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Running head: Precipitation impacts on switchgrass

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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.

Keywords: Aboveground net primary production, bioenergy crop, leaf gas exchange, *Panicum virgatum*, precipitation change, soil respiration, switchgrass, water use efficiency

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 1.1-6.4°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 (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 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 C_4 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 Kszo, 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 Ш 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 CO_2 from switchgrass fields varied drastically, ranging from 1.8-13 μ mol CO_2 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, 2012). 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 distributed immediately following each rainfall event to avoid a change in natural rainfall frequency (Fay et al., 2003, 2008). For each PPT treatment, there are four replicates (i.e. blocks). In total, twenty (20) 3 m × 2 m plots were used. There was a one-meter buffer strip between two adjacent plots. To minimize disturbance, drainage pipes (20 cm diameter) with holes were embedded in the surface soils between two adjacent plots to cut off lateral movement of soil water. A total 80 kg N ha^{-1} of solid compound fertilizer (29% N, 5% K_2O, and 2% Fe) was applied in each plot at the beginning of growing season in 2016.

2.2. Field measurements

Maximum leaf photosynthetic rate, stomatal conductance, and transpiration were measured monthly on average during each growing season (from April to October) in 2015 and 2016 using a Li-6400XT Portable Photosynthesis System (Li-Cor Inc., Lincoln, NE). The fully expanded young leaves of four or five selected tillers in each plot were measured between 9:00 am and 2:00 pm. Leaf chamber photosynthetic photon flux density was set at 2000 μmol $m^{-2}s^{-1}$. Instantaneous water use efficiency (WUE) was calculated as a ratio of leaf photosynthesis and transpiration. Leaf area index (LAI) was also measured during the growing season in 2016 using an LAI-2000 (Li-Cor Inc.). Aboveground biomass was measured in November, 2015 and 2016 by harvesting the aboveground tillers within 50 cm × 50 cm in the plots, dried at 75^{o}C for 24 hr and weighted. After the measurement of aboveground biomass, all of aboveground tiller in the plots were harvested and removed every year.

To measure SR, four polyvinal chloride (PVC) soil collars (10 cm diameter, 8 cm height) were permanently installed 5 cm into the soil in each plot. The rate of SR was measured bi-monthly on average during the growing season in 2015 and 2016 with a Li-Cor 6400 infrared gas analyzer coupled to a Li-Cor 6400-09 chamber. The measurements of SR were mainly made between 8:00 am and 12:00 am local time, accompanied by recordings of soil temperature and soil moisture at 10 cm depth.

2.3. Statistical analysis

Data analysis was performed using SAS software 9.3 (SAS Inc., Cary, NC) (Hui and Jiang, 1996). Repeated-measures Analysis of Variance (ANOVA) was used to determine the statistical significance of PPT treatment, year, and their interactive effects on soil moisture, soil temperature, ANPP, leaf gas exchange (leaf photosynthetic rate, stomatal conductance, transpiration and WUE) and SR. When a significant effect was detected, least significant difference (LSD) was used for multiple comparisons. One-way ANOVA with LSD test was used to test the difference of LAI among the five PPT treatments. Regression analysis was conducted to develop the relationships among SR, soil temperature, and soil moisture.

3. Results

3.1. Air temperature, precipitation, soil temperature and moisture

Air temperature ranged from -11°C to 30°C during the experimental period. The highest temperature appeared in June and the lowest temperature in February (Fig. 1). The mean daily air temperature was 16.4°C in 2015 and 16.9°C in 2016, respectively (Table 1). Precipitation was relatively uniform throughout the year, and the largest rain event of 59.9 mm appeared in February 2015 (Fig. 1). Annual PPT was 1249 mm in 2015 and 1189 mm in 2016, respectively (Table 1).

The seasonal variations of soil temperature and moisture showed similar patterns of air temperature and precipitation (Figs. S2a, b). The ANOVA test showed that the PPT treatments had no significant effect on soil temperature (Table 2; Fig. 2a), while significantly affecting soil moisture (Table 2). Soil moisture generally decreased with the declines in PPT and increased with the increases in PPT (Fig. 2b). The soil moisture in the +50% treatment was the highest, about 10% higher than that in the control (Fig. 2b). The -50% precipitation treatments had the lowest soil moisture, about 18% lower than that in the control (Fig. 2b). There were no significant differences in soil temperature and moisture between the two years (Tables 1).

