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Photosynthetic responses of switchgrass to light and CO₂ under different precipitation treatments

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Abstract

Switchgrass (*Panicum virgatum* L.) is a prominent bioenergy crop with robust resilience to environmental stresses. However, our knowledge regarding how precipitation changes affect switchgrass photosynthesis and its responses to light and CO₂ remains limited. To address this knowledge gap, we conducted a field precipitation experiment with five different treatments, including −50%, −33%, 0%, +33%, and +50% of ambient precipitation. To determine the responses of leaf photosynthesis to CO₂ concentration and light, we measured leaf net photosynthesis of switchgrass under different CO₂ concentrations and light levels in 2020 and 2021 for each of the five precipitation treatments. We first evaluated four light and CO₂ response models (i.e., rectangular hyperbola model, nonrectangular hyperbola model, exponential model, and the modified rectangular hyperbola model) using the measurements in the ambient precipitation treatment. Based on the fitting criteria, we selected the nonrectangular hyperbola model as the optimal model and applied it to all precipitation treatments, and estimated model parameters. Overall, the model fit field measurements well for the light and CO₂ response curves. Precipitation change did not influence the maximum net photosynthetic rate (P_{max}) but influenced other model parameters including quantum yield (α), convexity (θ), 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 α , and the ambient treatment had lower θ and LCP , higher R_d , and relatively lower LSP . Furthermore, precipitation significantly influenced all model parameters of CO₂ response. The ambient treatment had the highest P_{max} , largest α , and lowest θ , R_d , and CO₂ 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.

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KEYWORDS

bioenergy crop, CO₂-response curve, light-response curve, nonrectangular hyperbola model, precipitation change, switchgrass

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°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 (Douville et al., 2021; Pfahl et al., 2017; Pörtner et al., 2022; Trenberth, 2011; Vanaja et al., 2011). 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 (Deng et al., 2017; O'Keefe et al., 2013; Parrish & Fike, 2005; Tulbure et al., 2012).

Switchgrass (*Panicum virgatum* L.) is a C₄ 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 (Adler et al., 2006; Albaugh et al., 2014; Liu et al., 2022; Parrish & Fike, 2005; Ricketts et al., 2023; Rinehart, 2006). Extensive research has explored the effects of agricultural practices like nutrient applications, irrigation, and cutting systems, on switchgrass productivity (Hui et al., 2018; Keyser et al., 2022; Kieffer et al., 2023; Lemus et al., 2008; Miesel et al., 2017; Wullschlegel et al., 2010). 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 (Deng et al., 2017; Hartman et al., 2012; Hartman & Nippert, 2013; O'Keefe et al., 2013).

In addition, there is an incomplete understanding of switchgrass leaf photosynthesis responses to variations in light and carbon dioxide (CO₂) levels. Photosynthesis, a

fundamental biological process, plays a pivotal role in plant growth, development, biomass productivity, and yield potential (Ma et al., 2021; Song et al., 2021; Yang et al., 2010). Enhancements in plant productivity are often correlated with increased photosynthesis (Fischer et al., 1998; Song et al., 2021). Environmental factors such as cultivar, light, CO₂, 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 μmol CO₂ m⁻² 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 CO₂ concentration. The efficiency of light and CO₂ 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 (Baldocchi & Harley, 1995; Herrmann et al., 2020; Lobo et al., 2013; Yang et al., 2010).

Photosynthetic light response curves (Pn-I) and photosynthetic-CO₂ response curves (Pn-CO₂) are important for understanding how plants respond to climate change (Bukhov et al., 1995; Leverenz, 1988; Lobo et al., 2013; Ma et al., 2021; Xu et al., 2019). Pn-I response curves depict the relationship between the net photosynthetic rate (Pn) of plants and the photon flux density (Irradiance, I), while Pn-CO₂ response curves describe the relationship between Pn and CO₂ concentration (Song et al., 2021). These response curves enable the description of essential physiological parameters in plants (Herrmann et al., 2020; Liu et al., 2022; Lobo et al., 2013; Ma et al., 2021; Song et al., 2021), including the maximum net photosynthetic rate (P_{max}), apparent quantum yield (α), convexity (θ), dark respiration rate (R_d), light or CO₂ compensation point (LCP), and light or CO₂ saturation point (LSP) (Lang et al., 2013; Ma et al., 2021; Ye, 2007). The construction of Pn-I or Pn-CO₂ response curves involves measuring leaf photosynthesis at varying light or CO₂ levels, ranging from zero to saturating levels (1500 or 2000 μmol photon m⁻² s⁻¹ for light, 1200 ppm for CO₂). Various mathematical models can be employed to derive parameters from

