Frontiers in Plant Science

TYPE Original Research
PUBLISHED 28 March 2024
DOI 10.3389/fpls.2024.1291630

OPEN ACCESS

EDITED BY
Michael Moustakas,
Aristotle University of Thessaloniki, Greece

REVIEWED BY
Emerson Alves da Silva,
Instituto de Pesquisas Ambientais, Brazil
Yansheng Li,
Chinese Academy of Sciences (CAS), China

*CORRESPONDENCE
Zi-Piao Ye
yezp@jgsu.edu.cn
Zi-Fa Deng
dzf@ntu.edu.cn

RECEIVED 09 September 2023
ACCEPTED 23 February 2024
PUBLISHED 28 March 2024

CITATION
Yang X-L, Ma X-F, Ye Z-P, Yang L-S, Shi J-B, Wang X, Zhou B-B, Wang F-B and Deng Z-F (2024) Simulating short-term light responses of photosynthesis and water use efficiency in sweet sorghum under varying temperature and CO_2 conditions.
Front. Plant Sci. 15:1291630.
doi: 10.3389/fpls.2024.1291630

Simulating short-term light responses of photosynthesis and water use efficiency in sweet sorghum under varying temperature and CO_2 conditions

Xiao-Long Yang[1,2], Xiao-Fei Ma[3], Zi-Piao Ye[4]*, Long-Sheng Yang[1], Jun-Bo Shi[1], Xun Wang[1], Bei-Bei Zhou[1], Fu-Biao Wang[4] and Zi-Fa Deng[1]*

[1]School of Life Sciences, Nantong University, Nantong, China, [2]State Key Laboratory of Environmental Chemistry and Ecotoxicology, Research Center for Eco-Environmental Sciences, Chinese Academy of Sciences, Beijing, China, [3]Key Laboratory of Ecological Safety and Sustainable Development in Arid Lands, Northwest Institute of Eco-Environment and Resources, Chinese Academy of Sciences, Lanzhou, China, [4]Institute of Biophysics in Maths & Physics College, Jinggangshan University, Ji'an, China

Climate change, characterized by rising atmospheric CO_2 levels and temperatures, poses significant challenges to global crop production. Sweet sorghum, a prominent C_4 cereal extensively grown in arid areas, emerges as a promising candidate for sustainable bioenergy production. This study investigated the responses of photosynthesis and leaf-scale water use efficiency (WUE) to varying light intensity (I) in sweet sorghum under different temperature and CO_2 conditions. Comparative analyses were conducted between the A_n-I, g_s-I, T_r-I, WUE_i-I, and WUE_{inst}-I models proposed by Ye et al. and the widely utilized the non-rectangular hyperbolic (NRH) model for fitting light response curves. The Ye's models effectively replicated the light response curves of sweet sorghum, accurately capturing the diminishing intrinsic WUE (WUE_i) and instantaneous WUE (WUE_{inst}) trends with increasing I. The fitted maximum values of A_n, g_s, T_r, WUE_i, and WUE_{inst} and their saturation light intensities closely matched observations, unlike the NRH model. Despite the NRH model demonstrating high R^2 values for A_n-I, g_s-I, and T_r-I modelling, it returned the maximum values significantly deviating from observed values and failed to generate saturation light intensities. It also inadequately represented WUE responses to I, overestimating WUE. Across different leaf temperatures, A_n, g_s, and T_r of sweet sorghum displayed comparable light response patterns. Elevated temperatures increased maximum A_n, g_s, and T_r but consistently declined maximum WUE_i and WUE_{inst}. However, WUE_{inst} declined more sharply due to the disproportionate transpiration increase over carbon assimilation. Critically, sweet sorghum A_n saturated at current atmospheric CO_2 levels, with no significant gains under 550 μmol mol^{-1}. Instead, stomatal closure enhanced WUE under elevated CO_2 by coordinated g_s and T_r reductions rather than improved carbon assimilation. Nonetheless, this response diminished under simultaneously high temperature, suggesting intricate interplay between CO_2 and temperature in modulating plant responses. These findings provide valuable insights into photosynthetic dynamics of sweet sorghum, aiding predictions of yield and optimization of cultivation practices. Moreover, our methodology serves as a valuable reference for evaluating leaf photosynthesis and WUE dynamics in diverse plant species.

KEYWORDS

sweet sorghum, leaf gas exchange, photosynthetic light response, intrinsic water use efficiency, instantaneous water use efficiency, model, temperature, CO2 concentration

Introduction

Water plays a crucial role in maintaining the structural integrity and functionality of plants, facilitating nutrient transport, and regulating temperature (Fracasso et al., 2017; Bykova et al., 2019). Specially, it is essential for photosynthesis, providing the electrons necessary to fuel the light-dependent reactions of the process. Due to the growing population, uncontrolled urbanization, and industrialization, atmospheric CO_2 concentration has markedly risen from a pre-industrial value of 280 to 414 $\mu mol\ mol^{-1}$ in 2020, and it is projected to exceed 700 $\mu mol\ mol^{-1}$ by the end of 21st century (Asadi and Eshghizadeh, 2021). If the increase in CO_2 continues, global mean temperatures are expected to rise by 2.6~4.8°C (Hatfield and Dold, 2019). Consequently, alterations in precipitation patterns have been observed in numerous regions in recent years, leading to the frequent occurrence of extreme events such as recurrent droughts and durative high temperatures. This phenomenon is particularly pronounced in arid and semi-arid areas where water resources are significantly stressed (Grillakis, 2019; Feng et al., 2022). As a consequence, crop production in these regions has been significantly limited by availability of water (Kubien et al., 2003; Prasad et al., 2009; Scafaro et al., 2011; Soltani et al., 2023).

Sweet sorghum [*Sorghum bicolor* (L.) Moench], a C_4 species with high photosynthetic efficiency, ranks as the fifth most cereal crop globally, with the total yield lower than that of wheat, rice, maize, and barley (Loreto et al., 1995; Prasad et al., 2009; Asadi and Eshghizadeh, 2021). Due to its excellent drought tolerance, sweet sorghum is extensively cultivated in arid and semi-arid regions with annual precipitation of only 350~700 mm (Appiah-Nkansah et al., 2019; Asadi and Eshghizadeh, 2021). In 2019, global sorghum production reached 56.7 million tons, with Asia contributing 13%, and cultivation concentrated primarily in India and China (Mundia et al., 2019). Sweet sorghum can be utilized for various purposes, including starchy grains for human food, soluble sugar juice as a feedstock for producing spirits, syrup, and vinegar, and lignocellulosic biomass for manufacturing animal feed, fuel ethanol, and fiber. The crop is generating significant interest in industrial circles as a leading candidate for bioenergy production, given the remarkable accumulation of high sugar content in its stems (9~15% of dry biomass) (Appiah-Nkansah et al., 2019; Asadi and Eshghizadeh, 2021).

Photosynthesis stands as one of the pivotal life processes for plants, serving as the foundation for their growth and development. Crop yield is closely related to leaf photosynthesis (von Caemmerer and Farquhar, 1981; Allen et al., 2011; McAusland et al., 2016). During photosynthesis, leaves inevitably lose water to fix carbon gained when they open their stomata (Farooq et al., 2019). The dynamic changes between carbon flux driven by photosynthesis and water flux dominated by transpiration can be characterized by water-use efficiency (WUE; see Table 1 for the list of abbreviations), also known as intrinsic water use efficiency (WUE_i) or instantaneous water use efficiency (WUE_{inst}) at the leaf level (von Caemmerer and Farquhar, 1981; Fracasso et al., 2017). WUE_i is closely correlated with leaf photosynthetic capacity and stomatal behavior (von Caemmerer and Farquhar, 1981). It is commonly used to explain photosynthetic characteristics that are independent of evaporative demand (Ye et al., 2020). WUE_{inst} represents plant dry yield per unit of water loss, which can be considered as the WUE of the whole plant. WUE changes immediately within minutes of becoming water deprived. WUE is regarded as a key physiological indicator for assessing crop growth in arid regions, illuminating the link between crop production and water consumption (McAusland et al., 2016; Fracasso et al., 2017; Bykova et al., 2019; Hatfield and Dold, 2019). Currently, research has been undertaken to explore how crops respond to environmental stress based on the functional characterization of WUE (Gago et al., 2014; Xue et al., 2016; Silva et al., 2020), revealing that an elevated CO_2 concentration can enhance WUE_{inst} (Wall et al., 2001; Hatfield and Dold, 2019).

However, the process of photosynthesis in plants is inherently dynamic in natural conditions, with the photosynthetic rate exhibiting rapid responses to diverse environmental factors. The intensity of light incident on a leaf experiences fluctuations due to the movement of the sun, clouds, canopies, or the leaf itself, thereby influencing the photosynthetic rate (Gyimah and Nakao, 2007; McAusland et al., 2016). Plants demonstrate varied capabilities in harnessing light of different strengths, ranging from weak to strong, each with specific light requirements (Yan et al., 2019). Characterizing light response of plant photosynthesis is thus essential for elucidating photosynthetic dynamics, cultivation

TABLE 1 Definitions of the abbreviations.

Abbreviation	Definition	Units
WUE	Water use efficiency	
NRH	Non-rectangular hyperbolic	
WUE$_i$	Intrinsic water use efficiency	μmol mol^{-1}
WUE$_{i\text{-max}}$	Maximum intrinsic water use efficiency	μmol mol^{-1}
WUE$_{inst}$	Instantaneous water use efficiency	μmol mmol^{-1}
WUE$_{inst\text{-max}}$	Maximum instantaneous water use efficiency	μmol mmol^{-1}
A_n	Net photosynthetic rate	μmol m^{-2} s^{-1}
A_{nmax}	Maximum net photosynthetic rate	μmol m^{-2} s^{-1}
g_s	Stomatal conductance	mol m^{-2} s^{-1}
$g_{s\text{-max}}$	Maximum stomatal conductance	mol m^{-2} s^{-1}
T_r	Transpiration rate	mmol m^{-2} s^{-1}
$T_{r\text{-max}}$	Maximum transpiration rate	mmol m^{-2} s^{-1}
I	Light intensity	μmol m^{-2} s^{-1}
I_c	Light compensation point	μmol m^{-2} s^{-1}
I_{sat}	Saturation light intensity corresponding to A_{nmax}	μmol m^{-2} s^{-1}
$I_{g\text{-sat}}$	Saturation light intensity corresponding to $g_{s\text{-max}}$	μmol m^{-2} s^{-1}
$I_{T\text{-sat}}$	Saturation light intensity corresponding to $T_{r\text{-max}}$	μmol m^{-2} s^{-1}
$I_{i\text{-sat}}$	Saturation light intensity corresponding to WUE$_{i\text{-max}}$	μmol m^{-2} s^{-1}
$I_{inst\text{-sat}}$	Saturation light intensity corresponding to WUE$_{inst\text{-max}}$	μmol m^{-2} s^{-1}
α	Initial slope of the A_n-I response curve	μmol μmol^{-1}
α_s	Initial slope of the g_s-I response curve	mol μmol^{-1}
α_T	Initial slope of the T_r-I response curve	mmol μmol^{-1}
α_i	Initial slope of the WUE$_i$-I response curve	m^2 s mol^{-1}
α_{inst}	Initial slope of the WUE$_{inst}$-I response curve	m^2 s mmol^{-1}
R_d	Mitochondrial CO$_2$ release in the dark	μmol m^{-2} s^{-1}
g_{s0}	Residual stomatal conductance	mol m^{-2} s^{-1}
T_{r0}	Residual transpiration rate	mmol m^{-2} s^{-1}
K_i	Residual intrinsic water-use efficiency	μmol mol^{-1}
K_{inst}	Residual instantaneous water use efficiency	μmol mmol^{-1}
VPD	Vapor pressure deficit	Kpa
C_i	Intercellular CO$_2$ concentration	μmol mol^{-1}

management, and growth potential in changing environments (von Caemmerer and Farquhar, 1981; Gyimah and Nakao, 2007; Yan et al., 2019; Ye et al., 2020). While studies have explored changes in crop WUE (mainly WUE$_{inst}$) under water deficit stress and climate change (Wall et al., 2001; Allen et al., 2011; Fracasso et al., 2017; Hatfield and Dold, 2019; Asadi and Eshghizadeh, 2021), limited information exists on how WUE$_i$ and WUE$_{inst}$ respond to variations in light intensity and their evolution under concurrent rising CO$_2$ concentration and warming (Hatfield and Dold, 2019).