3.2. Switchgrass aboveground net primary production

Results of ANOVA showed that both PPT treatment and year had significant effects on switchgrass ANPP, but had no significant interactive effects (Table 3). Switchgrass ANPP was generally higher in 2016 than those in 2015 under all the PPT treatments (Table 1). Compared to the control, the -50% treatment significantly decreased switchgrass ANPP by 25% on an average across two years (Fig. 3a). For the other precipitation treatments, no significant change of switchgrass aboveground biomass was found (Fig. 3a). Thus, the ANPP-PPT relationship displayed a single negative asymmetry in both years (Fig. 3b).

3.3. Soil respiration

The seasonal patterns of SR were similar for all the PPT treatments (Fig. S2c), and were exponentially correlated with soil temperature (Fig. S3a). There was no significant relationship between SR and soil moisture in seasonal patterns (Fig. S3b).

Results of ANOVA showed that SR was significantly affected by the PPT treatment (Table 2). The SR in both years significantly decreased with the declines in PPT and increased with the increases in PPT compared to the control (Fig. 3c). But there was no significant difference between the two drought treatments or between the two wet treatments (Fig. 3c). Thus, the SR-PPT relationships displayed an “S” curve model (Fig. 3c). There were also significant differences in SR between the two years (Table 1). The mean SR across all the PPT treatments was 3.24 μmol CO_2 $m^{-2}s^{-1}$ in 2015, slightly lower than that (3.41 μmol CO_2 $m^{-2}s^{-1}$) in 2016. No significantly interactive effect of PPT treatment and year was detected for SR (Table 2). However, SR tended to increase more under the wet treatment during the hot/dry period and decrease more under the drought treatment during relatively cold/wet period (Fig. S2c).

3.4. Leaf gas exchange

The seasonal patterns in leaf photosynthesis, stomatal conductance, transpiration rates and WUE were similar for all the PPT treatments (Fig. S3). Results of ANOVA showed no significant effect of the PPT treatment on leaf photosynthesis (Table 3; Fig. 4a), while PPT treatment significantly influenced all the other physiological variables measured (Table 3). The LAI was significantly decreased by 18% only under the -50% treatment, compared to the control (5.17 m^2 m^{-2}) (Fig. 3b). For other precipitation treatments, no significant change of LAI was found (Fig. 3b). For the stomatal conductance, the lowest rates occurred in the -50% treatment (0.15 mol H_2O s^{-1} m^{-1}), significantly lower than those in the +33 and +50% treatments (Fig. 4c). The highest transpiration rates occurred in the +50% treatment (4.74 m mol H_2O s^{-1} m^{-1}), significantly higher than that in the control (4.11 m mol H_2O s^{-1} m^{-1}) (Fig. 4d). The transpiration rate was significantly decreased by 16% under the -33% treatment and by 21% under the -50% treatment, compared to the control (Fig. 4c). The WUE was significantly enhanced by 17% under the -33% treatment and by 19% under the -50% treatment, compared to the control (5.62 μmol CO_2 $mmol^{-1}$ H_2O) (Fig. 4e). No significant effect of increased PPT on WUE was found (Fig. 4e).

Switchgrass leaf photosynthesis, stomatal conductance and transpiration rates were generally higher in 2016 than 2015 across all the PPT treatments (Table 1), but the annual mean

WUE values were similar in the two years (Table 1). No significantly interactive effects of PPT treatment and year were detected for all above leaf variables (Table 3).

4. Discussion

Contrary to our expectation, we only found a single negative asymmetry response of switchgrass ANPP to the PPT treatments (Fig. 3b). The lack of a positive asymmetry response of switchgrass ANPP to the nominal variations in PPT was probably due to the relative high annual PPT in the region (1249 mm in 2015 and 1189 mm in 2016, respectively) that have reached the maximum value in nominal PPT range in Knapp et al. (2017) model. Thus, we believed that switchgrass grown at our study site was less limited by water. Increase in PPT could result in more nutrients loss via leaching, which may limit switchgrass response to the wet treatments (Garten et al., 2011). However, fertilizer inputs in 2016 significantly increased switchgrass ANPP (Table 1), but did not alter the PPT-ANPP relationships (Figs. 3a). Sanderson and Reed (2000) reported that switchgrass biomass responded to irrigation depending on plant density, with significant increase only under a low plant density. High LAI (>5 m^2 m^{-2}) observed in this study (Fig. 4b) may be responsible for the unchanged switchgrass ANPP under the wet treatments. The inconsistent responses of switchgrass ANPP to the wet treatments between our field study and some previous greenhouse studies (Sanderson and Reed, 2000; Barney et al., 2009; Hartman et al., 2012) were probably due to generally higher temperature in the greenhouses that could increase evaporation and plant transpiration, resulting in greater water limitation.

