



Environmental control of daytime net ecosystem exchange of carbon dioxide in switchgrass



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ABSTRACT

Net ecosystem CO₂ exchange (NEE) over a young switchgrass (*Panicum virgatum*) stand was measured with the eddy covariance technique across two growing seasons in the southern Great Plains of the United States at 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) was the most significant driver of NEE and explained over 90% of the NEE variation during optimum environmental conditions. The light-response curve showed hysteresis as carbon uptake by the ecosystem decreased up to 62% (monthly average) from morning to afternoon at similar light levels because of the stomatal closure control of photosynthesis at high vapor pressure deficit (VPD). This resultant large hysteresis 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 demonstrated 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. The results of this study are useful for the modeling community to develop, improve, and validate the models for global change studies, and for the eddy covariance community to develop more robust gap filling methods.

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1. Introduction

There is a growing interest to understand the influence of environmental factors, such as temperature and precipitation patterns, on net ecosystem CO₂ exchange (NEE, the balance between CO₂ 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; Pinging et al., 2010). Temperature response functions, based on leaf level photosynthetic processes and organic matter decomposition, have been used in all ecosystem-level carbon cycle models (Friedlingstein et al., 2006) because of the lack

of understanding of the ecosystem-level response to temperature. Similarly, production efficiency models estimate ecosystem-level gross primary production (GPP) by scaling up leaf level physiological processes (e.g., quantum yield or light use efficiency) (Monteith, 1972; Potter et al., 1993). Recently eddy covariance data are being used to determine ecosystem-level parameters and to evaluate land surface models for the carbon cycle (Bonan et al., 2011). These models can be improved by better understanding of the response of NEE to major climatic variables as the atmosphere–land fluxes of CO₂ are known to be sensitive to climate. Direct measurement of NEE between an ecosystem and the atmosphere, and the associated environmental factors by eddy covariance technique, provides an elucidation of the environmental controls on NEE (Baldocchi et al., 2001a). However, few studies have been reported on NEE measurements in switchgrass (*Panicum virgatum* L.) (Skinner and Adler, 2010; Zeri et al., 2011; Wagle and Kakani, 2013). Moreover, the previous studies lacked a detailed investigation of environmental controls on NEE. A detailed study of physiological processes at the ecosystem-level may improve our ability to parameterize ecosystem models.

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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 over the next two decades is one of the key assumptions of the ‘Billion Ton Study’ (Perlack and Stokes, 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 explain the underlying mechanisms for differences in productivity (Dohleman et al., 2009). Mechanistic models that employ photosynthetic CO₂ assimilation require comprehensive field data across multiple growing seasons under various environmental conditions for validating the models and understanding the physiological basis for observed differences in productivity (Dohleman et al., 2009). Although previous studies have simply evaluated productivity of switchgrass in relation to soil, climate, and management practices (Heaton et al., 2004; Wullschlegel et al., 2010), there is still a lack of information on the effect of environmental variables on ecosystem-level CO₂ fluxes, and the magnitude and seasonality of light-response parameters in switchgrass. Continuous field measurements of NEE and associated environmental factors over two growing seasons provide a unique dataset for this emerging bioenergy crop.

As NEE is the balance between carbon uptake (GPP) 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 eddy covariance studies to separate NEE into GPP and ER using a rectangular hyperbolic light-response function (Falge et al., 2001). Although the response of NEE to photosynthetic photon flux density (PPFD) is described by a rectangular hyperbola, Wagle and Kakani (2013) demonstrated that vapor pressure deficit (VPD) modified the NEE–PPFD relationship at high VPD and the light-response function failed to provide good fits to daytime NEE. Few other studies also reported the failure of the light-response function to describe daytime NEE in other ecosystems (Li et al., 2005; Lasslop et al., 2010; Pongintha et al., 2010).

To provide an improved understanding of switchgrass ecosystem responses, the objectives of this study were to determine the response of switchgrass NEE to major environmental factors (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 temperature and VPD.

2. Materials and methods

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 switchgrass (cv. Alamo) field during the 2nd and 3rd years of establishment (2011 and 2012, respectively). The eddy covariance 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 38 cm apart in 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.

2.1. Net ecosystem CO₂ exchange and meteorological measurements

Continuous CO₂ fluxes were measured using an eddy covariance 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 and 2012 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 (R_n) 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). Flux data quality was assessed by the degree of energy balance closure [$\{ \text{latent heat (LE)} + \text{sensible heat (H)} \} / (R_n - G)$]. The energy balance closures of 0.77 in 2011 and 0.83 in 2012 were typical for eddy covariance experiments (Wilson et al., 2002). Data for the period when wind was blowing from behind the tower and data for the periods of low turbulence (friction velocity, $u^* < 0.20 \text{ m s}^{-1}$) were removed. Unreasonable flux values and statistical outliers beyond ± 3.5 STD range from a 14-day running mean window were excluded. 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 CO₂ uptake from atmosphere is negative and a net CO₂ release to the atmosphere is positive.

2.2. Analysis of canopy CO₂ fluxes

The data sets used in this study were daytime half-hourly data for the two growing seasons (May–October for 2011 and March–October for 2012) and were analyzed separately. Simple and multiple regression analyses were performed at a monthly time scale between CO₂ fluxes and major environmental factors (monthly average PPFD, air temperature, and monthly total precipitation) to examine the response of the ecosystem to changes in major environmental factors.

The light-response of NEE was evaluated using the light-response function (Falge et al., 2001) as shown in equation (1) and the modified light-VPD-response function, that accounted for an exponential reduction in the light saturated maximum canopy CO₂ uptake rate at high VPD, as shown in equations (2 and 3).

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

where α is the apparent quantum yield [i.e., the initial slope of the light-response curve (mol CO₂ mol⁻¹ of photons)], PPFD is measured photosynthetic photon flux density ($\mu\text{mol m}^{-2} \text{ s}^{-1}$), GP_{\max} is the maximum canopy CO₂ uptake rate ($\mu\text{mol m}^{-2} \text{ s}^{-1}$) at light

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