Accurate characterization of the response curves of net photosynthetic rate (A_n) and WUE to light intensity (I) is paramount, serving as a prerequisite for determining key photosynthetic parameters including the maximum net photosynthetic rate (A_{nmax}), the maximum intrinsic water use efficiency (WUE$_{i\text{-max}}$), the maximum instantaneous water use efficiency (WUE$_{inst\text{-max}}$), and their corresponding saturation light intensity (i.e., I_{sat}, $I_{i\text{-sat}}$, $I_{inst\text{-sat}}$) (von Caemmerer, 2013; Ye et al., 2020; Yin et al., 2021). This process is essential for evaluating the impact of temperature and CO$_2$ concentration on plant WUE and elucidating the relationship between carbon assimilation and water use. Various models have been established to characterize the light response curve of photosynthesis (A_n-I curve) in plants, such as the rectangular hyperbola (Thornley, 1998), non-rectangular hyperbolic model (hereafter called NRH model) (Thornley, 1976; Farquhar and Wong, 1984), exponential-based functions (Leakey et al., 2006), and the mechanistic model by Ye et al. (2013) (hereafter called Ye's models). While utilized to predict photosynthesis, most lack assessment of the light response of WUE$_i$ and WUE$_{inst}$. Consequently, the NRH model has also been employed to describe WUE$_i$-I and WUE$_{inst}$-I curves. However, studies fitting the A_n-I curve have shown the NRH model significantly over/underestimates A_{nmax} and cannot estimates I_{sat}. Recently, we have developed WUE$_i$-I and WUE$_{inst}$-I models based on a mechanistic photosynthesis model, demonstrating accurate fitting of WUE$_i$-I and WUE$_i$-I curves for *Glycine max* and *Amaranthus hypochondriacus* at ambient temperature (Ye et al., 2020). However, their applicability across species and environments remains unknown.

In this study, we examined sweet sorghum leaf gas exchange across light levels under varying temperatures and CO$_2$ concentrations using a portable LI-6800 photosynthesis system. Light response curves of A_n, stomatal conductance (g_s), transpiration rate (T_r), WUE$_i$, and WUE$_{inst}$ were modeled and analyzed. Specifically, we compared the widely used NRH model against the A_n-I, g_s-I, T_r-I, WUE$_i$-I, and WUE$_{inst}$-I models by Ye et al. (Ye and Yu, 2008; Ye et al., 2013; Ye et al., 2020) for accuracy in representing response curves and deriving key photosynthetic parameters. The primary objectives were threefold: (a) to assess the flexibility of the Ye's models and the NRH model in photosynthesis in sweet sorghum under different CO_2 and temperature conditions; (b) to evaluate applicability of the WUE$_i$-I and WUE$_{inst}$-I models based on the Ye's models and the NRH model to the C_4 cereal crop sweet sorghum; (c) to elucidate light response characteristics of photosynthesis and WUE in sweet sorghum leaves under short-term exposure to elevated CO_2 and temperature. These founding not only provide methodological insights for evaluating photosynthesis and water use efficiency dynamics in other crops but also contribute to a deeper understanding of the intricate associations among temperature, CO_2 and light in modulating sweet sorghum photosynthesis to guide optimal cultivation in a shifting climate.

Materials and methods

Plant material and growth conditions

Sweet sorghum cultivar KF-JT-4 were obtained by the Institute of Modern Physics, Chinese Academic of Sciences. This early maturing cultivar was developed via heavy ion irradiation of the parental line KFJT-CK. Thirty seeds were surface sterilized by soaking in 0.025% carbendazim and germinated in Petri dishes on filter paper at 25°C in darkness until radicle emergence. Each seedling was then transplanted into a 1.86 L volume inverted truncated cone-shaped pots (top diameter 15 cm, bottom diameter 10 cm, height 15 cm) filled with field soil. Plants were grown in a controlled environment growth chamber (120 cm long, 75 cm wide, 200 cm high) (RDN-1000E-4, Ningbo Dongnan Instrument Co. Ltd., China) under conditions of 25°C, approximately 260 μmol photons m^{-2} s^{-1} radiation with a 12 h photoperiod, and 70% relative humidity. Plants were routinely watered and fertilized to prevent growth limitation.

After 40 days of cultivation (pre-jointing period), the plants were moved from the growth chamber to a natural laboratory environment to conduct measurements of leaf CO_2 gas exchange. Subsequent to the completion of each measurement, the plants were promptly returned to the growth chamber. The experiment involved the selection of five healthy and uniform seedlings for analysis. Growth performance of plants is shown in Supplementary Figure 1. Key growth traits including plant height, stem diameter, and leaf dimensions were measured with a LI-3000C leaf area meter and are provided in Supplementary Table S1.

Gas exchange measurements and experimental setup

Leaf gas exchange measurement was performed using a portable photosynthesis system (LI-6800, Li-Cor Inc., USA) equipped with an integrated fluorometer chamber head (Li-6800-01A, Li-Cor Inc., USA). From the central leaf, the downward second mature and fully expanded leaf was used for measurement. Prior to each measurement, leaf was clamped in the leaf chamber and acclimated at an irradiance intensity of 1800 μmol m^{-2} s^{-1} for 30~40 min until a steady-state CO_2 exchange was obtained. The system, featuring red and blue light sources, along with an integrated CO_2 mixer set to 500 μmol s^{-1} flow rate, facilitated the light-response measurements of CO_2 gas exchange.

Light-response measurements were systematically conducted in a descending order of light intensity levels: 2000, 1800, 1600, 1400, 1200, 1000, 800, 600, 400, 200, 150, 100, 50, 25, and 0 μmol m^{-2} s^{-1} at the leaf surface level. A minimum wait time of 2 minutes and a maximum of 3 minutes were set at each intensity level before recording data. The instrument automatically aligned reference and sample chamber conditions to ensure accuracy. Each measurement was replicated three times to enhance data reliability and mitigate potential variations.

The internal settings of the LI-6800 photosynthesis system enabled control of leaf temperature and CO_2 concentration during gas exchange measurements. This allowed simulation of different temperature and CO_2 treatments to assess short-term photosynthetic responses. Three leaf temperature treatments were imposed: 25, 30, and 35°C at 60-70% relative humidity. CO_2 treatments included sub-ambient (250 μmol mol^{-1}), ambient (410 μmol mol^{-1}), and elevated (550 μmol mol^{-1}) levels. Under each condition, total leaf exposure spanned 65-80 minutes, encompassing light acclimation (30-40 min) and light response measurements from 0 to 2000 μmol m^{-2} s^{-1} (30-45 min). Measurements occurred between 9:00-11:30 and 14:00-17:00 in April within a ~60 m^2 laboratory under natural air circulation. This experimental design examined dynamic changes in sweet sorghum photosynthesis under short-term warming and elevated CO_2 to elucidate plant responses to varying environmental conditions.

Analytical models and calculation

The dependence of A_n on I in Ye's models (Ye et al., 2013) is expressed as follows:

$$A_n = \alpha \frac{1-\beta I}{1+\gamma I} I - R_d \tag{1}$$

where A_n is the net photosynthetic rate, α is the initial slope of the A_n-I response curve, β and γ are the two parameters reflecting light limitation and light saturation, respectively, and R_d is the dark respiration rate.

The saturation light intensity (I_{sat}) corresponding to A_{nmax} can be calculated by the following equations:

$$I_{sat} = \frac{\sqrt{(\beta+\gamma)/\beta} - 1}{\gamma} \tag{2}$$

and

$$A_{nmax} = \alpha \left(\frac{\sqrt{\beta+\gamma} - \sqrt{\beta}}{\gamma} \right)^2 - R_d \tag{3}$$

The g_s-I model established by Ye and Yu (2008) was given as follows:

$$g_s = \alpha_s \frac{1-\beta_s I}{1+\gamma_s I} I + g_{s0} \quad (4)$$

where α_s is the initial slope of the g_s-I response curve, β_s and γ_s are the two coefficients independent of I. g_{s0} is the residual stomatal conductance when $I = 0$.

The saturation light intensity ($I_{\text{g-sat}}$) corresponding to the maximum stomatal conductance ($g_{\text{s-max}}$) can be found by the following equations:

$$I_{g-\text{sat}} = \frac{\sqrt{(\beta_s+\gamma_s)/\beta_s}-1}{\gamma_s} \quad (5)$$

and

$$g_{s-\max} = \alpha_s \left(\frac{\sqrt{\beta_s+\gamma_s}-\sqrt{\beta_s}}{\gamma_s} \right)^2 + g_{s0} \quad (6)$$

WUE$_i$ can be calculated by the ratio of A_n to g_s (A_n/g_s) in µmol mol^{-1}. The WUE$_i$-I model established by Ye et al. (2020) was given as follows:

$$\text{WUE}_i = \alpha_i \frac{1-\beta_i I}{1+\gamma_i I} I - K_i \quad (7)$$

where α_i denotes the initial slope of WUE$_i$-I response curve, β_i and γ_i are the two coefficients that are independent of I, and K_i is the residual WUE$_i$.