Although our results did not support the double asymmetry model, the responses of switchgrass ANPP to the drought (-33% and -50%) treatments were quite similar with those described by the model (Fig. 3b). We found that switchgrass ANPP only slightly decreased under the drought (-33%) treatment within the nominal PPT range, while decreasing much more under the severe drought (-50%) treatment (Fig. 3a). The slight decrease in switchgrass ANPP under the -33% treatment was probably due to increased WUE, one of the important indexes for plant drought tolerance (Liu et al., 2015). The enhanced WUE without significant change in leaf photosynthesis under the -33% treatment (Fig. 4a, e) confirms that switchgrass is a drought tolerant grass. The significant decrease in switchgrass ANPP under the -50% treatment suggests that drought stress of this degree likely exceeds switchgrass's tolerance threshold. Moreover, our results indicate that the severe drought affected switchgrass ANPP primarily through depressing canopy development rather than leaf physiology, as significant decrease in LAI but not leaf photosynthesis was detected under the -50% treatment (Fig. 4a, b). Because of very few and sometime even only one switchgrass grown in a pot, the greenhouse studies might not detect such ecosystem-level decrease in LAI under the severe drought, thus usually decreasing leaf photosynthesis (Barney et al., 2009). In field conditions, however, switchgrass biomass appears to have a poor relationship with photosynthetic rate (Nippert et al., 2007). A recent study of 10 switchgrass genotypes showed that variations in leaf-level photosynthesis did not scale up to biomass production, while leaf area, leaf architecture, and canopy development could contribute to final biomass yield (Cordero and Osborne, 2016). Another study of 9 switchgrass genotypes also showed that shifts in ANPP with climate changes were mainly related to tiller mass, tiller number, canopy height, LAI, flowering time (Aspinwall et al., 2013, 2017).

Soil respiration in our switchgrass field responded strongly to the PPT treatments with significant decreases under the drought treatments and increases under the wet treatments (Fig. 3c), suggesting that switchgrass belowground processes had higher PPT sensitivities than aboveground processes. Several biological processes may help explain such contrasting PPT sensitivities. First, plant roots usually move toward deeper soils in response to water stress, which is a typical drought tolerance mechanism of mesic species in the tallgrass prairie (Heckathorn and DeLucia, 1994; Knapp, 1984). Such shifts of roots in different soil layers could have significant effects on root activity and hence soil respiration, as the release of CO_2 in soils is almost entirely from surface root respiration and microbial decomposition of organic matter. Second, soil microbial community structure could rapidly change with altered PPT, as fungi can usually tolerate greater water stress than can bacteria (Holland and Coleman, 1987; Yuste et al., 2011). Shifts in fungi to bacteria ratios could significantly decrease soil respiration, but still maintaining constant nutrients supply due to their different carbon and nutrient use efficiency (Mouginot et al., 2014).

We found that SR responded nonlinearly to PPT (Fig. 3c), when extending the PPT-ANPP relationships to include extreme drought and wet conditions. This was inconsistent with some previous studies, showing SR responded linearly to PPT (Zhou et al., 2009). However, a recent global meta-analysis of PPT impacts on SR showed similar nonlinear relationships that SR tended to be more sensitive to increased PPT in more arid areas and more responsive to decreased PPT in more humid areas (Liu et al., 2016). The no SR change in the +50% treatment compared to the +33% treatment should be attributed to a trade-off between increased soil moisture and decreased soil O_2 concentration (e.g. Cleveland et al., 2010; Deng et al., 2012). Shifts in soil microbial community structure affected soil respiration and likely also altered its drought sensitivity (Holland and Coleman, 1987; Yuste et al., 2011), while a clear explanation for the no difference in SR between the -33% and -50% treatments was not readily apparent.

Contrary to Zhou et al. (2016), our results, using a multi-level PPT experiment including extreme drought and wet conditions, clearly demonstrate that switchgrass ANPP and SR responded differently to PPT changes (Fig. 3). While the switchgrass ANPP responded to PPT changes in a single negative asymmetry model, the response of SR to PPT change showed a “S” curve model (Fig. 3). This indicates that the wet treatment may decrease soil carbon pool, as it increased SR but not ANPP. Similarly, the moderate drought (-33%) treatment may increase soil carbon pool as it decreased SR but not ANPP. However, extension of drought to more extreme condition may shift switchgrass from carbon accumulation toward debt. The -50% treatment decreased both ANPP and SR, but more so ANPP, suggesting that carbon inputs are more strongly reduced, while losses continue with less reduction. Therefore, our findings provide new insights as to how switchgrass responds to altered PPT. The relationships gained from nominal variations in PPT may not be simply extrapolated to those in extreme PPT conditions (Knapp et al., 2017). Future switchgrass management, if not given sufficient attention to such different consequences of extreme PPT conditions, may cause unexpected economic losses and environmental issues. Findings from this PPT experiment may also have significant implications for development and improvement of land surface models that usually applied similar linear relationships between PPT and ecosystem C processes (plant and soil) to simulate the responses to altered precipitation (Cowling and Shin, 2006). Future land surface models may need to incorporate more complex but different PPT relationships for ecosystem aboveground and belowground processes.

