Microtopography-induced transient waterlogging affects switchgrass (Alamo) growth in the lower coastal plain of North Carolina, USA

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Abstract

Very limited information is currently available on growth responses of switchgrass (lowland cultivars) to transient waterlogging in lowland or poorly drained areas. This study investigated impacts of microtopography-induced transient waterlogging on switchgrass (Alamo cultivar) growth, represented by leaf-level gas exchange and biomass yield, in an established experimental field located in the Atlantic coastal plain of North Carolina, USA. Intensive leaf-level gas exchange measurements were conducted on switchgrass at paired spots with distinct elevations in three sub-blocks. Aboveground biomass was randomly collected across the study field to explore the potential impacts of the transient waterlogging on biomass yield. The sum of excess water (SEW) was calculated based on measured instantaneous water table depth to generalize the relationship between biomass yield and intensity of transient waterlogging. Results showed significant ($P \leq 0.0001$) treatment effects on leaf-level gas exchange, characterized by evident reduction in both $CO_2$ assimilation rate and stomatal conductance when water table was at or near the soil surface at low positions. Negative impacts of transient waterlogging on leaf-level gas exchange became more evident with the increasing of elevation differences between paired subplots. Stomatal closure was found to be the main mechanism responsible for the decline of net assimilation under transient waterlogging. Aboveground biomass yields of switchgrass showed relatively high spatial variability and were positively and linearly correlated with microtopography (represented by elevation in the analysis) ($P < 0.03$, $R^2 > 0.77$). Further analysis showed that biomass yields were negatively correlated with SEW ($P < 0.001$, $R^2 > 0.6$) with an exponential relationship. Results of this study strongly demonstrated transient waterlogging could negatively affect switchgrass growth by suppressing leaf-level gas exchange rates and ultimately reducing biomass yield. Findings from this study have critical implications for evaluating the economic viability of growing switchgrass on marginal lands that are subject to transient waterlogging stresses.

Keywords: gas exchange, marginal land, microtopography, productivity, switchgrass, waterlogging

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Introduction

Bioenergy derived from the second-generation bioenergy crops, such as lignocellulosic perennial grasses (e.g., switchgrass and Miscanthus), can potentially contribute to future global energy security (Mclaughlin & Kszos, 2005; Heaton et al., 2008; Schmer et al., 2008; Dale et al., 2014). They have received significant attention because of their ability to grow in suboptimal conditions with considerably less inputs (e.g., fertilizer and pesticides) and management (e.g., soil disturbance and tillage) compared to other crops (e.g., corn) (Tilman et al., 2006; Schmer et al., 2008). They can therefore be possibly grown on marginal lands to avoid interference with food production on fertile land, which is a limited resource worldwide (Emery et al., 2017). Marginal land, though not strictly defined, generally refers to fields that are unsuitable for food production due to various biotic and/or abiotic stresses, among which water stress is frequently mentioned (Jones et al., 2015; Quinn et al., 2015). Therefore, understanding the impacts of water stress (e.g., drought and waterlogging) on growth and productivity of bioenergy grasses on marginal land is important for selecting site suitable genotypes with specific...
morphological and physiological traits (Jones et al., 2015; Song et al., 2016). Such information is also fundamental for developing proper management practices with minimum inputs to secure expected ecological benefits and economic viability (Lemus et al., 2014; Blanco-Canqui, 2016).

Switchgrass (*Panicum virgatum* L.), a C4 perennial grass native to the North American prairie, was chosen by the United States Department of Energy (DOE) as a model herbaceous energy crop (Sanderson et al., 1997) with high annual biomass productivity (Mclaughlin & Kszos, 2005; Wullschleger et al., 2010). Previous studies have investigated growth responses of various ecotypes of switchgrass to several nonwater-related stresses, such as salinity (Kim et al., 2012; Anderson et al., 2015; Hu et al., 2015), nutrients (Ma et al., 2001; Stroup et al., 2003; Heaton et al., 2004; Arundale et al., 2014; Liu & Basso, 2016; Fike et al., 2017), high temperature (Knapp, 1985; Hartman & Nippert, 2013), and low temperature (Cordeiro & Osborne, 2017). With respect to water stress, switchgrass, especially upland cultivars, has been believed to be drought tolerant (Sanderson & Reed 2000; Heaton et al., 2004; Hartman et al., 2012) because of its high capability to develop deep root systems under dry conditions. While responses of switchgrass growth to drought are subject to switchgrass ecotypes, studies typically reported negative impacts of water deficit on switchgrass productivity (Stroup et al., 2003; Heaton et al., 2004; Xu et al., 2006; King et al., 2013; Liu et al., 2015; Joo et al., 2016; Liu & Basso, 2016; Hawkes & Kiniry, 2017).

