

ORIGINAL RESEARCH

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## Photosynthetic responses of switchgrass to light and CO<sub>2</sub> under different precipitation treatments

Running title: Photosynthetic responses of switchgrass

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## 27 **Abstract**

28 Switchgrass (*Panicum virgatum* L.) is a prominent bioenergy crop with robust resilience to  
29 environmental stresses. However, our knowledge regarding how precipitation changes affect  
30 switchgrass photosynthesis and its responses to light and CO<sub>2</sub> remains limited. To address this  
31 knowledge gap, we conducted a field precipitation experiment with five different treatments,  
32 including -50%, -33%, 0%, +33%, and +50% of ambient precipitation. To determine the  
33 responses of leaf photosynthesis to CO<sub>2</sub> concentration and light, we measured leaf net  
34 photosynthesis of switchgrass under different CO<sub>2</sub> concentrations and light levels in 2020 and  
35 2021 for each of the five precipitation treatments. We first evaluated four light and CO<sub>2</sub> response  
36 models (i.e., rectangular hyperbola model, nonrectangular hyperbola model, exponential model,  
37 and the modified rectangular hyperbola model) using the measurements in the ambient  
38 precipitation treatment. Based on the fitting criteria, we selected the nonrectangular hyperbola  
39 model as the optimal model and applied it to all precipitation treatments, and estimated model  
40 parameters. Overall, the model fit field measurements well for the light and CO<sub>2</sub> response

curves. Precipitation change did not influence the maximum net photosynthetic rate ( $P_{max}$ ) but influenced other model parameters including quantum yield ( $\alpha$ ), convexity ( $\theta$ ), dark respiration ( $R_d$ ), light compensation point ( $LCP$ ), and saturated light point ( $LSP$ ). Specifically, the mean  $P_{max}$  of five precipitation treatments was  $17.6 \mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$ , and the ambient treatment tended to have a higher  $P_{max}$ . The +33% treatment had the highest  $\alpha$ , and the ambient treatment had lower  $\theta$  and  $LCP$ , higher  $R_d$ , and relatively lower  $LSP$ . Furthermore, precipitation significantly influenced all model parameters of  $\text{CO}_2$  response. The ambient treatment had the highest  $P_{max}$ , largest  $\alpha$ , and lowest  $\theta$ ,  $R_d$ , and  $\text{CO}_2$  compensation point  $LCP$ . Overall, this study improved our understanding of how switchgrass leaf photosynthesis responds to diverse environmental factors, providing valuable insights for accurately modeling switchgrass ecophysiology and productivity.

## KEYWORDS

switchgrass, bioenergy crop, precipitation change, nonrectangular hyperbola model, light-response curve,  $\text{CO}_2$ -response curve

## 1 | INTRODUCTION

Climate change is escalating due to continued greenhouse gas emissions. These emissions primarily result from human activities such as deforestation, burning of fossil fuels, and agricultural practices (Mann & Kump 2015; Ritchie et al. 2020). The global average surface temperature has increased, with projections indicating an additional  $0.5^\circ\text{C}$  rise by 2050 (Fawzy et al. 2020; Stein 2022). Consequently, the water cycle is expected to accelerate. Heightened atmospheric moisture from a warmer planet is anticipated to lead to more frequent and intense

extreme precipitation events, such as severe drought and flooding (Trenberth, 2011; Vanaja et al. 2011; Pfahl et al. 2017; Douville et al. 2021; Pörtner et al. 2022). These altered precipitation patterns could significantly impact the structure and functioning of ecosystems (Hajek & Knapp 2022). Despite this, the specific effects of climate change, including changes in precipitation, on bioenergy crops like switchgrass (*Panicum virgatum* L.), remain insufficiently explored (Parrish and Fike 2005; Tulbure et al. 2012; O’Keefe et al. 2013; Deng et al. 2017).

Switchgrass (*Panicum virgatum* L.) is a C<sub>4</sub> perennial warm-season grass native to North America, originally spanning most of North America. Its habitat extends from southern Canada to Central Mexico (Lemus et al. 2008; Vogel et al. 2011). Remarkably productive, switchgrass thrives in a wide range of abiotic conditions and flourishes in soils with pH ranging from 3.9 to 7.6 (Rinehart 2006). Notably, it possesses favorable attributes, including lower nutrient demands and high below-ground carbon sequestration, making it a model bioenergy crop (Parrish and Fike 2005; Adler, et al. 2006; Rinehart 2006; Albaugh et al. 2014; Liu et al. 2022; Ricketts et al. 2023). Extensive research has explored the effects of agricultural practices like nutrient applications, irrigation, and cutting systems, on switchgrass productivity (Alder et al. 2006; Lemus et al. 2008; Wulschleger et al. 2010; Miesel et al. 2017; Hui et al. 2018; Keyser et al. 2022; Kieffer et al. 2023). However, there have been limited studies focused on understanding the impacts of climate change, such as changes in precipitation, on switchgrass, particularly in field conditions (Hartman et al. 2012; Hartman and Nippert 2013; O’Keefe et al. 2013; Deng et al. 2017).