In addition to the annually summed responses, ANPP and SR may respond differently to the changes in PPT on a seasonal basis. For example, the response of SR to the PPT treatments varied significantly over time. Overall, SR tended to be more sensitive to the wet treatment during the hot/dry period and more responsive to the drought treatment during relatively cold/wet period (Fig. S2). In contrast, change in PPT did not significantly change the seasonal pattern of leaf photosynthesis (Fig. S3a). Future study of the seasonal patterns of ANPP responses to changes in PPT is needed, which could reveal optimum irrigation timing for switchgrass during extreme drought. In addition, change in PPT could reinforce or offset the effects of other aspects of climate change on C cycling. Both experiments and models have indicated that warming would accelerate SR, thus reduce soil C storage (Cox et al., 2000; Luo, 2007). Our results suggest that the predicted losses of soil C under future warming may be reduced during moderate drought, but may increase under extreme drought. Previous studies have also indicated that drought could decrease temperature sensitivity of SR (Harper et al., 2005; Deng et al., 2012), which was not detected in our study (Fig. S4a). Future studies should follow an actual climate change scenario that includes both warming and drought treatments to allow the results to be better integrated into land surface models.

5. Conclusions

This study displayed a single negative asymmetry model for switchgrass ANPP in response to the PPT treatments. The lack of a positive asymmetry in switchgrass ANPP response to the nominal variations in PPT was probably due to regionally abundant PPT. Shifts in leaf WUE under the PPT treatments might contributed to unchanged photosynthetic rate. The severe drought decreased switchgrass ANPP primarily through depressing canopy development rather than leaf physiology. This study also demonstrated that SR responded to PPT changes differently from ANPP, showing higher sensitivity in nominal variations in PPT but nonlinear response when extending the PPT-ANPP relationships to include extreme drought and wet conditions. These findings suggested that future climate changes may have greater but more complex effects on switchgrass belowground than aboveground processes in mesic ecosystems, and result in significant yet different consequences for ecosystem carbon balance. Information generated from this study will improve model prediction of switchgrass carbon storage potential, and is useful for sustainable switchgrass management to maximize biofuel production and climate change mitigation. However, future experiments with more multi-year and multi-level PPT treatments are needed to test the relationships between PPT and ecosystem aboveground and belowground processes.

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Table 1. The mean values (± SE) of climatic factors, soil environment, switchgrass aboveground net primary production, soil respiration and leaf gas exchange across all precipitation treatments during the growing seasons in 2015 and 2016, respectively. Different letters indicate statistically significant differences between the two years.

Source	2015 (Unfertilized)	2016 (Fertilized)
Air temperature (^{o}C)	22.37±0.43	22.89±0.55
Precipitation (mm)	1249.43	1189.28
Soil temperature (^{o}C)	20.26±0.18	19.88±0.23
Soil moisture (%Vol.)	17.74±0.20	17.16±0.29
ANPP (t ha^{-1})	7.11±0.3^{b}	8.64±0.33^{a}
SR (μmol CO$_2$ m^{-2}s^{-1})	3.24±0.06^{a}	3.41±0.04^{b}
Photosynthesis (μmol CO$_2$ m^{-2}s^{-1})	18.78±0.34^{b}	21.26±0.37^{a}
Stomatal conductance (mol H$_2$O m^{-2}s^{-1})	0.16±0.005^{b}	0.18±0.004^{a}
Transpiration (mmol H$_2$O m^{-2}s^{-1})	3.48±0.07^{b}	4.47±0.10^{a}
WUE (μmol CO$_2$ mmol^{-1} H$_2$O)	5.85±0.10	5.89±0.005
LAI (m^{2} m^{-2})	-	4.91±0.09

ANPP: Aboveground net primary production; SR: Soil respiration; WUE: Water use efficiency; LAI: Leas area index; -: Unavailable data.

Table 2. Significance of the effects of precipitation treatment, year, and their interaction on soil temperature (^{o}C), soil moisture (%Vol.) and soil respiration (μmol CO_2 $m^{-2}s^{-1}$) using ANOVA. Numbers are F values. Stars indicate the level of significance (*=p<0.05, **=p<0.01).