On the other hand, excessive water in the root zone, that is, waterlogging, which may result in hypoxic or anoxic condition, has long been identified as a major abiotic factor constraining plant growth and development (Parent et al., 2008) and is a widespread problem for crop production (Feick et al., 2005; Lesk et al., 2016). However, impacts of waterlogging on switchgrass growth have not been adequately investigated. Past greenhouse studies using transplanted switchgrass showed that the lowland ecotypes (Alamo and Kanlow) could be relatively productive under flooding conditions (Porter, 1966; Barney et al., 2009). Such laboratory results might imply that lowland ecotypes are not susceptible to excess soil water conditions, which is contrary to our field observations (Fig. 1a, unpublished information) and annual biomass yield measurements (Fig. 1b) in the coastal plain of North Carolina, USA. We observed that switchgrass (Alamo) in our study fields was susceptible to excess water stress with severely poorer growth in depressions compared to adjacent high microtopographic positions (Fig. 1a). The uneven microtopography of the soil surface could induce spot specific transient waterlogging condition. Annual aboveground biomass yield in 2012 (the 4th year after planting), with an extremely wet period early in the growing season (wettest May on record), was much lower compared to yields in 2011 and 2013 (Fig. 1b). We therefore surmised that the lower yield in 2012 and the overall low annual biomass yield of our study site (less than 5 Mg ha$^{-1}$) were possibly caused by the excessive wet condition of the naturally poorly drained soil on the site. Our deductions are consistent with a recent field study conducted in Boone County, Iowa, showing a significant drop in switchgrass (Kanlow) yield during a year with historical flooding from June until August (Wilson et al., 2014). Another field study reported significantly lower biomass yield of switchgrass (Alamo) in a floodplain, compared to a nearby upland zone in Tennessee, USA (Mooney et al., 2009). Very limited information from field experiments is available with respect to physiological responses of lowland ecotypes of switchgrass to waterlogging conditions. Such information is very critical for cultivating...
switchgrass for bioenergy production in waterlogging susceptible regions, especially waterlogging that is likely to be exacerbated by the increase in frequency of extreme events caused by climate change (Alexander et al., 2006).

The main objective of this study was to investigate the impacts of transient waterlogging induced by uneven microtopography of soil surface on switchgrass (Alamo) growth in two established switchgrass fields located in the lower coastal plain of North Carolina, USA. Field experimental measurements including leaf-level gas exchange rates and spatial variations of biomass yield were used to demonstrate local switchgrass growth responses to transient waterlogging.

Materials and methods

Study site

Field measurements were conducted at an established experimental site (35°15’N, 77°27’W) located in Lenoir County in the Coastal Plain of North Carolina, USA (Fig. 2a and b). The experimental site is owned and operationally managed by Weyerhaeuser NR Company. The soils on the site are naturally poorly drained Pantego and Rains soil series. The top 10 cm of the soil profile has a mean bulk density of 1.17 g cm⁻³ and a mean porosity of 0.5 cm³ cm⁻³ (Cacho et al., 2015). In early 1970s, a network of open ditches (Fig. 2c) were dug 1.0–1.2 m deep at 100 m spacing to improve trafficability and provide desirable soil water conditions for loblolly pine (Pinus taeda L.). Long-term mean annual precipitation and temperature were 1252 mm and 16.5 °C, respectively (Albaugh et al., 2012). On average, the greatest seasonal amount of precipitation occurred during summer (Fig. 2d). The study site was initiated to investigate sustainability and productivity of loblolly pine and switchgrass intercropping to produce sawtimber and bioenergy feedstocks (Albaugh et al., 2012; Tian et al., 2015, 2017). Multiple experimental treatments including switchgrass and pine monocultures, and pine-switchgrass intercropping were established in a randomized complete block design (Albaugh et al., 2012). The pre-existing 34-year-old loblolly pine stand was harvested in September 2008 and prepared (V-shearing and root-raking) for switchgrass (Alamo cultivar) planting in June 2009. This current study was conducted on two blocks of the experimental site (Fig. 2c). Switchgrass was machine-seeded at a depth of 6 cm in June 2009 at 9 kg pure live seed ha⁻¹ in rows spaced 38 cm apart. The switchgrass received coated urea Arborite fertilizer (65.6 kg N ha⁻¹, 6.6 kg P ha⁻¹, and 0.2 kg boron ha⁻¹) during 2010, 2012, and 2014, but not during 2015 and 2016). Detailed descriptions of the study site, experimental design, and treatments can be found elsewhere (Albaugh et al., 2012, 2014; Tian et al., 2015, 2017).

Data collection

Physiological measurements. Leaf-level gas exchange (CO₂ and H₂O) was measured at Block 1 (Fig. 2) during the peak growing season (May to September) of 2015 to quantify net CO₂ assimilation ($A_{net}$) and stomatal conductance to water...
Table 1 Summary of six plots within three sub-blocks where the intensive physiological summer campaign was conducted on Block 1 (Fig. 2) in 2015

| Sub-block | Treatment | Plot indication | A | B | C |
|-----------|-----------|-----------------|---|---|---|
|           | High      | P1              | 0.26 | 0.20 | 0.20 |
|           | Low       | P2              | −0.09 | 0.03 | 0.08 |
| A          | High      | P3              | 0.20 | 0.03 | 0.08 |
|           | Low       | P4              | 0.09 | 0.20 | 0.03 |
| B          | High      | P5              | 0.09 | 0.20 | 0.03 |
|           | Low       | P6              | 0.09 | 0.20 | 0.03 |

The information includes plot relative elevation and soil properties, leaf area index (LAI), and aboveground biomass productivity. 'High' and 'low' indicate the assignment to replicated treatment (high vs. low elevation subplots) within each sub-block.

vapor (g). We also computed leaf-level intrinsic water-use efficiency (WUE), which is defined as the instantaneous ratio between $\Lambda_{\text{sat}}$ and $g$. These variables were used to represent leaf-level physiological responses of switchgrass to soil water conditions. Following the principle of randomized block design, three sub-blocks in Block 1 were chosen, and within each sub-block, two nearby plots with contrasting elevations were set up (Fig. 2 and Table 1). In other words, we triplicated two treatments (high and low microtopographic positions) in three sub-blocks, which were the main statistical units. At each subplot of 1 m², we selected 10 leaves from 10 stems and measured gas exchange from 08:00 to 14:00 hours. We used the same plants for the entire campaign unless they showed symptoms of obvious stress or damage (change in color, curling etc.). The measurements of leaf-level gas exchange rates were conducted only during the growing season of 2015, which should be representative and replicable because the site has been well established since 2009.

