO_2 uptake rate at high VPD as shown in equations 2 and 3.

$$NEE = \frac{\alpha \times GP_{\max} \times PPFD}{\alpha \times PPFD + GP_{\max}} + ER \qquad (1)$$

where α is the apparent quantum yield [i.e., the initial slope of the light-response curve (mol CO_2 mol^{-1} of photons)], PPFD is measured photosynthetic photon flux density (µmol m^{-2} s^{-1}), GP_{max} is the maximum canopy CO_2 uptake rate (µmol m^{-2} s^{-1}) at light saturation, and ER is respiration rate at zero PPFD (y-intercept of the light-response curve, µmol m^{-2} s^{-1}).

$$GP_{\max} = GP_0 \exp[-k(VPD - VPD_0)], if\ VPD > VPD_0 \qquad (2)$$

$$GP_{\max} = GP_0, if\ VPD < VPD_0 \qquad (3)$$

where k indicates the sensitivity of GP_{max} to VPD, and VPD_0 threshold was set to 1 kPa (Lasslop et al., 2010). Changing this threshold to 2 kPa did not alter the results, but the coefficient of determination (R^2) of the model fits was slightly decreased when threshold was set to 3 kPa. Fitted parameters were estimated using nonlinear least squares regression in SAS software (SAS Institute Inc., 2009, Cary, NC, USA). Measured daytime NEE data (not gap-filled) were fitted to the above mentioned models separately for each month of the growing seasons to obtain monthly estimates of GP_{max}, α, and ER to assess seasonality of the model parameters.

To determine the magnitude of NEE hysteresis (reduction in NEE rates in the afternoon hours when compared to the morning hours at similar light levels), we compared NEE rates at similar light levels (around 1000-1100 µmol m^{-2} s^{-1} PPFD) in the morning and afternoon hours across two growing seasons. To examine the relationship between NEE and PPFD, NEE observations for each season were separated into 10 different bins of PPFD (< 100, 100-200, 200-400, 400-600, 600-800, 800-1000, 1000-1200, 1200-1400, 1400-1600, and > 1600 µmol m^{-2} s^{-1}). The mean NEE and PPFD per bin was calculated to analyze the NEE trends with PPFD. We also sorted NEE data into thirteen different temperature classes (<16, 16-18, 18-20, 20-22, 22-24, 24-26, 26-28, 28-30, 30-32, 32-34, 34-36, 36-38, and > 38 °C) and six different VPD classes (< 1.2, 1.2-2, 2-3, 3-4, 4-5, > 5 kPa) to investigate the response of NEE to temperature and VPD. The light-response models were fitted across temperature and VPD classes separately to determine the coefficients of light-response parameters for each temperature/VPD class.

Results and Discussion

Seasonal weather conditions

The site experienced a relatively milder winter and cooler summer in 2012 as compared with 2011 (Fig. 13a). Mean monthly average air temperature ranged from 1.2 °C (January) to 32.4 °C (July) in 2011, while it ranged between 5.2 °C (February) and 30.1 °C (July) in 2012. Table 7 shows that monthly mean daily maximum air temperature for the growing seasons ranged from 23.9 °C (October) to 39.6 °C (July) in 2011 and 20.5 °C (March) to 37.1 °C (July) in 2012. The site received timely rainfall in 2012 as compared with 2011 which was dry throughout most of the year (Fig. 13b). However, both years were drier than the average, with the annual precipitation 41% below the 30-year average of 896 mm in 2011 and 25% below in 2012.

Response of NEE to major environmental drivers

Simple and multiple regression analyses showed that there were no relationships between NEE and the chosen environmental variables (PPFD, air temperature, and precipitation) at a monthly time scale, most likely due to different variance and covariance at different time scales as suggested by Baldocchi et al. (2001b). Wohlfahrt et al. (2008) also reported no significant relationships between annual NEE and environmental controls during the various periods in temperate mountain grassland. It is widely acknowledged that PPFD is the most significant environmental factor for variation in NEE. In general, photosynthetic activity and carbon uptake by the ecosystem increase as PPFD levels increase. But our study indicates that the correlation between NEE and PPFD is obscured by warm air temperature and high VPD in the summer. This is because a higher PPFD is associated with warm air temperature and high VPD. These conditions in the summer enhance respiration and reduce photosynthesis rates. The lack of a significant correlation between NEE and PPFD at a monthly time scale is associated with the limitation of photosynthesis by other environmental factors. Thus, we have investigated the response of NEE to PPFD, temperature, and VPD separately in the following sections.

Response of NEE to PPFD

When NEE was plotted against PPFD using mean values of NEE and PPFD per bin we observed rectangular hyperbolic-like response of NEE to PPFD in both seasons (Fig. 14). As a result, the LRF (equation 1) provided excellent fits for the data ($R^2 = 0.99$ for the

2011 growing season and $R^2 = 0.96$ for the 2012 growing season). The confounding effects of other environmental factors were masked when the bin averages were used to examine the NEE-PPFD relationship. But the confounding effect of high VPD limited the applicability of the LRF when the NEE-PPFD relationship was evaluated using half-hourly data for short periods (i.e., weekly) (Table 8). The table shows that the LRF successfully described the relationship between NEE and PPFD ($R^2 > 0.90$) at low VPD (< 3 kPa). The LRF, widely used by the EC community for NEE partitioning, became inadequate at VPD > 3 kPa. In contrast, the LVRM performed significantly better for the periods of high VPD. Different magnitudes of sensitivity of GP_{max} to VPD (represented by k in Table 8) for different ranges of VPD across two growing seasons concur with the finding of a previous study (Ludlow and Jarvis, 1971), that the response of photosynthesis to VPD is different for the same species when grown under different climatic conditions.

Limitation of VPD on the NEE-PPFD relationship

To further investigate the effect of VPD on the NEE-PPFD relationship, scatter plots (Fig. 15) of NEE vs. PPFD were plotted for two selected periods: one with smaller VPD (May 24-31, 2011: diurnal mean VPD ranged from 1.22 to 2.94 kPa) and the other with larger VPD (July 13-23, 2011: diurnal mean VPD range of 1.97-6.1 kPa). For the period of a smaller VPD, NEE increased with PPFD and there was no indication of canopy light saturation up to 2000 µmol m^{-2} s^{-1} PPFD (Fig. 15a). This result supports the finding of a previous study that photosynthesis in a warm-season prairie did not saturate at as high as

2100 µmol m^{-2}s^{-1} PPFD (Verma et al., 1992). The result suggests that VPD is not a limiting factor in the response of switchgrass NEE to PPFD when the maximum VPD < 3 kPa. During July 16-23, a period with high VPD, we observed larger scatter of the data at high PPFD and NEE decreased considerably when PPFD exceeded about 1300 µmol m^{-2} s^{-1} (Fig. 15b). A distinct hysteresis loop was evident for the NEE-PPFD relationship in the morning and afternoon hours. It highlights the confounding effect of VPD on the NEE-PPFD relationship. This NEE hysteresis is a result of the limitation of photosynthesis due to stomatal closure at high VPD and larger rate of respiration in the afternoon (Körner, 1995, Lasslop et al. 2010).

Seasonal patterns of VPD and asymmetric diurnal NEE cycles

To illustrate the underlying physiological mechanisms of reduction in NEE at high VPD, we examined the diurnal courses of NEE and VPD across the growing seasons. We observed great variations in VPD patterns with smaller values in the spring and late fall, and higher values during June to September (Table 7). As a result, NEE showed symmetric diurnal NEE cycles in the spring and late fall with a peak NEE at around 2:00 PM (CST) when the maximum radiation occurred as shown in Figure 16. However, NEE reached a maximum at or before noon, before radiation reached a peak, due to the limitation of high VPD on photosynthesis, and asymmetric diurnal NEE cycles were observed from June through September (e.g. July in Fig. 16). These asymmetric diurnal NEE cycles are typical (Price and Black, 1990), most probably due to different physiological responses of an ecosystem to environmental conditions in the afternoon than in the morning.

The reduction in NEE rates in the afternoon hours when compared to the morning hours at similar light levels were evaluated across the growing seasons and presented in Table 9. The table shows that carbon uptake by the ecosystem was of a similar magnitude in the morning and afternoon hours in March and April at similar light levels. The NEE rates slightly decreased from morning to afternoon in May (7 – 9%) and October (0 – 2.5%). The NEE rates decreased in the afternoon hours by 16 – 47% in June, 57 – 62% in July, 28 – 41% in August, and 35 – 36% in September, when compared to the morning hours. The greater reduction in NEE was observed during severe dry periods (high VPD). The results indicate that the NEE hysteresis phenomenon is associated with VPD effects on stomatal openings. Similar results were reported by Niu et al. (2011), that the magnitude of NEE hysteresis was larger in warmer than colder sites, with larger hysteresis during water stressed periods. These observations of NEE hysteresis are useful for understanding seasonal and inter-annual variability in NEE.

Magnitude and seasonality of light-response parameters

The values of GP_{max}, α, and ER increased to a maximum that coincided with periods of peak growth (May/June) and decreased towards senescence (Table 10) as observed previously for agricultural fields and grasslands (Gilmanov et al., 2003;Fischer et al., 2007). The values of the model parameters were greater in 2012 than in 2011 because of a greater crop growth and more optimal growing conditions. The maximum monthly average GP_{max} reached up to 31.1 μmol m^{-2} s^{-1} in 2011 and 50.3 μmol m^{-2} s^{-1} in 2012 during peak growth. The monthly average values of α during the period of maximum GP_{max} were 0.045 and 0.074 mol CO_2 mol^{-1} of photons in 2011 and 2012, respectively. Similarly, the highest value of ER during the peak growing period was 5.93 and 8.16 μmol m^{-2} s^{-1} in 2011 and 2012, respectively. We observed a strong correlation (GP_{max} = 8.31 x ER – 18.11, $R^2 = 0.74$, for pooled monthly estimates across both seasons) between GP_{max} and ER since changes in photosynthetic capacity alter the primary processes (i.e., protein turnover and active transport) accounting for respiration (De Vries, 1975). Our estimate of monthly average α (0.074 mol CO_2 mol^{-1} of photons) during the period of maximum GP_{max} in 2012 was higher than the value 0.044 mol CO_2 mol^{-1} of photons suggested by Ruimy et al. (1995) as the upper limit for C_3 and C_4 grasslands. However, this estimate generally agrees with other studies on C_4 species. The average α for NAD-ME type C_4 grasses, to which switchgrass belongs, was 0.060 mol CO_2 mol^{-1} of photons under normal atmospheric conditions (Ehleringer and Pearcy, 1983) and it was 0.068 in maize (*Zea mays*) (Dohleman and Long, 2009), a NADP-ME type C_4 species. Our estimates of maximum GP_{max} (50.3 μmol m^{-2} s^{-1}) and ER (8.2 μmol m^{-2} s^{-1}) were of similar magnitudes to estimates by Gilmanov et al. (2003). Their estimates of GP_{max} and ER in a tallgrass prairie in Oklahoma were 52.5 and 8.3 μmol CO_2 m^{-2} s^{-1}, respectively.

Dependency of light-response parameters to temperature and VPD

Light-response parameters showed great variations with temperature (Fig. 17a,b,c) and VPD (Fig. 17d,e,f). All light-response parameters (GP_{max}, α, and ER) were smaller at below optimum temperatures. A maximum GP_{max} occurred at an optimum temperature range between 30 and 32 °C. The maximum GP_{max} was higher (42.85 ± 3.96 µmol m^{-2} s^{-1}) in 2012 than in 2011 (33.51 ± 2.2 µmol m^{-2} s^{-1}). The higher values of α were achieved at a temperature range of 20-25 °C. The ER increased with increasing temperature up to an optimum temperature range of 23-25 °C and then it delined. The GP_{max} increased as VPD increases up to a certain range and decreased thereafter. In 2011, the maximum rate of GP_{max} (29.9 ± 1.4 µmol m^{-2} s^{-1}) was observed at a VPD range of 3-4 kPa. In 2012, GP_{max} exhibited a relatively flat response to VPD between 1.2 and 3 kPa, ranging from 35 ± 2 to 36.6 ± 2.3 µmol m^{-2} s^{-1}. Values of ER and α decreased with increasing VPD.

Response of NEE to temperature and VPD

The daytime NEE data, averaged over thirteen different bins of air temperature and six different bins of VPD, were plotted against air temperature and VPD (Fig. 18). The NEE increased rapidly with the temperature in the lower temperature range to reach a maximum and then declined as the temperature increased further. At high temperatures, the NEE decreases because photorespiration increases as a result of more increase in oxygenating reaction of RuBISCO than the carboxylating reaction (Long, 1991). In addition, high temperature enhances heterotrophic respiration as well. The optimum temperature for NEE was 33.8 °C in 2011 and 28.1 °C in 2012 (Fig. 18a). The optimum temperature range for GP_{max} (30-32 °C) and NEE (28-34 °C) in this study was in agreement with the result of a previous study that switchgrass photosynthesis was maximum at 30-35 °C (Warner et al., 1987). Higher optimum temperature for NEE in

2011 than in 2012 suggests that the optimum temperature shifts to a higher temperature in a warmer year, most probably due to thermal acclimation and overcompensation of increases in respiration by increases in photosynthesis at a higher temperature (Baldocchi et al., 2001a;Niu et al., 2012), as switchgrass is a native C_4 warm-season grass. Niu et al. (2012) reported a positive correlation between optimum temperature for NEE and annual mean temperature.

The NEE increased with increasing VPD at a smaller VPD, with higher values of NEE at a VPD range of 2-4 kPa in 2011 and at a VPD range of 1.2-3 kPa in 2012, and decreased thereafter (Fig. 18b). The result concurs with the finding of a previous study (Ludlow and Jarvis, 1971), that the response of photosynthesis to VPD is different for the same species when grown under different climatic conditions. The increase of NEE with increasing VPD at low VPD is because of increasing air temperature (VPD and temperature increase simultaneously) that enhances RuBISCO activity and in turn higher CO_2 assimilation (Sage and Kubien, 2007) and not due to the alleviation of VPD related stomatal limitation.

Conclusions

The goals of this study were to characterize the effects of key environmental factors (PPFD, air temperature, and VPD) on daytime NEE and to explore the underlying mechanisms. The result shows that PPFD is the most significant environmental factor for variation in NEE in switchgrass under optimal conditions. However, warm air temperature and high VPD obscured the NEE-PPFD relationship, and thereby affected the light-response parameters. As a result, the rectangular hyperbolic light-response curve failed to provide good fits for daytime NEE at high VPD (> 3 kPa). The carbon uptake by the ecosystem decreased up to 62% (monthly average) from morning to afternoon at equal light levels because of the limitation of photosynthesis due to stomatal closure at high VPD. The NEE exhibited an optimum temperature range of 28-34 °C and decreased markedly beyond 35 °C. The consistent presence of NEE hysteresis at higher VPDs suggests that asymmetric diurnal NEE cycles should be considered when simulating carbon cycle models.

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Table 7. Peak diurnal monthly mean values of vapor pressure deficit (VPD) and air temperature across two growing seasons.

	2011		2012	
Month	VPD (kPa)	Air Temp. (°C)	VPD (kPa)	Air Temp. (°C)
Mar			1.21	20.5
Apr			1.25	23.4
May	2.74	27	2.17	28.2
Jun	5.2	36.9	2.92	32
Jul	6.22	39.6	4.74	37.1
Aug	6.09	39.1	4.42	35.5
Sep	3.84	30.3	2.41	27.2
Oct	3.28	23.9	2.06	24.4

Table 8. Comparison of rectangular hyperbolic light-response function (LRF) and modified rectangular hyperbolic light-VPD-response model (LVRM) fits for selected time periods with different VPD ranges.

Time periods	LRF (R^2)	LRVM (R^2)	k	VPD range (kPa)
May 24-31, 2011	0.96	0.96	0.01	1.22-2.94
Jul 16-23, 2011	0.24	0.82	0.31	1.97-6.1
Aug 24-31, 2011	0.38	0.82	0.22	2.04-6.59
Apr 16-23, 2012	0.90	0.90	0.02	0.50-1.42
Jun 24-30, 2012	0.45	0.89	0.32	0.84-5.30
Aug 1-7, 2012	0.60	0.93	0.17	1.64-6.76

Vapor pressure deficit (VPD) range is the diurnal mean of VPD for the week, R^2 is the coefficient of determination, and k represents the response of maximum canopy CO_2 uptake rate at light saturation (GP_{max}) to VPD.

Table 9. Magnitude of reduction (expressed in percentage) in net ecosystem CO_2 exchange (NEE) in the afternoon (PM) hours as compared to the morning (AM) hours at similar photosynthetic photon flux density (PPFD) across growing seasons.