Source	Soil temperature	Soil moisture	Soil respiration
Precipitation	1.07	25.78^{**}	21.26^{**}
Year	0.91	0.47	6.14^{*}
Precipitation*Year	0.02	0.59	0.66

Table 3. Significance of the effects of precipitation treatment, year, and their interaction on switchgrass aboveground net primary production (ANPP, t ha^{-1}), leaf photosynthesis (μmol CO_2 $m^{-2}s^{-1}$), stomatal conductance (mol H_2O $m^{-2}s^{-1}$), transpiration (mmol H_2O $m^{-2}s^{-1}$) and water use efficiency (WUE, μmol CO_2 $mmol^{-1}$ H_2O) using ANOVA. Numbers are F values. Stars indicate the level of significance (*=p<0.05, **=p<0.01).

Source	ANPP	Photosynthesis	Stomatal conductance	Transpiration	WUE
Precipitation	3.14^{*}	1.93	4.08^{**}	18.94^{**}	15.38^{**}
Year	12.07^{**}	22.82^{**}	7.11^{**}	58.56^{**}	0.21
Precipitation*Year	0.22	1.87	0.31	2.10	0.68

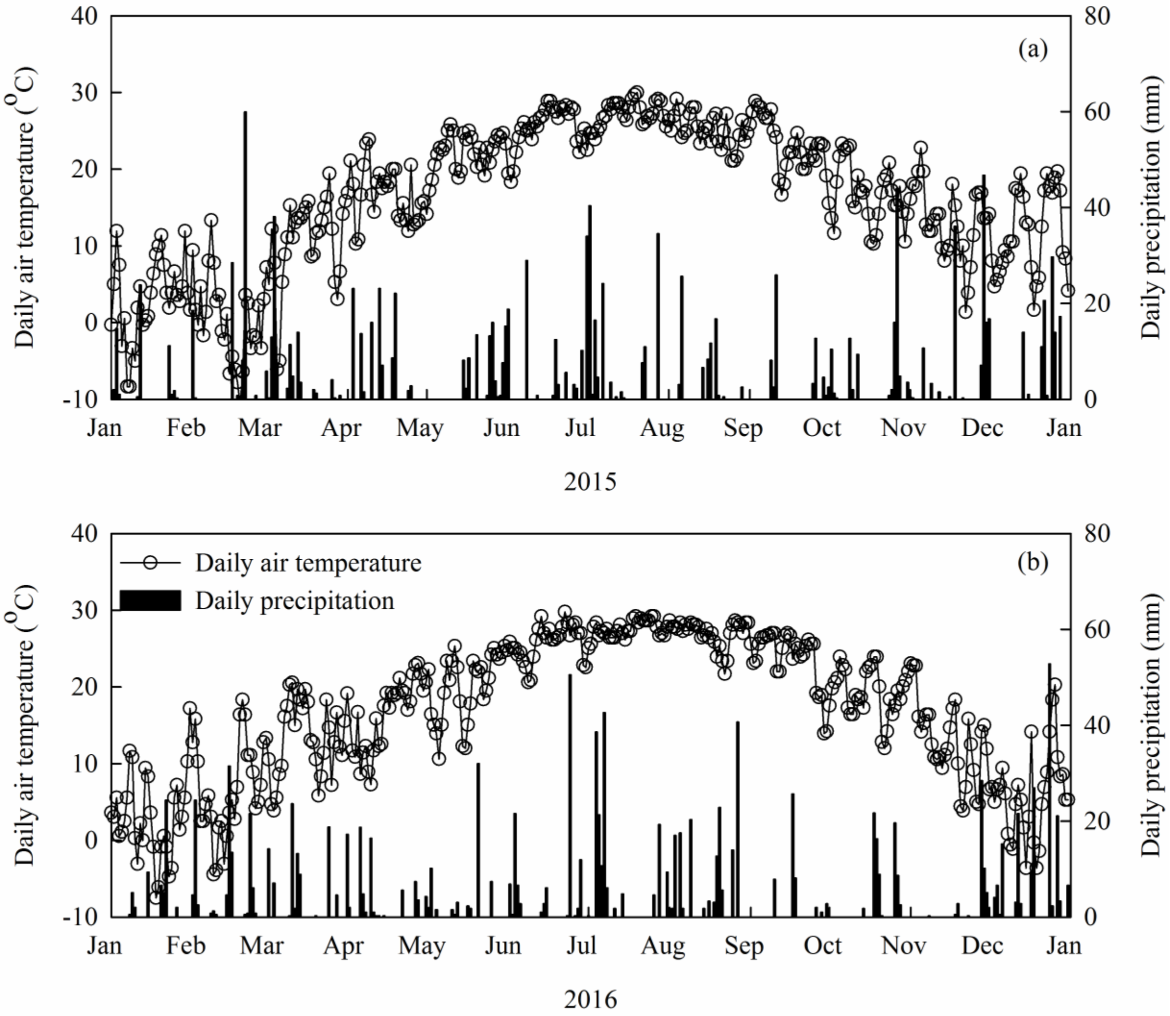
Figure legends

Fig. 1. Daily air temperature and precipitation in 2015 (a) and 2016 (b).