For each plant, we selected sunlit leaves from the upper quarter of the canopy and measured gas exchange using two LI-COR 6400 instruments (LI-COR Inc., Lincoln, NE, USA). The air temperature and humidity within the cuvettes were kept at ambient conditions (i.e., within 30–38 °C and 40–60%, respectively), CO₂ concentration was set to 400 µmol mol⁻¹, and photosynthetically active radiation (PAR) to 1500 µmol m⁻² s⁻¹, that is, close to light saturated level (Tian et al., 2017). We conducted field measurements bivewely during most of the expediments period and weekly after heavy storm events with a total of 11 field campaigns of gas exchange measurements during the 2015 growing season. The measurements were typically split into two sampling periods: the first was conducted between 08:00 and 11:00 hours and the second from 11:00 to 14:00 hours. Given the number of the plots and leaves, we had 120 data points for each day except on DOY 133, 244, and 259 when we only made 60 measurements (either due to instrument malfunction or adverse weather conditions) during the first sampling period. To minimize any potential instrument artifact, we calibrated both gas exchange systems at the beginning of the campaign and then regularly checked stability of the system by comparing zero and span against the reference gas in the laboratory. In addition, (i) we shifted the instruments between two measurement periods so each leaf was measured by both instruments within a day; and (ii) we initiated each measurement campaign with a different instrument as compared to preceding campaign at the same plot. We did not observe any significant effect of the instrument nor time of measurement, so all measurements made on the same day for each leaf were aggregated. The cuvette of LI-COR 6400 has dimensions of 2 × 3 cm. As switchgrass leaves were typically thinner than 2 cm, we measured the diameter of each leaf to scale up all leaf gas exchange measurements into proper units of 1 m² of leaf area. Data from all gas exchange measurements were visually screened for assessing data quality and obvious outliers were removed. We removed all data points which were of the 95% confidence interval of the Gaussian distribution. On average, data filtering resulted in less than 20% removal of data. One-sided projected stand leaf area index (LAI, m² m⁻²) was measured using an AccuPAR LP-80 (Decagon Devices Inc., Pullman, WA, USA) at each plot during 5 days throughout the 2015 intensive summer campaign. The LAI measurements were conducted around noon time under clear sky conditions by taking 10 readings within each plot.

Annual aboveground biomass yield. Destructive samples of switchgrass were collected from multiple plots with different microtopography at the end of growing season (November) of 2015 and 2016 to determine the impacts of microtopography on aboveground biomass yield. Four sampling transects were set up across each block, and five samples were randomly taken from each transect to represent the average site condition. Six additional grass samples were collected from each subplot where gas exchange rates measurements were conducted in 2015. Sampling area was restricted by a 1 × 1 m quadrat made of polyvinyl chloride (PVC) pipes. Switchgrass shoots were cut 10 cm above the ground surface using hedge shears. Samples were placed in paper bags and transported to the laboratory for processing. Grass samples were oven-dried at 70 °C for approximately 48 h to a constant mass and weighed to obtain the dry weight biomass. Overall, a total of 46 and 40 grass samples was collected in 2015 and 2016, respectively. Each subplot
was surveyed at five random points to get its mean relative elevation based on a datum set up at the groundwater-level monitoring well located at the center of each block.

**Soil chemical and textural analyses.** To account for possible effect of soil physical and chemical properties on the observed spatial variation of biomass yield, we collected soil samples along with grass sampling at each subplot in November of 2016. Two composite samples at two depths (0–20 and 20–40 cm) were collected from three soil samples randomly collected from individual subplot using a hand auger (2 cm diameter). A portion of well-mixed soil samples was air-dried and analyzed for total carbon (TC) and total nitrogen (TN) via total combustion method using TruMac CNS Determinators (LECO, Saint Joseph, MI, USA). Particle size distribution analysis was conducted using the hydrometer method.

**Water table depth.** Water table depth (WTD) was recorded every 15 min at the center of each study field since September of 2009 using a U20 HOBO (Onset Computer Corp., Inc., Bourne, MA, USA) water-level logger, a pressure-based logger with an accuracy of 3 mm. The logger was placed inside a monitoring well made of 5-cm-diameter nonstructural PVC pipes to record pressure and temperature simultaneously. The pipe was installed about 2.3 m deep and the logger located approximately 6–8 cm from the bottom of the well. In addition to the water table measuring wells, an additional logger was placed in a pipe above water level to collect barometric pressure. Water-level data were collected using HOBO waterproof shuttle (U-DTW-1) with a coupler (COUPLER2-B) (Onset Computer Corp., Inc.). The collected data were processed using HOBOware pro software (Onset Computer Corp., Inc.) to obtain accurate water-level reading after compensating for barometric pressure, temperature, and water density.