		2011			2012		
Month	Time	PPFD (μmol m^{-2} s^{-1})	NEE (μmol m^{-2} s^{-1})	Change (%)	PPFD (μmol m^{-2} s^{-1})	NEE (μmol m^{-2} s^{-1})	Change (%)
Mar	AM				957	-6.08 ± 1.07	+2.8
	PM				983	-6.25 ± 1.36	
Apr	AM				1027	-25.39 ± 2.3	-0.5
	PM				1008	-25.26 ± 1.66	
May	AM	1113	-13.02 ± 1.29	-9.3	1023	-27.46 ± 2.38	-7.7
	PM	1088	-11.81 ± 1.65		1003	-25.34 ± 2.28	
Jun	AM	1009	-16.7 ± 0.71	-47.3	1004	-21.46 ± 1.78	-16.8
	PM	1026	-8.8 ± 0.57		1085	-17.85 ± 2.29	
Jul	AM	1033	-12.17 ± 0.53	-62.5	992	-13.46 ± 0.91	-57.2
	PM	1069	-4.56 ± 0.76		999	-5.75 ± 0.82	
Aug	AM	1004	-11.04 ± 1.04	-41.2	1061	-10.35 ± 0.90	-28.4
	PM	1039	-6.49 ± 0.94		1077	-7.41 ± 0.94	
Sep	AM	1067	-8.81 ± 0.56	-36.2	1057	-7.49 ± 0.5	-35.1
	PM	1100	-5.62 ± 0.72		1030	-4.86 ± 0.57	
Oct	AM	1101	-8.39 ± 0.55	0	956	-7.74 ± 1.2	-2.5
	PM	1110	-8.40 ± 1.36		956	-7.54 ± 1.15	

Negative sign for change (%) indicates reduction in NEE in the afternoon hours as compared to the morning hours. The NEE rates and PPFD were half-hourly binned diurnal mean values for the entire month.

Table 10. Coefficients estimated from rectangular hyperbolic light-VPD (vapor pressure deficit)-response model (LVRM) fits for each month of the growing seasons.

	2011				2012			
Month	α	GP_{max}	ER	R^2	α	GP_{max}	ER	R^2
Mar					0.029	15.0	3.79	0.32
Apr					0.074	45.2	6.01	0.82
May	0.044	30.6	5.93	0.71	0.074	50.3	8.16	0.87
Jun	0.045	31.1	5.62	0.86	0.063	40.4	7.11	0.85
Jul	0.037	19.0	4.46	0.6	0.037	27.8	4.65	0.73
Aug	0.033	24.6	5.50	0.5	0.050	21.9	5.43	0.81
Sep	0.032	18.7	4.73	0.73	0.074	13.1	5.26	0.49
Oct	0.035	14.9	3.56	0.56	0.046	17.9	4.87	0.66

Here α is the apparent quantum yield (mol CO_2 mol^{-1} of photons), GP_{max} is the maximum canopy CO_2 uptake rate (μmol m^{-2} s^{-1}) at light saturation, and ER is respiration rate (μmol m^{-2} s^{-1}) at zero photosynthetic photon flux density, and R^2 is the coefficient of determination.

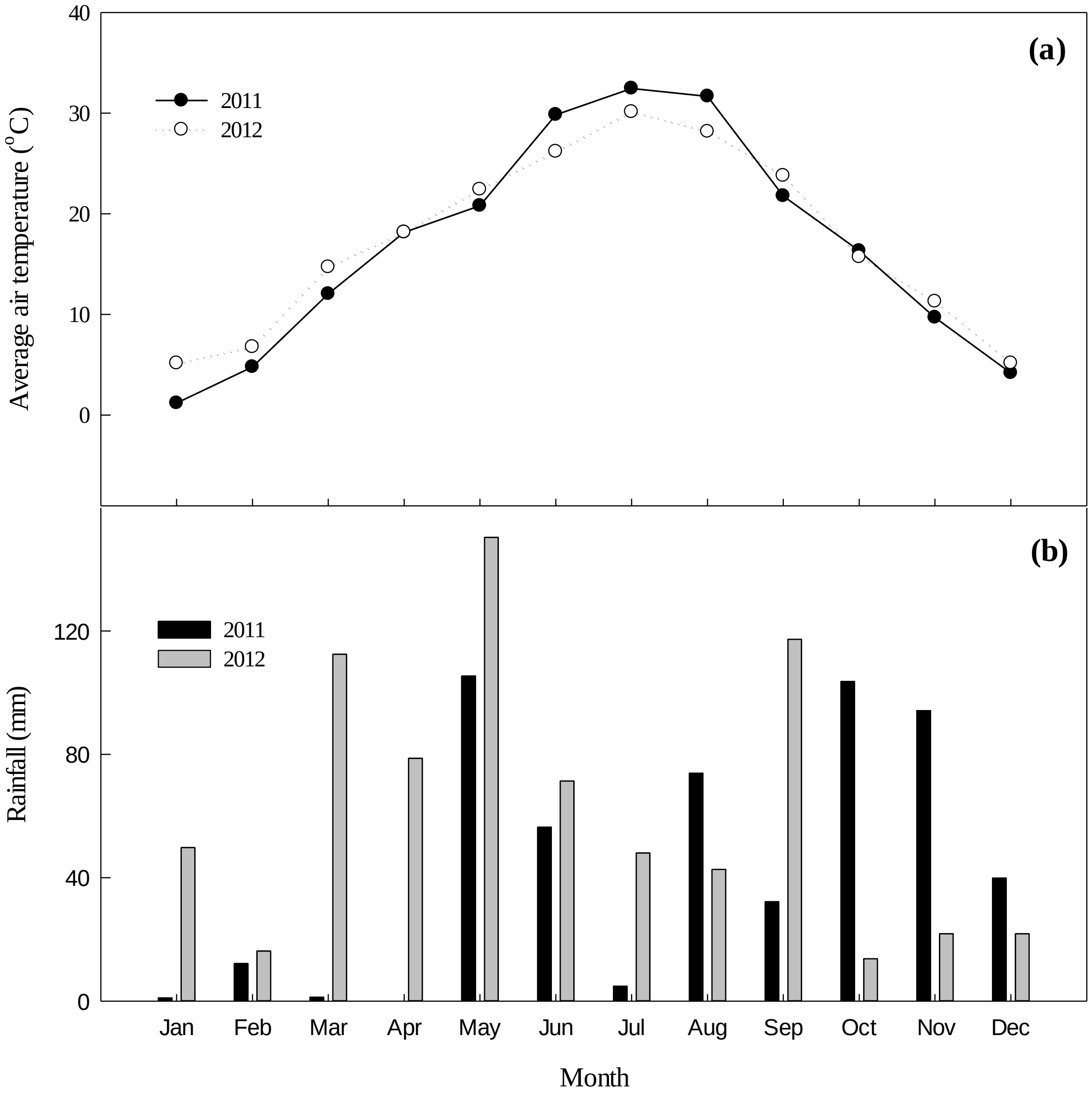

Fig. 13. Monthly average air temperature (a) and monthly total rainfall (b) in 2011 and 2012 for Chickasha, Oklahoma, USA.

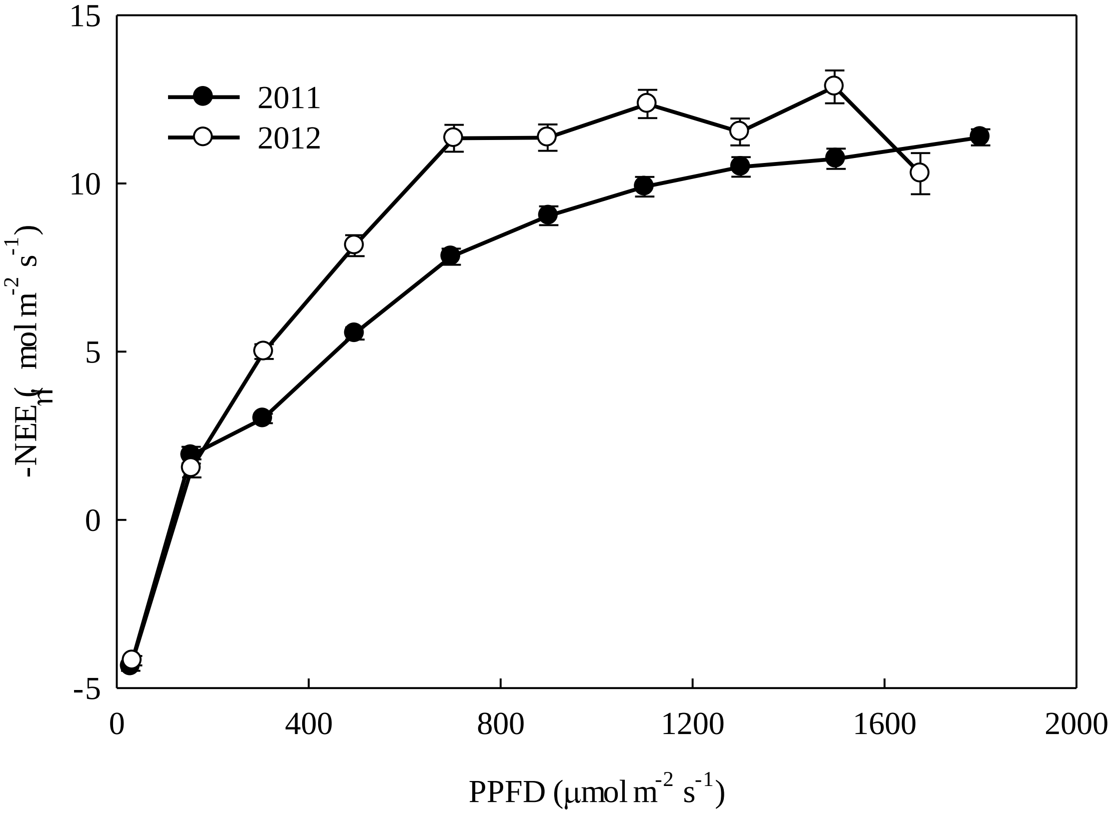

Fig. 14. Response of net ecosystem CO_2 exchange (NEE) to photosynthetic photon flux density (PPFD). Each data point is the seasonal mean NEE at a PPFD class. Bars represent standard errors of the means. Minimum significant differences from Tukey's HSD groupings were 1.95 and 2.22 for 2011 and 2012, respectively.

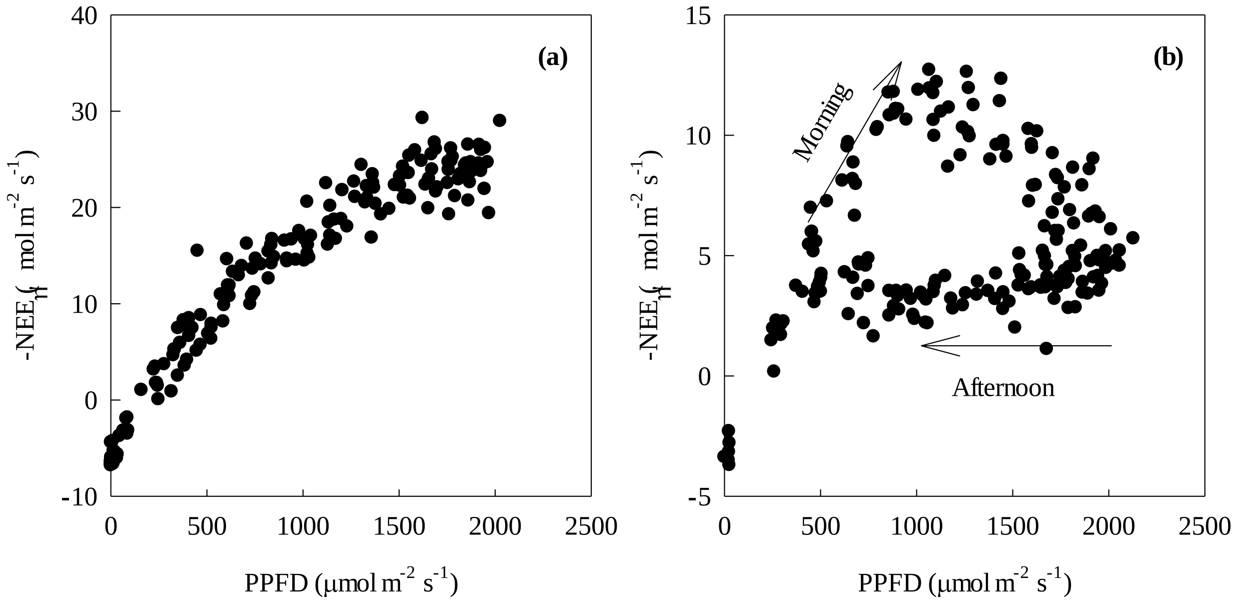

Fig. 15. The relationship between net ecosystem CO_2 exchange (NEE) and photosynthetic photon flux density (PPFD) for two selected time periods: (a) May 24-31, 2011 and (b) July 16-23, 2011.

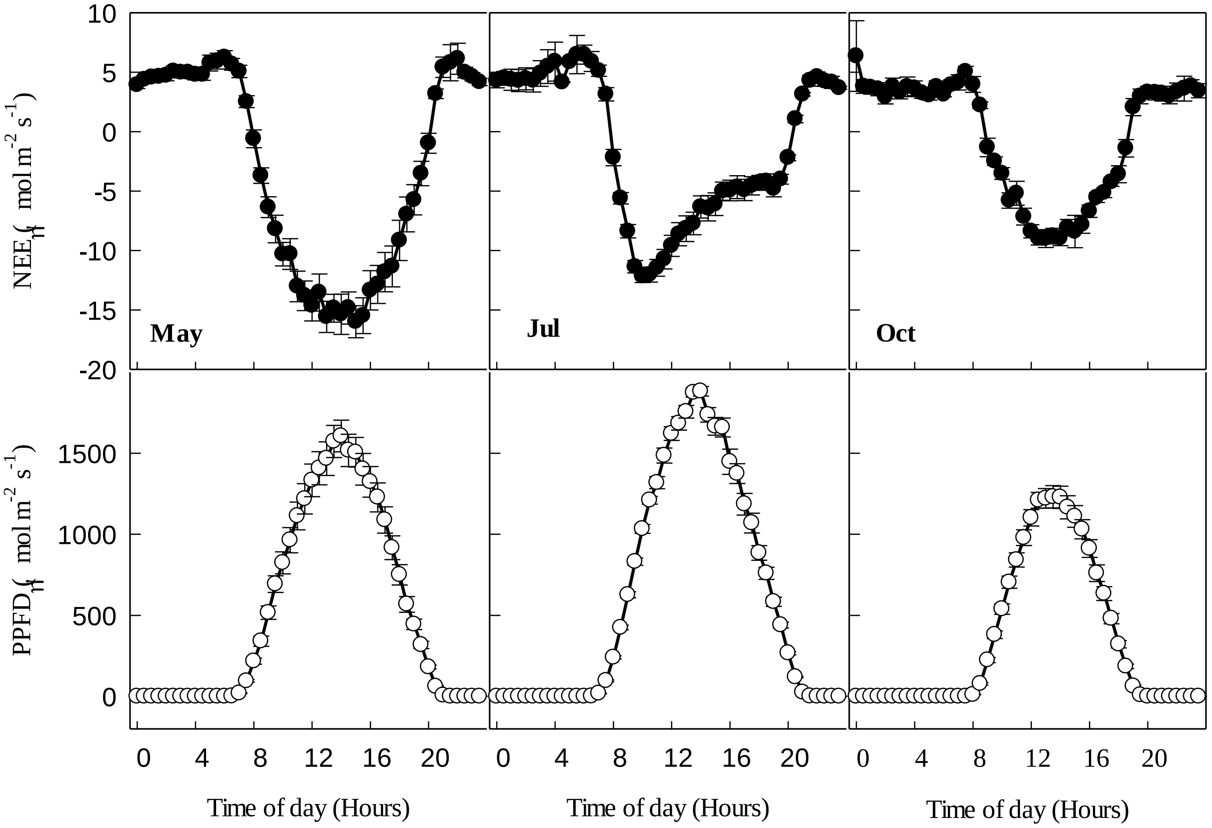

Fig. 16. Half-hourly binned diurnal courses of net ecosystem CO_2 exchange (NEE) and photosynthetic photon flux density (PPFD) for May, July, and October 2011. Negative values of NEE indicate net carbon uptake and positive values indicate carbon release by the ecosystem. Bars represent standard errors of the means.