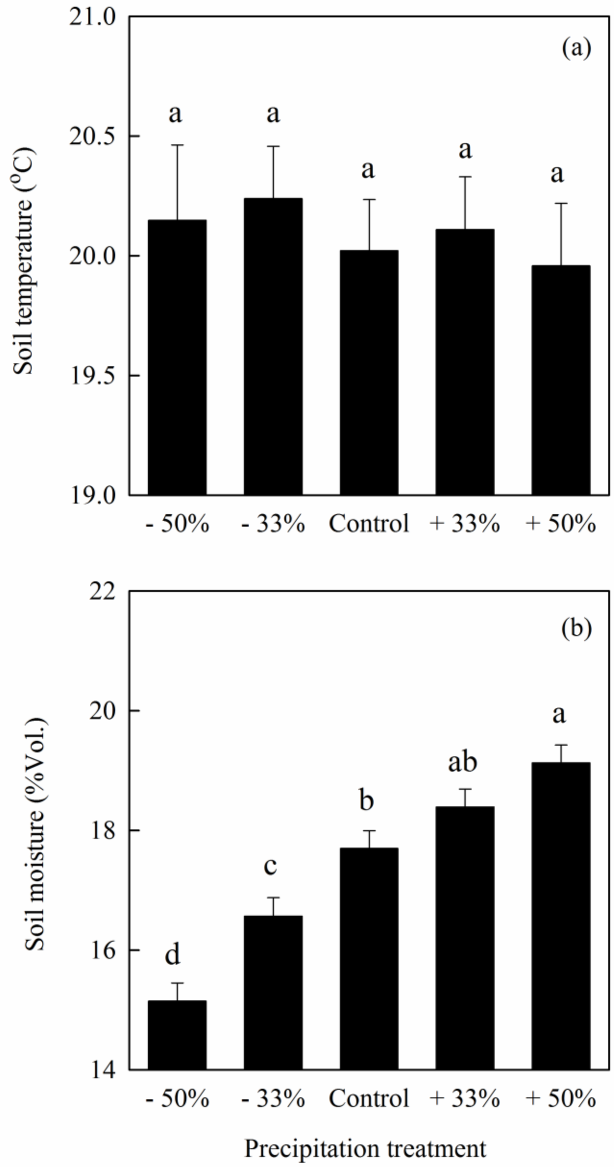
Fig. 2. Mean soil temperature and soil moisture at 10 cm depth in each precipitation treatment during the growing seasons. Error bars represent standard errors. Different letters over the bars of litter indicate statistically significant differences among the precipitation treatments. There was no significant difference in soil temperature among the precipitation treatments.