The saturated light intensity ($I_{\text{i-sat}}$) corresponding to the maximum WUE$_i$ (WUE$_{\text{i-max}}$) can be calculated by the following equations:

$$I_{i-\text{sat}} = \frac{\sqrt{(\beta_i+\gamma_i)/\gamma_i}-1}{\gamma_i} \quad (8)$$

and

$$\text{WUE}_{i-\max} = \alpha_i \left(\frac{\sqrt{\beta_i+\gamma_i}-\sqrt{\beta_i}}{\gamma_i} \right)^2 - K_i \quad (9)$$

WUE$_{\text{inst}}$ is expressed as the ratio between A_n and T_r (A_n/T_r) in µmol mmol^{-1}. The WUE$_{\text{inst}}$-I model established by Ye et al. (2020) was given as follows:

$$\text{WUE}_{\text{inst}} = \alpha_{\text{inst}} \frac{1-\beta_{\text{inst}} I}{1+\gamma_{\text{inst}} I} I - K_{\text{inst}} \quad (10)$$

where α_{inst} denotes the initial slope of WUE$_{\text{inst}}$-I response curve, β_{inst} and γ_{inst} are the two coefficients that are independent of I, and K_{inst} is the residual WUE$_{\text{inst}}$.

The saturation light intensity ($I_{\text{inst-sat}}$) corresponding to the maximum WUE$_{\text{inst}}$ (WUE$_{\text{inst-max}}$) can be calculated by the following equations:

$$I_{\text{inst}-\text{sat}} = \frac{\sqrt{(\beta_{\text{inst}}+\gamma_{\text{inst}})/\gamma_{\text{inst}}}-1}{\gamma_{\text{inst}}} \quad (11)$$

and

$$\text{WUE}_{\text{inst}-\max} = \alpha_{\text{inst}} \left(\frac{\sqrt{\beta_{\text{inst}}+\gamma_{\text{inst}}}-\sqrt{\beta_{\text{inst}}}}{\gamma_{\text{inst}}} \right)^2 - K_{\text{inst}} \quad (12)$$

The dependence of A_n on I in NRH model (Thornley, 1976; Farquhar and Wong, 1984) is expressed as follows:

$$A_n = \frac{\alpha I + A_{n\max} - \sqrt{(\alpha I + A_{n\max})^2 - 4\alpha\theta I A_{n\max}}}{2\theta} - R_d \quad (13)$$

where A_n is the net photosynthetic rate at light intensity I, $A_{n\max}$ is the maximum net photosynthetic rate, α is the initial slope of A_n-I response curve, θ is the convexity of curve, and R_d is the dark respiration rate. The NRH model has also been used to characterize the responses of g_s, T_r, WUE$_i$, and WUE$_{\text{inst}}$ to I (Ye et al., 2020).

Statistical analysis

The data of A_n-I, g_s-I, T_r-I, WUE$_i$-I, and WUE$_{\text{int}}$-I were fitted by non-linear regression using the Levenberg-Marquardt algorithm in SPSS version 24.0 and the *Photosynthesis Model Simulation Software* (PMSS, http://photosynthetic.sinaapp.com). Goodness of fit was evaluated by the coefficient of determination (R^2). Student's *t*-tests assessed differences in parameter values between the photosynthetic models and between fitted and observed values. The effects of temperature and CO$_2$ on photosynthetic parameters were analyzed by one-way ANOVA with Duncan's *post-hoc* test. Data were expressed as group mean ± standard errors (n = 3). Statistical significance was accepted at $p<0.05$.

Results

Performance of models in reproducing light response curves and quantifying photosynthetic traits

Both the Ye's models (Equations 1, 4) and the NRH model (Equation 13) successfully reproduced the A_n-I, g_s-I, and T_r-I curves of sweet sorghum under varying temperatures (Figures 1A-I). The NRH model showed slightly higher R^2 values in comparison to the Ye's models. However, NRH model predictions for $A_{n\max}$ values significantly exceeded observed values (Supplementary Table 2) ($p<0.05$). Additionally, $g_{\text{s-max}}$ and $T_{\text{r-max}}$ values exhibited disparities with the measured values, either overestimated or underestimated. Focusing on the curves depicting the relationship between WUE$_i$ or WUE$_{\text{inst}}$ and I, the Ye's WUE models (Equations 7, 10) outperformed the NRH model across all temperature treatments by accurately captured the decline in WUE$_i$ and WUE$_{\text{inst}}$ as I increased under high light intensity, a trend not reflected by the NRH model (Figures 1J-O). WUE$_{\text{i-max}}$ and WUE$_{\text{inst-max}}$ values from the Ye's WUE models closely matched observed values, with no statistically significant differences ($p>0.05$) (Supplementary Table 2). In addition, saturation light intensities (I_{sat}, $I_{\text{g-sat}}$, $I_{\text{T-sat}}$, $I_{\text{i-sat}}$ and $I_{\text{inst-sat}}$) corresponding to $A_{n\max}$, $g_{\text{s-max}}$, $T_{\text{r-max}}$, WUE$_{\text{i-max}}$ and WUE$_{\text{inst-max}}$ were directly obtained from the Ye's models fitting but not from the NRH model fitting (Table 2). WUE$_{\text{i-max}}$ and WUE$_{\text{inst-max}}$ values from the NRH model were significantly

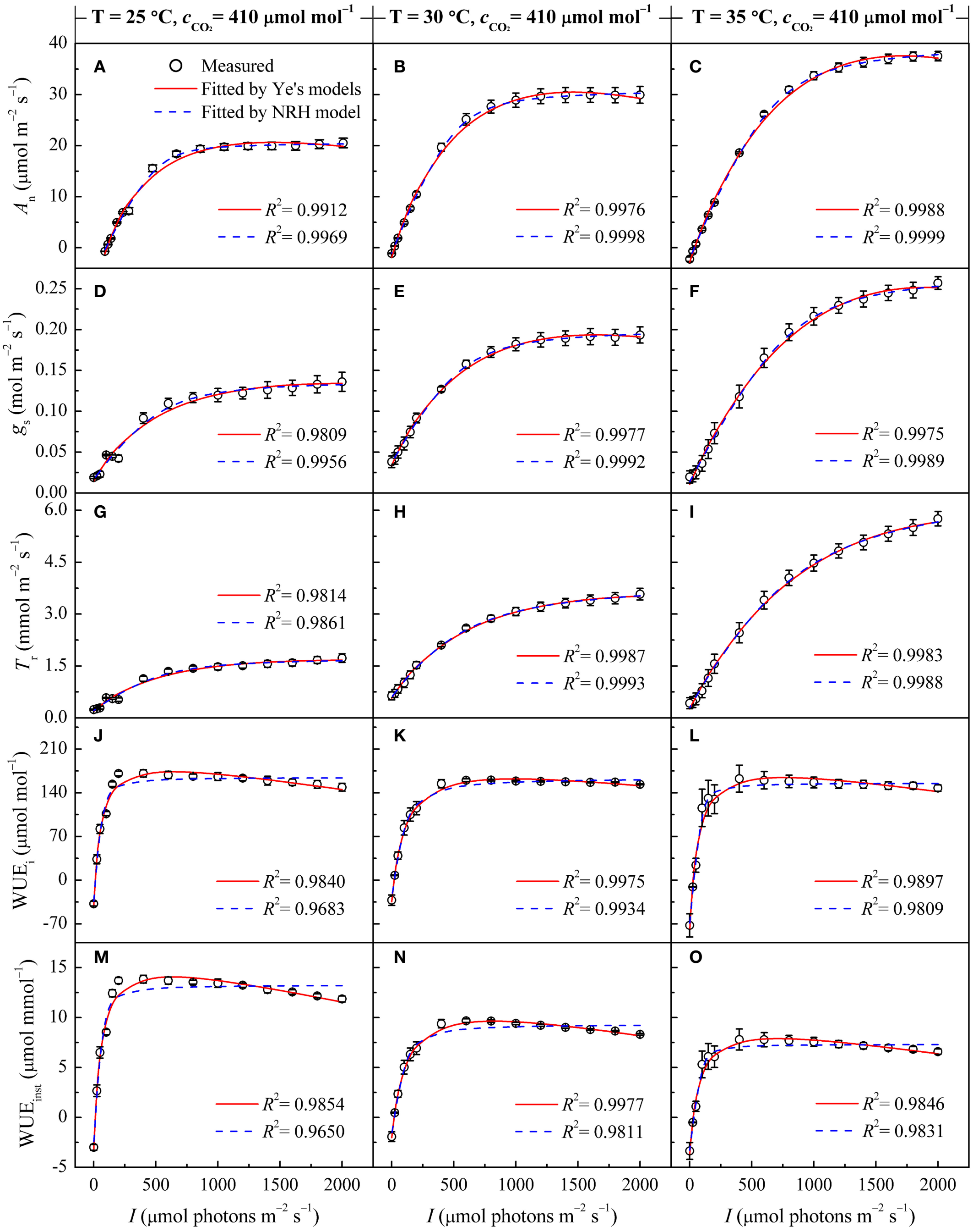

FIGURE 1
Changes in gas exchange parameters of sweet sorghum leaves across varied air temperatures (25, 30, and 35°C) under atmospheric CO_2 level (410 μmol mol^{-1}), alongside comparison of light response curves fitted by the Ye's models and the NRH model. **(A-C)** present the net photosynthetic rate (A_n); **(D-F)** stomatal conductance (g_s); **(G-I)** Transpiration rate (T_r); **(J-L)** intrinsic water-use efficiency (WUE$_i$); and **(M-O)** instantaneous water-use efficiency (WUE$_{inst}$).

overestimated compared to observed values across all temperature conditions ($p<0.05$) (Supplementary Table 2).

Similar to its performance under varying temperatures, the NRH model was employed to fit the A_n-I curves under different CO_2 concentrations, yielding A_{nmax} values that exceeded their observed counterparts (Supplementary Table 3). While successfully reproducing the g_s-I and T_r-I curves (Figures 2D-I), the NRH model struggled to accurately predict $g_{s\text{-max}}$ and $T_{r\text{-max}}$, consequently failing to determine corresponding saturation light intensities (Table 3). In contrast, the Ye's models performed exceptionally well in fitting these curves. When used to fit the WUE$_i$-I and WUE$_{inst}$-I curves under different CO_2 concentrations, Ye's WUE models consistently demonstrated outstanding performance, with R^2 exceeding 0.995 (Figures 2J-O). The fitted WUE$_{i\text{-max}}$ and WUE$_{inst\text{-max}}$ values showed no significant differences from their respective measured values ($p>0.05$) (Supplementary

TABLE 2 Comparison analysis of photosynthetic parameters in sweet sorghum under varied temperature conditions at 410 μmol mol^{-1} CO_2 based on fitting values from light response curves using different photosynthetic models.