**Data analysis**

**Intensity of waterlogging.** In order to quantify the impacts of waterlogging on aboveground biomass yield, we adopted a metric called the sum of excess water (SEW) to quantify the intensity of waterlogging. This empirical metric is based on soil WTD and has been widely used to determine waterlogging intensity and provide a quantitative way of determining the amount of stress on crop growth during the growing season (Shaw & Meyer, 2015). Several studies found strong correlation between the SEW and crop yield (Kanwar et al., 1988; Malik et al., 2002; Marti et al., 2015). It has also been adapted by various models, such as DRAINMOD (Skaggs et al., 2012), Agricultural Production Systems Simulator (APSIM) (McCown et al., 1996), and Salt Water And Groundwater MANagement (SWAGMAN) Destiny (Destiny) model (Shaw & Meyer, 2015). The SEW method (Sieben, 1964) for a growing season lasting N days is calculated as:

\[
\text{SEW} = \sum_{i=0}^{N-1} \max(\text{WTD}_{\text{ct}} - \text{WTD}_{0}),
\]

where WTD is the water table depth (m) at day \(i\); \(\text{WTD}_{\text{ct}}\) is a specified water table depth smaller than that considered to cause excess water stress. In our study, we set the WTD as 0.30 m and the sum of excess water is abbreviated as SEW30. As switchgrass is a perennial species and may be vulnerable to waterlogging during the dormant period as well, we computed the SEW30 separately for growing season only (April to September), which is termed as SEW30GW and the whole year (October of the previous year to September of the current year), which is termed as SEW30WY.

**Statistical analysis.** Statistical analysis was completed using the generalized linear model (GLM) in SAS 9.4 (SAS Institute Inc. 2012). The statistical model in this analysis is described in Eqn (2):

\[
Y_{ijk} = \mu + a_i + b_j + (ab)_{ij} + (bt)_{jk} + (bt)_{ijk} + e_{ijk},
\]

where, \(Y_{ijk}\) = predicted response variables (\(A_{\text{net}}\), \(S\), and WUE) in \(i\)th treatment, \(j\)th sub-block, and \(k\)th time; \(\mu\) = overall mean; \(a_i\) = fixed effect of \(i\)th treatment; \(b_j\) = random effect of \(j\)th sub-block; \(t_k\) = fixed effect of \(k\)th time; \((ab)_{ij}\) = \(i\)th treatment-\(j\)th sub-block interaction; \((bt)_{jk}\) = \(i\)th treatment-\(k\)th time interaction; \((bt)_{ijk}\) = \(i\)th treatment-\(j\)th sub-block-\(k\)th time interaction; \(e_{ijk}\) = error in observation on a response variable at the \(i\)th block, \(j\)th treatment, and \(k\)th time.

Sub-block was treated as a random effect to account for not only variation in soil or other environmental conditions across the field, but also the variation of elevation difference among sub-blocks (Table 1). Interactions between sub-block and other factors were also treated as random factors. Tukey’s honestly significant difference post hoc test with Westfall’s adjustment for multiplicity (Westfall, 1997; Bretz et al., 2010) was subsequently applied on the mixed effects linear models to identify statistically significant differences in particular interactions between the fixed effects. Assumptions on distributions of residuals of the linear models were checked by visual inspection of quantile-quantile probability plots and by analysis of skewness and kurtosis and additionally by Shapiro–Wilks test. Effects were considered as significant when \(P < 0.05\) and as marginally significant for \(0.05 < P \leq 0.1\).

Given the fact that elevations of each subplot with gas exchange measurements are different, a pairwise comparison was carried out to further explore the impacts of microtopography-induced transient waterlogging on switchgrass growth. We computed ratios of the daily mean gas exchange rates (\(A_{\text{net low}}/A_{\text{net high}}\), \(S_{\text{low}}/S_{\text{high}}\), \(G_{\text{low}}/G_{\text{high}}\)) between each pair of all investigated subplots (low divided by high plot) and further correlated with concurrent WTD of the measurement day. Consequently, the six subplots yielded 15 pairwise comparisons. Ratio less than 1 suggests higher gas exchange rates for high elevation subplots and \textit{vice versa}. In other words, values of \(A_{\text{net low}}/A_{\text{net high}}\) could be less than or higher than unity, suggesting waterlogging and drought stresses, respectively, or close to unity, suggesting no water stress. Calculated ratios of each pair were plotted against concurrent WTD of the measurement day, and a linear relationship was established to describe their correlations. In addition, we conducted the Tukey’s honestly significant difference (THSD) post hoc test with Westfall’s adjustment for multiplicity of the mixed linear model (treating
each day as a separate experiment) to assist the pairwise comparisons (results shown as Table S1).

A linear mixed effect model was used to determine the impacts of elevation, soil chemical, and physical properties on aboveground biomass yield of switchgrass at each subplot with clipping samples. Sub-block was considered as a random factor. Collinearity examination was checked based on the variance inflation factor (VIF) and removed factors with VIF larger than 10. The collinearity examination suggested removal of either TN or TC and sand or silt from soil chemical and physical properties, respectively. The remaining independent variables were elevation, total carbon content, clay fraction, and sand fraction (Fig. S1). We used simple linear regression to analyze the effects of elevation and SEW30 on spatial variations of aboveground biomass yield.