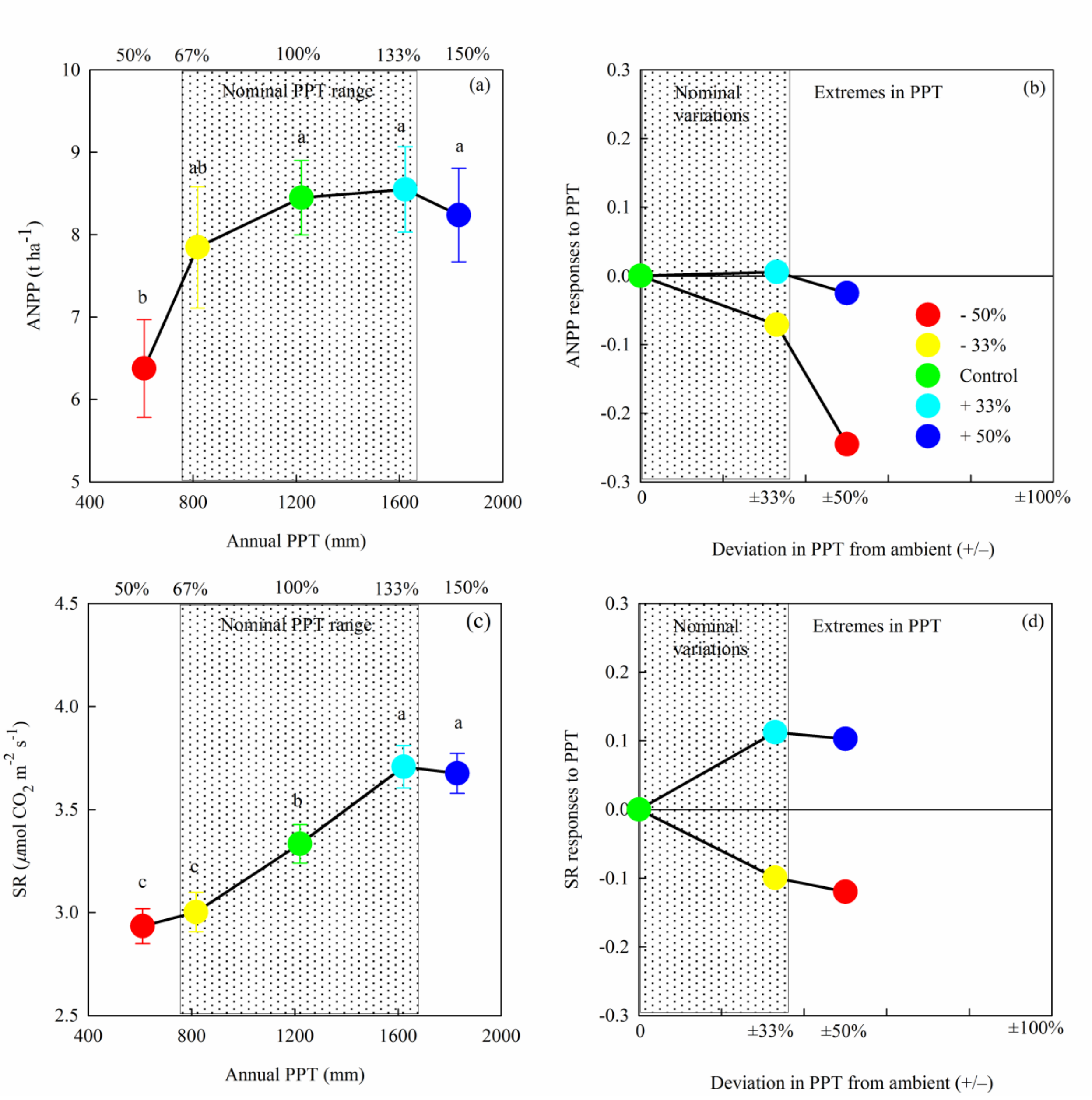
Fig. 3. The relationships between aboveground net primary production (ANPP) and annual precipitation (PPT) or between soil respiration (SR) and PPT across two-year data. (a) ANPP-PPT relationship displayed single negative asymmetry model and (c) SR-PPT relationship displayed an “S” curve model. (b) ANPP-PPT relationship and (d) SR-PPT relationship re-drawn to emphasize the comparative magnitudes in ANPP and SR, respectively. Error bars represent standard errors. Different letters over the bars of litter indicate statistically significant differences among the PPT treatments.