these response curves (Lang et al., 2013; Lobo et al., 2013; Song et al., 2021). Accurately estimating the parameters of $Pn-I$ or $Pn-CO_2$ 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_2 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_2 concentrations; (2) Quantifying the impact of precipitation intensity on leaf photosynthetic parameters under varying light and CO_2 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 1200 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 four replicate plots for each treatment. Each plot measured 3 m $\times$ 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 $Pn-I$ and $Pn-CO_2$ response curves were constructed using the preset programs in the LI-6800. For $Pn-CO_2$ response curves, photosynthesis measurements were taken at CO_2 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_2 response curve measurements. For $Pn-I$ 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_2 concentration was set at 400 ppm. Temperature was not controlled during the measurements. In total, 5–12 light response curves and 7–10 CO_2 response curves were generated for each precipitation treatment over the two-year period. Totally, 38 light response curves and 45 CO_2 response curves were measured.

2.3 | Data analysis

2.3.1 | Light and CO_2 response curves modeling

Four models have been commonly fitted to light- or CO_2 -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; Lee et al., 2022; Liu et al., 2019).

Rectangular hyperbola model

The equation of the rectangular hyperbola model is shown below:

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

where P_n is the net photosynthetic rate ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), α is the initial quantum efficiency at lower light or 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:

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

where θ represents convexity (curvature or rate of bending) of the response curve, and P_n , α , P_{max} , R_d and I have been defined above (Ma et al., 2021; Thornley, 1998). To calculate light- or 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:

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

where P_n , α , 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 β is the photoinhibition and γ is light saturation and P_n , α , 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_2 response curves, we calculated mean square errors (MSE), Akaike information criterion corrected (AIC_c), Bayesian information criterion (BIC), and the coefficient of determination (R^2) (Brewer et al., 2016; Ma et al., 2021). The optimal fit of the model is determined through the minimization of MSE, AIC_c and BIC values, alongside the maximization of R^2 (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_2 . Following an evaluation of how well the models fitted to the light and CO_2 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 CO_2 response (P_n - CO_2) curves. Consequently, the nonrectangular hyperbola model was applied to the P_n -I and P_n - 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 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

(Figure 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 Pn -I response. In the case of Pn -CO₂, both the rectangular hyperbolic and exponential models did not fit the data (Figure 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 α , produced by the nonrectangular hyperbolic model, this model was chosen for fitting both Pn -I and Pn -CO₂ responses across all precipitation treatments.

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.