Results

Temporal and spatial variation of switchgrass leaf-level gas exchange

During the study period of gas exchange measurements, WTD fluctuated from soil surface to as deep as 1.5 m. Both \( A_{\text{net}} \) and \( g_s \) showed significant \((P < 0.001)\), relatively consistent, decreasing trends with time (Fig. 3). Throughout the season, \( A_{\text{net}} \) decreased from 34 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) to 17 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) on average in the high microtopographic positions (Fig. 3, Table 2). While less pronounced, the decline trend of \( A_{\text{net}} \) from about 27 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) to less than 16 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) for switchgrass growing at low positions was still detectable. Measured \( g_s \) showed similar seasonal trends in both treatments. The mean \( g_s \) in high positions declined from 203 mmol m\(^{-2}\) s\(^{-1}\) in May to 110 mmol m\(^{-2}\) s\(^{-1}\) in September, while it decreased from 175 to 100 mmol m\(^{-2}\) s\(^{-1}\) in the low positions. In contrast to \( A_{\text{net}} \) and \( g_s \), WUE did not show a consistent decreasing trend, yet its overall decline trend was still significant \((P = 0.04 \text{ and } P = 0.005 \text{ for high and low positions, respectively})\). Remarkably, WUE was initially increasing and positively correlated with WTD during May and June. During the same period, we observed the most pronounced differences in gas exchange between the high and low positions and the most rapid leaf area growth (Fig. 3), indicating the importance of this period for the aboveground biomass accumulation.

Statistical analysis (Table 2) showed that \( A_{\text{net}}, g_s, \) and WUE were significantly dependent on DOY \((P < 0.0001)\), treatment \((P \leq 0.0001)\), sub-block \((P \leq 0.001)\), and their interactions \((P \leq 0.04)\). There were three large storm events raising WTD to less than 30 cm during the study period. After the first two storm events (occurred on DOY 131 and 155), \( A_{\text{net}} \) and \( g_s \) of switchgrass at high positions were significantly \((P < 0.05)\) higher, compared to switchgrass growing at low positions. The observed difference became insignificant between the two storm events, as suggested by the measurement on DOY 149. After the storm event on DOY 207, \( A_{\text{net}} \) and \( g_s \) of switchgrass declined sharply for both treatments and the treatment effect was undetectable \((P > 0.3)\). On the contrary, \( A_{\text{net}} \) of switchgrass at high positions was significantly \((P < 0.05)\) lower than \( A_{\text{net}} \) of switchgrass growing at low positions when the WTD reached approximately 1 m deep (measurements on DOY 184 and 196). Nevertheless, measurements of \( A_{\text{net}} \) and \( g_s \) did not show statistically significant \((P > 0.4)\) difference between grass at high and low positions on DOY 245 when WTD reached 1.2 m deep. These temporal changes of treatment effects on gas exchange led to a significant \((P < 0.001)\) treatment \( \times \) DOY interaction for both \( A_{\text{net}} \) and \( g_s \). Because of the similar responses of \( A_{\text{net}} \) and \( g_s \) to treatments and DOY, impacts of treatments, sub-block, DOY, and their interactions on WUE, were less evident, but still significant (Table 2).

In line with the relatively narrow range of observed WUE, \((P < 0.001)\), \( A_{\text{net}} \) was closely related to \( g_s \) (Fig. 4a). This significant \((P < 0.001)\) nonlinear relationship was characterized by smaller increases of \( A_{\text{net}} \) under high \( g_s \) values indicating lower WUE, when stomata were fully open and higher WUE, when stomata were partly closed (Fig. 4b). Overall, we did not observe significant \((P > 0.4)\) differences between high and low positions for \( A_{\text{net}} \) vs. \( g_s \) relationships, nor the corresponding WUE, vs. \( g_s \) relationships.

Pairwise comparisons of gas exchange rates between subplots

The pairwise comparison of \( A_{\text{net}} \) (Fig. 5) generally showed positive relationships between WTD and \( A_{\text{net,low}}/A_{\text{net,high}} \). Specifically, significant \((P < 0.05)\) linear relationships were found for six pair comparisons, including P1–P2, P1–P6, P3–P2, P4–P2, P3–P5, and P4–P6 (Fig. 5) and marginally significant \((0.05 < P < 0.1)\) linear relationship for three pair comparisons (P1–P4, P1–P5, and P3–P6). These pairs typically had larger elevation differences, and correlation coefficients of \((A_{\text{net,low}}/A_{\text{net,high}})\) vs. WTD relationships were higher than 0.65. On the other hand, correlation coefficients became close to zero or even negative for pairs (e.g., P5–P4, P5–P6, and P6–P2) with small elevation differences. Overall, correlation coefficients significantly \((P = 0.004)\) increased with elevation difference between pairs (Fig. 5). Mean daily WTD was shallower than 0.6 m for 5 of 11 days with gas exchange measurements (Fig. 3). There were 11 of 15 paired plots with elevation differences larger than 0.1 m. Integrating these two conditions yielded a total of 55 pair comparisons, of which 44 pair comparisons with ratios of \( A_{\text{net,low}}/A_{\text{net,high}} \) less
than a unity. Furthermore, the ratios of $A_{\text{net,low}}/A_{\text{net,high}}$ were significantly ($P < 0.05$) less than unity for all 18 pair comparisons with elevation differences larger than 0.2 m during days with WTD shallower than 0.6 m (Table S1). The lowest ratio of $A_{\text{net,low}}/A_{\text{net,high}}$ occurred for P1–P5 on DOY 133 with WTD of 0.07 m.