In addition, there is an incomplete understanding of switchgrass leaf photosynthesis responses to variations in light and carbon dioxide (CO<sub>2</sub>) levels. Photosynthesis, a fundamental biological process, plays a pivotal role in plant growth, development, biomass productivity, and

yield potential (Yang et al. 2010; Ma et al. 2021; Song et al. 2021). Enhancements in plant productivity are often correlated with increased photosynthesis (Fischer et al., 1998; Song et al. 2021). Environmental factors such as cultivar, light, CO<sub>2</sub>, humidity, temperature, and nutrient availability, have the potential to significantly influence leaf photosynthesis (Ma et al. 2021). For example, Barney et al. (2009) observed a variation in leaf photosynthesis ranging from 16 to 22  $\mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$  among six switchgrass cultivars. In a mesocosm study, Hui et al. (2018) found that increased precipitation enhanced leaf photosynthesis, while reduced precipitation did not induce changes in leaf photosynthesis. However, there is a limited understanding of how photosynthesis responds to different precipitation intensities. Few studies have examined how changes in precipitation alter the interplay of photosynthesis with light availability and CO<sub>2</sub> concentration. The efficiency of light and CO<sub>2</sub> use in photosynthesis is critical to switchgrass biomass production and environmental adaptation (Hui et al. 2001; Song et al. 2021) and is key to parameterizing photosynthesis in plant growth and ecosystem-scale models (Harley and Baldocchi 1995, Yang et al. 2010; Lobo et al. 2013; Herrmann et al. 2020)

Photosynthetic light response curves ( $P_n$ -I) and photosynthetic-CO<sub>2</sub> response curves ( $P_n$ -CO<sub>2</sub>) are important for understanding how plants respond to climate change (Leverenz 1988; Bukhov et al. 1995; Lobo et al. 2013; Xu et al. 2019; Ma et al. 2021).  $P_n$ -I response curves depict the relationship between the net photosynthetic rate ( $P_n$ ) of plants and the photon flux density (Irradiance, I), while  $P_n$ -CO<sub>2</sub> response curves describe the relationship between  $P_n$  and CO<sub>2</sub> concentration (Song et al. 2021). These response curves enable the description of essential physiological parameters in plants (Lobo et al. 2013; Herrmann et al. 2020; Song et al. 2021; Ma et al. 2021; Liu et al. 2022), including the maximum net photosynthetic rate ( $P_{max}$ ), apparent quantum yield ( $\alpha$ ), convexity ( $\theta$ ), dark respiration rate ( $R_d$ ), light or CO<sub>2</sub> compensation point

(*LCP*), and light or CO<sub>2</sub> saturation point (*LSP*) (Ye 2010; Lang et al., 2013; Ma et al. 2021). The construction of *Pn-I* or *Pn-CO<sub>2</sub>* response curves involves measuring leaf photosynthesis at varying light or CO<sub>2</sub> levels, ranging from zero to saturating levels (1500 or 2000  $\mu\text{mol photon m}^{-2}\text{s}^{-1}$  for light, 1200 ppm for CO<sub>2</sub>). Various mathematical models can be employed to derive parameters from these response curves (Lobo et al. 2013; Lang et al. 2013; Song et al. 2021). Accurately estimating the parameters of *Pn-I* or *Pn-CO<sub>2</sub>* response curve under diverse environmental conditions is crucial for revealing the physiological changes that occur under these conditions (Song et al. 2021).

In this study, we conducted a field precipitation experiment in Nashville, TN, simulating a range of precipitation intensities spanning from -50% to +50% of the ambient precipitation levels. These treatments were chosen based on the assessment of the region's interannual precipitation variability, encompassing 80% of the total observed variation in precipitation amount over the past 50 years (Deng et al. 2017). Our aim was to investigate how switchgrass photosynthesis responds to varying levels of light intensity and CO<sub>2</sub> concentration under distinct precipitation scenarios. The main objectives of this study included: 1) Determining the most appropriate model for characterizing leaf photosynthetic responses of switchgrass plants to variations in light and CO<sub>2</sub> concentrations; 2) Quantifying the impact of precipitation intensity on leaf photosynthetic parameters under varying light and CO<sub>2</sub> conditions. Our results will be instrumental in improving model simulations that address the responses of switchgrass photosynthesis under different environmental conditions. Additionally, this research will enhance our understanding of the photo-physiological characteristics of switchgrass in the context of future climate change conditions.