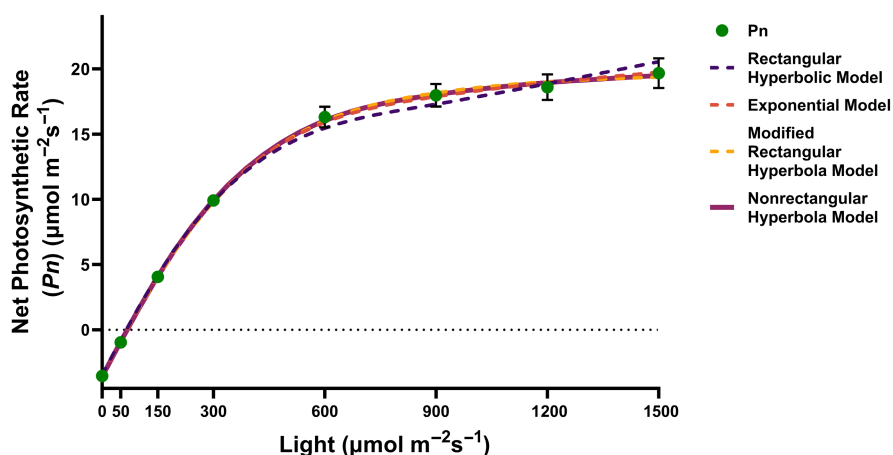
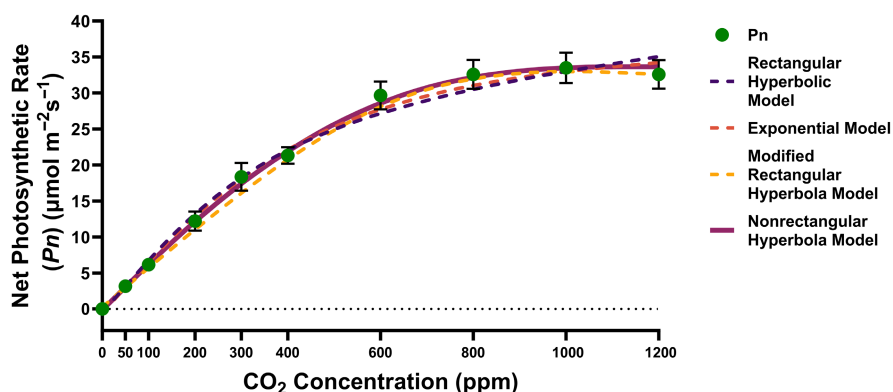


TABLE 1 Comparison of modeling fitting of four commonly used photosynthesis-light (Pn -I) and photosynthesis-CO₂ (Pn -CO₂) models of the net photosynthesis with light in the ambient plots: rectangular hyperbolic model, nonrectangular hyperbola model, exponential model, and modified rectangular hyperbola model.

Response	Fitting accuracy	Rectangular hyperbolic model	Nonrectangular hyperbolic model	Exponential model	Modified rectangular hyperbolic model
Light	AIC _C	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
CO ₂	AIC _C	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

Note: AICc, BIC, R^2 and Root MSE were used to determine the fitting accuracy for the response models.

FIGURE 2 Graphical representation of the model comparison for CO₂ concentration. Data points with standard error bars are mean values of measurements in the ambient treatment plots.



3.2 | Impact of precipitation on model parameters

3.2.1 | Light response

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

The photosynthetic parameters, including $P_{\max}$, α , θ 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; Figures 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 θ 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 α values, the $+50\%$ treatment had the lowest (0.030 ± 0.02), while the $+33\%$ treatment had the highest (0.053 ± 0.003). No significant differences