Conversely, we also observed that $A_{\text{net,low}}/A_{\text{net,high}}$ was significantly ($P < 0.05$) higher than unity for 13 pairwise comparisons (Table S1), all of which occurred on DOY with mean WTD deeper than 0.9 m and for paired plots with elevation difference higher than 0.2 m. By examining the scatter plots of $A_{\text{net,low}}/A_{\text{net,high}}$...
A\text{net\_high}) vs. WTD (Fig. 5), one can identify a narrow range of WTD (between 0.6 and 0.8 m) at which A\text{net\_low}/A\text{net\_high} ratios were close to unity. That range can be considered as the desired WTD range at our research site with the established root system.

Similar positive relationships were observed between WTD and $g_{s\_low}/g_{s\_high}$ ratios (Fig. 6). However, the relationships were less evident compared to those of $A_{\text{net}}$, with fewer pair comparisons showing significant positive relationships. Relationships of $(g_{s\_low}/g_{s\_high})$ vs. WTD were found statistically significant ($P < 0.05$) for only three pairwise comparisons (P1–P2, P1–P6, and P4–P6) and marginally significant ($0.05 < P < 0.1$) for two pairs (P1–P4 and P3–P6) (Fig. 6). The ratio of $g_{\text{net\_low}}/g_{\text{net\_high}}$ was less than unity for 37 paired plots with elevation difference greater than 0.1 m on days with WTD shallower than 0.6 m. Additionally, the ratio of $g_{\text{net\_low}}/g_{\text{net\_high}}$ during days with WTD shallower than 0.6 m was significantly ($P < 0.05$) less than unity for all 18 pair comparisons with elevation differences larger than 0.2 m (Table S1). The lowest ratio of $g_{\text{net\_low}}/g_{\text{net\_high}}$ was 0.71 and occurred for P1–P5 on DOY 133 with 0.07 m WTD. Ratio of $g_{\text{net\_low}}/g_{\text{net\_high}}$ was also significantly ($P < 0.05$) greater than unity for nine pairwise comparisons (Table S1), all of which occurred on DOY with mean WTD deeper than 0.9 m and for paired plots with elevation difference higher than 0.2 m. Ratio of $g_{\text{net\_low}}/g_{\text{net\_high}}$ was also close to unity when WTD was between 0.6 and 0.8 m deep.

Effects of microtopography and SEW\textsubscript{30} on aboveground biomass yield

Sampled aboveground biomass yields across study blocks were significantly ($R^2 > 0.75$, $P < 0.001$) and positively correlated with relative elevations for both years (Fig. 7). In spite of the relatively small range of elevations (<0.4 m), aboveground biomass yield depicted very large spatial variations. Mean biomass yield of all samples in both blocks declined from about 1 kg m\textsuperscript{-2} in 2015 to approximately 0.7 kg m\textsuperscript{-2} in 2016. Standard deviations of sampled aboveground biomass yield for both blocks were about 0.7 kg m\textsuperscript{-2} for 2015 and 0.3 kg m\textsuperscript{-2} for 2016. Slopes of linear regression equations significantly ($P = 0.001$) declined from 2015 to 2016 for both blocks. The decline of biomass yield from 2015 to 2016 could be mainly attributed to the wetter growing season in 2016 and the continuous depletion of soil mineral N since the last fertilizer application was in 2014. Except for elevation, effects of all other factors including soil chemical and physical properties on sampled aboveground biomass yields of 2016 (Fig. S1) were not significant.

The relationships between SEW\textsubscript{30} and aboveground biomass yield depicted an exponentially declining trend (Fig. 8) as opposed to the linear relationships between relative elevation and biomass yield at each sampling point (Fig. 7). Aboveground biomass yield sharply declined from above 2 kg m\textsuperscript{-2} to about 0.6 kg m\textsuperscript{-2} as SEW\textsubscript{30,WY} increased from less than 4 m day to 25 m day or as SEW\textsubscript{30,GW} increased from less than 2 m day to 7 m day. Further increase in SEW\textsubscript{30} (SEW\textsubscript{30,WY} > 20 m day or SEW\textsubscript{30,GW} > 6 m day) resulted in smaller decreases in biomass yield. The regression equations of individual years at each block can explain more than 75% of spatial variations in aboveground biomass yield. The overall regression equations combining 2015 and 2016 data explained more than 57% of the spatial variations in aboveground biomass yield at both blocks. The comparable coefficient of determinations between biomass yield and SEW\textsubscript{30,WY} (or SEW\textsubscript{30,GW}) suggested that
SEW30 is a good predictor of biomass productivity response to waterlogging intensity.

Discussions

This study investigated switchgrass gas exchange rates and aboveground biomass yield at subplots with elevation differences (up to 0.34 m) on a study site with poorly drained soil. Seasonal changes and magnitudes of $A_{net}$ and $g_s$ of switchgrass in the present study were comparable to results published elsewhere (Barney et al., 2009; Dohleman et al., 2009; Hartman & Nippert, 2013; Albaugh et al., 2014; Liu et al., 2015; Taylor et al., 2016; Cordero & Osborne, 2017). Estimated aboveground biomass yields were about 7.5 Mg ha$^{-1}$, which is at the lower end of reported switchgrass yields

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but comparable to estimated harvestable biomass production in marginal lands (Qin et al., 2015). Nevertheless, the estimated yield is higher than previously reported biomass yield based on harvested bales (≈6 Mg ha⁻¹ typically measured during December or January) from the same site (Albaugh et al., 2012; Tian et al., 2016). Given the relatively large number of random samplings, we suspect that the discrepancy was possibly caused by previously late harvesting (Waramit et al., 2014) and biomass loss due to inherently lower efficiency of machine operations (Sanderson et al., 1997).