## **2 | MATERIALS AND METHODS**

### **2.1 | Experimental facility and design**

In 2015, the Precipitation Experimental Facility was established on pre-existing field switchgrass stands at the Tennessee State University Agricultural Research and Education Center, Nashville, TN (latitude 36.12°N, longitude 86.89°W at an elevation of 127.6 m) (Deng et al. 2017). The seeds of Alamo switchgrass were initially planted in April 2012 in a no-tillage field, and switchgrass stands were already well-established by the time the precipitation facility was built. The area where the precipitation facility is located experiences a warm humid temperate climate, with mean annual precipitation of 1,200 mm and a mean annual temperature of 15.1°C. The soil, classified as Talbott silt clay loam, is slightly acidic.

The detailed experimental design and implementation were provided in Deng et al. (2017). In brief, the experiment included five precipitation treatments: a 50% reduction in precipitation from ambient conditions (-50%), a 33% reduction (-33%), the ambient level (0%), a 33% increase (+33%), and a 50% increase from ambient conditions (+50%). A total of 20 plots were constructed with 4 replicate plots for each treatment. Each plot measured 3 m x 2 m. Precipitation was manipulated using a combined modified rainfall-interception-redistribution (RIR) system (Deng et al. 2017) following the design of Yahdjian and Sala (2002). For drought treatments, precipitation was intercepted using transparent PVC half-tubes. The treatments were validated by collecting precipitation in the treatment plots. The rainwater collected from these PVC half-tubes in the drought plots was subsequently redistributed to the wet treatment plots (Deng et al. 2017).

### **2.2 | Leaf gas exchange measurements**

Leaf photosynthesis measurements were conducted during the peak growing seasons of 2020 and 2021. Field measurements were primarily taken in the morning on sunny days to ensure consistent environmental conditions. For each treatment, two to three healthy and young fully expanded switchgrass leaves were randomly selected and measured using a Li-Cor Portable Photosynthesis System (Li-6800, Li-Cor Inc., Lincoln, NE) connected with LED chamber. The measurements were conducted directly on leaves attached to the plants and completed in two days each time. The  $P_n$ -I and  $P_n$ -CO<sub>2</sub> response curves were constructed using the preset programs in the LI-6800. For  $P_n$ -CO<sub>2</sub> response curves, photosynthesis measurements were taken at CO<sub>2</sub> concentrations descending from near ambient: 400, 300, 200, 100, 50, and 0 ppm, then ascending to saturation: 400, 400, 600, 800, 1000, and 1200 ppm. The light level was set at 1500  $\mu\text{mol photon m}^{-2}\text{s}^{-1}$  during CO<sub>2</sub> response curve measurements. For  $P_n$ -I response curves, photosynthesis measurements were taken at descending light levels: 1500, 1200, 900, 600, 300, 150, 50, and 0  $\mu\text{mol photon m}^{-2}\text{s}^{-1}$ , while CO<sub>2</sub> concentration was set at 400 ppm. Temperature was not controlled during the measurements. In total, 5 to 12 light response curves and 7 to 10 CO<sub>2</sub> response curves were generated for each precipitation treatment over the two-year period. Totally, 38 light response curves and 45 CO<sub>2</sub> response curves were measured.

## **2.3 | Data analysis**

### **2.3.1 | Light and CO<sub>2</sub> response curves modeling**

Four models have been commonly fitted to light- or CO<sub>2</sub>-response curves: the rectangular hyperbola model, the nonrectangular hyperbola model, the exponential model, and the modified rectangular hyperbola model (Fang et al. 2015; Ma et al. 2021). We applied these four models to the ambient plot response curves measurements and used a model selection approach to identify

the best-fitting model. The selected model was then applied uniformly across all treatments to estimate the physiological parameters at each precipitation treatment. A concise description of each model tested is provided below (Fang et al. 2015; Liu et al. 2019; Lee et al. 2022).

### ***Rectangular hyperbola model***

The equation of the rectangular hyperbola model is shown below:

$$P_n = \frac{\alpha I P_{max}}{\alpha I + P_{max}} - R_d$$

where  $P_n$  is the net photosynthetic rate ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ),  $\alpha$  is the initial quantum efficiency at lower light or  $\text{CO}_2$  condition,  $P_{max}$  is the maximum net photosynthetic rate ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ),  $R_d$  is the dark respiration rate ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ), and  $I$  is photosynthetic active radiation ( $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$ ) (Ma et al. 2021).

### ***Nonrectangular hyperbola model***

The equation of the nonrectangular hyperbola model is shown below:

$$P_n = \frac{\alpha I + P_{max} - \sqrt{(\alpha I + P_{max})^2 - 4\alpha\theta I P_{max}}}{2\theta} - R_d$$

where  $\theta$  represents convexity (curvature or rate of bending) of the response curve, and  $P_n$ ,  $\alpha$ ,  $P_{max}$ ,  $R_d$ , and  $I$  have been defined above (Thornley 1998; Ma et al. 2021). To calculate light- or  $\text{CO}_2$ -  $LSP$ , we set  $P_n=80\%$  of  $P_{max}$  and  $90\%$  of  $P_{max}$  and calculated  $LSP$  (0.8) and  $LSP$  (0.9), respectively.