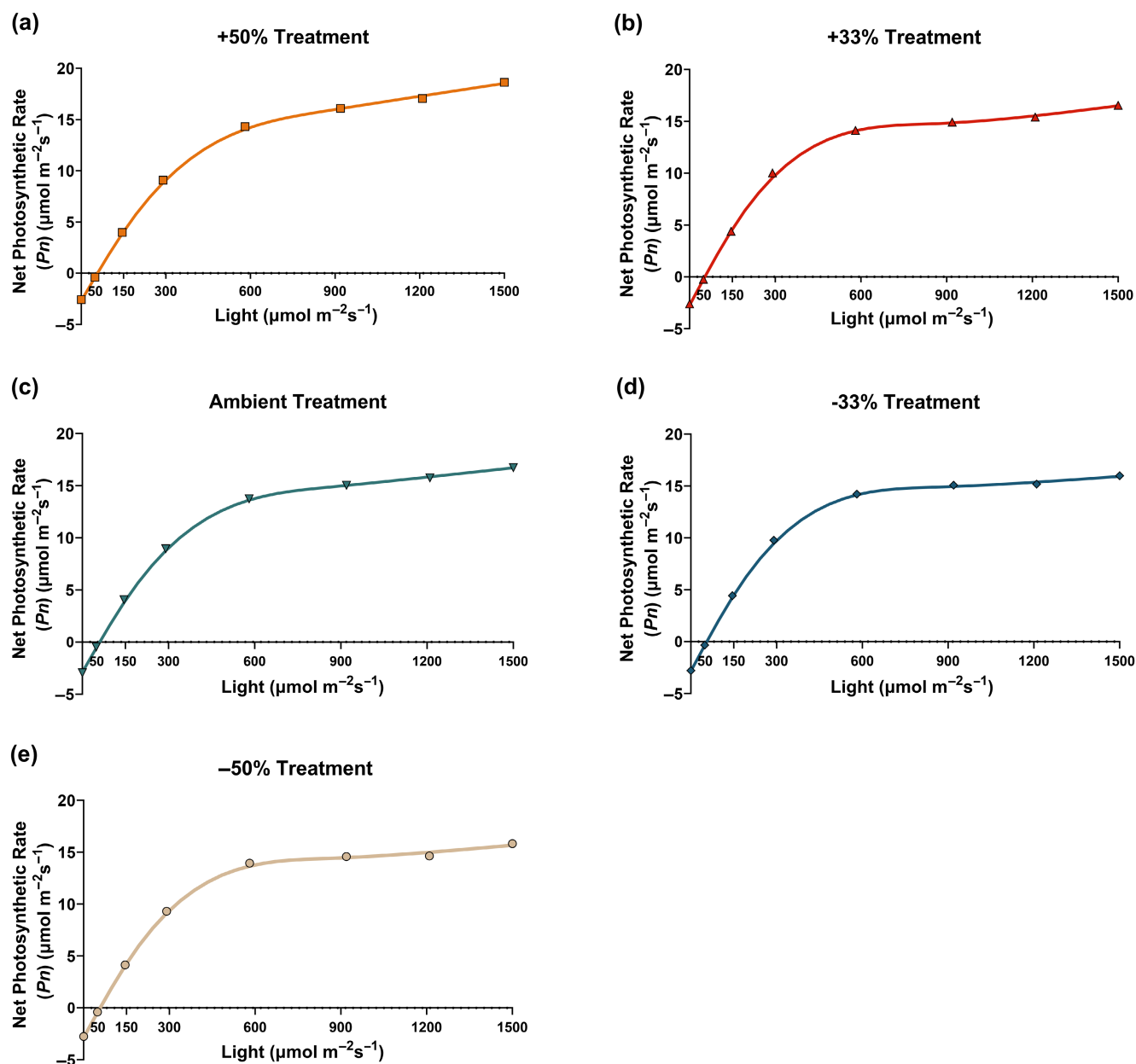


FIGURE 3 Light response curve using the nonrectangular hyperbola model for each precipitation treatment. Points are observed values and the lines are the modeled curves.

TABLE 2 The ANOVA results, with the significant levels, for the effects of precipitation treatment on light response curves using the nonrectangular hyperbola model.

Model parameter	+50%	+33%	Ambient	−33%	−50%
θ	0.966 ± 0.02ab	0.955 ± 0.02ab	0.912 ± 0.02a	0.957 ± 0.01ab	0.969 ± 0.02b
α	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
$LSP(0.9)$	2237.52 ± 585.18a	2243.21 ± 596.71a	1330.35 ± 228.36b	895.16 ± 142.89c	1451.72 ± 406.41b
$LSP(0.8)$	1142.17 ± 230.70a	1082.47 ± 245.44a	741.10 ± 101.31b	557.76 ± 70.12c	770.60 ± 166.05b
n	5	5	8	12	8

Note: The model parameters include θ , α , P_{max} , R_d , LCP , and LSP . N is the number of measurements.

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 | CO₂ response

The observed P_n also exhibited a typical response curve to CO₂ concentration. P_n was negative when CO₂ 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 (Figure 5).

Similarly, we employed the nonrectangular hyperbola model across the precipitation treatments to fit the CO₂ response curves. Then we compared the estimated and calculated photosynthetic parameters across treatments. Overall, all model parameters associated with CO₂ response curves exhibited statistical significance across the precipitation treatments (Table 3; Figures 5 and 6). The P_{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 exceeding those in the +33% and −33% treatments. Notably, the ambient treatment displayed the lowest θ among all treatments, while the −33% and +33% treatments exhibited the largest θ . The largest α 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 CO₂ 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 CO₂ response curves. The rectangular hyperbola model assumes a hyperbolic relationship between photosynthetic rate and either light intensity or CO₂ 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., 2021). 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 (Ma et al., 2021; Thornley, 1998). 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., 2021). 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 (Song et al., 2021; Ye, 2007). In this study, all four models could fit the photosynthetic light and CO₂ response