Photosynthetic parameters	Fitted by the Ye's models			Fitted by the NRH model		
	25 °C	30 °C	35 °C	25 °C	30 °C	35 °C
α (μmol μmol^{-1})	0.0726 ± 0.0048 ^{b}	0.0839 ± 0.0035 ^{a}	0.0732 ± 0.0026 ^{b}	0.0459 ± 0.0039 ^{b}	0.0598 ± 0.0025 ^{a}	0.0575 ± 0.0013 ^{a}
A_{nmax} (μmol m^{-2} s^{-1})	20.70 ± 0.73 ^{c}	30.54 ± 0.76 ^{b}	37.67 ± 0.96 ^{a}	21.07 ± 1.02 ^{c}	32.25 ± 1.68 ^{b}	42.30 ± 1.21 ^{a}
I_{sat} (μmol m^{-2} s^{-1})	1434.87 ± 92.87 ^{b}	1460.77 ± 169.70 ^{b}	1710.8 ± 31.3 ^{a}	——	——	——
I_c (μmol m^{-2} s^{-1})	16.90 ± 0.11 ^{b}	23.30 ± 1.16 ^{b}	39.27 ± 5.19 ^{a}	8.08 ± 2.03 ^{b}	18.01 ± 0.91 ^{b}	36.87 ± 6.02 ^{a}
R_d (μmol m^{-2} s^{-1})	1.19 ± 0.08 ^{b}	1.89 ± 0.02 ^{b}	2.80 ± 0.44 ^{a}	0.39 ± 0.12 ^{b}	1.07 ± 0.05 ^{b}	2.12 ± 0.39 ^{a}
α_s (mol μmol^{-1})	0.0003 ± 0.0000 ^{b}	0.0004 ± 0.0000 ^{a}	0.0004 ± 0.0000 ^{a}	0.0002 ± 0.0000 ^{b}	0.0003 ± 0.0000 ^{a}	0.0003 ± 0.0000 ^{a}
$g_{s\text{-}max}$ (mol m^{-2} s^{-1})	0.138 ± 0.012 ^{c}	0.194 ± 0.010 ^{b}	0.252 ± 0.008 ^{a}	0.123 ± 0.012 ^{c}	0.167 ± 0.011 ^{b}	0.260 ± 0.004 ^{a}
$I_{g\text{-}sat}$ (μmol m^{-2} s^{-1})	1765.96 ± 158.02 ^{a}	1654.96 ± 22.29 ^{a}	1900.89 ± 74.45 ^{a}	——	——	——
g_{s0} (mol m^{-2} s^{-1})	0.014 ± 0.001 ^{ab}	0.033 ± 0.007 ^{a}	0.011 ± 0.008 ^{b}	0.017 ± 0.001 ^{ab}	0.036 ± 0.007 ^{a}	0.013 ± 0.008 ^{b}
α_r (mmol μmol^{-1})	0.0034 ± 0.0002 ^{b}	0.0060 ± 0.0006 ^{a}	0.0072 ± 0.0006 ^{a}	0.0025 ± 0.0002 ^{b}	0.0068 ± 0.0005 ^{a}	0.0065 ± 0.0006 ^{a}
$T_{r\text{-}max}$ (mmol m^{-2} s^{-1})	1.68 ± 0.11 ^{c}	3.56 ± 0.15 ^{b}	5.83 ± 0.27 ^{a}	1.54 ± 0.11 ^{c}	4.01 ± 0.48 ^{b}	6.52 ± 0.26 ^{a}
$I_{T\text{-}sat}$ (μmol m^{-2} s^{-1})	2292.28 ± 392.15 ^{a}	2578.42 ± 319.24 ^{a}	2663.16 ± 310.52 ^{a}	——	——	——
T_{r0} (mmol m^{-2} s^{-1})	0.18 ± 0.02 ^{a}	0.56 ± 0.12 ^{a}	0.25 ± 0.16 ^{a}	0.21 ± 0.02 ^{a}	0.53 ± 0.11 ^{a}	0.28 ± 0.16 ^{a}
α_i (m^2 s mol^{-1})	4.7330 ± 0.3587 ^{a}	2.3849 ± 0.6450 ^{b}	3.9871 ± 1.412 ^{ab}	2.8690 ± 0.5946 ^{a}	1.5512 ± 0.5053 ^{a}	2.7595 ± 0.6064 ^{a}
$WUE_{i\text{-}max}$ (μmol mol^{-1})	174.17 ± 3.62 ^{a}	163.14 ± 2.14 ^{a}	151.34 ± 6.46 ^{b}	200.22 ± 9.84 ^{a}	192.49 ± 8.96 ^{a}	225.74 ± 18.60 ^{a}
$I_{i\text{-}sat}$ (μmol m^{-2} s^{-1})	615.35 ± 32.16 ^{a}	965.35 ± 76.79 ^{a}	859.94 ± 222.47 ^{a}	——	——	——
K_i (μmol mol^{-1})	40.74 ± 1.79 ^{b}	34.91 ± 8.32 ^{b}	75.18 ± 19.12 ^{a}	35.30 ± 4.22 ^{b}	29.40 ± 9.64 ^{b}	72.47 ± 17.54 ^{a}
α_{inst} (m^2 s $mmol^{-1}$)	0.3665 ± 0.0274 ^{a}	0.1367 ± 0.0354 ^{b}	0.1706 ± 0.0618 ^{b}	0.2204 ± 0.0424 ^{a}	0.0850 ± 0.0281 ^{b}	0.1209 ± 0.029 ^{ab}
$WUE_{inst\text{-}max}$ (μmol $mmol^{-1}$)	14.12 ± 0.22 ^{a}	9.70 ± 0.20 ^{b}	7.21 ± 0.35 ^{c}	16.03 ± 0.64 ^{a}	10.94 ± 0.58 ^{b}	10.45 ± 0.89 ^{b}
$I_{inst\text{-}sat}$ (μmol m^{-2} s^{-1})	602.71 ± 18.01 ^{a}	799.13 ± 63.61 ^{a}	728.23 ± 30.09 ^{a}	——	——	——
K_{inst} (μmol $mmol^{-1}$)	3.22 ± 0.13 ^{a}	2.07 ± 0.48 ^{a}	3.43 ± 0.88 ^{a}	2.75 ± 0.33 ^{a}	1.66 ± 0.60 ^{a}	3.32 ± 0.80 ^{a}

Mean and standard errors of three replicates are shown. Statistically significant differences ($p<0.05$) between temperature treatment groups are denoted by different letters under the Ye's models and the NRH model.

Table 3). Nevertheless, the NRH model inadequately captured changes in the responses of WUE_i and WUE_{inst} to I, particularly evident in a low fitting coefficient for WUE_{inst}-I (Figures 2J-O). Consequently, the fitted $WUE_{i\text{-}max}$ and $WUE_{inst\text{-}max}$ values exceeded their measured counterparts by more than 20% (Supplementary Table 3).

Light response curves of A_n, g_s, T_r, WUE_i and WUE_{inst} in sweet sorghum under varied leaf temperatures

In Figures 1A-I, the responses of A_n, g_s, and T_r to varying I under different leaf temperatures exhibited comparable patterns. Below 800 μmol m^{-2} s^{-1}, A_n, g_s, and T_r increased rapidly with increasing I until reaching their respective peaks (A_{nmax}, $g_{s\text{-}max}$, and $T_{r\text{-}max}$) at the specific saturation light intensities (I_{sat}, $I_{g\text{-}sat}$, and $I_{T\text{-}sat}$). Notably, at high light intensity levels (I >1400 μmol m^{-2} s^{-1}), a decrease in A_n with increasing I was not observed, indicating the absence of photoinhibition. Figures 1J-O illustrates the variations in WUE_i and WUE_{inst} in response to I at different temperatures. Both WUE_i and WUE_{inst} showed almost linear increases within the 200 μmol m^{-2} s^{-1} range, indicating improving WUE with increasing I. In other words, the plant became more efficient in utilizing water for photosynthesis relative to the amount of light it received. However, upon reaching the $WUE_{i\text{-}max}$ and $WUE_{inst\text{-}max}$ at corresponding $I_{i\text{-}sat}$ and $I_{inst\text{-}sat}$, gradual decreases were observed (Table 2), suggesting that additional light did not proportionally increase photosynthesis but potentially led to increased water loss without a corresponding increase in carbon gain. It should be noted that T_r for sweet sorghum under varying CO_2 and temperature conditions did not reach saturation within the values of I applied for the T_r-I curve and hence values for $I_{T\text{-}sat}$ (and $T_{r\text{-}max}$) are an extrapolation.

The photosynthetic processes in sweet sorghum leaves were significantly influenced by temperature (one-way and two-way ANOVA $p<0.05$) (Tables 2, 4). At an ambient CO_2 level (410 μmol mol^{-1}), elevating temperature led to significant increases in A_{nmax}, $g_{s\text{-}max}$, and $T_{r\text{-}max}$ ($p<0.05$). This rise in temperature also corresponded with amplified values in I_{sat}, I_c, and R_d. However, both $WUE_{i\text{-}max}$ and $WUE_{inst\text{-}max}$ consistently declined with