### ***Exponential model***

The equation of the exponential model is shown below:

$$P_n = P_{max} \cdot \left(1 - e^{\frac{-\alpha I}{P_{max}}}\right) - R_d$$

where  $P_n$ ,  $\alpha$ ,  $P_{max}$ ,  $R_d$ , and  $I$  have already been defined above (Ma et al., 2021) and  $e$  represents the base of natural logarithm.

### ***Modified rectangular hyperbola model***

The equation of the modified rectangular hyperbola model is shown below:

$$P_n = \alpha \times \frac{1 - \beta I}{1 + \gamma I} I - R_d$$

where  $\beta$  is the photoinhibition and  $\gamma$  is light saturation and  $P_n$ ,  $\alpha$ ,  $R_d$ , and  $I$  have already been defined above (Ma et al. 2021).

### **2.3.2 | Model fitting and validation**

To determine the optimal model for switchgrass light and CO<sub>2</sub> response curves, we calculated mean square errors (MSE), Akaike Information Criterion Corrected (AIC<sub>C</sub>), Bayesian Information Criterion (BIC), and the coefficient of determination (R<sup>2</sup>) (Brewer et al. 2016; Ma et al. 2021). The optimal fit of the model is determined through the minimization of MSE, AIC<sub>C</sub>, and BIC values, alongside the maximization of R<sup>2</sup> (Brewer et al. 2016).

The data from the eight  $P_n$ -I response curves collected in the ambient precipitation treatment were averaged and used to fit the four models. The same was done for  $P_n$ -CO<sub>2</sub>. Following an evaluation of how well the models fitted to the light and CO<sub>2</sub> response curves derived from ambient conditions, and taking into consideration the biological significance of the model parameters, the nonrectangular hyperbola model was selected as the best performance

model for both light response ( $P_n$ -I) and  $\text{CO}_2$  response ( $P_n$ - $\text{CO}_2$ ) curves. Consequently, the nonrectangular hyperbola model was applied to the  $P_n$ -I and  $P_n$ - $\text{CO}_2$  measurements across the rest of the precipitation treatments and estimate the photosynthetic physiological parameters. To assess the impact of varying precipitation on these parameters, an analysis of variance (ANOVA) with PROC GLM was conducted, accounting for the imbalance in the measured data. Multiple comparison was conducted using Least Significant Difference (LSD) method when a significant effect was detected.

All statistical analyses were conducted using the SAS software (SAS 9.4, SAS Institute Inc., Cary, NC). Model fitting and parameter estimations were conducted using the Proc NLIN. Curves and graphs were constructed using the graphical program GraphPad Prism (GraphPad Software, San Diego, CA USA).

## **3 | RESULTS**

### **3.1 | Model comparison and selection**

Four models were used to fit  $P_n$  with increasing light levels and increasing  $\text{CO}_2$  levels from the ambient/control plots. The modified rectangular hyperbola model demonstrated suboptimal fit for the  $P_n$ -I, contrasting with the superior performance of the nonrectangular hyperbolic model among the four models considered (Fig. 1, Table 1). The nonrectangular hyperbolic model had the lowest BIC and root MSE, highest  $R^2$ , and intermediate AICc, establishing it as the best model for capturing the  $P_n$ -I response. In the case of  $P_n$ - $\text{CO}_2$ , both the rectangular hyperbolic and exponential models did not fit the data (Fig. 2; Table 1). In contrast, both the modified rectangular hyperbolic and the nonrectangular hyperbolic models exhibited the best fit based on

AICc, BIC, and  $R^2$  (Table 1). Given the more biologically meaningful values of certain parameters, such as  $P_{\max}$  and  $\alpha$ , produced by the nonrectangular hyperbolic model, this model was chosen for fitting both  $Pn$ -I and  $Pn$ -CO<sub>2</sub> responses across all precipitation treatments.

## 3.2 | Impact of precipitation on model parameters

### 3.2.1 | Light response

The observed  $Pn$  exhibited a typical response curve to light intensity. Initially negative at zero light intensity,  $Pn$  increased progressively, reaching saturation as light intensity increased. The highest  $Pn$  values ranged from 15 to 20  $\mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$ , depending on the specific precipitation treatment (Fig. 3).