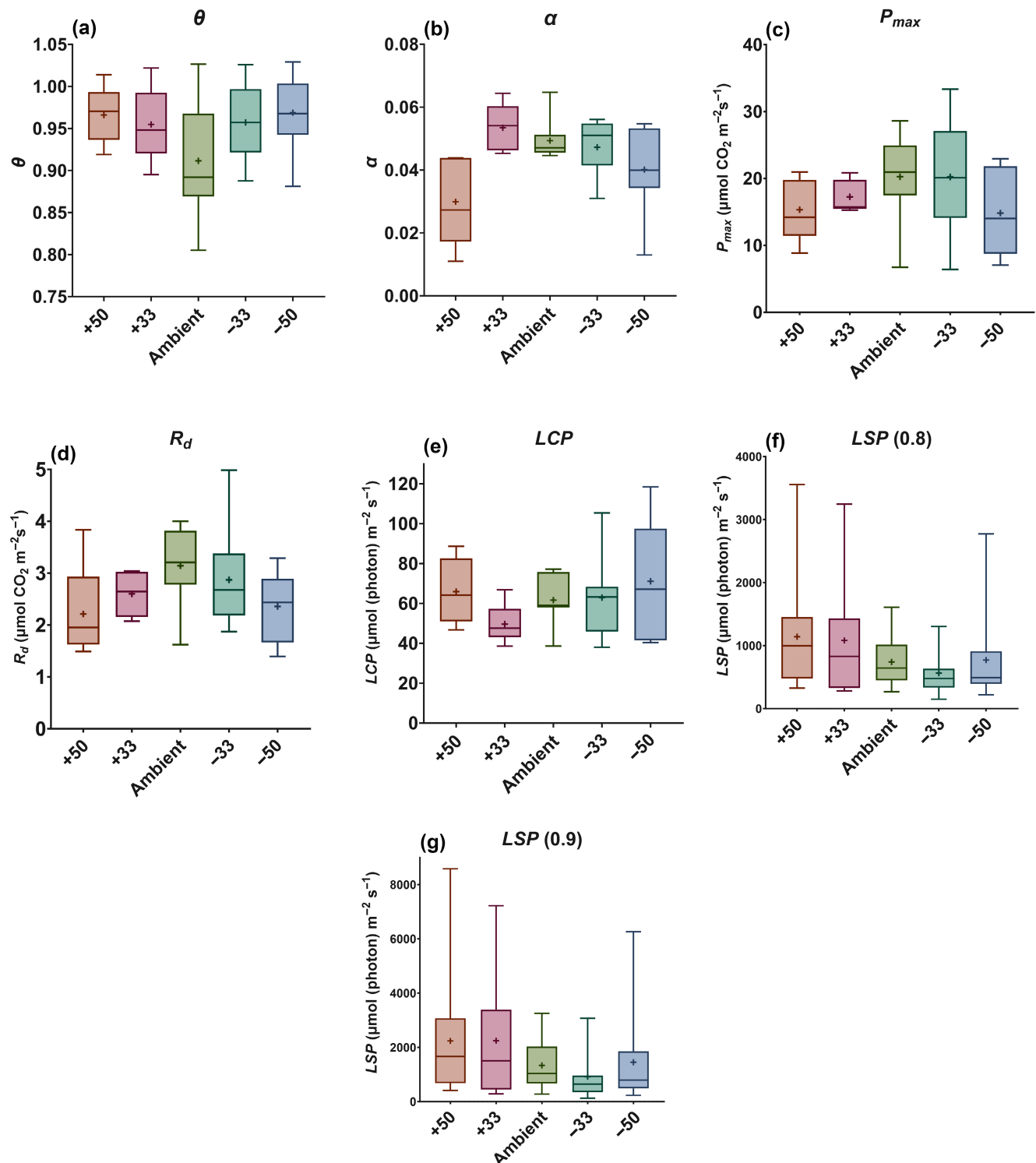


FIGURE 4 The distribution of data is show for each of the model parameter values including the average, median, minimum value, maximum value, first quartile, and third quartile values. The data are from the nonrectangular hyperbola model for light response results.