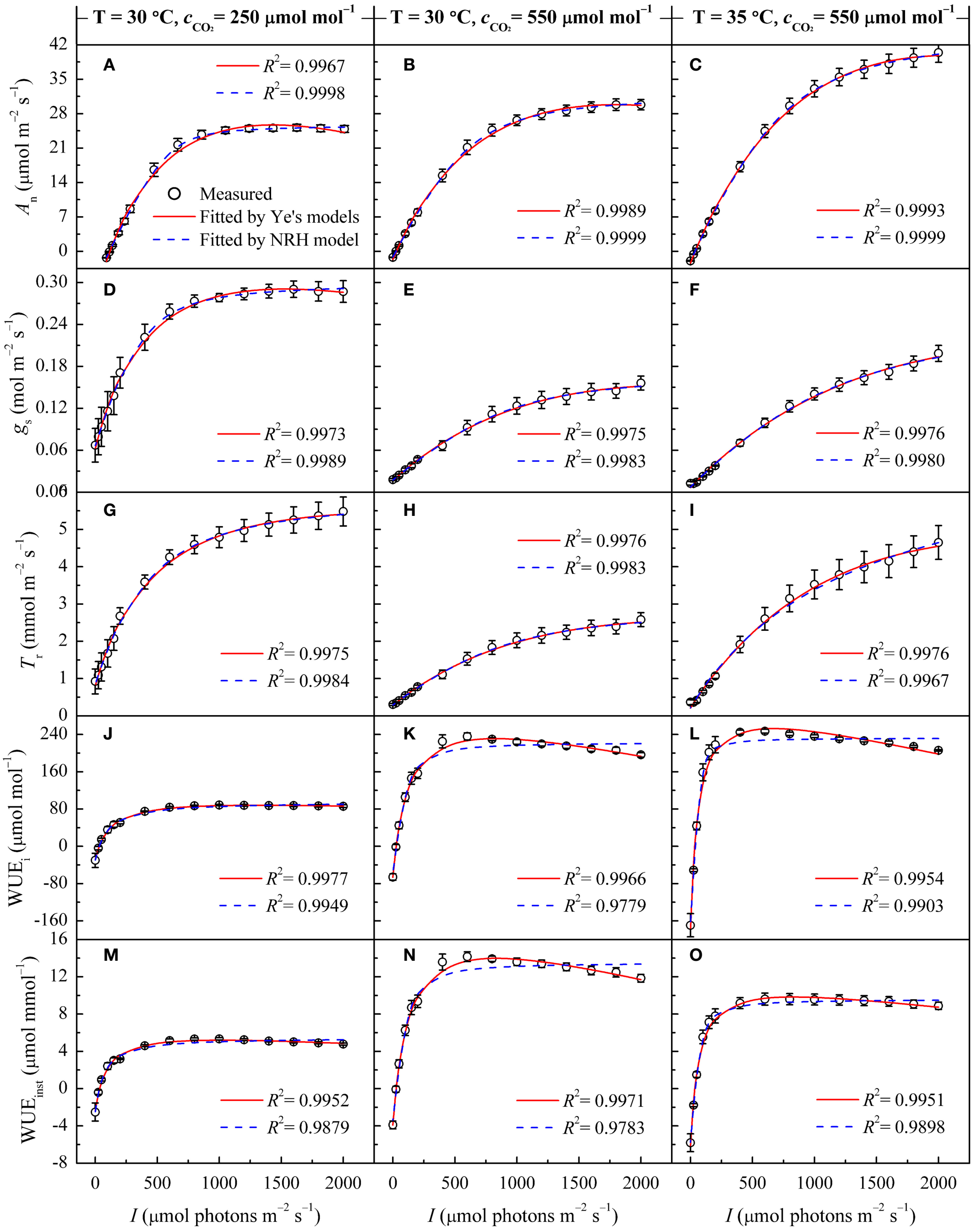

FIGURE 2
Changes in gas exchange parameters of sweet sorghum leaves across varied CO$_2$ concentrations, as well as comparison of light response curves fitted by the Ye's models and the NRH model. Figures **(A, B)**, **(D, E)**, **(G, H)**, **(J, K)** and **(M, N)** present changes in A_n, g_s, T_r, WUE$_i$, and WUE$_{inst}$ at 30°C under CO$_2$ concentrations of 250 and 550 μmol mol^{-1}, respectively. Figures **(C, F, I, L)** and **(O)** show the changes in A_n, g_s, T_r, WUE$_i$, and WUE$_{inst}$ at 35°C under a CO$_2$ concentrations of 550 μmol mol^{-1}.

increasing temperature, with WUE$_{inst\text{-}max}$ displaying the most pronounced decrease and significant differences across temperature levels (p<0.05). For instance, increasing the temperature from 25°C to 30°C caused increase of 47.54%, 40.58%, and 111.91% in A_{nmax}, $g_{s\text{-}max}$, and $T_{r\text{-}max}$, respectively (p<0.05). No significant changes were observed in I_{sat} and $I_{g\text{-}sat}$, while $I_{T\text{-}sat}$ exhibited a non-significant increase (p>0.05). WUE$_{i\text{-}max}$ only decreased by 6.33% without significant differences, whereas WUE$_{inst\text{-}max}$ significantly decreased by 31.30% (Table 2). Further increasing the temperature from 30°C to 35°C, despite the moderated enhancements in A_{nmax}, $g_{s\text{-}max}$, and $T_{r\text{-}max}$ (increases of 23.34%, 29.90%, and 63.76%, respectively), the reduction in WUE$_{i\text{-}max}$ expanded to 7.23%, and WUE$_{inst\text{-}max}$ declined by 25.67%. Higher temperature raised the saturation light intensities corresponding to WUE$_{i\text{-}max}$ and WUE$_{inst\text{-}max}$ (Table 2). However, at an elevated CO$_2$ level (550 μmol mol^{-1}), rising temperature from

30°C to 35°C significantly increased WUE$_{\text{i-max}}$, while expanding the decline of WUE$_{\text{inst-max}}$ to 29.47% due to a substantial 88.55% increase in $T_{\text{r-max}}$ (Supplementary Table 4).

Light response curves of A_n, g_s, T_r, WUE$_i$ and WUE$_{\text{inst}}$ in sweet sorghum under varied air CO$_2$ concentrations

In Figures 2A-D, under sub-ambient CO$_2$ concentration, A_n and g_s exhibited consistent response trends to I, rapidly increasing and reaching $A_{\text{n-max}}$ and $g_{\text{s-max}}$ at corresponding I_{sat} and $I_{\text{g-sat}}$. With increasing CO$_2$ concentration, the responses of g_s and T_r to I gradually shifted from a single-peaked pattern to an approximately linear increase (Figures 2D-I). Under elevated CO$_2$, A_n reached saturation within the measured light intensity range, whereas g_s and T_r increased nearly linearly with I, especially at 35°C (Figures 2F, I). Across varying CO$_2$ concentrations, the patterns in WUE$_i$-I and WUE$_{\text{inst}}$-I curves displayed distinct divisions into light-limited, light-saturated, and light-inhibited segments (Figures 2J-O). At high light intensity (I>1000 μmol m^{-2} s^{-1}) under elevated CO$_2$, both WUE$_i$ and WUE$_{\text{inst}}$ showed a significant reduction.

At a specific temperature (30°C), increasing CO$_2$ concentration from 250 to 410 μmol mol^{-1} resulted in increased A_{nmax} and α for sweet sorghum, while decreasing I_c and R_d (Table 3). I_{sat} corresponding to A_{nmax} remained unchanged. However, further increasing the concentration to 550 μmol mol^{-1} did not cause a continual increase in A_{nmax}; instead, it raised both I_{sat} and I_c. Elevated CO$_2$ significantly weakened photosynthesis under light-limited conditions, as evidenced by reductions in α, α_g, and α_T (Table 3). For g_s and T_r, their values decreased as CO$_2$ levels rose, and their response curves to light became less steep (Figures 2D-I), leading to a significant decrease in $g_{\text{s-max}}$ and $T_{\text{r-max}}$ (p<0.05). Consequently, there was a substantial increase in both WUE$_{\text{i-max}}$ and WUE$_{\text{inst-max}}$ with elevated CO$_2$ (p<0.05). Specifically, upon elevating CO$_2$ concentration from 410 to 550 μmol mol^{-1}, $g_{\text{s-max}}$ decreased by 19.59%, $T_{\text{r-max}}$ by 26.40%, while WUE$_{\text{i-max}}$ increased by 42.44% and WUE$_{\text{inst-max}}$ by 44.85% (Table 5).

TABLE 3 Comparison analysis of photosynthetic parameters in sweet sorghum under varied CO$_2$ levels at 30°C based on fitting values from light response curves using different photosynthetic models.

Photosynthetic parameters	Fitted by the Ye's models			Fitted by the NRH model		
	250 μmol mol^{-1}	410 μmol mol^{-1}	550 μmol mol^{-1}	250 μmol mol^{-1}	410 μmol mol^{-1}	550 μmol mol^{-1}
α (μmol μmol^{-1})	0.0728 ± 0.0078^{ab}	0.0839 ± 0.0035^{a}	0.0610 ± 0.0068^{b}	0.0491 ± 0.0037^{a}	0.0598 ± 0.0025^{a}	0.0481 ± 0.0048^{a}
A_{nmax} (μmol m^{-2} s^{-1})	25.84 ± 0.65^{b}	30.54 ± 0.76^{a}	29.88 ± 1.07^{a}	27.01 ± 0.71^{b}	32.25 ± 1.68^{a}	33.43 ± 1.10^{a}
I_{sat} (μmol m^{-2} s^{-1})	1393.79 ± 71.49^{b}	1460.8 ± 169.7^{b}	1782.36 ± 30.13^{a}	——	——	——
I_c (μmol m^{-2} s^{-1})	30.42 ± 2.13^{a}	23.30 ± 1.16^{b}	28.87 ± 1.90^{ab}	25.56 ± 2.49^{a}	18.01 ± 0.91^{b}	25.00 ± 1.61^{a}
R_d (μmol m^{-2} s^{-1})	2.09 ± 0.08^{a}	1.89 ± 0.02^{ab}	1.70 ± 0.13^{b}	1.23 ± 0.03^{a}	1.07 ± 0.05^{a}	1.19 ± 0.09^{a}
α_s (mol μmol^{-1})	0.0007 ± 0.0000^{a}	0.0004 ± 0.0000^{b}	0.0002 ± 0.0000^{c}	0.0005 ± 0.0000^{a}	0.0003 ± 0.0000^{b}	0.0001 ± 0.0000^{c}
$g_{\text{s-max}}$ (mol m^{-2} s^{-1})	0.293 ± 0.011^{a}	0.194 ± 0.010^{b}	0.156 ± 0.008^{c}	0.237 ± 0.040^{a}	0.167 ± 0.011^{a}	0.161 ± 0.002^{a}
$I_{\text{g-sat}}$ (μmol m^{-2} s^{-1})	1484.64 ± 184.44^{b}	1654.9 ± 22.3^{b}	2533.57 ± 328.53^{a}	——	——	——
g_{s0} (mol m^{-2} s^{-1})	0.061 ± 0.026^{a}	0.033 ± 0.007^{a}	0.016 ± 0.001^{a}	0.066 ± 0.026^{a}	0.036 ± 0.007^{a}	0.017 ± 0.001^{a}
α_r (mmol μmol^{-1})	0.0123 ± 0.0007^{a}	0.0060 ± 0.0006^{b}	0.0028 ± 0.0003^{c}	0.0105 ± 0.0005^{a}	0.0068 ± 0.0005^{b}	0.0025 ± 0.0002^{c}
$T_{\text{r-max}}$ (mmol m^{-2} s^{-1})	5.48 ± 0.36^{a}	3.56 ± 0.15^{b}	2.62 ± 0.13^{c}	5.13 ± 0.76^{a}	4.01 ± 0.48^{ab}	2.74 ± 0.04^{b}
$I_{\text{T-sat}}$ (μmol m^{-2} s^{-1})	2378.80 ± 142.08^{a}	2578.4 ± 319.2^{a}	2837.28 ± 396.25^{a}	——	——	——
T_{r0} (mmol m^{-2} s^{-1})	0.79 ± 0.38^{a}	0.56 ± 0.12^{a}	0.27 ± 0.02^{b}	0.84 ± 0.37^{a}	0.53 ± 0.11^{a}	0.29 ± 0.02^{b}
α_i (m^2 s mol^{-1})	1.4960 ± 0.8689^{a}	2.3849 ± 0.6450^{a}	3.1903 ± 0.5037^{a}	1.1939 ± 0.7342^{a}	1.5512 ± 0.5053^{a}	2.0450 ± 0.2548^{a}
WUE$_{\text{i-max}}$ (μmol mol^{-1})	88.60 ± 2.71^{c}	163.14 ± 2.14^{b}	232.37 ± 6.57^{a}	120.79 ± 13.65^{c}	192.49 ± 8.96^{b}	281.68 ± 12.86^{a}
$I_{\text{i-sat}}$ (μmol m^{-2} s^{-1})	1227.71 ± 62.57^{a}	965.35 ± 76.79^{b}	806.83 ± 54.02^{b}	——	——	——
K_i (μmol mol^{-1})	30.38 ± 15.56^{b}	34.91 ± 8.32^{b}	66.68 ± 7.90^{a}	28.68 ± 16.28^{b}	29.40 ± 9.64^{b}	57.72 ± 7.35^{a}
α_{inst} (m^2 s mmol^{-1})	0.1307 ± 0.0583^{a}	0.1367 ± 0.0354^{a}	0.1849 ± 0.0293^{a}	0.1009 ± 0.0464^{a}	0.0850 ± 0.0281^{a}	0.1196 ± 0.0159^{a}
WUE$_{\text{inst-max}}$ (μmol mmol^{-1})	5.26 ± 0.19^{c}	9.70 ± 0.20^{b}	14.05 ± 0.47^{a}	7.65 ± 0.94^{c}	10.94 ± 0.58^{b}	16.95 ± 0.91^{a}
$I_{\text{inst-sat}}$ (μmol m^{-2} s^{-1})	985.69 ± 14.90^{a}	799.13 ± 63.61^{b}	815.71 ± 49.94^{b}	——	——	——
K_{inst} (μmol mmol^{-1})	2.53 ± 0.98^{a}	2.07 ± 0.48^{a}	3.91 ± 0.47^{a}	2.39 ± 1.05^{a}	1.66 ± 0.60^{a}	3.38 ± 0.45^{a}

Mean and standard errors of three replicates are shown. Statistically significant differences (p<0.05) between temperature treatment groups are denoted by different letters under the Ye's models and the NRH model.