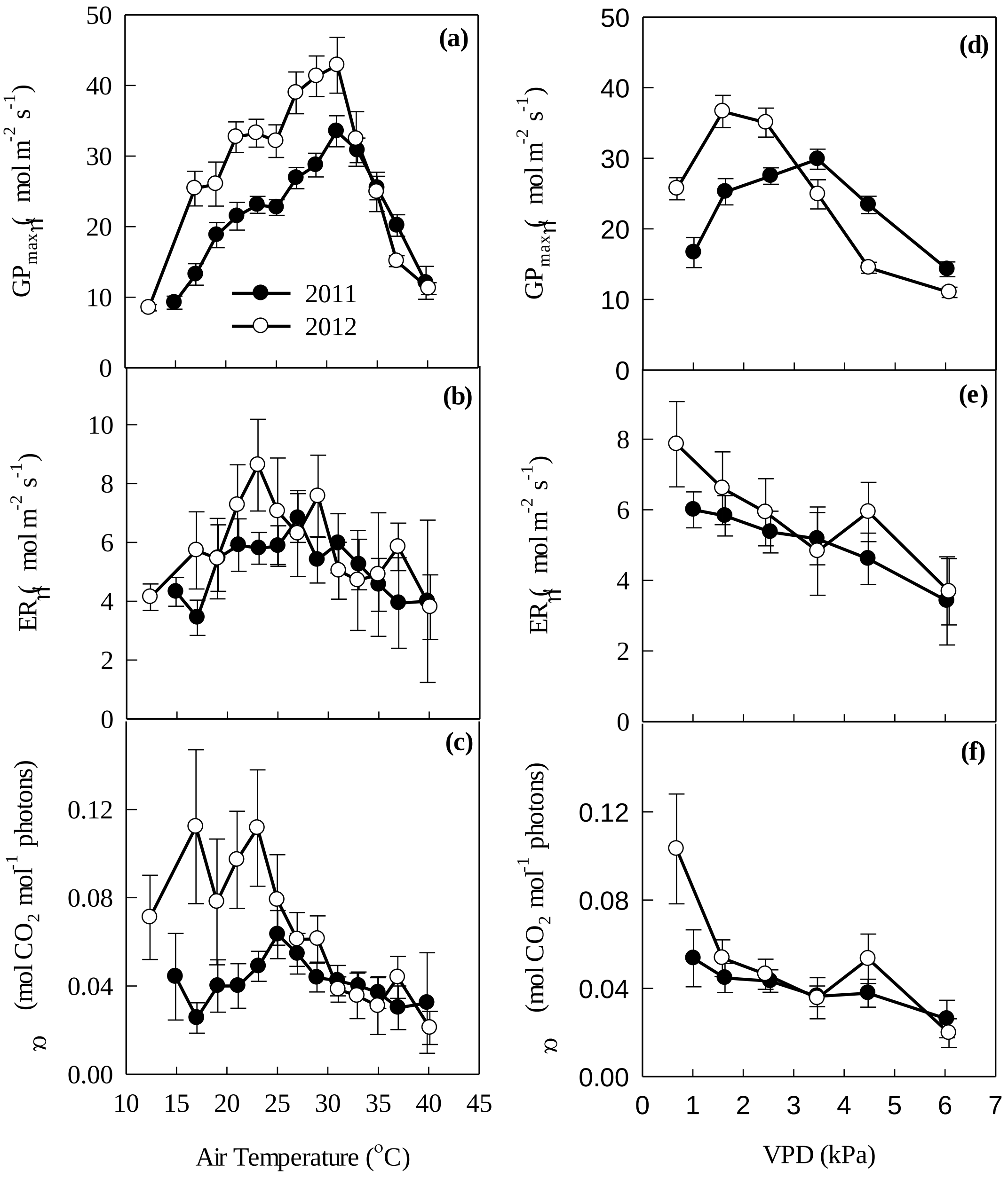

Fig. 17. Light-response parameters: maximum canopy CO_2 uptake rate (GP_{max}) at light saturation, respiration (ER) at zero light levels, and apparent quantum yield (α) as a function of air temperature and vapor pressure deficit (VPD). The parameters were determined from daytime net ecosystem CO_2 exchange (NEE) data categorized by air temperature and VPD classes and fit to the non-linear least square regression. Bars represent standard errors of the means.

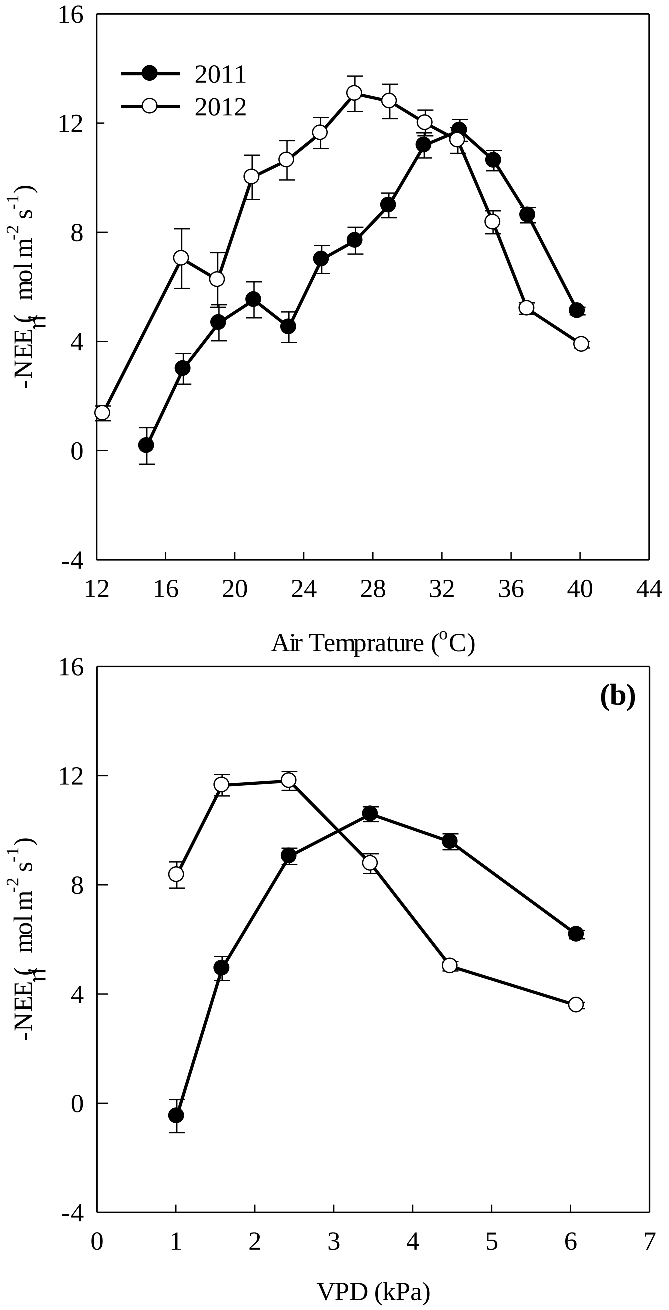

Fig. 18. The response of daytime net ecosystem CO_2 exchange (NEE) to (a) air temperature and (b) vapor pressure deficit (VPD). Each data point is the mean NEE at a temperature/VPD class. Bars represent standard errors of the means. Minimum significant differences from Tukey's HSD groupings for temperature were 2.86 and 2.92, and for VPD were 1.7 and 1.75 for 2011 and 2012, respectively.

CHAPTER V

COMPARISON OF NET ECOSYSTEM CO_2 EXCHANGE OF SWITCHGRASS AND HIGH BIOMASS SORGHUM

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ABSTRACT. We analyzed eddy covariance carbon dioxide flux measurements from co-located switchgrass (*Panicum virgatum* L.) and high biomass sorghum (*Sorghum bicolor* L. Moench) fields during a growing season in 2012. The major objective of this study was to quantify and contrast net ecosystem CO_2 exchange (NEE) between ecosystems. Monthly ensemble averaged NEE reached seasonal peak values of -33.02 ± 1.96 (May) and -35.86 ± 2.32 µmol m^{-2} s^{-1} (June) in switchgrass and sorghum, respectively. The weekly average of daily integrated NEE reached seasonal peaks of -8.5 g C m^{-2} d^{-1} in switchgrass and -10.3 g C m^{-2} d^{-1} in sorghum. Daily gross ecosystem production (GEP) reached seasonal peaks of 18.15 and 19.03 g C m^{-2} d^{-1} in switchgrass and sorghum, respectively. The growing season (March-October) GEP and ecosystem respiration (ER) totals in switchgrass were 2017 ± 295 and 1527 ± 236 g C m^{-2}, respectively. Similarly, the growing season (May-October) cumulative GEP and ER of sorghum were 1164 ± 183 and 903 ± 134 g C m^{-2}, respectively. The result shows that the switchgrass ecosystem was a larger carbon sink with a cumulative seasonal carbon uptake of -490 ± 59 g C m^{-2} compared to -261 ± 48 g C m^{-2} by sorghum. Because the magnitude of CO$_2$ exchange was similar, the difference in carbon sink strength between two ecosystems was driven mainly by the length of the growing season. Switchgrass was a net sink of carbon during five months (April-August), but the sorghum ecosystem appeared to be a net carbon sink for only three months (June-August).

Keywords: Biofuels, Eddy covariance, High biomass sorghum, Net ecosystem exchange, Seasonal variation, Switchgrass.

Introduction

America consumes about 25% of the world's oil as one-third of the automobiles (230 million) are in America (NBAP, http://www1.eere.energy.gov/biomass/pdfs/nbap.pdf, verified April 11, 2013). According to the projection of the U.S. Energy Information Administration (EIA), the reliance on foreign producers for oil will increase 30% by 2030 and the transport sector's greenhouse gas emissions will rise by 40% (Annual Energy Outlook, 2007, ftp://ftp.eia.doe.gov/forecasting/0383(2007).pdf, verified April 11, 2013). The demand and cost of energy are increasing, and oil and gas reserves are declining.

Moreover, CO_2 concentration is increasing in the atmosphere since the Industrial Revolution of the mid-nineteenth century. Most of the released CO_2 into the atmosphere is a result of burning fossil fuels (Revelle and Suess, 1957). It is, therefore, necessary to produce alternative fuels from renewable sources to supplement transportation fuel requirement. Current ethanol production from sugar/starch may not be sustainable because of the direct competition with food/feed sources. Thus, biofuels production from biomass is a viable choice of energy production. The U.S. has the capability of producing about 1.3 billion dry tons of biomass each year (Perlack et al., 2005). Switchgrass (*Panicum virgatum* L.) and high biomass sorghum (hereafter referred to as sorghum) (*Sorghum bicolor* L. Moench) have been proposed as dedicated biomass feedstocks for the southern Great Plains of the U.S.

In recent years, direct measurements of net ecosystem CO_2 exchange (NEE), the balance between carbon uptake through photosynthesis and carbon loss through respiration, have increased. The North American Carbon Program Science Plan (Wofsy and Harriss, 2002) emphasized quantifying the carbon sink of the North America by NEE measurements in a variety of ecosystems. Long-term eddy covariance monitoring networks such as Ameriflux, Euroflux, and Asiaflux have been established to measure NEE across a range of land-use categories, and data from several ecosystems are available for scientific communities. FLUXNET, an international network of micrometeorological tower sites, coordinates regional and global analysis of continuous observations of exchanges of CO_2, H_2O, and energy between terrestrial ecosystems and the atmosphere from over 500 tower sites using the eddy covariance method (http://fluxnet.ornl.gov/, verified December 18, 2012). However, few studies of NEE in switchgrass have been reported to date (Skinner and Adler, 2010;Zeri et al., 2011;Wagle and Kakani, 2013). To our knowledge there has been no NEE study in high biomass sorghum yet. This paper not only quantifies NEE but also compares the magnitudes of NEE and its two components, gross ecosystem production (GEP, total carbon gained by the ecosystem) and ecosystem respiration (ER, total carbon lost by the ecosystem), between two contrasting (perennial and annual) feedstock species at the same experiment site.

The objective of this study was to quantify and contrast the magnitude of CO_2 flux exchange between switchgrass and sorghum ecosystems under the same growing condition. In this study, NEE was compared between annual sorghum and perennial switchgrass in its third year of production in South Central (Chickasha) Oklahoma.

Material and Methods

Site description and weather conditions

Eddy covariance measurements were performed over switchgrass (*cv*. Alamo) and sorghum (*cv*. ES 5200) fields located at adjacent plots at Oklahoma State University, South Central Research Station, Chickasha, Oklahoma. Switchgrass stand was established in spring 2010 and sorghum was planted in the second week of May. We applied ammonium nitrate at 75 kg N ha^{-1} in April for switchgrass and in May for sorghum. Both crops relied on rainfall. The site has been described in detail previously (Wagle and Kakani, 2013). Two flux towers were about 500 m from each other. Thus, both ecosystems experienced similar weather conditions. Monthly mean daily maximum and minimum temperatures, and monthly rainfall in 2012 in comparison with the 30-year mean for the site are presented in Table 11. Winter and spring in 2012 were slightly warmer and wetter than the average, but summer and fall seasons in 2012 were slightly warmer and drier when compared with the 30-year average for the site.

Micrometeorological and biometric measurements, and data screening

Net ecosystem CO_2 exchange from switchgrass and sorghum fields was measured using the eddy covariance technique in the 2012 growing season. At both ecosystems, a three-dimensional sonic anemometer (Model CSAT3, Campbell Scientific Inc., Logan, UT, USA) and an open path infrared gas analyzer (IRGA; model LI-7500, LI-COR Inc., Lincoln, NE, USA) were mounted over the crop canopy. Sensor heights were adjusted according the canopy height not to measure fluxes in roughness sub-layer. Other climatic variables like photosynthetic photon flux density (PPFD), near surface soil temperature, moisture, soil heat (G) flux measurements (top 5 cm), and net radiation (R_n) were also collected. We also took periodic (mostly biweekly) biometric measurements for the better understanding of flux values. Leaf area index (LAI) was measured using a plant canopy analyzer (LAI 2000, LI-COR Inc., Lincoln, NE, USA). Biomass samples were destructively collected from three different 1 m^2 areas in each field throughout the growing season and dried in an oven for a week at 70 °C before recording dry weights. Canopy height was also recorded.

Flux measurements were collected at 10 Hz frequency and finally half-hourly CO_2 fluxes were calculated from the covariance between CO_2 density and vertical wind speed. The eddy flux data was processed using eddy covariance processing software, *EddyPro* (LI-COR Inc., Lincoln, NE, USA). We screened data for the periods of low turbulent intensity (u* < 0.20 m s^{-1}). The CO_2 and turbulent fluxes were filtered to keep in the reliable range of fluxes. In addition, statistical outliers beyond ±3.5 standard deviation range were removed using a 14-day running mean window. Measurement details and data screening techniques have been provided in previous publications (Wagle and Kakani, 2012;Wagle and Kakani, 2013). Sign convention of NEE in this study is that a net CO_2 uptake by the ecosystem is negative and a net CO_2 release by the ecosystem is positive.

Gap filling and partitioning of CO_2 fluxes

To fill missing data we employed different gap filling approaches based on the length of data gaps. Half-hourly gaps were filled using an average value immediately before and after the gap (Wever et al., 2002). Less than two hour gaps were filled using linearly interpolated values (Flanagan et al., 2002). Empirical models based on dominant physiological processes were developed to fill longer data gaps. Simple and multiple regression equations or exponential relationships were derived between nighttime NEE and soil temperature, air temperature, and soil moisture. Relationships with the highest level of significance were selected to fill nighttime NEE data gaps (Flanagan et al., 2002). Mean NEE rates were calculated and filled the gaps for the periods when no significant relationships of the variables were observed (Flanagan et al., 2002). Initially, we partitioned daytime NEE into GEP and ER using a widely used rectangular hyperbolic light-response curve function as shown below:

$$NEE = \frac{\alpha \times GP_{\max} \times PPFD}{\alpha \times PPFD + GP_{\max}} + ER \qquad (1)$$

where α, i.e. apparent quantum yield, is the initial slope of the light response curve (mol CO_2 mol^{-1} of photons), PPFD is photosynthetic photon flux density (μmol m^{-2} s^{-1}), GP_{max} is the maximum canopy CO_2 uptake rate (μmol m^{-2} s^{-1}) at light saturation, and ER is respiration rate at zero PPFD. We reported asymmetric diurnal NEE cycles in switchgrass mainly from June to September at this site (Wagle and Kakani, 2013) because of the limitation of higher vapor pressure deficit (VPD) on photosynthesis. Thus, the equation 1 failed to provide good fits for the data. To address this problem, GP_{max} was calculated as the exponential decreasing function at high VPD to include the effect of VPD on photosynthesis as shown in a previous study (Lasslop et al., 2010):

$GP_{max} = GP_0 \exp[-k (VPD-VPD_0)]$, if $VPD > VPD_0$ (2)

$GPmax = GP_0$, if $VPD < VPD_0$ (3)

where VPD_0 threshold was set to 1 kPa (Lasslop et al., 2010). Parameters were estimated using nonlinear least squares regression in SAS software (SAS Institute Inc. 2009, Cary, NC, USA). All empirical functions were developed for short time periods (mostly a week and sometimes up to 14 days in case of insufficient data points or lack of good fits) to account for climatic variability. Non-gap filled data were used for the optimization of model parameters. Daytime NEE data gaps were filled using these empirical functions. Seasonal total of NEE were calculated by summing the gap-filled half-hourly values. The sampling uncertainty (gap filling) errors with in seasonal estimates of CO_2 fluxes were determined as the standard error of the gap filling models as described in a previous study (Black et al., 2007).