The photosynthetic parameters, including  $P_{\max}$ ,  $\alpha$ ,  $\theta$ , and  $R_d$ , estimated by the nonrectangular hyperbole model and the calculated  $LCP$  and  $LSP$  at 80% and 90% of  $P_{\max}$  were compared across precipitation treatments (Table 2). ANOVA found no significant differences among the precipitation treatments for  $P_{\max}$  (Table 2; Figs. 3 and 4). The mean  $P_{\max}$  across all precipitation treatments was  $21.97 \pm 0.95 \mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$ . There was a slight variation in  $\theta$  among the five treatments, with the smallest observed in the ambient treatment and the largest in the -50% treatment. These variations were not statistically different from the other treatments. For the  $\alpha$  values, the +50% treatment had the lowest ( $0.030 \pm 0.02$ ), while the +33% treatment had the highest ( $0.053 \pm 0.003$ ). No significant differences were found among the ambient, -33%, and -50% treatments. Regarding  $R_d$ , the +50% treatment had the lowest, and the ambient treatment had the highest, with no significant differences from other treatments. For the calculated parameters, the +33% treatment showed the lowest  $LCP$ . Light saturation point ( $LSP$  (0.9))

ranged from  $895.2 \pm 142.89 \mu\text{mol photon m}^{-2}\text{s}^{-1}$  in the -33% treatment to a maximum of  $2243.2 \pm 596.71 \mu\text{mol photon m}^{-2}\text{s}^{-1}$  in the +33% treatments.

### 3.2.2 | CO<sub>2</sub> response

The observed  $P_n$  also exhibited a typical response curve to CO<sub>2</sub> concentration.  $P_n$  was negative when CO<sub>2</sub> concentration was very low and increased progressively. The highest  $P_n$  values ranged from 27 to 33  $\mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$ , depending on the specific precipitation treatment (Fig. 5).

Similarly, we employed the nonrectangular hyperbola model across the precipitation treatments to fit the CO<sub>2</sub> response curves. Then we compared the estimated and calculated photosynthetic parameters across treatments. Overall, all model parameters associated with CO<sub>2</sub> response curves exhibited statistical significance across the precipitation treatments (Table 3; Figs. 5,6). The  $P_{\text{max}}$  reached its peak in the ambient treatment at  $36.1 \pm 2.75 \mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$ ), significantly higher than the rates estimated in the +50% and -50% treatments and exciding those in the +33% and -33% treatments. Notably, the ambient treatment displayed the lowest  $\theta$  among all treatments, while the -33% and +33% treatments exhibited the largest  $\theta$ . The largest  $\alpha$  was observed in the ambient treatment, surpassing those in the +50% and -50% treatments, and exceeding the values in the +33% and -33% treatments. The ambient treatment had the lowest  $R_d$  at  $0.08 \pm 0.04 \mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$ , but no significant difference was observed when compared to the +50% and -50% treatments. The CO<sub>2</sub> compensation point was highest in the -33% treatment ( $7.17 \pm 3.49 \text{ ppm}$ ) and lowest in the ambient treatment ( $0.63 \pm 0.36 \text{ ppm}$ ). Slight but significant variations in  $LSP$  (0.9) were observed across ambient and +33 and -33. +50 and -50 treatments had no significant differences among treatments. Values ranging from  $618.5 \pm 57.09 \text{ ppm}$  in the -33% treatment to  $864.2 \pm 138.0 \text{ ppm}$  in the ambient treatment.

## 4 | DISCUSSION

### 4.1 | Model determination

We first evaluated four commonly used models for fitting photosynthesis with light and CO<sub>2</sub> response curves. The rectangular hyperbola model assumes a hyperbolic relationship between photosynthetic rate and either light intensity or CO<sub>2</sub> concentration (Farquhar, 1989; Hui et al. 2001; Ma et al. 2021). Although this model is simple and widely used, its ability to accurately represent complex physiological responses might be limited (Ma et al. 2001). The nonrectangular hyperbola model is similar to the rectangular hyperbola model but provides a more flexible fit because it contains an additional parameter related to the curvature of the response curve (Tornley, 1998; Ma et al. 2021). The exponential model can effectively capture exponential growth or decline in photosynthetic rate but may not fit well with more intricate patterns in the data (Chen et al. 2011; Song et al. 2020). The modified rectangular hyperbola model is a variation of the rectangular hyperbola model with additional parameters to account for various factors influencing photosynthetic response. However, its application requires careful consideration of parameter interpretation and the potential for overfitting (Ye 2007; Song et al. 2020). In this study, all four models could fit the photosynthetic light and CO<sub>2</sub> response curves. However, based on Root MSE, R<sup>2</sup>, AICc, and BIC metrics and considering biological relevance, the nonrectangular hyperbola model was the best at characterizing switchgrass photosynthesis. Similar results were reported in previous studies. For example, Song et al. (2020) compared six photosynthesis light response models for four different mulching treatments of spring wheat and found that the nonrectangular hyperbolic model provided better fit.