At a high temperature of 35°C, elevated CO_2 concentration positively impacted photosynthesis in sweet sorghum, resulting in a 5.8% increase in A_{nmax} (Table 5, Supplementary Table 4). Similar decreases occurred in $g_{\mathrm{s\text{-}max}}$ and $T_{\mathrm{r\text{-}max}}$, but the plants' dependence on light increased, as evidenced by I_{sat}, $I_{\mathrm{g\text{-}sat}}$ and $I_{\mathrm{T\text{-}sat}}$, all exceeding 2000 µmol photons m^{-2} s^{-1}. Notably, $\mathrm{WUE}_{\mathrm{i\text{-}max}}$ showed significant improvement, reaching 255.46 ± 5.26 µmol mol^{-1}, significantly higher than all other treatment groups (one-way and two-way ANOVA $p<0.05$) (Tables 4, 5). However, the increase in $\mathrm{WUE}_{\mathrm{inst\text{-}max}}$ was significantly lower compared to the increase observed under elevated CO_2 at 30°C, reaching only 37.45% (Supplementary Table 4).

Interactive effect of temperature and CO_2 concentration on key photosynthetic parameters

The interactive effect of temperature and CO_2 concentration on key photosynthetic parameters was assessed in sweet sorghum using a two-way analysis of variance (ANOVA) (Table 4). Temperature provoked highly significant main effects ($p<0.001$) on A_{nmax}, I_{sat}, I_c, R_d, $g_{\mathrm{s\text{-}max}}$, $T_{\mathrm{r\text{-}max}}$, and $\mathrm{WUE}_{\mathrm{inst\text{-}max}}$, suggesting increasing the temperature from 30°C to 35°C profoundly impacted these traits independently of CO_2 concentration. Meanwhile, elevated CO_2 concentration induced highly significant main effect ($p<0.001$) on I_{sat}, $g_{\mathrm{s\text{-}max}}$, $T_{\mathrm{r\text{-}max}}$, and $\mathrm{WUE}_{\mathrm{i\text{-}max}}$, regardless of temperature. Statistically significant interaction effects between temperature and CO_2 were observed for the intrinsic quantum yield (α) at $p<0.05$, as well as for $\mathrm{WUE}_{\mathrm{i\text{-}max}}$, and $\mathrm{WUE}_{\mathrm{inst\text{-}max}}$. Quantum yield represents the photon requirement for assimilating one CO_2 molecule during photosynthesis. This suggests that the impact of temperature differed across CO_2 levels in determining the ability of sweet sorghum to acquire and use water.

DISCUSSION

Applicability of Ye's models to NRH model

In this study, we employed a methodological approach that involved a comparative analysis of models against observed data. This facilitated a systematic assessment and differentiation of the Ye's models and the NRH model concerning their abilities to replicate the A_n-I, g_s-I, T_r-I, WUE_i-I, and $\mathrm{WUE}_{\mathrm{inst}}$-$I$ curves of sweet sorghum. We also focused on quantifying the key traits defining these curves. Remarkably, the Ye's models excelled not only in capturing the diminishing trends in photosynthetic parameters (e.g. A_n, WUE_i, $\mathrm{WUE}_{\mathrm{inst}}$) with increased light intensity, but also in accurately determining critical photosynthetic traits across diverse temperatures and CO_2 conditions. These findings align with previous research applying the Ye's models to Cyanobacteria (Yang et al., 2022; Yang et al., 2023), Chlorophyta, Bacillariophyta (Yang et al., 2020), and other plants (Xu et al., 2012; Atsushi et al., 2017; Martínez-García et al., 2017; Liu et al., 2018; Ye et al., 2020), demonstrating its broad utility.

TABLE 4 Summary of two-way ANOVA analysis between the effects of temperature and CO_2 concentration on key photosynthetic parameters of sweet sorghum.

Dependent variables	Factors	DF	F	*p* value
α (µmol $µmol^{-1}$)	Temperature	1	1.072	0.321
	CO_2 concentration	1	22.831	< 0.001
	Temperature × CO_2 concentration	1	4.981	**0.045**
A_{nmax} (µmol m^{-2} s^{-1})	Temperature	1	50.299	< 0.001
	CO_2 concentration	1	0.406	0.536
	Temperature × CO_2 concentration	1	1.411	0.258
I_{sat} (µmol m^{-2} s^{-1})	Temperature	1	76.254	< 0.001
	CO_2 concentration	1	122.789	< 0.001
	Temperature × CO_2 concentration	1	0.285	0.603
I_c (µmol m^{-2} s^{-1})	Temperature	1	27.790	< 0.001
	CO_2 concentration	1	1.029	0.331
	Temperature × CO_2 concentration	1	1.606	0.229
R_d (µmol m^{-2} s^{-1})	Temperature	1	19.273	0.001
	CO_2 concentration	1	2.247	0.160
	Temperature × CO_2 concentration	1	0.232	0.639
$g_{\mathrm{s\text{-}max}}$ (mol m^{-2} s^{-1})	Temperature	1	63.950	< 0.001
	CO_2 concentration	1	25.771	< 0.001
	Temperature × CO_2 concentration	1	0.007	0.934
$T_{\mathrm{r\text{-}max}}$ (mmol m^{-2} s^{-1})	Temperature	1	81.140	< 0.001
	CO_2 concentration	1	12.919	0.004
	Temperature × CO_2 concentration	1	0.009	0.927
$\mathrm{WUE}_{\mathrm{i\text{-}max}}$ (µmol mol^{-1})	Temperature	1	2.191	0.165
	CO_2 concentration	1	514.088	< 0.001
	Temperature × CO_2 concentration	1	20.812	**0.001**
$\mathrm{WUE}_{\mathrm{inst\text{-}max}}$ (µmol $mmol^{-1}$)	Temperature	1	78.809	< 0.001
	CO_2 concentration	1	89.111	< 0.001
	Temperature × CO_2 concentration	1	4.911	**0.047**

The bold p value indicates a significant interactive effect between temperature and CO_2 concentration on the parameter.

Since its establishment by Thornley in 1976, the NRH model has been extensively utilized to study the response of plant photosynthesis to light, elucidating changes in plant growth and

TABLE 5 Comparison of results fitted by the Ye's models and the NRH model with measured data in sweet sorghum under elevated CO_2 concentration (410 μmol mol^{-1}) and high temperature (35°C) in combination.

Photosynthetic parameters	Temperature of 35°C and CO_2 concentration of 550 μmol mol^{-1}		
	Fitted by the Ye's models	Fitted by the NRH model	Measured by LI-6800
α (μmol μmol^{-1})	0.0649 ± 0.0033 ^{a}	0.0557 ± 0.003 ^{a}	——
A_{nmax} (μmol m^{-2} s^{-1})	39.87 ± 1.92 ^{b}	47.62 ± 2.11 ^{a}	40.42 ± 1.98 ^{b}
I_{sat} (μmol m^{-2} s^{-1})	2064.90 ± 45.82 ^{a}	——	2000.00 ± 0.00 ^{a}
I_c (μmol m^{-2} s^{-1})	38.64 ± 2.9 ^{a}	37.15 ± 2.95 ^{a}	37.99 ± 1.25 ^{a}
R_d (μmol m^{-2} s^{-1})	2.43 ± 0.18 ^{a}	2.04 ± 0.14 ^{ab}	1.95 ± 0.08 ^{b}
α_s (mol μmol^{-1})	0.0002 ± 0.0000 ^{a}	0.0002 ± 0.0000 ^{a}	——
$g_{s\text{-}max}$ (mol m^{-2} s^{-1})	0.215 ± 0.01 ^{b}	0.256 ± 0.013 ^{a}	0.198 ± 0.012 ^{b}
$I_{g\text{-}sat}$ (μmol m^{-2} s^{-1})	3484.01 ± 395.74	——	>2000
g_{s0} (mol m^{-2} s^{-1})	0.006 ± 0.003 ^{a}	0.007 ± 0.003 ^{a}	0.013 ± 0.003 ^{a}
α_r (mmol μmol^{-1})	0.0053 ± 0.0007 ^{a}	0.0049 ± 0.0004 ^{a}	——
$T_{r\text{-}max}$ (mmol m^{-2} s^{-1})	4.94 ± 0.45 ^{b}	7.03 ± 0.23 ^{a}	4.65 ± 0.45 ^{b}
$I_{T\text{-}sat}$ (μmol m^{-2} s^{-1})	2561.44 ± 123.51	——	>2000
T_{r0} (mmol m^{-2} s^{-1})	0.21 ± 0.06 ^{a}	0.24 ± 0.04 ^{a}	0.37 ± 0.07 ^{a}
α_i (m^2 s mol^{-1})	9.1759 ± 1.8803 ^{a}	4.5104 ± 0.7748 ^{b}	——
$WUE_{i\text{-}max}$ (μmol mol^{-1})	255.46 ± 5.26 ^{b}	404.47 ± 27.6 ^{a}	247.05 ± 4.14 ^{b}
$I_{i\text{-}sat}$ (μmol m^{-2} s^{-1})	644.44 ± 49.65 ^{a}	——	525.00 ± 47.87 ^{a}
K_i (μmol mol^{-1})	181.31 ± 25.48 ^{a}	170.53 ± 26.28 ^{a}	169.55 ± 24.90 ^{a}
α_{inst} (m^2 s mmol^{-1})	0.2941 ± 0.0656 ^{a}	0.1633 ± 0.0292 ^{a}	——
$WUE_{inst\text{-}max}$ (μmol mmol^{-1})	9.91 ± 0.64 ^{b}	15.36 ± 1.24 ^{a}	9.66 ± 0.64 ^{b}
$I_{inst\text{-}sat}$ (μmol m^{-2} s^{-1})	816.50 ± 54.83 ^{a}	——	950.02 ± 132.29 ^{a}
K_{inst} (μmol mmol^{-1})	6.19 ± 0.99 ^{a}	5.75 ± 0.93 ^{a}	5.82 ± 0.96 ^{a}