Results and Discussion

Energy balance closure

The plausibility of eddy covariance measurements is assessed from energy balance closure (EBC) test. The EBC was determined by comparing turbulent heat fluxes [sensible heat (H) + latent heat (LE)] with the available energy fluxes (R_n – G) as given below:

$$EBC = (H + LE)/(R_n - G) \quad (4)$$

We observed EBC of 0.83 for switchgrass and 0.82 for sorghum for half-hourly measurements in the 2012 growing season. Our result matches well with the typical range of eddy covariance measurements. The EBC for many field-experiments and for the CO_2 flux networks is about 80% (Aubinet et al., 1999;Wilson et al., 2002). Even a careful application of all corrections of the turbulent fluxes reduced the residual only slightly (Mauder and Foken, 2006). Recently it has been reported that the time-averaged fluxes (Finnigan et al., 2003) or spatially averaged fluxes including turbulent-organized structures (Kanda et al., 2004) can close the energy balance. These findings indicate that the unclosed EBC problem may not be related to errors involve in eddy covariance measurements. Instead, it may be related to the atmospheric phenomena which the eddy covariance system fails to measure.

Information on crop growth

Because of mild winter in 2012 switchgrass growth began earlier in March, about 1.5-2 months earlier than seen in 2011 and 2013. Even though sorghum was planted in the first week of May, sorghum growth occurred rapidly and the peak LAI was observed during mid-July for both ecosystems. The peak value of LAI was about 5.9 m^2 m^{-2} for switchgrass and 5.7 m^2 m^{-2} for sorghum. The highest recorded aboveground biomass in switchgrass was about 17 t ha^{-1} during mid-July while in sorghum it was about 27.6 t ha^{-1} during mid-August. Canopy height reached a maximum of about 1.8 m in switchgrass and 2.2 m in sorghum. The result shows that the aboveground biomass of sorghum increased more rapidly and produced more aboveground biomass compared to switchgrass.

Growing season patterns of ecosystem CO_2 exchange

Growing season distributions of daily NEE, GEP, and ER for both crops are shown in Figure 19. A similar seasonal phenology of CO_2 uptake and release were observed over both ecosystems, with maximum carbon uptake during the active growing season followed by a rapid decrease in the late growing season due to dominance of ER over GEP. High rates of carbon assimilation (GEP) and low rates of ER resulted in substantial rates of carbon uptake by the ecosystems in the spring (Fig. 19). The magnitude of carbon uptake rate (NEE) was slightly greater in sorghum (-10.3 g C m^{-2} d^{-1}) than in switchgrass (-8.5 g C m^{-2} d^{-1}) because of slightly larger magnitude of GEP (19.03 g C m^{-2} d^{-1}) and a smaller magnitude of ER (10.24 g C m^{-2} d^{-1}) in sorghum when compared to switchgrass. The peak GEP and ER of switchgrass reached 18.15 and 10.66 g C m^{-2} d^{-1}, respectively. In both ecosystems, peak NEE values occurred in June and this period corresponded to the active growing periods. Both GEP and ER showed similar seasonal cycles as NEE (Fig. 19b,c), with higher rates of fluxes during the active growing phase and smaller rates of fluxes in the late growing season. The switchgrass ecosystem was able to acquire CO_2 at relatively higher rates during the late growing season (Fig. 19b). Both GEP and ER rates were also slightly larger in switchgrass than in sorghum during the late growing season. This is most probably because of deep-rooted switchgrass vegetation could have better access to groundwater. Relatively little rainfall was recorded in the late growing season for this site. The site received 293 mm of total rainfall from June to October while the 30-year average rainfall for the site was 418 mm. The site received 86% below the 30-year average rainfall of 99 mm in October 2012. This led to an early yellowing of sorghum compared with switchgrass.

The maximal NEE daily value of -8.5 g C m^{-2} d^{-1} in switchgrass in our study was a similar magnitude of the peak NEE for native tallgrass prairie (-8.4 g C m^{-2} d^{-1}) in north-central Oklahoma (Suyker and Verma, 2001). We observed a slightly larger magnitude of daily peak NEE of -10.3 g C m^{-2} d^{-1} in sorghum, but it was a smaller magnitude of peak NEE of -17 g C m^{-2} d^{-1} in maize in eastern Nebraska (Suyker et al., 2005). Peak GEP values of 19.03 g C m^{-2} d^{-1} (sorghum) and 18.15 g C m^{-2} d^{-1} (switchgrass) in our study were smaller than those reported for irrigated maize (28-30 g C m^{-2} d^{-1}) and rainfed maize (22-27 g C m^{-2} d^{-1}) in eastern Nebraska (Suyker and Verma, 2012), but were comparable to values reported for soybean (18 g C m^{-2} d^{-1}) (Suyker et al.,

2005) and a tallgrass prairie (19 g C m^{-2} d^{-1}) (Turner et al., 2003). Similarly, peak ER values of about 10 g C m^{-2} d^{-1} in both switchgrass and sorghum in this study were also smaller than those reported by Suyker and Verma (2012) in irrigated maize (12-15 g C m^{-2} d^{-1}) and rainfed maize (9-13 g C m^{-2} d^{-1}). But they were comparable to values reported by Xu and Baldocchi (2004) for a California grassland (9-10 g C m^{-2} d^{-1}) and mentioned by Suyker et al. (2005) as unpublished data for a tallgrass prairie (9-9.5 g C m^{-2} d^{-1}).

Seasonal NEE, GEP, and ER

Weekly cumulative NEE plotted in Figure 20 shows steadily increasing (more negative – more carbon uptake by the ecosystem) cumulative NEE from the beginning of the growing season to the end of August. In both ecosystems, increasing cumulative NEE switched to decreasing NEE after August due to dominance of ER over GEP. The result shows that the switchgrass ecosystem was a larger carbon sink throughout the growing season. The seasonal carbon uptake was -490 ± 59 and -261 ± 48 g C m^{-2} at switchgrass and sorghum ecosystems, respectively.

The growing season cumulative values of GEP, ER, and NEE for both crops are shown in Table 12. Cumulative seasonal values of all three NEE, GEP, and ER fluxes from the switchgrass field were larger than those from the sorghum field. The growing season GEP total was 2017 ± 295 g C m^{-2} in switchgrass compared to 1164 ± 183 g C m^{-2} in sorghum (a ratio of 1.73:1). Similarly, the growing season ER total in switchgrass was 1527 ± 236 g C m^{-2} compared to 903 ± 134 g C m^{-2} in sorghum (a ratio of 1.69:1). Because peak daily values of GEP (18-19 g C m^{-2} d^{-1}) and ER (about 10 g C m^{-2} d^{-1}) were similar between ecosystems, the cumulative difference of about 1.7 times higher GEP and ER in switchgrass is likely related to the earlier canopy development in switchgrass. It is important to mention here that switchgrass greened up in March and sorghum was planted in May and both crops were killed by frost in the first week of November. It shows that the switchgrass had two months longer growing season compared to the sorghum.

Our study shows that the growing season ER/GEP ratio was about 0.76 in switchgrass and 0.78 in sorghum. March-August ER/GEP ratio was 0.70 in switchgrass and May-August ER/GEP ratio was 0.68 in sorghum. During the late growing season (September-October) the ER/GEP ratio increased at both ecosystems. For switchgrass it was 1.14, whereas for sorghum it was 1.42. The higher ER/GEP ratio after the crop senescence in the late growing season suggests that the carbon balance is linked to plant activity. The higher ER/GEP ratio in sorghum than switchgrass during the September-October period indicates that carbon uptake by sorghum was inhibited more in this period due to dry conditions. Growing season ER/GEP ratios of 0.76 and 0.78 in our study were higher than the previously reported ratios for other ecosystems, most probably due to higher respiration rates and the limitation of photosynthesis in the afternoon hours during warm growing periods in this region. Growing season ER/GEP of 0.56 for maize and 0.76 for soybean (Suyker and Verma, 2012), 0.6 for winter wheat and 0.4 for potato and sugarbeets (Aubinet et al., 2009) have been reported.

Variability in NEE

Diurnal NEE trends at switchgrass and sorghum ecosystems across the growing season are compared in Figure 21. Large seasonal and inter-species differences were observed for NEE rates. As expected, higher NEE rates were observed during the peak growth due to more canopy photosynthetic capacity. The NEE rates declined during the late growing season because of crop senescence. In switchgrass NEE rates reached a maximum in May, while the maximum NEE rates were observed in June in sorghum. The NEE rates in sorghum were larger during June and July than those in switchgrass, and they were smaller from August to October. The magnitudes of diurnal peak NEE (monthly average) reached up to -33.02 ± 1.96 (May) and -35.86 ± 2.32 µmol m^{-2} s^{-1} (June) in switchgrass and sorghum, respectively. These magnitudes of NEE matched with the results of previous studies in native tallgrass prairie for this region: -32 µmol m^{-2} s^{-1} in north-central Oklahoma (Suyker and Verma, 2001) and -30 µmol m^{-2} s^{-1} in northeastern Kansas (Kim and Verma, 1990).

Nighttime respiration rates in switchgrass were higher in May, but they were similar during June and July when compared to the nighttime respiration rates in sorghum. Similar to daytime NEE rates, slightly smaller nighttime respiration rates were observed in sorghum from August to October.

Average daily NEE at both ecosystems for the entire growing season is provided in Table 13. The switchgrass ecosystem was a net carbon sink from April through August with a peak daily uptake of -6.57 g C m^{-2} d^{-1} in May. The sorghum ecosystem was a net carbon sink from June through August with a peak daily uptake of -7.99 g C m^{-2} d^{-1} in

June. The result shows that the switchgrass was a net sink of carbon for five months (April-August) while the sorghum was a net sink of carbon only for three months (June-August). Both ecosystems were carbon source in September and October, with larger rates of carbon release from the sorghum.

Response of NEE to VPD

We demonstrated that large VPD of over 3 kPa limited photosynthesis in switchgrass and caused asymmetric diurnal NEE cycles (substantially higher rates of NEE in the morning hours as compared to the afternoon hours at similar light levels) in our previous publication (Wagle and Kakani, 2013). To examine the effect of VPD on NEE in sorghum, we plotted diurnal trends of VPD and NEE (Fig. 22) for two ranges of VPD [one with the maximum VPD of about 3 kPa (June 16-30) and the other with the maximum VPD of over 5 kPa (August 1-14)]. During June 16-30, the maximum NEE was -40.78 ± 1.88 μmol m^{-2} s^{-1} at 1:30 PM when VPD was 2.8 kPa. But the NEE reached a peak (-6.98 ± 1.19 μmol m^{-2} s^{-1}) at 11 PM during August 1-14 when VPD was 3.03 kPa and then decreased as VPD increased further. The result shows that the threshold VPD to affect photosynthesis in sorghum is also about 3 kPa as in switchgrass. As a result, both ecosystems had similar diurnal trends of NEE across the growing season except in June and July (most notably in July, Fig. 21). More symmetric diurnal NEE cycles were observed in sorghum during June and July. June and July were the active growing periods for sorghum as it was planted in May, but switchgrass had already lost some photosynthetic capacity after May. This is well supported by the higher NEE rates of sorghum in June and July, and the declining trends of NEE in switchgrass after May as shown in Figure 21. Our result illustrates that plant's response to VPD is not a constant property and the crop phenology alters the response of photosynthesis to VPD. Ludlow and Jarvis (1971) also reported that the response of photosynthesis to VPD varies for the same species when grown under different climatic conditions.

Conclusions

Net ecosystem CO_2 exchange (NEE) was measured using eddy covariance system from co-located switchgrass and sorghum fields in south central Oklahoma, USA during the growing season in 2012. The purpose of this study was to quantify and contrast NEE in these two ecosystems. Monthly ensemble averaged NEE at switchgrass and sorghum reached seasonal peak values of -33.02 ± 1.96 and -35.86 ± 2.32 μmol m^{-2} s^{-1}, respectively. Daily integrated NEE reached seasonal peaks of -8.5 and -10.3 g C m^{-2} d^{-1} in switchgrass and sorghum, respectively. Our result shows that both ecosystems were carbon sinks with the growing season carbon uptake of -490 ± 59 and -261 ± 48 g C m^{-2} by switchgrass and sorghum, respectively. Because peak values of gross ecosystem production (GEP, 18-19 g C m^{-2} d^{-1}) and ecosystem respiration (ER, about 10 g C m^{-2} d^{-1}) were similar at both ecosystems, the difference in carbon sink potential is likely related primarily to the length of the growing season. Switchgrass was a net sink of carbon during five months (April-August) while the sorghum was a net sink of carbon only during three months (June-August).

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Table 11. Monthly daily mean maximum and minimum temperatures, and monthly total rainfall in 2012 in comparison with the 30-year mean (1981 to 2010) for Chickasha, Oklahoma, USA.

	2012			30-year mean		
Month	Max T (^{o}C)	Min T (^{o}C)	Rain (mm)	Max T (^{o}C)	Min T (^{o}C)	Rain (mm)
Jan	13.56	-2.57	49.78	10.06	-3.44	33.5
Feb	13.00	0.25	16.26	14	-0.78	45.2
Mar	21.66	8.35	112.52	18.83	4.06	71.9
Apr	24.11	12.03	78.74	24.06	9.06	91.9
May	29.48	15.88	150.37	28.06	14.72	133.1
Jun	33.51	19.33	71.37	32.39	19.5	104.6
Jul	37.98	22.59	48.01	35.28	21.56	53.6
Aug	36.04	20.61	42.67	34.56	20.61	69.3
Sep	31.56	16.16	117.35	30.61	16.22	91.4
Oct	22.61	9.02	13.72	24.89	9.83	98.6
Nov	20.3	3.0	21.84	17.06	3.22	54.4
Dec	12.19	-2.19	21.84	11.5	-1.72	48.5

Table 12. Growing season sums of net ecosystem CO_2 exchange (NEE), gross ecosystem production (GEP), and ecosystem respiration (ER) (± uncertainty) from switchgrass and sorghum fields during their respective growing seasons in 2012.

	Switchgrass (DOY 61-305)	Sorghum (DOY 122-305)
GEP (g C m^{-2})	2017 ± 295	1164 ± 183
ER (g C m^{-2})	1527 ± 236	903 ± 134
NEE (g C m^{-2})	-490 ± 59	-261 ± 48

Table 13. Average daily net ecosystem exchange (NEE) of carbon (g C m^{-2} d^{-1}) from switchgrass and sorghum fields across a growing season in 2012. Negative values of NEE indicate uptake (i.e., sink) and positive values indicate loss (i.e., source).