curves. However, based on Root MSE, R^2 , 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. (2021) 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

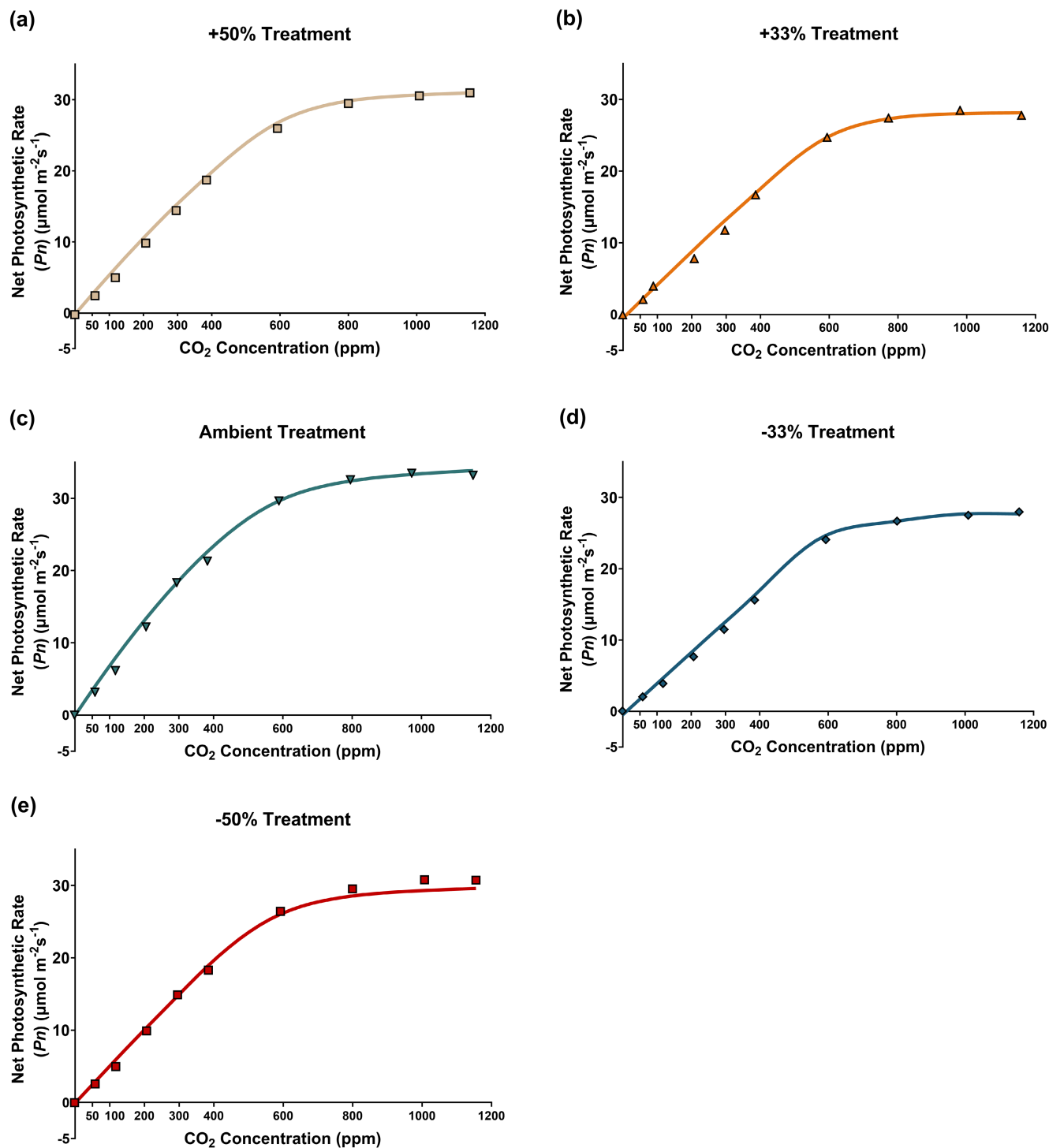


FIGURE 5 Effects of precipitation treatment on the CO_2 response curve using the nonrectangular hyperbola model. Points are observed values and the lines are the modeled curves.