Ye (2007) and Ye and Yu (2008) proposed the modified rectangular hyperbola model could fit the light-response curves and main model parameters more accurately than other models (Lang et al. 2013; Ma et al. 2021). However, while in our study the modified rectangular hyperbola model was the best fitting model for the CO<sub>2</sub> response curve, it was the poorest model for the light response curve. Lobo et al. (2013) reported that the maximum photosynthetic rate and saturated light intensity produced by the modified rectangular hyperbola model can occasionally exceed expected physiological ranges. Our study corroborated these issues, suggesting that the modified rectangular hyperbole model cannot be applied to both *P<sub>n</sub>-I* and *P<sub>n</sub>-CO<sub>2</sub>* curves under all situations (Lobo et al. 2013). So, like in Lobo et al., (2013) the non-rectangular hyperbola model was the best fitting model.

#### **4.2 | Impact of precipitation intensity on leaf photosynthesis and physiological parameters**

The response patterns of leaf photosynthesis to light and CO<sub>2</sub> were similar to the reported patterns in previous studies (Barney et al. 2009; Dohleman et al. 2009; Hartman et al. 2012; Gao et al. 2017). Leaf net photosynthesis was negative when light intensity and CO<sub>2</sub> concentration was set at 0 or very low levels and increased with increase of light and CO<sub>2</sub> concentration. It leveled off at high light intensity or CO<sub>2</sub> concentration. Only a few measurements during the late growing seasons showed a decline in leaf photosynthesis when light and CO<sub>2</sub> concentration were high, perhaps due to the potential damage to the leaf at the late stages of the measurements.

Our results showed significant differences in the majority of model parameters for both light and CO<sub>2</sub> response curves across the various precipitation treatments. Precipitation changes significantly influenced all model parameters except for *P<sub>max</sub>* in light response curves. Only a few studies have investigated the photosynthetic response to light in switchgrass. Our results were comparable to these previous studies. For example, Albaugh et al. (2014) estimated *P<sub>n</sub>-I*

model parameters for switchgrass observing  $P_{\max}$  at  $28.7 \mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$ ,  $\alpha$  at 0.059,  $\theta$  at 0.74, and  $R_d$  at  $3.4 \mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$ . In addition, they found that different cropping systems or measurement dates did not influence parameter estimates. Similarly, Gao et al. (2015) estimated switchgrass photosynthesis responses to spacing over three years and found that  $\alpha$  remains stable over time, ranging between 0.0328 and 0.0424. Neither spacing nor time influenced  $LCP$ , ranging from 36 to 51, and  $LSP$ , ranging from 1399 to 1442. Their findings reported a substantially higher  $LSP$  than observed in our study. It is worth noting that  $LSP$  estimated in our study showed large variations within and among precipitation treatments (Fig. 4). Overall,  $LSP$  decreased from the +50% to -50% precipitation treatments. The main reason could be that in the drought treatments, plants may experience water stress, affecting their ability to photosynthesize efficiently. Their mean maximum photosynthesis was about  $18.4 \mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$ . Mulching treatments in Song et al. (2020) impacted maximum net photosynthetic rates. Our results fell within the range of these studies reported values. Regarding photosynthesis and  $\text{CO}_2$  response in switchgrass, Albaugh et al. (2014) estimated the maximum photosynthetic rate at  $27.6 \mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$ , with no other study, to our knowledge, reporting the response of switchgrass photosynthesis to  $\text{CO}_2$ .

Despite the significant influence of precipitation on model parameters such as  $P_{\max}$  and  $\alpha$ , variations were limited to narrow ranges. Switchgrass exhibited a remarkable tolerance to changes in precipitation, and performed well under the various precipitation conditions in Nashville, TN. This adaptability may be attributed to inherent adaptive mechanisms within switchgrass, enabling it to thrive across a wide range of environmental conditions in its extensive native range.

While switchgrass has been the subject of relatively few studies, numerous prior studies have investigated the responses of photosynthesis to light and CO<sub>2</sub> for various species (Muraoka et al. 2010; Ali et al. 2015; Miner and Bauerle 2017; Zhao et al. 2020). These studies confirmed that model parameter often differ among different studies (Zhao et al. 2020). For example, Lobo et al. (2013) reported a  $P_{\max}$  range of 42 to 59  $\mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$  for C<sub>3</sub> species and 57 to 75  $\mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$  for C<sub>4</sub> species, significantly exceeding the estimated switchgrass  $P_{\max}$  in this study and other previous studies (Barney et al. 2009; Gao et al. 2017). The measured maximum photosynthetic rate of switchgrass leaves typically falls between 14 to 30  $\mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$  (Hartman et al. 2012; Wagle and Kakani 2014; Gao et al. 2015; Hui et al. 2018). In contrast, Lobo et al. (2013) reported  $P_{\max}$  for *Vochysia divergens* ranging from 14.4 to 15.7  $\mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$ , depending on different models, while Ma et al. (2021) found a  $P_{\max}$  of around 8  $\mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$  for larch (*Larix principis-rupprechtii* Mayr (Larch)).