	NEE (g C m^{-2} d^{-1})	
Months	Switchgrass	Sorghum
March	0.71	
April	- 4.87	
May	-6.57	0.94
June	-4.82	-7.99
July	-1.36	-3.25
August	-0.45	-0.41
September	0.71	0.81
October	0.44	1.21

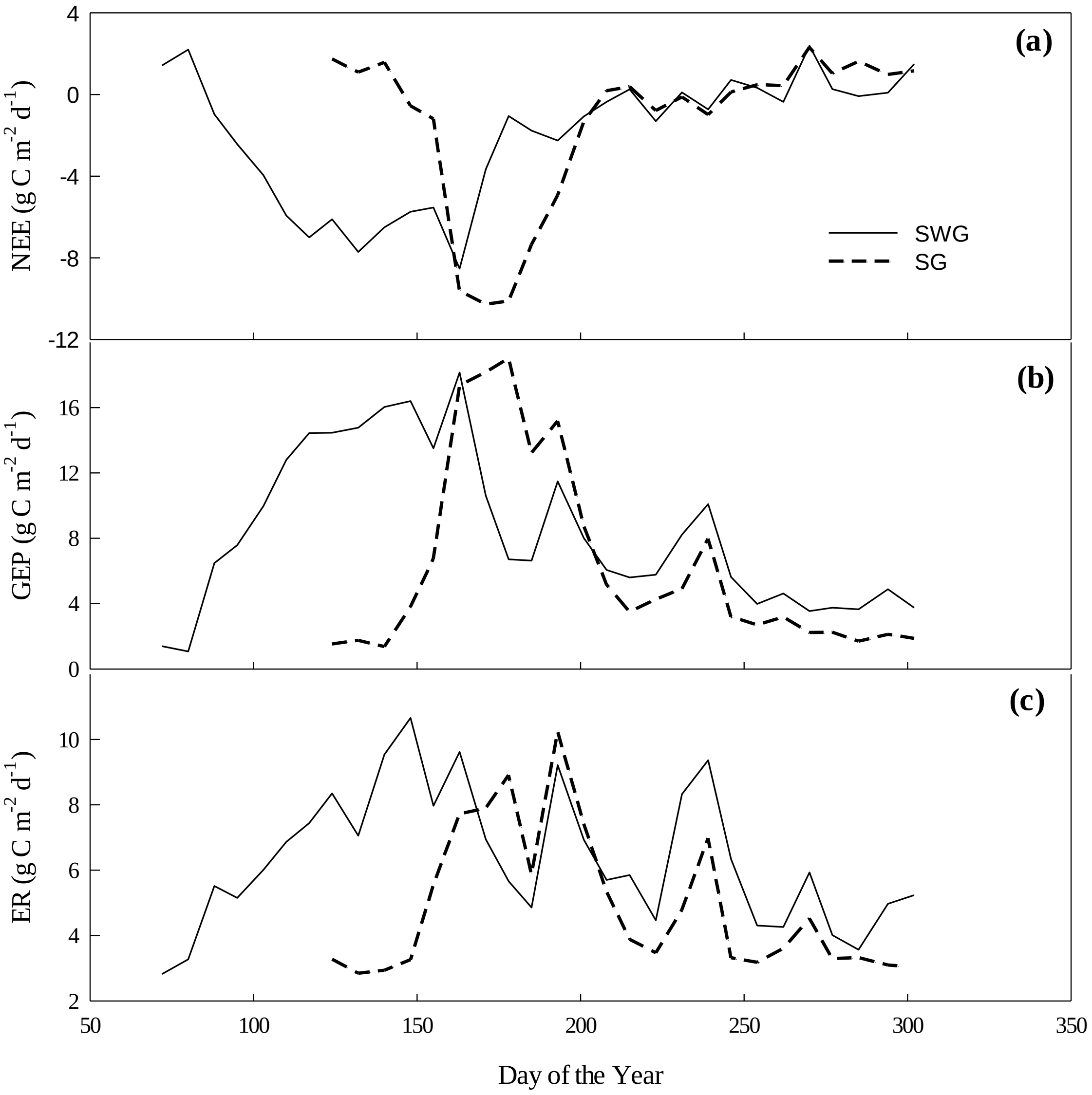

Fig. 19. Growing season patterns of net ecosystem CO_2 exchange (NEE), gross ecosystem production (GEP), and ecosystem respiration (ER) in switchgrass (SWG) and sorghum (SG) ecosystems. Data lines represent 7-day average values of CO_2 fluxes.

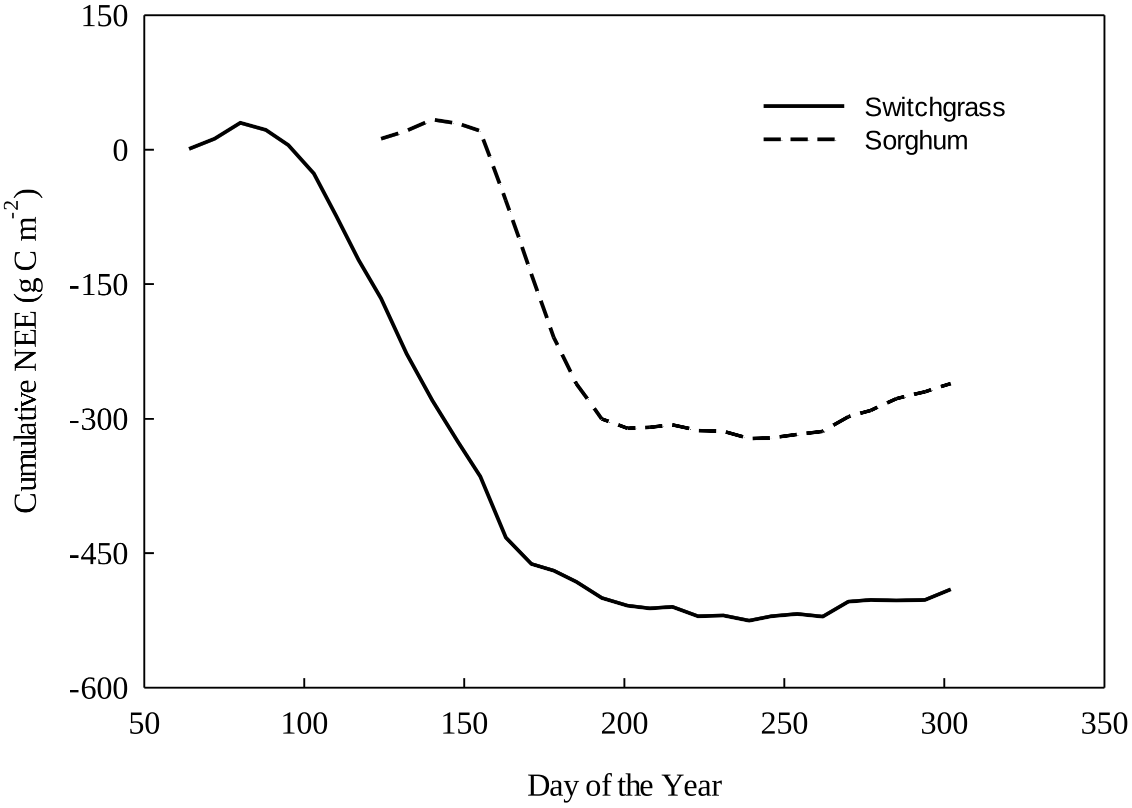

Fig. 20. Cumulative weekly net ecosystem CO_2 exchange (NEE) in switchgrass and sorghum. Negative value of NEE indicates a net carbon uptake by the ecosystem.

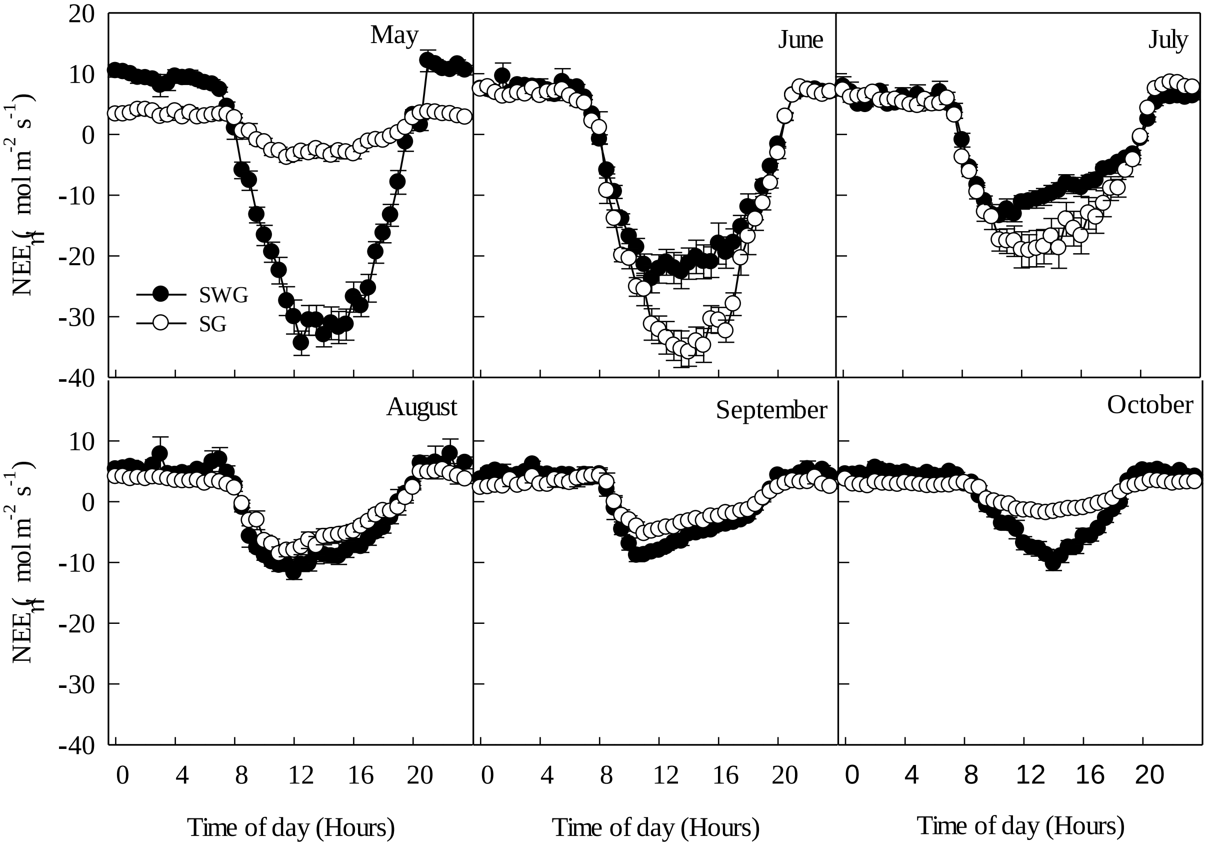

Fig. 21. Half-hourly binned diurnal courses of net ecosystem CO$_2$ exchange (NEE) in switchgrass (SWG) and sorghum (SG) across the growing season. Each data point is a 30-min time-stamp average value for the entire month. Bars represent standard errors of the means. Negative values of NEE indicate uptake (i.e., sink) and positive values indicate loss (i.e., source).

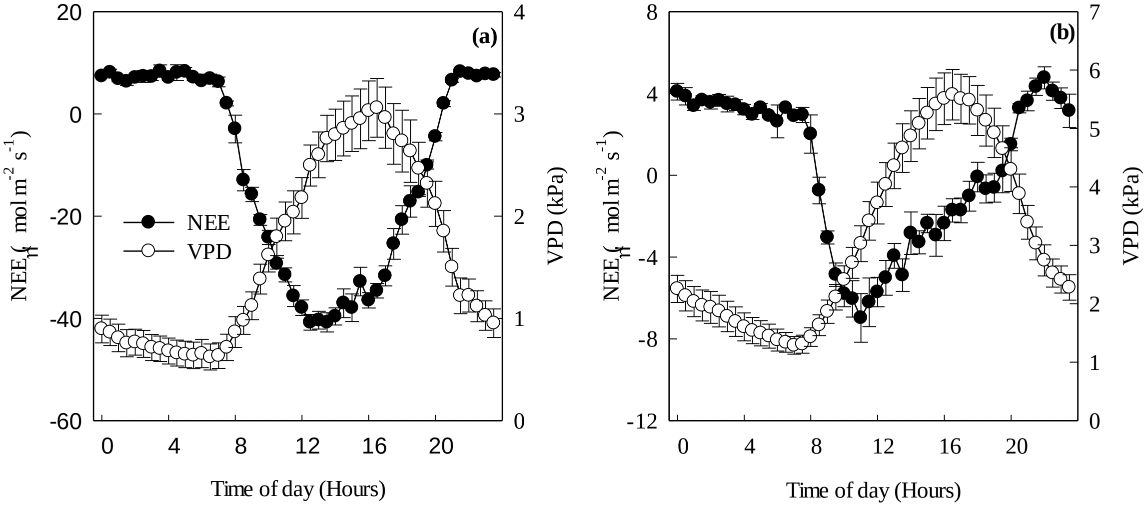

Fig. 22. Half-hourly binned diurnal courses of net ecosystem CO_2 exchange (NEE) and vapor pressure deficit (VPD) in sorghum during two selected periods: June 16-30, 2012 (a) and August 1-14, 2012 (b). Each data point is a 30-min time-stamp average value for entire two weeks. Bars represent standard errors of the means.

CHAPTER VI

COMPARISON OF CANOPY EVAPOTRANSPIRATION AND ECOSYSTEM WATER USE EFFICIENCY FOR SWITCHGRASS AND HIGH BIOMASS SORGHUM

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ABSTRACT. We measured water and energy flux densities over co-located switchgrass (*Panicum virgatum* L.) and high biomass sorghum (*Sorghum bicolor* L. Moench) using eddy covariance systems during the 2012 growing season. The major objective of this study was to compare differences in water use between these contrasting ecosystems at the growing season scale. During the growing season, the daily ET (weekly average) was 1.0-6.2 mm day^{-1} for switchgrass and 0.7-6.7 mm day^{-1} for sorghum. Total ET from both ecosystems was similar (487 mm from switchgrass and 465 mm from sorghum field) for the overlapping period of the growing season (May-October). Moreover, the magnitude of ET rate was similar at both ecosystems during the active growing periods. However,.

growing season total ET was higher in switchgrass (653 mm, March-October) than in sorghum (465 mm, May-October) due to two months longer growing season of switchgrass. This result indicates that the difference in water use between two species was mainly attributed to the length of crop growing season. Monthly gross ecosystem production (GEP) showed a strong positive linear relationship with ET (R^2 = 0.88 and 0.91 in switchgrass and sorghum, respectively), suggesting a strong linkage between carbon gain and water loss over the season. The ratio of cumulative GEP to the respective ET yielded monthly ecosystem water use efficiency (EWUE) from 6.3 (March) to 16.1 (June) g CO_2 mm^{-1} ET in switchgrass and from 4.7 (May) to 13.6 (June) g CO_2 mm^{-1} ET in sorghum, with seasonal averages of 12.6 and 9.9 g CO_2 mm^{-1} ET for switchgrass and sorghum, respectively. The results illustrated the great production potential of both feedstocks in this region. The higher EWUE of switchgrass suggests that the carbon gain by the switchgrass ecosystem was enough to offset its higher water use for a longer growing season.

Key words: Bioenergy, Ecosystem water use efficiency, Eddy covariance, Evapotranspiration, High biomass sorghum, Switchgrass.

Introduction

In the United States of America, 136 billion liters of biofuel production, including 79 billion liters from cellulosic biofuels, is mandated by 2022 (http://www.gpo.gov/fdsys/pkg/BILLS-110hr6enr/pdf/BILLS-110hr6enr.pdf, verified

April 30, 2013). This 2022 biofuel goal requires developing alternative feedstock sources to traditional feedstock like maize (*Zea mays* L.) for food security and to meet increasing biofuel feedstock demand. Cellulosic crops switchgrass (*Panicum virgatum* L.) and high biomass sorghum (*Sorghum bicolor* L. Moench) are considered as viable alternative sources. Ethanol production capacity has increased exponentially, from 0.66 billion liters in 1980 to more than 49 billion litters in recent years (RFA 2012, http://www.ethanolrfa.org/pages/statistics, verified May 1, 2013). Thus, the acreage of cellulosic feedstocks is increasing in the recent years (Biomass Crop Assistance Program, BCAP, http://www.fsa.usda.gov/FSA/webapp?area=home&subject=ener&topic=bcap, verified November 21, 2013). This increased deployment of dedicated biomass crops has sparked numerous environmental concerns, including the impact on the regional hydrologic cycle. Fewer environmental impacts are predicted from advanced cellulosic fuel production compared with grain-based ethanol production (Heaton et al., 2004). It is more likely that lignocellulosic crops provide positive effects on soil properties, biodiversity, energy balance, greenhouse gas mitigation, and carbon footprint (Rowe et al., 2009). However, environmental impacts and ecosystem services of biofuel production should not be neglected (Rowe et al., 2009). Therefore, we have to consider several factors when selecting environmentally and economically viable bioenergy feedstocks (Hill et al., 2006).

Understanding the efficiency of bioenergy crops in using available water to produce biomass and store carbon in soil is an important metric of bioenergy crop performance (Zeri et al., 2013). Quantifying and understanding of evapotranspiration (ET) and ecosystem water use efficiency (EWUE, net carbon uptake by the ecosystem per amount of water use) of bioenergy crops is very critical to assess the impacts of increased deployment of dedicated biomass crops on local and regional hydrology. In most cases, ET is the second largest term after precipitation in the hydrological balance (Ford et al., 2007), indicating a major component of water balance in terrestrial ecosystems. The associated flux of latent heat, a major component of energy balance, has a major role on the planetary boundary layer dynamics (Baldocchi et al., 2000). Moreover, several hydrological and biological processes in an ecosystem are tightly linked via ET (McNulty et al., 1994;Wilson and Baldocchi, 2000). The study of ET is, therefore, fundamental for better understanding of terrestrial ecosystems. The EWUE, a key component of the hydrologic cycle which relates biomass production or carbon gain to water use, is intricately linked to biogeochemical cycles (Sellers et al., 1997). The EWUE can be considered as a determinant of the sustainability of newly introduced crop species (Wallace, 2000). Thus, the study of ET and EWUE in a variety of terrestrial ecosystems is an essential for the assessment of local, regional, and global water balances. However, the study and comparison of ET and EWUE between commercial-scale production of two contrasting cellulosic feedstocks, switchgrass and high biomass sorghum, at adjacent plots is lacking. We measured water and energy flux densities over co-located switchgrass and high biomass sorghum ecosystems in the southern Great Plains of the United States (Chickasha, OK) using two independent eddy covariance systems. Direct and continuous field-scale measurements of net ecosystem exchange (NEE) of CO_2 and H_2O by the eddy covariance system offer a great opportunity to compute and compare ET and EWUE between ecosystems. Such an estimation of ET demand and EWUE provides bases for the selection of best suited feedstocks for bioenergy production for the region.