Gas exchange measurements in this study suggested negative responses of switchgrass to both waterlogging and drought (Fig. 3). Leaf-level gas exchange of switchgrass can be negatively affected by transient waterlogging stresses (Fig. 3) after heavy rainfall events that raised WTD to <0.3 m, as suggested by the statistical
analysis results (Table 2). Waterlogging impacts on gas exchange by switchgrass reported in this study are distinct from a greenhouse study that reported no negative impacts of waterlogging on gas exchange of lowland switchgrass cultivar (Barney et al., 2009). Given the lack of information on the impacts of waterlogging on gas exchange of switchgrass in the available literature, more studies are necessary to investigate switchgrass responses to waterlogging under different environmental conditions (e.g., more extreme drought/flooding events) and for other lowland cultivars to validate our findings for broader generalizing. While it was not the objective of this field experiments, gas exchange measurements additionally demonstrated that switchgrass growth was also negatively affected by temporary drought stress, which evidently occurred when WTD is deeper than 0.9 m (Figs 3, 5, and 6). The reductions of $A_{\text{net}}$ and $g_s$ of switchgrass (Alamo) due to drought were comparable to findings of other studies (Barney et al., 2009; Liu et al., 2015; Taylor et al., 2016). Given the relatively high precipitation (Fig. 2) and poorly drained conditions at our study site resulting in high WTD for most of the time, switchgrass could have developed a relatively shallow rooting system (Ferchaud et al., 2015), making the plant more vulnerable to occasional summer water deficit. Additionally, the distribution of precipitation at the site is highly skewed with up to 25% of annual precipitation possibly occurring in a very short period (Fig. 2). In this regard, annual precipitation alone may not be a reliable indicator of water availability for switchgrass growth (Heaton et al., 2004; Wullschleger et al., 2010; King et al., 2013).

We found that treatment impacts on leaf-level gas exchange were significantly subjected to sub-block ($P \leq 0.04$) and DOY ($P \leq 0.03$) (Table 2). The interaction effects between treatment and sub-block mainly due to the elevation differences in paired subplots among sub-blocks (Table 1). This was further confirmed by results of THSD post hoc test (Table S1) and visual pairwise comparisons among all subplots (Figs 5 and 6). The existed interaction between treatment and DOY was mainly due to two mechanisms. First, our 11 times of gas exchange measurements spanned the major growing season and it is known that switchgrass sensitivity to water stress varies at different growing stages (Shaw et al., 2004; Wullschleger et al., 2010; King et al., 2013).
& Meyer, 2015). Secondly, large natural fluctuations of WTD during our study period led to changes of treatment impacts on switchgrass leaf-level gas exchange or even opposite treatment impacts under waterlogging and drought conditions (Fig. 3). The fluctuations of WTD also represented by different antecedent soil water condition and duration of specific event, which will affect switchgrass responses to both waterlogging and drought. The waterlogging condition (WTD shallower than 30 cm) occurring in mid-May lasted for 6 days and was preceded by an extended period (several months) with shallow WTD (about 40 cm deep). In contrast, the WTD was deeper than 1 m for a month prior to the waterlogging event in late July, which lasted for 3 days only. Pairwise comparisons of $A_{\text{net}}$ and $g_s$, measured at subplots with different elevations, further confirmed that switchgrass growing at lower positions tended to have lower gas exchange rates under shallow WTD, and vice versa (Figs 5 and 6).

Stomatal closure was found as one controlling factor that contributed to the decline of $A_{\text{net}}$ of switchgrass under transient waterlogging or drought conditions. This is supported by the strong and significant relationship between $A_{\text{net}}$ and $g_s$ (Fig. 4a) as well as similar responses of $g_s$ to waterlogging (Figs 3 and 6). Decline of CO$_2$ assimilation under transient waterlogging condition could be caused by either stomatal closure and/or nonstomatal metabolic alterations (Liao & Lin, 2001; Parent et al., 2008; Ghannoum, 2009). A reduction in stomatal conductance is the earliest plant physiological response to hypoxic and/or anoxic soil conditions induced by waterlogging or flooding (Parent et al., 2008). The observed responses of switchgrass to waterlogging in this study were clearly associated with this process. However, the differences between treatments were significant mostly for $A_{\text{net}}$ but not for $g_s$ during the latter part of the growing season (Fig. 4). In addition, the ($g_s_{\text{low}}/g_s_{\text{high}}$) vs. WTD relationships of pairwise comparison (Fig. 6) were evidently weaker than that of ($A_{\text{net low}}/A_{\text{net high}}$) vs. WTD (Fig. 5). Thus, further studies are necessary to explore nonstomatal metabolic responses of switchgrass to transient waterlogging.

In the absence of soil water condition and texture information, topography can be used as a proxy variable and is considered a critical factor affecting crop yield (Delin et al., 2000; Iqbal et al., 2005; Huang et al., 2008; Kumbalova et al., 2008; Zipper et al., 2015). We observed significant relationships between aboveground biomass yield and relative elevation in 2015 and 2016 (Fig. 7). The significant relationship between SEW$_{30}$ and biomass yield (Fig. 8) suggests that soil water condition affected by microtopography is a major factor contributing to the large spatial variations of biomass yield of switchgrass at this site. In addition, higher waterlogging intensity in 2016 (Fig. 8) may be primarily responsible for the reduction in aboveground biomass when compared to that of 2015 (Fig. 7), as well as the low biomass yield in 2012 (Fig. 1). Crop susceptibility factors that are dependent on phenological stage need to be developed for switchgrass in order to determine stress day indices (Hiler, 1969), as has been done for other crops, that is, corn and soybean (Evans et al., 1991). Both soil chemical and physical properties did not significantly affect switchgrass yield (Fig. S1), which is different from findings of other studies showing that soil properties (e.g., texture) associated with topography could be a key factor contributing to observed spatial variations of crop yield (Jiang & Thelen, 2004; Iqbal et al., 2005; Hao et al., 2010; Zipper et al., 2015). This could be mainly due to the small scale of our study site with small ranges of soil properties (e.g., clay fraction of 22.4 ± 4.4% and total carbon content within 4.6 ± 1.3%).