Quantum yield, as reported by Lobo et al (2013), ranges from 0.0266 to 0.0800  $\mu\text{mol}^{-1}\mu\text{mol photon}^{-1}$ , a range within which our estimates also fall. In our study, the parameter  $\theta$ , representing the ratio of physical to total resistances of CO<sub>2</sub> diffusion and signifying the sharpness of the transition from light limitation to light saturation (Lobo et al. 2013) varied from 0.912 to 0.969 under different precipitation treatments. This range aligns with the observed norm of 0.70 to 0.99 (Ogren 1993; Lobo et al. 2013). In our study  $LCP$ , ranging from 49.69 to 71.12  $\mu\text{mol photon m}^{-2}\text{s}^{-1}$ , was higher than that of *Vochysia divergens* (20.2 to 23.4. In addition, Ma et al. (2021) demonstrated substantial variations in model parameters estimated by different models. For example, quantum yield may vary from 0.55 to 0.95 and  $LSP$  can fluctuate from 300 to 1000  $\mu\text{mol photon m}^{-2}\text{s}^{-1}$ . Because of these variations, it is evident that more studies on

switchgrass ecophysiology responses to environmental changes are needed, encompassing different cultivars and at diverse geographical locations.

## 5 | CONCLUSIONS

In this study, we evaluated the response models used for characterizing photosynthesis in relation to light and CO<sub>2</sub> and estimated the model parameters for switchgrass across five different precipitation treatments, employing the optimal model we selected. Among the four models tested (i.e., rectangular hyperbola model, nonrectangular hyperbola model, exponential model, and the modified rectangular hyperbola model), we found they all fitted the measurements obtained from the ambient precipitation treatment. However, the nonrectangular hyperbola model emerged as the optimal choice based on both fitting criteria and the biological significance of its parameters.

This optimal model was then applied across all precipitation treatments, revealing that alterations in precipitation did not exert influence on  $P_{\max}$ , but influenced other model parameters, including  $\alpha$ ,  $\theta$ , and  $R_d$ . In addition, precipitation significantly influenced all model parameters of CO<sub>2</sub> response. While the ambient treatment had the highest  $P_{\max}$  in the  $P_n$ -CO<sub>2</sub> response, it also had greater  $\alpha$  and  $R_d$ . Interestingly, the fluctuations in model parameters for  $\alpha$ ,  $\theta$ , and  $P_{\max}$  were relatively small.

Overall, this study improved our understanding of how switchgrass leaf photosynthesis responds to varying precipitation conditions, providing valuable insights for the accurately modeling of switchgrass ecophysiology and productivity. Switchgrass demonstrates extensive tolerance to precipitation variations, thriving under the diverse precipitation conditions in Nashville, TN. This adaptability likely stems from inherent adaptive mechanism, allowing

switchgrass to excel amidst the considerable environmental variations within its vast native range. However, improved parameter estimations could enhance our understanding and predictive accuracy regarding switchgrass ecophysiology and biomass productivity in future climate conditions.

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## AUTHOR CONTRIBUTIONS

D.H. developed the ideas for this manuscript. C.K. and N.K. collected data. C.K. and D.H. performed data analysis and wrote the first draft of the manuscript. All authors contributed to the writing of the manuscript.

## CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are opening available in the figshare at  
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TABLE 1. Comparison of modeling fitting of four commonly used photosynthesis-Light ( $Pn-I$ ) and photosynthesis- $CO_2$  ( $Pn-CO_2$ ) models of the net photosynthesis with light in the ambient plots: rectangular hyperbolic model, nonrectangular hyperbola model, exponential model, and modified rectangular hyperbola model. AICc, BIC,  $R^2$ , and Root MSE were used to determine the fitting accuracy for the response models.

| Response              | Fitting Accuracy | Rectangular Hyperbolic Model | Nonrectangular Hyperbolic Model | Exponential Model | Modified Rectangular Hyperbolic Model |
|-----------------------|------------------|------------------------------|---------------------------------|-------------------|---------------------------------------|
| <b>Light</b>          | AIC <sub>c</sub> | 37.0                         | 36.4                            | 25.9              | 48.3                                  |
|                       | BIC              | 24.0                         | 6.8                             | 12.9              | 18.7                                  |
|                       | $R^2$            | 0.99                         | 1.00                            | 0.99              | 0.82                                  |
|                       | Root MSE         | 0.98                         | 0.38                            | 0.66              | 1.87                                  |
| <b>CO<sub>2</sub></b> | AIC <sub>c</sub> | 53.2                         | 43.8                            | 47.2              | 39.6                                  |
|                       | BIC              | 46.4                         | 30.3                            | 40.4              | 26.1                                  |
|                       | $R^2$            | 0.96                         | 0.96                            | 0.96              | 0.96                                  |
|                       | Root MSE         | 2.67                         | 2.84                            | 2.46              | 2.33                                  |