The major objective of this study was to compare differences in water use between two candidate cellulosic bioenergy feedstocks switchgrass and high biomass sorghum at the growing season scale. We hypothesized that growing season total ET would be higher for switchgrass relative to sorghum due to a longer growing season. We also assumed that EWUE calculation based on total carbon uptake (GEP, gross ecosystem production) by the ecosystem yields higher EWUE in switchgrass because of higher total carbon uptake potential and higher below ground biomass when compared with sorghum. This study provides a unique opportunity to investigate the potential environmental impacts and services of large-scale productions of annual and perennial C_4 cellulosic feedstocks on water resources.

Materials and Methods

Description of study site

Switchgrass and high biomass sorghum plots of eight hectares each were established at Oklahoma State University, South Central Research Station, Chickasha, Oklahoma. As two ecosystems were located at adjacent plots, we can assume that they were exposed to the same weather and atmospheric water demand. Switchgrass (*cv*. Alamo) was sown at 0.38 m row spacing under no till conditions in spring 2010. . Sorghum (*cv*. ES 5200) was planted at 0.76 m row spacing on May 15, 2012. Ammonium nitrate was broadcasted at

75 kg N ha^{-1} in April for switchgrass and on May 18th for sorghum. Site description has been provided in a detail previously (Wagle and Kakani, 2013).

Flux measurements

Carbon dioxide, water, and energy flux densities were continuously measured over switchgrass and sorghum ecosystems during the 2012 growing season using eddy covariance systems. The eddy covariance systems were composed of an infrared gas analyzer (LI-7500, LI-COR Inc., Lincoln, NE, USA) and a three-dimensional sonic anemometer (CSAT3, Campbell Scientific Inc., Logan, UT, USA). Flux measurements were collected at 10 Hz frequency and computed for a 30-min averaging period. In addition to eddy covariance measurements, photosynthetic photon flux density (PPFD), net radiation (R_n), near top surface measurements of soil temperature, moisture, and soil heat (G) fluxes were collected at 10 Hz frequency and finally averaged for 30-min averaging periods using a datalogger (CR3000, Campbell Scientific Inc., Logan, UT, USA). Measurement details and data processing techniques have been described previously (Wagle and Kakani, 2013;Wagle and Kakani, 2012).

Biometric measurements

Because of mild winter in 2012, switchgrass greened up earlier in March. Biometric measurements were initiated on March 28, 2012 in switchgrass. Since sorghum was planted in May, the first biometric measurement was taken on June 12, 2012. Biometric measurements were taken mostly biweekly throughout the growing season. Three biomass samples were taken from 1 m^2 area at randomly located positions and oven dried in an oven for a week at around 70 °C. Leaf area index (LAI) was measured using a plant canopy analyzer (LAI-2000, LI-COR Inc., Lincoln, NE, USA). Canopy heights were also recorded periodically.

Screening and gap filling of fluxes

Statistical outliers beyond ± 3.5 STD range from a 14-day running mean window were removed. Sensible heat (H) and latent heat (LE) fluxes were filtered to keep in the range of -200 to 500 W m^{-2} and -200 to 800 W m^{-2}, respectively (Sun et al., 2010). In addition, we excluded unreliable flux data during low turbulent periods (friction velocity, $u^* <$ 0.20 m s^{-1}). Half-hourly gaps in H_2O fluxes were filled with an average value immediately before and after the gap (Wever et al., 2002). Shorter gaps (< 2 hours) were filled with linearly interpolated values (Flanagan et al., 2002). Larger gaps (> 2 hours) in H_2O fluxes were gap filled using a linear relationship between PPFD and H_2O fluxes as H_2O fluxes showed very strong positive relationship with PPFD ($R^2 > 0.80$, most of the cases) as shown in Figure 23. The PPFD-H_2O relationships were developed for each week to account for seasonal variability. Partitioning and gap filling techniques for CO_2 fluxes have been described in a detail previously (Wagle and Kakani, 2013).

ET and EWUE calculations

Total ET for 30-min periods (mm 30 min^{-1}) was calculated from measured H_2O flux (mmol m^{-2} s^{-1}) using the following equation:

$$ET = (H_2O \text{ flux} \times 18.01528 \times 1800)/10^6 \qquad (1)$$

Seasonal and monthly totals of ET were calculated by summing the gap-filled half-hourly values. Cumulative ET also included evaporation of intercepted water by the crop canopy. Although several methods of EWUE calculations are available in the literature, we estimated EWUE from the ratio of cumulative GEP to cumulative daytime ET over the growing season. Only ET for the daytime, when there was carbon uptake, was used to relate EWUE to carbon sequestration as suggested in a previous study (Tubiello et al., 1999).

Results and Discussion

Meteorology and crop growth

As compared with the 30-year mean, the site experienced relatively warmer and wetter spring, and slightly warmer and drier summer in 2012. Overall, the site received 25% less rainfall in 2012 compared with the 30-year average (896 mm). The switchgrass growing season (March-October) total rainfall was 11% less than the 30-year average for the period (714 mm) and the sorghum growing season (May-October) total rainfall was 20% less than the 30-year average for the period (551 mm). Late growing season was relatively drier in 2012. Total rainfall recorded from August to October, 2012 was 174 mm while the 30-year average rainfall for that period was 259 mm. For both crops, LAI reached a maximum during mid-July. In switchgrass, LAI reached a maximum of 5.9 m^2 m^{-2} while the maximum LAI was 5.7 m^2 m^{-2} in sorghum. The maximum recorded above ground biomass during the growing season was about 17 t ha^{-1} in switchgrass and 30 t ha^{-1} in sorghum.

Energy balance closure

Energy balance closure (EBC) is considered as an important test of data quality of eddy covariance measurements (Foken et al., 2006). The EBC for half-hourly measurements was 0.83 for the switchgrass and 0.82 for sorghum in the 2012 growing season. The result shows that the measured turbulent fluxes accounted for over 80% of the available energy, as calculated from a linear regression of (H+LE) vs. (R_n-G). These results fall within the typical range of eddy covariance experiments (Foken et al., 2006).

Energy fluxes

Seasonal variations in the diurnal courses of H and LE fluxes for the selected months are shown in Figure 24. Diurnal patterns of energy fluxes were similar for both species. Energy fluxes were high during daytime, starting at around 8:00 AM and reached a maximum at around 2:00 PM. Peak diurnal means of H and LE fluxes for both ecosystem across the growing season are provided in Table 14. The table shows that in the beginning of the crop growing season H started to decrease and LE began to increase until peak growing periods. The LE started to dominate over H in switchgrass from the first month of greening up (March), but H was the dominant turbulent flux in sorghum in May (the month of planting). The smallest H and the largest LE fluxes were observed during May and June in switchgrass and sorghum, respectively. The peak value of LE in switchgrass reached 390 (± 29) W m^{-2} in May while the peak LE in sorghum was 378 (± 23) W m^{-2} in June. Similarly, the smallest value of H in switchgrass was 111 (± 17) W m^{-2} in May while in sorghum it dropped down to 71 (± 9) W m^{-2} in June. The result shows that the smallest H and the largest LE fluxes coincided with the most active growing periods. After the most active growing periods, H began to increase and LE began to decrease in both ecosystems. As a result, H started to dominate over LE after June in switchgrass and after July in sorghum. The results demonstrate that a switch in energy partitioning is strongly associated with crop phenology (from H to LE after leaf emergence and from LE to H after crop senescence).

Response of H_2O flux to VPD

The H_2O flux data, averaged over seven different bins of VPD, was plotted against VPD (Fig. 25). The H_2O flux increased rapidly with increasing VPD up to a threshold value. The maximum rates of H_2O fluxes were observed in the VPD range of 2.5-3.5 kPa and declined thereafter. This result confirms the findings of previous studies (Anthoni et al., 1999; Brümmer et al., 2012), that stomata began to close to restrict transpiration water loss when VPD exceeded a threshold. Generally, the driving force for transpiration increases as VPD increases causing increase in transpiration rates. This leads to reduction in leaf water potential causing stomata to close and thereby reducing ET at higher VPD (Monteith, 1995). This concept of the response of H_2O flux to VPD is very important to understand the patterns of EWUE. Tallec et al. (2013) observed a hyperbolic relationship between VPD and EWUE. The VPD value increases with increasing temperature. Thus, EWUE increases with increasing VPD at smaller VPD because of increasing air temperature that enhances RuBISCO activity and in turn higher CO_2 assimilation (Sage and Kubien, 2007). Moreover, water loss through transpiration is limited at low temperatures (low VPD). Although decreased canopy conductance at high VPD reduces both carbon assimilation (GEP) and water loss (ET), more rapid reduction in GEP than ET (Tallec et al., 2013;Wagle and Kakani, 2012) leads to a decline in EWUE with increasing VPD at higher VPDs. Plants respond to an increasing VPD by partially closing stomata and potentially limiting carbon assimilation (Turner et al., 1985). A higher VPD can also inhibit photosynthesis, i.e. inhibition of CO_2-saturated photosynthesis, via non-stomatal effect (Morison and Gifford, 1983). Because of these reasons, the higher EWUE values are observed in the morning hours than in the afternoon (Wagle and Kakani, 2012).

Patterns of ET and rainfall

Seven-day averages of daily ET along with the patterns of rainfall across the growing season are presented in Figure 26. Seasonal patterns of ET exhibited similar trends at both ecosystems. As expected, ET rates were larger during wet periods and smaller during dry periods. The switchgrass growth initiated earlier due to milder winter and began to transpire earlier. Once sorghum started to grow, ET rates rapidly approached and exceeded those of the switchgrass field because of rapid gain of biomass and larger crop size. During the growing season, the weekly average of daily ET was 1.0-6.2 mm day^{-1} for switchgrass and 0.7-6.7 mm day^{-1} for sorghum. These magnitudes of ET were similar to ET from other major crops in this region. During the growing season, the daily ET was 2.5-7 mm for wheat (*Triticum aestivum* L.) and 3.5-5 mm for native tall grass prairie in north-central Oklahoma (Burba and Verma, 2005).

Higher rates of ET were associated with the peak growth of the crops and smaller values of ET were observed in the early and late growing seasons at both ecosystems. The 7-day running-mean of daily ET reached a maximum of 6.7 mm day^{-1} in the 4th week of June in sorghum, while in switchgrass it reached a maximum of 6.2 mm day^{-1} during the 3rd week of May. The patterns of ET in switchgrass for the 2012 growing season reveal larger values than those in 2011 reported previously for this site (Wagle and Kakani, 2012) due to more optimal growing conditions and increased maturity of the stand in 2012. These results show that patterns of precipitation and canopy development greatly affect ET patterns. However, the sensitivity of ET patterns was different between two ecosystems. The ET rates decreased more sharply in sorghum during the late growing season because of an earlier senescence of sorghum. The relatively drier late growing season in 2012 caused an earlier senescence of sorghum.

As determined from greening up to senescence for switchgrass and from planting to senescence for sorghum, the total growing season was longer for switchgrass by two months. Seasonal (March-October) cumulative ET (653 mm) in switchgrass was similar to cumulative rainfall (635 mm). Similarly, growing season (May-October) total ET (465 mm) in sorghum was similar to cumulative rainfall (443 mm) for the period. It shows a close correspondence between cumulative ET and rainfall for both ecosystems. Total ET from both ecosystems was similar (487 mm from switchgrass and 465 mm from sorghum field) for the overlapping period of the growing season (May-October). However, growing season total ET was higher in switchgrass (653 mm, March-October) than in sorghum (465 mm, May-October) due to the longer growing season of switchgrass. This result shows that switchgrass had 37% higher ET compared with sorghum over their respective growing seasons. While both species showed similar water use patterns during the active growing periods, the large difference in water use between two species was attributed to the length of crop growing season. It should be noted that some evaporation occurs during the time when sorghum field is fallow. The different growing season lengths make it more difficult to compare between ecosystems in this study.

Seasonal variability in ET

Typical diurnal trends of ET across the growing season at both ecosystems are provided in Figure 27. Great variation was observed for ET rates between species and among months of the growing season. Daytime ET was higher, starting at around 8 AM and reached a peak at around 2-3 PM. Unlike CO_2 fluxes the diurnal courses of ET were relatively symmetrical. We had reported asymmetrical diurnal NEE cycles, most notably during June to September, previously (Wagle and Kakani, 2013). This result suggests that CO_2 fluxes are more sensitive to environmental factors than H_2O fluxes.

The ET rates showed a clear pattern of seasonality. In both ecosystems, ET rates started to increase with increasing crop growth and the highest ET rates were observed during the peak growth period. The ET rates declined during the late growing season due to crop senescence and lower solar radiation in late fall. In switchgrass, ET rates were the highest in May, while in sorghum the rates were the highest in June. Peak diurnal mean (monthly) of ET rates across the growing season are provided in Table 15. In May, ET rates were larger in switchgrass than in sorghum, but sorghum had higher rates of ET in June and July. Again from August, slightly higher ET rates were observed in switchgrass. In switchgrass, the magnitude of peak diurnal ET rates ranged from 0.08 (September) to 0.28 mm 30-min^{-1} (May) whereas it ranged between 0.05 (October) and 0.28 mm 30-min^{-1} (June) in sorghum. The result showed that ET magnitudes were similar at both ecosystems during the active growing period. This result was further supported by the data presented in Figure 28. The figure shows that monthly total ET was 141 mm in May for switchgrass and in June for sorghum. The seasonal pattern of monthly ET was similar in both ecosystems with increasing ET in the early growing season, reaching their maximum values during the peak growth periods, and declining thereafter (Fig. 28). Peak growing periods were May and June for switchgrass and sorghum, respectively. During the growing season, the lowest monthly total ET (43 mm month^{-1} in switchgrass and 34 mm month^{-1} in sorghum) was observed in October at both ecosystems due to the crop senescence and less solar radiation.

Comparison of EWUE

We found very strong linear relationships between monthly GEP (g CO_2 m^{-2}) and ET (mm) at both ecosystems on the seasonal time scale (switchgrass: GEP = 14.1 x ET – 221.5, R^2 = 0.88, P = 0.0005 and sorghum: GEP = 13.2 x ET – 305.6, R^2 = 0.91, P = 0.002). Brümmer et al. (2012) also observed highly significant ($P < 0.001$) linear relationships between monthly GEP and ET. The result indicates a strong linkage between carbon gain and water loss over the season. The physiological control of gas exchange results in a strong coupling between carbon and water fluxes at the leaf and ecosystem levels (Valentini et al., 1991). The slope of the linear relationship between monthly GEP and ET represents EWUE, showing that EWUE of switchgrass and sorghum were 14.1 and 13.2 g CO_2 mm^{-1} ET, respectively. Estimation of EWUE from the ratio of monthly cumulative GEP to monthly daytime ET showed a smaller magnitude of EWUE in the early and late growing season and the highest EWUE during the peak growing season (June) at both ecosystems (Fig. 29). During the peak growing season, full canopy closure reduces the amount of radiation reaching the ground surface and ultimately reduces soil evaporation. On the other hand, radiation use efficiency is higher and thus increases photosynthesis. In switchgrass, EWUE was 6.3 g CO_2 mm^{-1} ET in March (the first month of green up) due to a smaller GEP and it reached to a maximum of 16.1 g CO_2 mm^{-1} ET in June, with seasonal (March-October) average EWUE of 12.6 g CO_2 mm^{-1} ET. The EWUE for switchgrass in our study was similar to the EWUE of 12-15 g CO_2 mm^{-1} ET reported by Skinner and Adler (Skinner and Adler, 2010) in a switchgrass field in southwestern Pennsylvania and of 12 g CO_2 mm^{-1} ET observed by

Eggemeyer et al. (2006) in the sandhill grassland of Nebraska. In a dry and warm growing season in 2011, monthly EWUE in switchgrass for the same site ranged between 10.5 and 14.1 g CO_2 mm^{-1} ET, with a seasonal average of 12 g CO_2 mm^{-1} ET (Wagle and Kakani, 2012). The result suggests a smaller year-to-year variability in EWUE. Similar to this study, Reichstein et al. (Reichstein et al., 2007) also observed very small interannual variability in EWUE of European forests. This is expected because of strong positive linear correlations between monthly GEP and ET, most likely due to the plant's nature of regulating exchange of CO_2 and H_2O fluxes (Monteith and Greenwood, 1986). Brümmer et al. (2012) also reported that a strong relationship between monthly values of GEP and ET resulted in EWUE being relatively constant at several sites. These results confirm the findings of the previous studies (Law et al., 2002;Jassal et al., 2009), that ET and GEP are affected in a similar manner by stomatal limitation. However, slightly different responses of the CO_2 and H_2O fluxes to environmental variables cause a smaller interannual variability. We had observed a smaller EWUE in drought because of more rapid reduction in carbon assimilation than water loss (Wagle and Kakani, 2012).