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_2 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_n -I and P_n - CO_2 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.

TABLE 3 ANOVA results for the effects of precipitation treatment on CO₂ response curves using the nonrectangular hyperbola model.

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

Note: Significant levels are indicated.

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

The response patterns of leaf photosynthesis to light and CO₂ were similar to the reported patterns in previous studies (Barney et al., 2009; Dohleman et al., 2009; Gao et al., 2017; Hartman et al., 2012). Leaf net photosynthesis was negative when light intensity and CO₂ concentration was set at 0 or very low levels and increased with increase of light and CO₂ concentration. It leveled off at high light intensity or CO₂ concentration. Only a few measurements during the late growing seasons showed a decline in leaf photosynthesis when light and CO₂ 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 CO₂ response curves across the various precipitation treatments. Precipitation changes significantly influenced all model parameters except for $P_{\max}$ 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 Pn-I model parameters for switchgrass observing $P_{\max}$ at 28.7 μmol CO₂ m^{−2} s^{−1}, α at 0.059, θ at 0.74, and R_d at 3.4 μmol CO₂ m^{−2} 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 3 years and found that α 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 (Figure 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 μmol CO₂ m^{−2} s^{−1}. Mulching treatments in Song et al. (2021) impacted maximum net photosynthetic rates. Our results fell within the range of these studies reported values. Regarding photosynthesis and CO₂ response in switchgrass, Albaugh et al. (2014) estimated the maximum photosynthetic rate at 27.6 μmol CO₂ m^{−2} s^{−1}, with no other study, to our knowledge, reporting the response of switchgrass photosynthesis to CO₂.

Despite the significant influence of precipitation on model parameters such as $P_{\max}$ and α , 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 CO₂ for various species (Miner & Bauerle, 2019; Muraoka et al., 2010; Zhao et al., 2021). These studies confirmed that model parameter often differ among different studies (Zhao et al., 2021). For example, Lobo et al. (2013) reported a $P_{\max}$ range of 42–59 μmol CO₂ m^{−2} s^{−1} for C₃ species and 57–75 μmol CO₂ m^{−2} s^{−1} for C₄ 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 and 30 μmol CO₂ m^{−2} s^{−1} (Gao et al., 2015; Hartman et al., 2012; Hui et al., 2018; Wagle & Kakani, 2014). In contrast, Lobo et al. (2013) reported $P_{\max}$ for *Vochysia divergens* ranging from 14.4 to 15.7 μmol CO₂ m^{−2} s^{−1}, depending on different models, while Ma et al. (2021) found a $P_{\max}$ of around 8 μmol CO₂ m^{−2} s^{−1} for larch (*Larix principis-rupprechtii* Mayr (Larch)).

