



Research Paper

Effects of precipitation changes on aboveground net primary production and soil respiration in a switchgrass field



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ABSTRACT

Switchgrass (*Panicum virgatum* L.) is widely selected as a model feedstock for sustainable replacement of fossil fuels and climate change mitigation. However, how climate changes, such as altered precipitation (PPT), will influence switchgrass growth and soil carbon storage potential have not been well investigated. We conducted a two-year PPT manipulation experiment with five treatments: -50% , -33% , $+0\%$, $+33\%$, and $+50\%$ of ambient PPT, in an “Alamo” switchgrass field in Nashville, TN. Switchgrass aboveground net primary production (ANPP), leaf gas exchange, and soil respiration (SR) were determined each growing season. Data collected from this study was then used to test whether switchgrass ANPP responds to PPT changes in a double asymmetry pattern as framed by Knapp et al. (2017), and whether it is held true for other ecosystem processes such as SR. Results showed that the wet ($+33\%$, and $+50\%$) treatments had little effects on ANPP and leaf gas exchange compared to the ambient precipitation treatment, regardless of fertilization or not. The -33% treatment did not change ANPP and leaf photosynthesis, but significantly decreased transpiration and enhanced water use efficiency (WUE). Only the -50% treatment significantly decreased ANPP and LAI, without changing leaf photosynthesis. SR generally decreased under the drought treatments and increased under the wet treatments, while there was no significant difference between the two drought treatments or between the two wet treatments. Our results demonstrate that switchgrass ANPP responded in a single negative asymmetry model to PPT changes probably due to relative high PPT in the region. However, even in such a mesic ecosystem, SR responded strongly to PPT changes in an “S” curve model, suggesting that future climate changes may have greater but more complex effects on switchgrass belowground than aboveground processes. The contrasting models for switchgrass ANPP and SR in response to PPT indicate that extreme wet or dry PPT conditions may shift ecosystem from carbon accumulation toward debt, and in turn provide government and policy makers with useful information for sustainable management of switchgrass.

1. Introduction

Due to fossil fuel combustion and land-use change, global land surface temperature has been increasing over the past decades, and is expected to further increase $1.1\text{--}6.4\text{ }^{\circ}\text{C}$ by the end of the century (IPCC, 2013). The increase in temperature will alter global air circulation patterns and the hydrological cycle (Huntington, 2006), resulting in more extreme droughts and flooding events in the future, particularly in the North American Great Plains (Easterling et al., 2000; Christensen

et al., 2007; Yoon et al., 2015). Such extremes in precipitation (PPT) regimes may have significant impacts on grassland structure and function (Knapp et al., 2008; van der Molen et al., 2011). However, most of previous studies have focused on examining the responses of grasslands to PPT within nominal variations (Knapp et al., 2002; Fay et al., 2003; Dukes et al., 2005; Hui and Jackson, 2006; Wu et al., 2011; Knapp et al., 2015; Zhou et al., 2016). How the ecosystem functions or processes respond to extreme PPT values remains unclear, but is essential both ecologically and for ecosystem models to forecast future

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grassland structure and function in changing PPT regimes.

Recently, Knapp et al. (2017) framed a new conceptual model for a full relationship between PPT and aboveground net primary production (ANPP), an important integrator of grassland ecosystem functions: a positive asymmetric response of ANPP to nominal variations of PPT and a negative asymmetric ANPP response to extremes in PPT. That means the increases in ecosystem function with increased PPT are of larger magnitude than decreases in function with decreased PPT within nominal variations of PPT, while for the extremes in PPT, the decreases in ecosystem function with decreased PPT are larger than are increases in function with increased PPT (Knapp et al., 2017). This nonlinear ‘double asymmetry’ model would improve prediction of grassland ANPP in responses to future PPT changes, but it has not been well tested (Luo et al., 2017).

Switchgrass (*Panicum virgatum* L.) is a perennial C₄ grass widely distributed in North America. Compared with other grass species, switchgrass is characterized by higher aboveground biomass production, lower herbicide and fertilizer input requirements, and more widespread adaptability to climatic conditions, and hence has stronger ability to sequester atmospheric carbon and to mitigate climate change (Gelfand et al., 2013; Eichelmann et al., 2016). As a result, the U.S. Department of Energy (DOE), partnering with the U.S. Department of Agriculture (USDA), has selected switchgrass as the model feedstock to be used for bioenergy production (McLaughlin and Kszos, 2005; Tulbure et al., 2012). Accordingly, the scope of switchgrass lands has rapidly increased in recent decades (Parrish and Fike, 2005; Schmer et al., 2008), and the U.S. switchgrass yield was expected to double or even triple for the goals of 36 billion gallons of biofuels production annually by 2022 (McLaughlin et al., 2006). However, information regarding of how switchgrass will respond to future climate change particularly to extremes in PPT regimes remains lacking, making the model prediction of switchgrass and its sustainable development largely uncertain (Ashworth et al., 2016; Aspinwall et al., 2017). For example, some studies found that annual PPT linearly influences switchgrass ANPP through either a spatial or temporal lens (Sanderson and Reed, 2000; Wang et al., 2010), but their PPT values mainly falls within the nominal range. To test whether the response of switchgrass ANPP to changing PPT follows the nonlinear ‘double asymmetry’ model, it is necessary to conduct a multi-level PPT experiment including both nominal variations and extreme PPT treatments (Estiarte et al., 2016; Luo et al., 2017).