In sorghum, EWUE was 4.7 g CO_2 mm^{-1} ET in the month of planting (May) and it reached to 13.6 g CO_2 mm^{-1} ET in June, with a seasonal average EWUE of 9.9 g CO_2 mm^{-1} ET. The ratio of seasonal sums of daily daytime GEP to daily daytime ET provided EWUE of 12.9 and 10.8 g CO_2 mm^{-1} ET for switchgrass and sorghum, respectively. These results show that switchgrass are more water efficient than sorghum.

In agricultural studies, harvested biomass (crop productivity) is generally used to compute water use efficiency (WUE). The larger harvestable above ground biomass and smaller seasonal ET of sorghum in this study yields higher WUE for sorghum than switchgrass if WUE is calculated based on above ground biomass and the amount of water used by the crops. The result indicates that the higher biomass productivity of sorghum comes at the expense of less carbon left in the field after removal of harvestable biomass when compared with switchgrass. A previous study also reported that row crops had higher WUE than perennials when this approach of WUE estimation was used (Zeri et al., 2013). However, calculation of WUE based on harvestable above ground biomass does not account for the total carbon uptake by the ecosystem. This agronomic metric neglects the several pools of carbon uptakes (soils, below ground biomass, litters, etc.). It accounts for only one carbon pool – harvestable above ground biomass (VanLoocke et al., 2012). A significant amount of resources is partitioned to below ground in perennial grasses (Anderson-Teixeira et al., 2009; Jackson et al., 1996). Studies of soil carbon storage shows that switchgrass sequesters significant carbon in soils (McLaughlin and Adams Kszos, 2005). Carbon allocated below ground offers several benefits such as contributing to soil fertility, carbon sequestration, and so on (Anderson-Teixeira et al., 2009). This important portion of carbon pool is neglected when calculating WUE from harvestable above ground biomass. The EWUE should represent all trade-offs associated with carbon uptake and water use by the ecosystems. This study showed that the higher water use of switchgrass was offset by higher total seasonal carbon uptake by the ecosystem. Thus, the result suggests that the higher EWUE of switchgrass should be associated with other ecosystem services, for example adding more carbon to the soil, beyond harvestable above ground biomass. Because of these reasons, EWUE calculation based on GEP and ET seems more suitable and applicable estimate of EWUE especially for feedstock production. This approach allows us to compare the water use associated with the total carbon gain by the ecosystem. Our results confirm the finding of VanLoocke et al. (2012) that the trade-off between carbon uptake and water loss for cellulosic feedstocks is variable depending on whether harvestable biomass or other ecosystem services are considered.

Conclusions:

The goal of this study was to compare ET patterns and EWUE of two candidate cellulosic feedstocks, switchgrass and high biomass sorghum, for the southern Great Plains of the United States using eddy covariance system. The results presented in this study illustrated that both species showed similar water use patterns during the active growing periods and the difference in water use between two species was mainly attributed to the length of crop growing season. While switchgrass had higher ET due to its longer growing season, the carbon gain by the switchgrass ecosystem was enough to offset this higher water use resulting in higher EWUE than that of high biomass sorghum. The results illustrated the great production potential of both feedstocks for this region.

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Table 14. Peak diurnal means (monthly) of sensible (H) and latent heat (LE) fluxes (± standard errors) across the growing season.

	Switchgrass		Sorghum	
Month	H (W m^{-2})	LE (W m^{-2})	H (W m^{-2})	LE (W m^{-2})
Mar	157 (± 11)	206 (± 22)		
Apr	126 (± 10)	285 (± 26)		
May	111 (± 17)	390 (± 29)	249 (± 15)	162 (± 20)
Jun	224 (± 23)	224 (± 22)	71 (± 9)	378 (± 23)
Jul	281 (± 17)	186 (± 18)	185 (± 18)	271 (± 28)
Aug	246 (± 26)	152 (± 17)	217 (± 26)	136 (± 14)
Sep	273 (± 17)	111 (± 10)	258 (± 22)	98 (± 9)
Oct	205 (± 16)	121 (± 20)	225 (± 18)	85 (± 13)

Table 15. Peak diurnal mean (monthly) of evapotranspiration (ET) rate (± standard errors) across the growing season.

	ET (mm 30-min^{-1})	
Month	Switchgrass	Sorghum
Mar	0.15 (±0.02)	
Apr	0.22 (±0.02)	
May	0.28 (±0.02)	0.13 (±0.02)
Jun	0.17 (±0.02)	0.28 (±0.02)
Jul	0.14 (±0.01)	0.20 (±0.02)
Aug	0.11 (±0.01)	0.10 (±0.01)
Sep	0.08 (±0.01)	0.07 (±0.01)
Oct	0.09 (±0.02)	0.05 (±0.01)

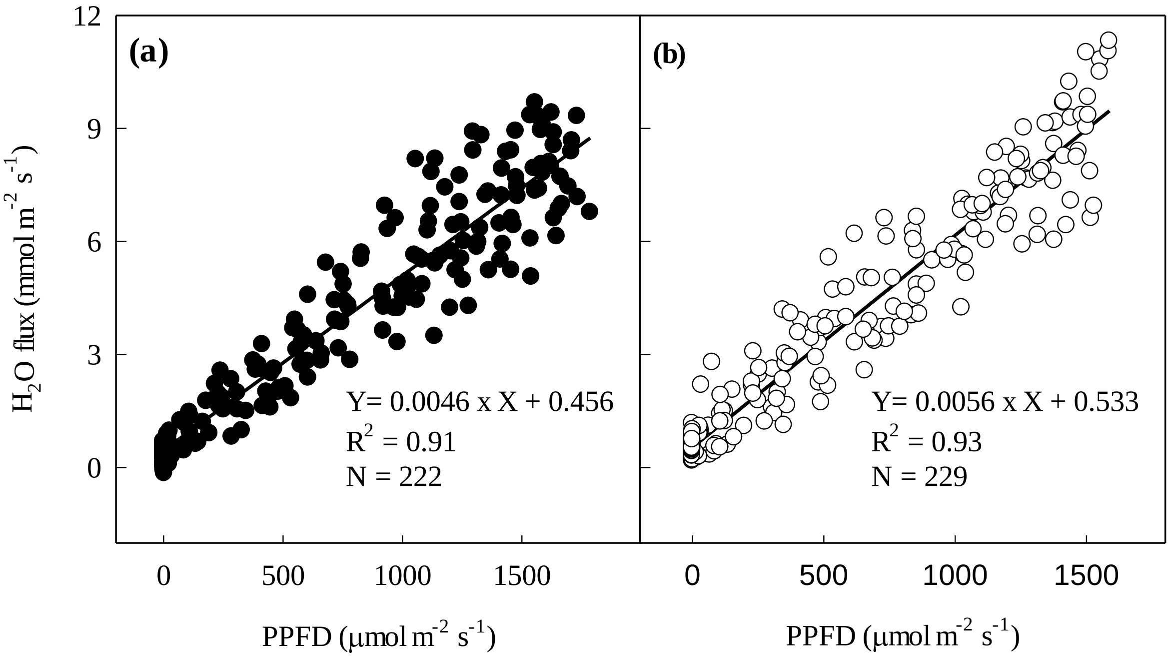

Fig. 23. Linear relationships between photosynthetic photon flux density (PPFD) and H_2O flux for selected time periods: June 8-15, 2012 in switchgrass (a) and June 16-23, 2012 in sorghum (b). The solid lines represent the best fit lines for linear regressions. Total half hourly data points are represented by N.

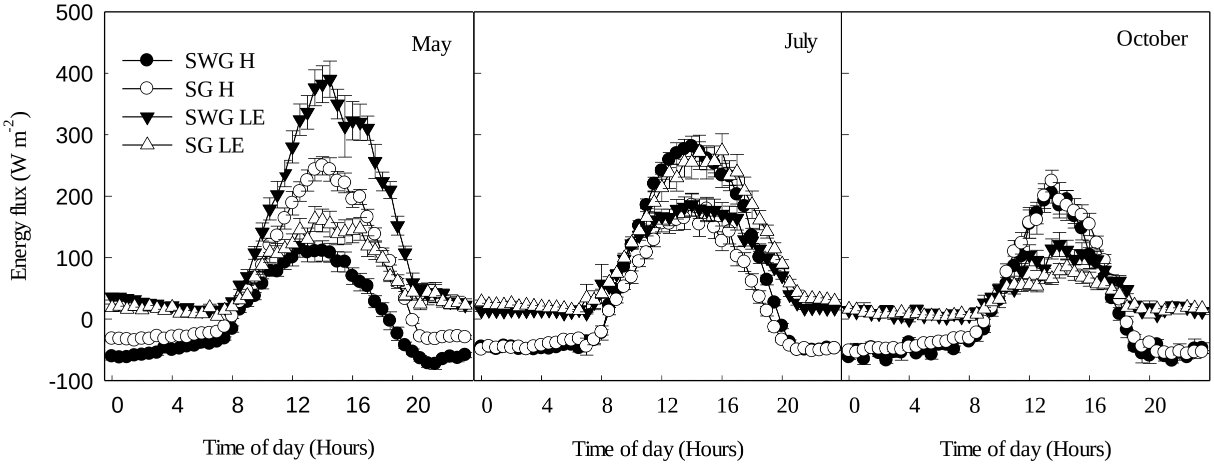

Fig. 24. Seasonal variation in the mean diurnal courses of sensible (H) and latent heat (LE) fluxes. Data points represent the diurnal mean of available data points for the entire months. Bars represent standard errors of the means.

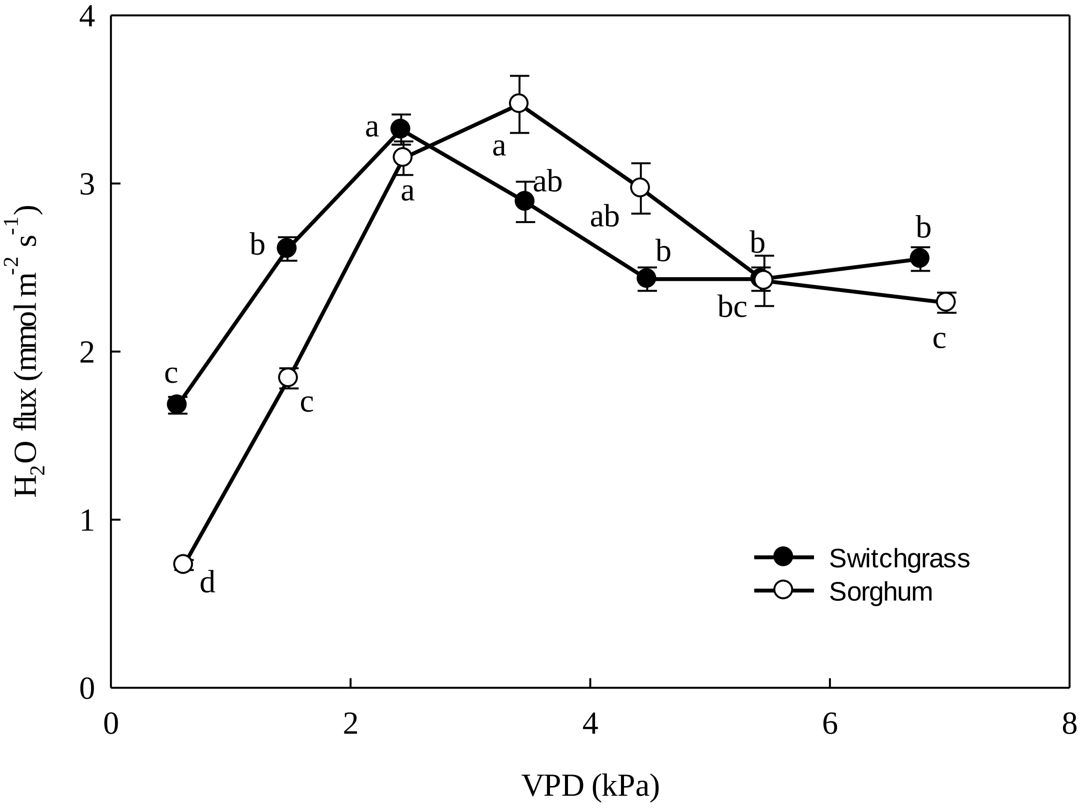

Fig. 25. Effect of vapor pressure deficit (VPD) on H_2O flux in switchgrass and sorghum. Bars represent standard errors of the means and letters represent Tukey’s HSD groupings at $\alpha = 0.05$ (same letter indicates means are not significantly different). Minimum significant differences were 0.56 and 0.64 for switchgrass and sorghum, respectively.

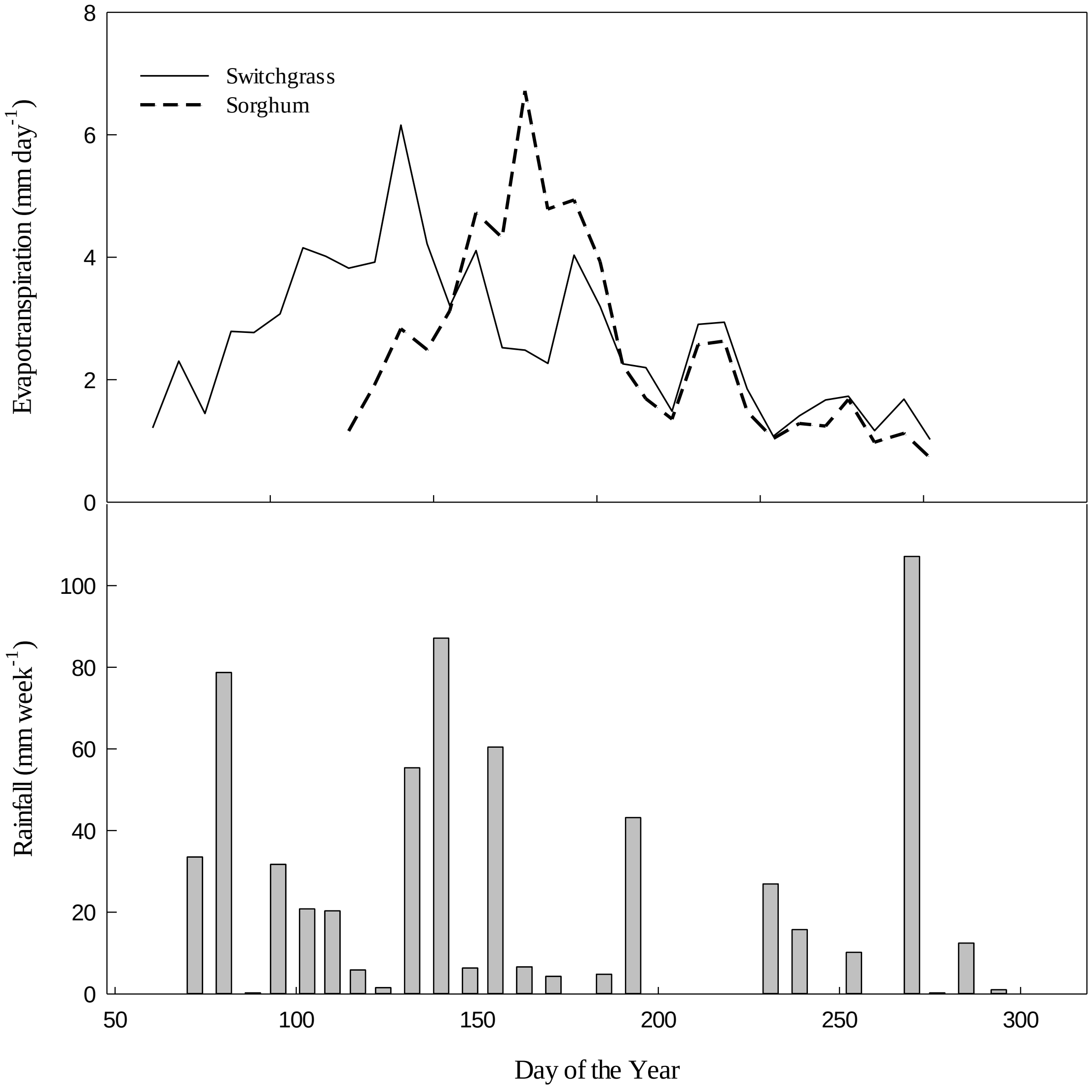

Fig. 26. Seasonal patterns of evapotranspiration and rainfall. The data lines represent weekly averages of daily evapotranspiration and vertical bars represent total weekly rainfall.