It could be an oversimplification to only consider impacts of waterlogging on physiological responses of switchgrass. The yield differences among subplots with gas exchange measurements (Table 1) cannot be fully explained solely by $A_{\text{net}}$ and LAI. Other nonphysiological factors thus deserve further investigations. For example, soil wetness may affect fine root decay during dormant seasons, and the nonstructural carbohydrate storage will further affect early sprouting during the early stage of the forthcoming year. It has been shown that off-season flooding could affect growth, photosynthesis, carbohydrate partitioning, and nutrient uptake of an evergreen shrub (Liu et al., 2014). Additionally, vegetation typically tends to allocate more assimilated carbon to aboveground components under wetter soil conditions (Chaves et al., 2002; Poorter et al., 2012). Waterlogging-induced reduction in root biomass has been observed for other C4 species such as ryegrass (McFarlane et al., 2003), some bluegrass cultivars (Jiang & Wang, 2006; Wang & Jiang, 2007), and some tropical forage grasses (Baruch, 1994). These legacies of localized transient waterlogging related to microtopography could accordingly increase the vulnerability of switchgrass to excess soil water conditions in the root zone. As an example, a recent field study reported that growth responses of switchgrass (both lowland and upland ecotypes) to drought are subject to precipitation legacies of previous years (Hawkes & Kiniry, 2017). These legacies effects in field studies could be the main factor contributing distinct findings between greenhouse studies using transplants (Porter, 1966; Barney et al., 2009) and the present field study, as well as others (Mooney et al., 2009; Wilson et al., 2014). Further, switchgrass may respond differently to transient waterlogging condition in the field, compared to continuous flooding in greenhouse studies (Morales-Olmedo et al., 2015).

Implications and recommendations

Waterlogging impacts on switchgrass yield have been largely overlooked. This study observed significant reductions of $A_{\text{net}}$ and $q_{\text{so}}$ and aboveground biomass yield of switchgrass in response to transient waterlogging (Fig. 2). The close relationships between SEW_{30} and aboveground biomass yield (Fig. 8) clearly suggested negative impacts of transient waterlogging on switchgrass productivity at our study site. Similar negative impacts of waterlogging on Miscanthus were reported in other studies (Zimmermann et al., 2014; Lord, 2015). Our findings have critical implications for cultivating switchgrass in low landscapes with naturally poorly drained soils. Crop cultivation, especially corn, another C4 species, on poorly drained lands of U.S. Midwest and U.S. Southeast typically requires improvement of land drainage via surface and subsurface drainage systems. Subsurface drain spacing typically ranges from 20 to 40 m (Skaggs et al., 2012), but can be as great as 100 m when improved surface drainage is used. Wide drain spacing of 100 m or greater with unimproved surface drainage is common for loblolly pine plantations in eastern North Carolina (Skaggs et al., 2016) as loblolly pine is not as susceptible as corn to periodic waterlogging. A process-based modeling tool, such as DRAINMOD-GRASS (Tian et al., 2016), can help design suitable water management systems for cultivating switchgrass on naturally poorly drained soils where excessive water in the root zone is expected to suppress grass growth and productivity.

Although the term ‘marginal land’ has not been strictly defined (Emery et al., 2017), waterlogging/poor drainage is certainly a characteristic that could lead to a designation of ‘marginal’ for land that is to be cultivated (NijSen et al., 2012; Shortall, 2013; Emery et al., 2017). Many studies have been conducted to assess the availability of marginal land regionally (Gopalakrishnan et al., 2011; Gelfand et al., 2013), nationally (Zumkehr & Campbell, 2013; Milbrandt et al., 2014; Emery et al., 2017), and globally (Campbell et al., 2008; Cai et al., 2011) for cultivating second-generation bioenergy crops including switchgrass and Miscanthus for bioenergy production. To our knowledge, however, existing studies seldom accounted for the negative impacts of waterlogging on biomass yield of bioenergy crops. While further validations of our results are necessary for other regions and other lowland cultivars of switchgrass, the present study evidently suggests that more emphasis must be given to this important abiotic factor on biomass yield and economic return of switchgrass grown on ‘marginal lands’ that are subject to transient waterlogging. Water-tolerant herbaceous species, such as reed canary grass (Phalaris arundinacea), or woody species such as American sycamore (Domenc et al., 2017; Fischer et al., 2017), may be better suited for bioenergy production in low topographic or otherwise poorly drained areas (Lord, 2015).

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Supporting Information

Additional Supporting Information may be found online in the supporting information tab for this article:

Table S1. A Tukey’s honestly significant difference (THSD) post-hoc test with Westfall’s adjustment for multiplicity of the mixed linear model treating each day as a separate experiment.

Figure S1. Relationships between aboveground biomass yield of 2016 and elevation, soil chemical and physical properties.