Mean and standard errors of three replicates are shown. Different letters denote statistically significant differences (p<0.05) among the values fitted by the Ye's models, the values fitted by the NRH model, and the measured values.

physiology across diverse environments (Yu et al., 2004; Ye and Yu, 2008; dos Santos Junior et al., 2012; Xu et al., 2012; Domingues et al., 2014; Wassenaar et al., 2022; Wu et al., 2023). However, upon taking the first derivative of the mathematical expression characterizing the relationship between the variables A_n and I, as defined by Equation 13 in the NRH model, an analytical solution was not obtained. This implies that the NRH model follows an asymptotic function for A_n rather than a closed-form solution. Consequently, the NRH model does not produce analytical solutions for the maximum A_n and the specific saturation light intensity for A_{nmax}. A_{nmax} may be numerically estimated from the NRH model through nonlinear least squares calculations (Ye et al., 2021). When parameters such as A_n, g_s, T_r, WUE_i, and WUE_{inst} of plants reach saturation or decrease with increasing I under high light intensities, the maximum values obtained by fitting their light response curves using the NRH model would inevitably deviate significantly from their observed values. This discrepancy explains why the A_{nmax}, $g_{s\text{-}max}$, $T_{r\text{-}max}$, $WUE_{i\text{-}max}$, and $WUE_{inst\text{-}max}$ derived from the NRH model fitting for sweet sorghum in this study significantly differed from the measured data. These findings are consistent with previous reports of similar discrepancies (dos Santos Junior et al., 2012; Xu et al., 2012; Atsushi et al., 2017; Martínez-García et al., 2017; Liu et al., 2018).

Photoinhibition is the well-documented, light-induced decrease in photosynthetic rate in plants that occurs upon exposure to excess irradiance exceeding their utilization capacity (Anderson et al., 2021). Similarly, in the present study, both the WUE_i-I and WUE_{inst}-I curves of sweet sorghum exhibited declining trends under high light intensities, consistent with our previous findings in *Glycine max* and *Amaranthus hypochondriacus* (Ye et al., 2020). This reduction in plant WUE under high irradiance appears to be common across species. Thus, light response models that do not effectively capture decreases in photosynthetic parameters under high light conditions are likely to fail in elucidate plant responses across varying irradiance environments and determine actual physiological states (Egea et al., 2011). In contrast, by incorporating light inhibition effect (β) and a light saturation parameter (γ), the Ye's model (Equations 1, 7, 10) provided excellent fits to the A_n-I, $WUE_{i\text{-}max}$-I, and $WUE_{inst\text{-}max}$-I curves of plants, irrespective of temperature or CO_2 concentration (Ye et al., 2013; Ye et al., 2020).

Effect of elevated temperature on dynamic photosynthesis and water use efficiency in sweet Sorghum leaves

Plants facing environmental stress commonly exhibit reduced leaf photosynthesis (Hatfield and Dold, 2019). However, our study revealed sweet sorghum exhibited robust photosynthesis and a lack of photoinhibition at high temperatures up to 35°C, aligning with literature suggesting greater photosynthetic thermotolerance in sorghum species (Loreto et al., 1995; Prasad et al., 2021; Sales et al., 2021). Specifically, previous evidence indicates that optimal temperatures exceeding 35°C sustain the enzymatic rates of key C_4 cycle enzymes like pyruvate orthophosphate dikinase and phosphoenolpyruvate carboxylase in sorghum (Loreto et al., 1995; Sales et al., 2021), thereby preserving carbon assimilation even at high temperatures. Through concentrating CO_2 at the site of Rubisco, C_4 plants effectively suppress photorespiration while simultaneously minimizing transpiration. This twin benefit confers advantages to C_4 species over C_3 plants in hot, arid climates (Sales et al., 2021). Therefore, the thermotolerant photosynthesis exhibited by sweet sorghum likely facilitates the ecological success of C_4 cereals including sorghum across tropical and subtropical agroecosystems prone to heat stress. Further examination of genotypic variation in thermal acclimation processes governing photosynthesis may inform climate-resilient crop development.

g_s has been considered one of the most vital indicators of a plant's response to environmental fluctuations, yet its reaction to temperature has been relatively understudied (Urban et al., 2017). Some earlier studies have suggested divergent responses of g_s to increasing temperatures, including an increase (Mott and Peak, 2010; Urban et al., 2017), no significant change, or even stomatal closure. Our present results are consistent with previous research in *Tradescantia pallida* (Mott and Peak, 2010), *Pinus taeda*, and *Populus deltoides x nigra* (Urban et al., 2017). As temperatures increased, g_s of sweet sorghum gradually increased, enhancing the exchange of CO_2 and H_2O and elevating the CO_2 uptake. In early research, g_s and A_n were commonly presumed to share a stable, linear relationship, with g_s and A_n exhibiting synergistic increases or decreases in response to varying environmental conditions. The patterns of g_s and A_n in sweet sorghum leaves showed some parallels when responding to light. However, because g_s is more thermally sensitive, a slight decline in WUE_i was observed when leaf temperatures increased from 30°C to 35°C. Typically, increased temperature coupled with heightened vapor pressure deficit (*VPD*) results in increased T_r, followed by cell shrinkage and stomatal closure (Urban et al., 2017; Sales et al., 2021). Interestingly in this study, even when the *VPD* of sweet sorghum leaves rose to 2.2 kPa at 35°C, the intercellular CO_2 concentration (C_i) remained relatively stable, implying stomata did not close. Instead, *VPD*, g_s, and A_n increased concurrently (Supplementary Figure 2, Figures 1A-F). This aligns with observations in *Oryza* and *Flaveria bidentis* under elevated temperatures (Kubien et al., 2003; Scafaro et al., 2011), contrasting the behavior of the C_4 Model *Setaria viridis* (Anderson et al., 2021). The differential stomatal responses to warming may be attributable to variances in plant functional type or evolutionary origin (Bykova et al., 2019). Therefore, the findings indicate photosynthesis in sweet sorghum was not suppressed by elevated temperatures; rather, it was stimulated by widening of stomatal openings to enhance CO_2 influx, expediting assimilation rates.

The variation in WUE_{inst} of sweet sorghum became more noticeable with increasing temperature. Notably, WUE_{inst} substantially decreased relative to WUE_i, primarily due to the disproportionate increase in transpiration compared to photosynthesis under elevated temperatures. For example, from 30°C to 35°C, $T_{r\text{-}max}$ increased 2.73 times compared to A_{nmax} and 2.02 times versus $g_{s\text{-}max}$. WUE_i indicates a long-term water use balance between assimilation and conductance, independent of vapor pressure deficit (von Caemmerer and Farquhar, 1981; Gyimah and Nakao, 2007; Ye et al., 2020). In this study, sweet sorghum exhibited a minor decrease in WUE_i with elevated temperatures, highlighting adaptation via prioritizing growth and survival over short-term heat stress. In contrast, WUE_{inst} experienced a significant decrease. As WUE_{inst} represents plant yield per water loss, aligning with whole-plant WUE (Wall et al., 2001). Its substantial reduction indicates a trade-off of water to ensure survival under high temperatures. This could be seen as a physiological mechanism employed by sweet sorghum for leaf cooling under short-term heat stress, as adopted in other species (Scafaro et al., 2011; Anderson et al., 2021). Collectively, these results reveal that sweet sorghum adjustments to maintain photosynthesis, transpiration and respiration could outweigh slower WUE adaptations, especially diminishing dynamic WUE_{inst}.

Effect of elevated CO_2 concentration on dynamic photosynthesis and water use efficiency in sweet sorghum leaves

Raising CO_2 levels from 250 to 410 μmol mol^{-1} enhanced photosynthesis in sweet sorghum at moderate temperatures, consistent with observations in many plants (Gago et al., 2014; Kimball, 2016). The heightened substrate availability drives this initial photosynthetic response. However, further elevating CO_2 concentration to 550 μmol mol^{-1} did not lead to a consistent and proportional increase in photosynthesis. In concordance with previous research indicating reduced sorghum yield under elevated CO_2 concentrations (Kimball, 2016; Asadi and Eshghizadeh, 2021), this suggests that sweet sorghum's photosynthetic system cannot fully capitalize on CO_2 levels beyond a saturation threshold. Instead, alternative factors such as light availability, may become limiting beyond this point. Despite lacking statistical significance, elevated CO_2 concentration did improve photosynthesis at 35°C. Two-way ANOVA analysis from Table 4 also indicated CO_2 level impacts on sweet sorghum's light use efficiency and WUE (including both intrinsic and instantaneous aspects) vary across temperatures, highlighting complex interplay between temperature and CO_2 in photosynthetic responses. Previous research emphasized that the magnitude of A_n at elevated temperatures is primarily determined by the electron transfer capacity, suggesting that sweet sorghum photosynthesis has been constrained by irradiance and temperature under current atmospheric CO_2 (Loreto et al., 1995; McAusland et al., 2016; Sales et al., 2021).

The CO_2 rise induced partial stomatal closure, reducing g_s and T_r, consequently improving WUE, a widely observed response (Conley et al., 2001; Allen et al., 2011). The reduction in g_s under high CO_2 levels is recognized as an adaptive response across various plant species (Farooq et al., 2019). Higher atmospheric CO_2 led to elevated C_i in leaves, increasing stomatal sensitivity and prompting adjustments to maintain C_i below ambient levels (Urban et al., 2017; Feng et al., 2023). Contrary to previous studies attributing heightened WUE_i to simultaneous increases in A_n and decreases in T_r under elevated CO_2 (Conley et al., 2001; Ye et al., 2020), improvements here arose primarily from reductions in g_s and T_r, rather than an increase in A_n. Furthermore, CO_2-induced reductions in g_s and T_r diminished at 35°C, suggesting that this stomatal response weakens with increasing leaf temperature. This interaction emphasizes the complex CO_2-temperature interplay in shaping plant responses. Despite the substantial increase in WUE_i to 255.46 ± 5.26 μmol mol^{-1} under the combined influence of elevated CO_2 and temperature implies the adaptive capacity of sweet sorghum to shifting environments, the precise mechanisms remain unclear and require further investigation. Optimizing WUE likely involves intricate signaling and physiological adjustments (Hatfield and Dold, 2019).