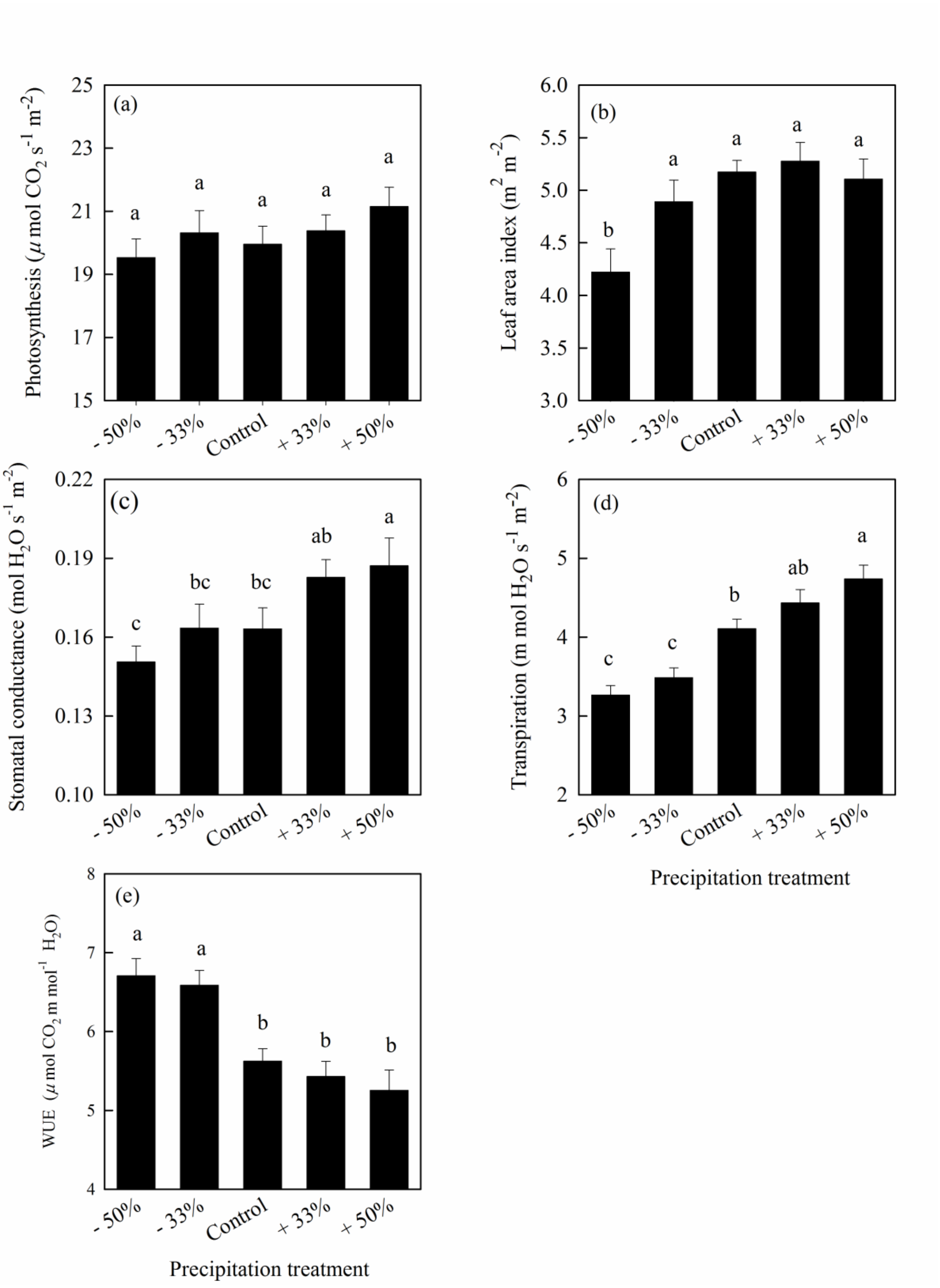
Fig. 4. Mean leaf photosynthesis (a), leaf area index (LAI) (b), stomatal conductance (c), transpiration (d), and water use efficiency (WUE) (e) in each precipitation treatment during the growing seasons. Error bars represent standard errors. Different letters over the bars of litter indicate statistically significant differences among the precipitation treatments.



(a)
Daily air temperature (^{o}C)
Daily precipitation (mm)
40
30
20
10
0
-10
80
60
40
20
0
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
2015
(b)
Daily air temperature
Daily precipitation
Daily air temperature (^{o}C)
Daily precipitation (mm)
2016


21.0
20.5
20.0
19.5
19.0
(a)
Soil temperature (^oC)
a
a
a
a
a
- 50%
- 33%
Control
+ 33%
+ 50%
22
20
18
16
14
(b)
Soil moisture (%Vol.)
d
c
b
ab
a
- 50%
- 33%
Control
+ 33%
+ 50%
Precipitation treatment


50%
67%
100%
133%
150%
Nominal PPT range
(a)
ANPP (t ha^{-1})
Annual PPT (mm)
b
ab
a
a
a
Nominal variations
Extremes in PPT
(b)
ANPP responses to PPT
Deviation in PPT from ambient (+/–)
0
±33%
±50%
±100%
- 50%
- 33%
Control
+ 33%
+ 50%
(c)
SR (μmol CO_2 m^{-2} s^{-1})
c
c
b
a
a
(d)
SR responses to PPT


(a)
Photosynthesis (μ mol CO_2 s^{-1} m^{-2})
25
23
21
19
17
15
a
a
a
a
a
- 50%
- 33%
Control
+ 33%
+ 50%
(b)
Leaf area index (m^2 m^{-2})
6.0
5.5
5.0
4.5
4.0
3.5
3.0
b
a
a
a
a
- 50%
- 33%
Control
+ 33%
+ 50%
(c)
Stomatal conductance (mol H_2O s^{-1} m^{-2})
0.22
0.19
0.16
0.13
0.10
c
bc
bc
ab
a
- 50%
- 33%
Control
+ 33%
+ 50%
(d)
Transpiration (m mol H_2O s^{-1} m^{-2})
6
5
4
3
2
c
c
b
ab
a
- 50%
- 33%
Control
+ 33%
+ 50%
Precipitation treatment
(e)
WUE (μ mol CO_2 m mol^{-1} H_2O)
8
7
6
5
4
a
a
b
b
b
- 50%
- 33%
Control
+ 33%
+ 50%
Precipitation treatment