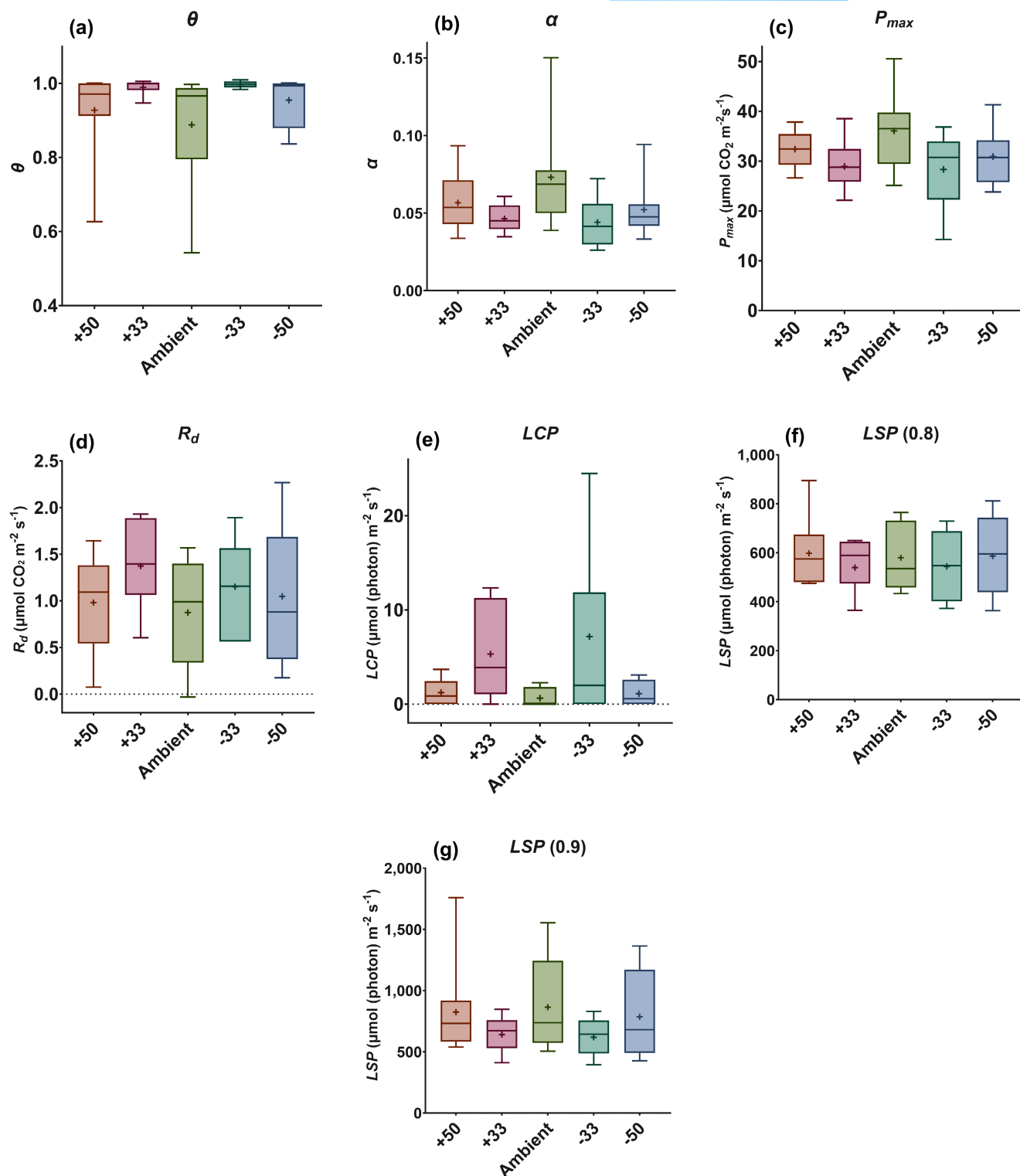


FIGURE 6 The distribution of data is show for each of the model parameter values including the average, median, minimum value, maximum value, first quartile, and third quartile values. The data are from the nonrectangular hyperbola model for CO₂ response results.

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 θ , representing the ratio of physical to total resistances of CO₂ 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 (Lobo et al., 2013; Ogren, 1993). In our study LCP , ranging from 49.69 to 71.12 μmol

photon $\text{m}^{-2}\text{s}^{-1}$, was higher than that of *Vochysia divergens* ($20.2\text{--}23.4 \mu\text{mol photon m}^{-2}\text{s}^{-1}$). 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_2 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 α , θ , and R_d . In addition, precipitation significantly influenced all model parameters of CO_2 response. While the ambient treatment had the highest P_{max} in the Pn-CO_2 response, it also had greater α and R_d . Interestingly, the fluctuations in model parameters for α , θ , 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.

AUTHOR CONTRIBUTIONS

Christina Kieffer: Data curation; formal analysis; investigation; methodology; writing – original draft;

writing – review and editing. **Navneet Kaur:** Data curation; formal analysis; investigation; methodology; writing – review and editing. **Jianwei Li:** Investigation; methodology; writing – review and editing. **Roser Matamala:** Investigation; methodology; writing – review and editing. **Philip A. Fay:** Funding acquisition; investigation; methodology; writing – review and editing. **Dafeng Hui:** Conceptualization; funding acquisition; investigation; methodology; supervision; writing – original draft; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

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 <https://doi.org/10.6084/m9.figshare.25345549.v1>.

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