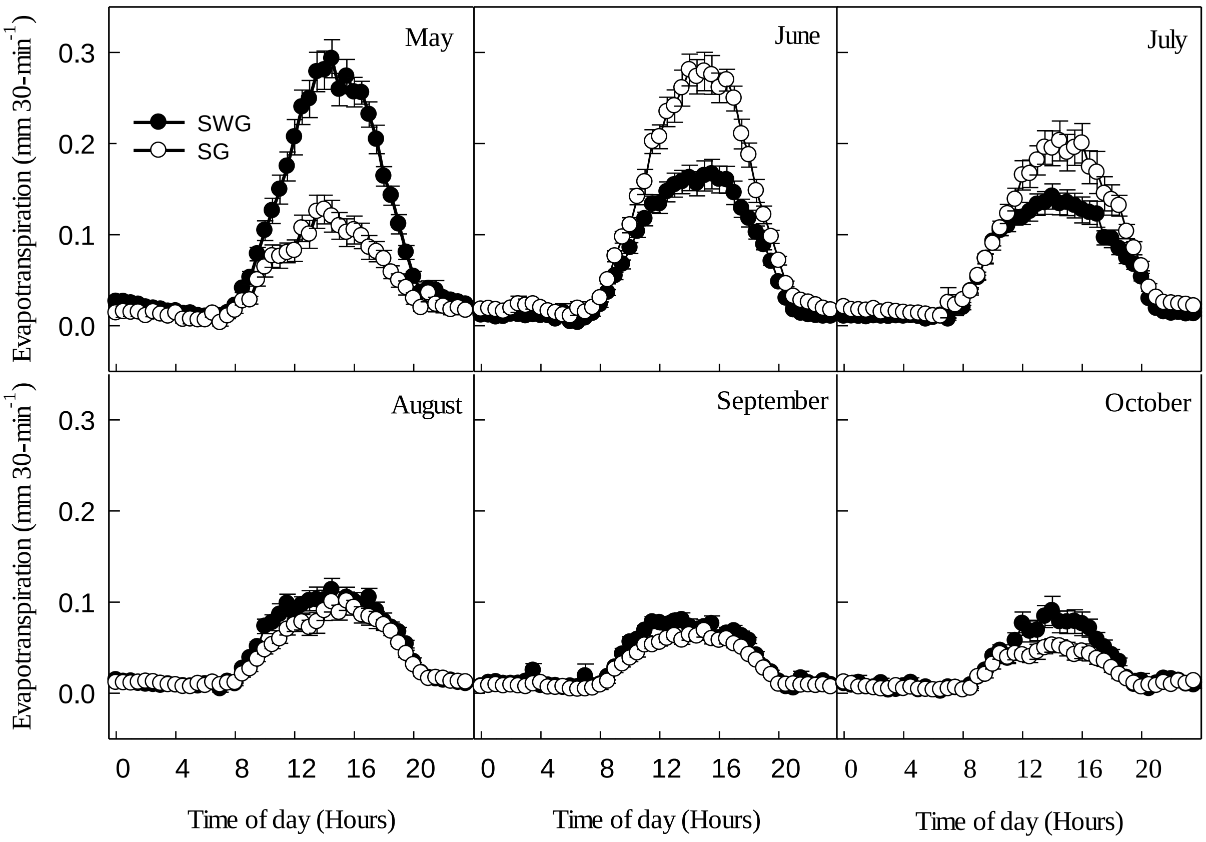

Fig. 27. Half-hourly binned diurnal courses of evapotranspiration rates in switchgrass (SWG) and sorghum (SG) across the growing season. Each data point is 30-min time-stamp average value for the entire month. Bars represent standard errors of the means.

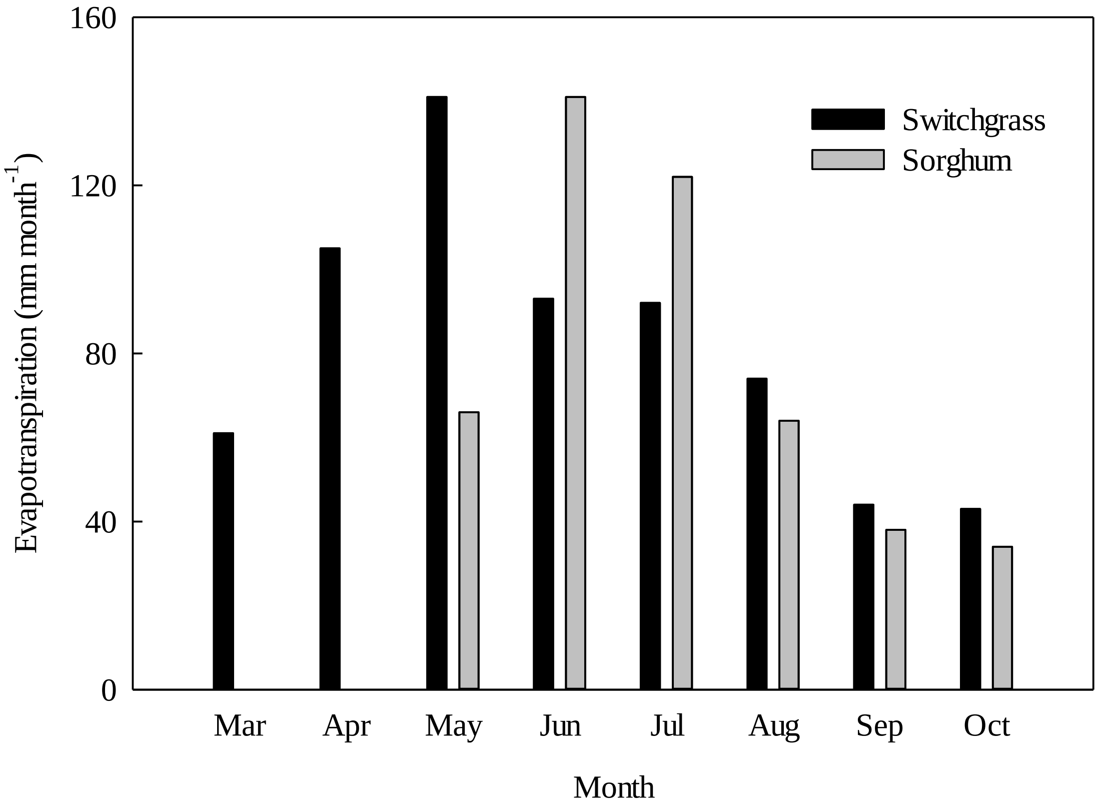

Fig. 28. Monthly cumulative evapotranspiration in switchgrass and sorghum across the growing season.

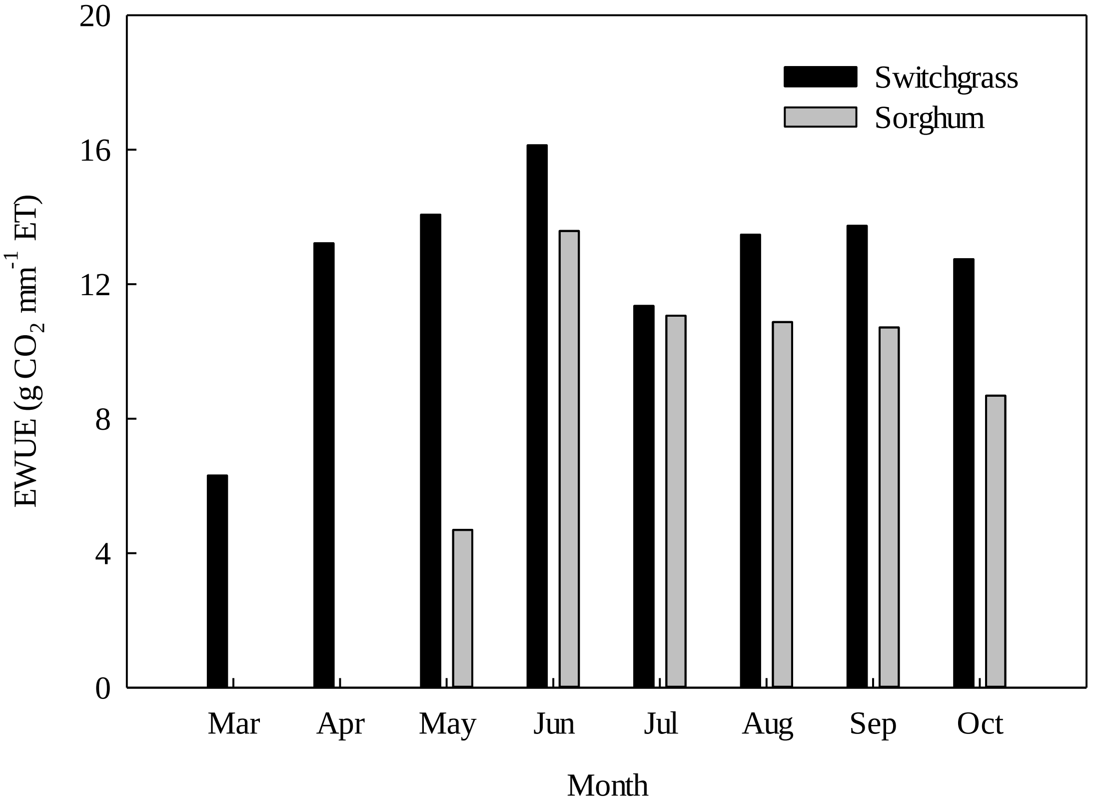

Fig. 29. Ecosystem water use efficiency (EWUE) for different months of the growing season.

CHAPTER VII

CONCLUSION

Ecosystem level CO_2 and H_2O fluxes were measured using eddy covariance (EC) system from co-located switchgrass and high biomass sorghum fields in south central Oklahoma, USA. The major objectives of this study were to quantify and examine seasonal variations in net ecosystem CO_2 exchange (NEE), evapotranspiration (ET), and ecosystem water use efficiency (EWUE) of switchgrass and sorghum in response to controlling factors, and to explore the underlying mechanisms.

Monthly ensemble averaged NEE at switchgrass and sorghum reached seasonal peak values of -33.02 ± 1.96 and -35.86 ± 2.32 µmol m^{-2} s^{-1}, respectively. Daily integrated NEE reached seasonal peaks of -8.5 and -10.3 g C m^{-2} d^{-1} in switchgrass and sorghum, respectively. These NEE rates were of similar magnitudes or higher as reported in productive prairie grasslands for this region. Switchgrass ecosystem was a net sink of CO_2 during 5 to 6 months and total seasonal uptakes were -1128 ± 130 and -1796 ± 217 g CO_2 m^{-2} in 2011 and 2012, respectively. The higher carbon uptake potential of switchgrass in 2012 as compared with 2011 can be attributed to better growing condition and increased maturity of the plant stand. The switchgrass stand was established in spring 2010. Sorghum ecosystem was a net sink of CO_2 for only three months (June to August) in 2012 with seasonal uptake of 956 ± 176 g CO_2 m^{-2}. Because peak values of gross ecosystem production (GEP, 18-19 g C m^{-2} d^{-1}) and ecosystem respiration (ER, about 10 g C m^{-2} d^{-1}) were similar at both ecosystems, the difference in carbon sink potential is likely related primarily to the length of the growing season. Interannual variability in NEE in switchgrass ecosystem seems to be mainly driven by spring temperature and rainfall distribution in summer. Mild spring temperature caused earlier greening up of switchgrass, resulting in a longer growing season. Actively growing leaves, relatively longer days, and optimal temperature for photosynthesis in the spring favored more carbon uptake and increased carbon uptake by the ecosystem. High vapor pressure deficit (VPD > 3 kPa) limited photosynthesis and caused asymmetrical diurnal NEE cycles (substantially higher NEE in the morning hours than in the afternoon at equal light levels), most notably from June to September. The result indicates that optimally warm and normal precipitation years can maximize net carbon sequestration of switchgrass and sorghum in this region. However, longer measurements are required to know about the timing that switches switchgrass ecosystem from carbon sinks to sources. We also observed that the response of ER to the environmental factors (soil and air temperatures, and soil moisture) was different throughout the entire study period, indicating that the response of ER to environmental factors should be evaluated for short time periods (preferably a week) to account for the changes in climate and plant phenology. Since NEE includes heterotrophic respiration as well additional measurements are needed to partition ER into autotrophic and heterotrophic components.

The effects of major environmental factors [photosynthetic photon flux density (PPFD), air temperature, and VPD] on daytime NEE in switchgrass was characterized to explore the underlying mechanisms. The result shows that PPFD is the most significant environmental factor for variation in switchgrass NEE (explained over 90% of the NEE variation) under optimum environmental conditions. Canopy photosynthesis did not saturate at as high as 2000 μmol $m^{-2}s^{-1}$ PPFD. However, this study indicates that the NEE-PPFD relationship is obscured by warm air temperature and high VPD in the summer. Carbon uptake by the switchgrass ecosystem decreased up to 62% (monthly average) from morning to afternoon at equal light levels because of the stomatal closure control of photosynthesis at high VPD (> 3 kPa). As a result, the light response function (LRF) provided biased estimates of light response parameters and yielded unreliable estimate (highly overestimated) of α (apparent quantum yield), which is used in several production efficiency (PEM) models to estimate GEP. Consequently these models highly overestimate GEP. The findings of this study suggest that the effect of VPD on carbon assimilation should be considered while partitioning NEE to account for the systematic presence of NEE hysteresis and determining light response parameters especially during dry and warm periods when temperature and VPD exceed thresholds. The NEE exhibited an optimum temperature range of 28-34 °C and decreased markedly beyond 35 °C. These observations will have implications for better understanding of temporal and spatial variation in fluxes. In addition, empirical functions developed based on the response of NEE to major environmental factors in this study can be used for the extrapolation of the site-specification measurements to the larger scales, and also for developing and testing ecosystem process models.

Patterns of ET and EWUE, and seasonal distributions of energy fluxes [sensible (H) and latent heat (LE) fluxes] were examined over switchgrass and sorghum fields. The results show that both species had similar water use patterns during the active growing periods. Diurnal patterns of energy fluxes were similar for both species. The results demonstrate that a switch in energy partitioning is strongly associated with crop phenology (from H to LE after leaf emergence and from LE to H after crop senescence) in both ecosystems. However, more energy was partitioned towards H during dry periods even in the mid-growing season of switchgrass (e.g. July 2011). Similarly, H was greater than LE even in wet periods during the late growing season due to crop senescence. The results suggest that energy partitioning is sensitive to both biological and climatic factors. Similar ET magnitude was observed (1.0-6.2 mm day^{-1} for switchgrass and 0.7-6.7 mm day^{-1} for sorghum) in both ecosystems in the 2012 growing season. These ET magnitudes were similar to ET from other major crops in this region. Total ET from both ecosystems was similar (487 mm from switchgrass and 465 mm from sorghum field) for the overlapping period of the growing season (May-October, 2012). However, seasonally integrated ET demand was higher in switchgrass due to longer growing season. As determined from greening up to senescence for switchgrass and from planting to senescence for sorghum, the total growing season was longer for switchgrass by two months in 2012. It should be noted that some evaporation occurs during the time when sorghum field is fallow. The difference in growing season lengths makes it more difficult to compare between ecosystems in this study.

The ET magnitude (1.0-6.2 mm day^{-1}) in switchgrass for the 2012 growing season was larger than in 2011 (0.5-4.8 mm day^{-1}) at this site due to more optimal growing conditions and increased maturity of the stand in 2012. These results show that patterns of precipitation and canopy development greatly affect ET patterns. Switchgrass ecosystem had a seasonal average EWUE of 12.6 g CO_2 mm^{-1} ET while high biomass sorghum had a seasonal average EWUE of 9.9 g CO_2 mm^{-1} ET in 2012. In a dry and warm growing season in 2011, seasonal average EWUE was 12 g CO_2 mm^{-1} ET in switchgrass, suggesting a smaller year to year variability in EWUE because of strong positive linear correlations between monthly GEP and ET. However, slightly different responses of CO_2 and H_2O flux to environmental variables caused a smaller inter annual variability in EWUE. Unlike CO_2 flux, the diurnal courses of ET were relatively symmetrical.

In conclusion, both ecosystems showed strong seasonal carbon sink potential and high water use efficiency in this region. However, evaluation over a longer term would be more valuable. The findings of this study will be helpful for quantifying the effects of stress and changes in climate and plant phenology on carbon and water vapor exchanges, and for developing and testing mechanistic models and remote-sensing algorithms for switchgrass and sorghum.

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