TABLE 2. The ANOVA results, with the significant levels, for the effects of precipitation treatment on light response curves using the nonrectangular hyperbola model. The model parameters include  $\theta$ ,  $\alpha$ ,  $P_{max}$ ,  $R_d$ ,  $LCP$ , and  $LSP$ . N is the number of measurements.

| <b>Model<br/>Parameter</b> | <b>+50%</b>      | <b>+33%</b>      | <b>Ambient</b>   | <b>-33%</b>    | <b>-50%</b>      |
|----------------------------|------------------|------------------|------------------|----------------|------------------|
| $\theta$                   | 0.966±0.02ab     | 0.955±0.02ab     | 0.912±0.02a      | 0.957±0.01ab   | 0.969±0.02b      |
| $\alpha$                   | 0.030±0.006c     | 0.053±0.003b     | 0.049±0.002ab    | 0.047±0.003ab  | 0.040±0.005ac    |
| $P_{max}$                  | 15.322±2.09a     | 17.245±1.09a     | 20.253±2.33a     | 20.229±2.34a   | 14.829±2.22a     |
| $R_d$                      | 2.214±0.42a      | 2.602±0.20ab     | 3.144±0.28b      | 2.872±0.25ab   | 2.360±0.24ab     |
| $LCP$                      | 65.631±9.27a     | 53.761±5.78c     | 65.062±3.75a     | 61.667±5.22ab  | 59.163±6.81bc    |
| $LSP(0.9)$                 | 2,237.52±585.18a | 2,243.21±596.71a | 1,330.35±228.36b | 895.16±142.89c | 1,451.72±406.41b |
| $LSP(0.8)$                 | 1,142.17±230.70a | 1,082.47±245.44a | 741.10±101.31b   | 557.76±70.12c  | 770.60±166.05b   |
| <b>n</b>                   | 5                | 5                | 8                | 12             | 8                |

TABLE 3. ANOVA results for the effects of precipitation treatment on CO<sub>2</sub> response curves using the nonrectangular hyperbola model. Significant levels are indicated.

| <b>Model<br/>Parameter</b>   | <b>+50%</b>     | <b>+33%</b>   | <b>Ambient</b> | <b>-33%</b>   | <b>-50%</b>     |
|------------------------------|-----------------|---------------|----------------|---------------|-----------------|
| <b><math>\theta</math></b>   | 0.93±0.04ab     | 0.99±0.007a   | 0.89±0.06b     | 1.00±0.004a   | 0.95±0.02ab     |
| <b><math>\alpha</math></b>   | 0.06±0.006ab    | 0.046±0.003b  | 0.073±0.01a    | 0.04±0.006b   | 0.05±0.007b     |
| <b><math>P_{max}</math></b>  | 32.40±1.16ab    | 28.94±1.45b   | 36.08±2.75a    | 28.32±2.97b   | 30.92±1.98ab    |
| <b><math>R_d</math></b>      | 0.16±0.06b      | 0.47±0.12a    | 0.08±0.04b     | 0.47±0.21a    | 0.10±0.05b      |
| <b><math>LCP</math></b>      | 1.23±0.45bc     | 5.31±1.47ab   | 0.63±0.36c     | 7.17±3.49a    | 1.10±0.47bc     |
| <b><math>LSP(0.9)</math></b> | 824.55±116.39ab | 639.74±41.96b | 864.25±138.00a | 618.54±57.09b | 785.69±126.16ab |
| <b><math>LSP(0.8)</math></b> | 597.39±40.66a   | 539.01±3145a  | 579.37±46.36a  | 543.81±50.25a | 586.21±56.38a   |
| <b>n</b>                     | 10              | 11            | 8              | 7             | 8               |

## Figure legends

FIGURE 1. Graphical representation of the model comparison for light irradiance. Data points with standard error bars are the mean values of measurements in the ambient treatment plots.

FIGURE 2. Graphical representation of the model comparison for CO<sub>2</sub> concentration. Data points with standard error bars are mean values of measurements in the ambient treatment plots.

FIGURE 3. Light response curve using the nonrectangular hyperbola model for each precipitation treatment. Points are observed values and the lines are the modeled curves.

FIGURE 4. The distribution of data is show for each of the model parameter values including the average, median, minimum value, maximum value, first quartile and third quartile values. The data are from the nonrectangular hyperbola model for light response results.

FIGURE 5. Effects of precipitation treatment on the CO<sub>2</sub> response curve using the nonrectangular hyperbola model. Points are observed values and the lines are the modeled curves.

FIGURE 6. The distribution of data is show for each of the model parameter values including the average, median, minimum value, maximum value, first quartile and third quartile values. The data are from the nonrectangular hyperbola model for CO<sub>2</sub> response results.