Switchgrass is a drought tolerant grass, and one of its drought tolerance mechanisms is associated with altered leaf gas exchange and enhanced water use efficiency (WUE) (Aspinwall et al., 2013; Liu et al., 2015), which likely contributes to the positive asymmetric responses in ANPP to PPT (Knapp et al., 2017). Indeed, several studies have reported that after a short-term drought treatment, switchgrass seedlings could decrease stomatal conductance and transpiration but increase WUE, resulting in no significant change in leaf photosynthetic rate and aboveground biomass compared to the control plants (Barney et al., 2009; Hartman et al., 2012; Ye et al., 2016). In contrast, increased water input could stimulate switchgrass leaf photosynthesis and biomass production (Sanderson and Reed, 2000; Barney et al., 2009; Hartman et al., 2012). However, most of these experiments were performed in a greenhouse condition, which have significantly limited our ability in incorporating the positive asymmetric relationship into ecosystem models used to analyze effects of possible future climate change on switchgrass biomass productivity (Morrow III et al., 2014; Liu et al., 2015; Lovell et al., 2016). To improve our understanding of the PPT-ANPP relationships, an in-depth field investigation of responses of switchgrass leaf gas exchange to changing PPT regimes is urgently required.

While a double asymmetry model is proposed to characterize responses of ANPP to future changing PPT, other ecosystem processes such as soil respiration (SR) likely respond differently to PPT than ANPP, because SR is controlled by different mechanisms than ANPP

(Thomey et al., 2011; Luo et al., 2017). For example, SR from grasslands increased linearly along a PPT gradient from 430 to 1200 mm in the Great Plains, USA (Zhou et al., 2009). However, a recent meta-analysis with single-level PPT experiments suggested that SR and ANPP probably responded similarly to changing PPT, with decreases in both ANPP and SR under the drought treatment and increases in both under the irrigation treatment, resulting in minor increases in soil carbon pools (Zhou et al., 2016). The release of soil CO₂ from switchgrass fields varied drastically, ranging from 1.8 to 13 m mol CO₂ m⁻² s⁻¹ depending on regional climate conditions (Skinner and Adler, 2010; Mbonimpa et al., 2015; Huang et al., 2016), suggesting that SR in the switchgrass fields is highly sensitive to climate variability. However, our understanding of how SR will respond to the changing PPT regimes in switchgrass fields remains limited (Wagle and Kakani, 2014; Creutzig et al., 2015).

In this study, we conducted a two-year (2015–2016) field experiment in middle Tennessee to examine the effects of sustained PPT changes (50%, 67%, 100%, 133%, and 150% of ambient PPT) on switchgrass ANPP, leaf gas exchange (photosynthetic rate, stomatal conductance, transpiration, and WUE), leaf area index (LAI) and SR. The ± 33% PPT treatments represent nominal variations in PPT that encompass 80% of the interannual variation of PPT over the past 50 years in the region and the ± 50% PPT treatments represent extremes in PPT that exceed the highest and lowest historic values. We hypothesized that the response of switchgrass ANPP to the PPT treatments followed a double asymmetry model as framed by Knapp et al. (2017), with a positive asymmetric response to the ± 33% PPT treatments and a negative asymmetric response to the ± 50% PPT treatments. We further hypothesized that shifts in leaf gas exchange would contribute to the PPT-ANPP relationships. Finally, we hypothesized that SR responded to the PPT treatments differently from ANPP did.

2. Materials and methods

2.1. Experimental facility and design

This study was conducted in 2015 and 2016 at the Tennessee State University (TSU) Agricultural Research and Education Center (Latitude 36.12°N, Longitude 86.89°W, elevation 127.6 m) in Nashville, TN, USA. Climate in the region is a warm humid temperate climate (Deng et al., 2015), with an average annual temperature of 15.1 °C, and total annual PPT of 1200 mm. The experimental site is a Talbott silt clay loam soil with slight acidity and low in both carbon (2.37 g kg⁻¹) and nitrogen (0.14 g kg⁻¹).

Seeds of “Alamo” switchgrass were initially planted in a no-tillage field (about 50 m × 60 m) with a small seed planter in May 2011, but the germination was poor due to drought in 2011. Seed were re-planted in April 2012 at a rate of 6.73 kg ha⁻¹ and about 19 cm row spacing. The land was mowed grassland and used for hay production for over 30 years. Before planting, herbicide (Accent®) were sprayed. Due to the severe drought in June of 2012, all plots were irrigated to help switchgrass stand establishment.

A PPT manipulation facility was constructed in the switchgrass field in March 2015. Five levels of PPT treatments were considered, including -50%, -33%, +0%, +33%, and +50% of ambient precipitation. The ambient PPT was control), ± 33% PPT (equal to 67% and 133% of ambient PPT) were set to simulate nominal variations in PPT that encompass 80% interannual variations of PPT over the past 50 years in the region (Fig. S1), and ± 50% PPT (equal to 50% and 150% of ambient PPT) were set to simulate extremes in PPT regimes. We used a rainfall-interception-redistribution (RIR) system that combines a modified rainout shelter originally designed by Yahdjian and Sala (2002) with a water redistribution system described by Zhou et al., 2006. The reduced PPT treatments were achieved using a rainout shelter. The increases in PPT were achieved by redistributing rainwater collected by the nearby rainout shelters to the plots. Rainwater was

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