While providing unique insights into immediate photosynthetic responses, our short-term exposures are constrained in comparison to long-term open-top chamber (OTC) and free-air CO_2 enrichment (FACE) studies. Prolonged OTC and FACE exposures over weeks or months facilitate a thorough characterization of gradual acclimation processes, revealing cumulative impacts on physiology, metabolism, tissue structure, gene/protein expression, yield, and overall plant adaptation. Looking ahead, it is imperative to conduct systematic and long-term investigations to gain a more nuanced understanding of sweet sorghum's adaptability to climate change scenarios and its potential under predicted climatic conditions. These future studies should meticulously explore morphological, physiological, and biochemical differences within the plant, encompassing variations in responses among roots, stems, and leaves. Additionally, our use of indoor-cultivated seedlings differs from field-grown plants. While growth chambers allow precise regulation of conditions like temperature, humidity, and lighting to reduce variability and stressors, indoor cultivation may heighten sensitivity to environmental shifts. Transferring seedlings from controlled growth chamber to the lab with open gas circulation for gas exchange measurements may induce physiological changes due to altered growth conditions. Despite efforts to minimize variation, the transition between environments could result in transient responses that would not occur in plants already acclimated to field settings.

Conclusion

Our study further validates the superiority of the photosynthesis models proposed by Ye et al. for simulating the light response curves of A_n, g_s, T_r, WUE_i, and WUE_{inst}. Particularly, when employed to fit the WUE_i-I and WUE_{inst}-I curves, the models uniquely capture the decline in both WUE_i and WUE_{inst} with increasing I under high light intensity. Across all experimental conditions, it returns the values for A_{nmax}, $g_{s\text{-}max}$, $T_{r\text{-}max}$, $WUE_{i\text{-}max}$, and $WUE_{inst\text{-}max}$ closely matching measured data. In contrast, the NRH model inadequately reproduces the WUE_i-I and WUE_{inst}-I curves and severely overestimates A_{nmax}, $WUE_{i\text{-}max}$, and $WUE_{inst\text{-}max}$ relative to measurements. It also fails to determine the corresponding saturation light intensities for these traits. In addition, sweet sorghum exhibits remarkable heat tolerance up to 35°C, achieving higher A_n through stimulated g_s. However, disproportionate increase in T_r lead to a sharp decline in WUE_{inst}. Increasing CO_2 concentration from sub-ambient to ambient levels has a significant positive effect on photosynthesis in sweet sorghum, but no consistent and proportional increase is observed at 550 μmol mol^{-1}. Elevated CO_2 causes partial stomatal closure in sweet sorghum leaves, markedly reducing g_s and T_r, thereby improving WUE_i and WUE_{inst}. Nevertheless, the effect of CO_2-induced stomatal closure in reducing transpiration progressively diminishes at high temperature owing to stomatal opening. Elucidating the physiological mechanisms governing plant responses to combined environmental factors will enable identifying adaptive traits to accelerate resilient crop development amidst intensifying environments.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding authors.

Author contributions

X-LY: Conceptualization, Data curation, Formal Analysis, Investigation, Writing – original draft. X-FM: Writing – review and editing, Resources, Supervision, Software. Z-PY: Funding acquisition, Methodology, Writing – review and editing, Software. L-SY: Writing – review and editing, Investigation. J-BS: Writing – review and editing, Investigation. XW: Writing – review and editing, Investigation. B-BZ: Writing – review and editing, Visualization. F-BW: Writing – review and editing. Z-FD: Funding acquisition, Supervision, Writing – review and editing, Project administration.

Funding

The author(s) declare financial support was received for the research, authorship, and/or publication of this article. This research was supported by the Natural Science Foundation of China (Grant No. 31960054 and 32260063) and the China Postdoctoral Science Foundation (Grant No. 2023M733681).

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpls.2024.1291630/full#supplementary-material

References

Allen, L. H., Kakani, V. G., Vu, J. C. V., and Boote, K. J. (2011). Elevated CO_2 increases water use efficiency by sustaining photosynthesis of water-limited maize and sorghum. *J. Plant Physiol.* 168, 1909–1918. doi: 10.1016/j.jplph.2011.05.005

Anderson, C., Mattoon, E., Zhang, N., Becker, E., Mchargue, W., Yang, J., et al. (2021). High light and temperature reduce photosynthetic efficiency through different mechanisms in the C_4 model *Setaria viridis*. *Commun. Biol.* 4, 1092. doi: 10.1038/s42003-021-02576-2

Appiah-Nkansah, N. B., Li, J., Rooney, W., and Wang, D. (2019). A review of sweet sorghum as a viable renewable bioenergy crop and its techno-economic analysis. *Renew. Energ.* 143, 1121–1132. doi: 10.1016/j.renene.2019.05.066

Asadi, M., and Eshghizadeh, H. R. (2021). Response of sorghum genotypes to water deficit stress under different CO_2 and nitrogen levels. *Plant Physiol. Bioch.* 158, 255–264. doi: 10.1016/j.plaphy.2020.11.010

Atsushi, S., Tatsuya, K., Shigeto, T., and Masashi, Y. (2017). Effect of temperature on photosynthesis characteristics in the passion fruits 'Summer Queen' and 'Ruby Star'. *Horticult. J.* 86, 194–199. doi: 10.2503/hortj.OKD-023

Bykova, O., Chuine, I., and Morin, X. (2019). Highlighting the importance of water availability in reproductive processes to understand climate change impacts on plant biodiversity. *Perspect. Plant Ecol.* 37, 20–25. doi: 10.1016/j.ppees.2019.01.003

Conley, M. M., Kimball, B. A., Brooks, T. J., Pinter, P. J.Jr., Hunsaker, D. J., Wall, G. W., et al. (2001). CO_2 enrichment increases water-use efficiency in sorghum. *New Phytol.* 151, 407–412. doi: 10.1046/j.1469-8137.2001.00184.x

Domingues, T. F., Martinelli, L. A., and Ehleringer, J. R. (2014). Seasonal patterns of leaf-level photosynthetic gas exchange in an eastern Amazonian rain forest. *Plant Ecol. Divers.* 7, 189–203. doi: 10.1080/17550874.2012.748849

dos Santos Junior, U. M., de Carvalho Gonçalves, J. F., and Fearnside, P. M. (2012). Measuring the impact of flooding on Amazonian trees: photosynthetic response models for ten species flooded by hydroelectric dams. *Trees* 27, 193–210. doi: 10.1007/s00468-012-0788-2

Egea, G., Verhoef, A., and Vidale, P. L. (2011). Towards an improved and more flexible representation of water stress in coupled photosynthesis–stomatal conductance models. *Agr. For. Meteorol.* 151, 1370–1384. doi: 10.1016/j.agrformet.2011.05.019

Farooq, M., Hussain, M., Ul-Allah, S., and Siddique, K. H. M. (2019). Physiological and agronomic approaches for improving water-use efficiency in crop plants. *Agric. Water Manage.* 219, 95–108. doi: 10.1016/j.agwat.2019.04.010

Farquhar, G. D., and Wong, S. C. (1984). An empirical model of stomatal conductance. *Aust. J. Plant Physiol.* 11, 191–210. doi: 10.1071/PP9840191

Feng, S., Hao, Z., Zhang, X., Wu, L., Zhang, Y., and Hao, F. (2022). Climate change impacts on concurrences of hydrological droughts and high temperature extremes in a semi-arid river basin of China. *J. Arid Environ.* 202, 104768. doi: 10.1016/j.jaridenv.2022.104768

Feng, X., Liu, R., Li, C., Zhang, H., and Slot, M. (2023). Contrasting responses of two C_4 desert shrubs to drought but consistent decoupling of photosynthesis and stomatal conductance at high temperature. *Environ. Exp. Bot.* 209, 105295. doi: 10.1016/j.envexpbot.2023.105295

Fracasso, A., Magnanini, E., Marocco, A., and Amaducci, S. (2017). Real-time determination of photosynthesis, transpiration, water-use efficiency and gene expression of two *Sorghum bicolor* (Moench) genotypes subjected to dry-down. *Front. Plant Sci.* 8. doi: 10.3389/fpls.2017.00932

Gago, J., Douthe, C., Florez-Sarasa, I., Escalona, J. M., Galmes, J., Fernie, A. R., et al. (2014). Opportunities for improving leaf water use efficiency under climate change conditions. *Plant Sci.* 226, 108–119. doi: 10.1016/j.plantsci.2014.04.007

Grillakis, M. G. (2019). Increase in severe and extreme soil moisture droughts for Europe under climate change. *Sci. Total Environ.* 660, 1245–1255. doi: 10.1016/j.scitotenv.2019.01.001

Gyimah, R., and Nakao, T. (2007). Early growth and photosynthetic responses to light in seedlings of three tropical species differing in successional strategies. *New Forest.* 33, 217–236. doi: 10.1007/s11056-006-9028-1

Hatfield, J. L., and Dold, C. (2019). Water-use efficiency: Advances and challenges in a changing climate. *Front. Plant Sci.* 10, 103. doi: 10.3389/fpls.2019.00103

Kimball, B. A. (2016). Crop responses to elevated CO_2 and interactions with H_2O, N, and temperature. *Curr. Opin. Plant Biol.* 31, 36–43. doi: 10.1016/j.pbi.2016.03.006

Kubien, D. S., Caemmerer, S. V., Furbank, R. T., and Sage, R. F. (2003). C_4 photosynthesis at low temperature. A study using transgenic plants with reduced amounts of Rubisco. *Plant Physiol.* 132, 1577–1585. doi: 10.1104/pp.103.021246

Leakey, A. D. B., Uribelarrea, M., Ainsworth, E. A., Naidu, S. L., and Long, S. P. (2006). Photosynthesis, productivity, and yield of maize are not affected by open-air elevation of CO_2 concentration in the absence of drought. *Plant Physiol.* 140, 779–790. doi: 10.1104/pp.105.073957

Liu, S., Liu, W., Shi, X., Li, S., Hu, T., Song, L., et al. (2018). Dry-hot stress significantly reduced the nitrogenase activity of epiphytic cyanolichen. *Sci. Total Environ.*, 619–620, 630–637. doi: 10.1016/j.scitotenv.2017.11.179

Loreto, F., Tricoli, D., and Marco, G. D. (1995). On the relationship between electron transport rate and photosynthesis in leaves of the C_4 plant *Sorghum bicolor* exposed to water stress, temperature changes and carbon metabolism inhibition. *Aust. J. Plant Physiol.* 22, 885–892. doi: 10.1071/PP9950885

Martínez-García, E., Rubio, E., García-Morote, F. A., Andrés-Abellán, M., Miettinen, H., and López-Serrano, F. R. (2017). Net ecosystem production in a Spanish black pine forest after a low burn-severity fire: Significance of different modelling approaches for estimating gross primary production. *Agr. For. Meteorol.* 246, 178–193. doi: 10.1016/j.agrformet.2017.06.017

McAusland, L., Vialet-Chabrand, S., Davey, P., Baker, N. R., Brendel, O., and Lawson, T. (2016). Effects of kinetics of light-induced stomatal responses on photosynthesis and water-use efficiency. *New Phytol.* 211, 1209–1220. doi: 10.1111/nph.14000

Mott, K. A., and Peak, D. (2010). Stomatal responses to humidity and temperature in darkness. *Plant Cell Environ.* 33, 1084–1090. doi: 10.1111/j.1365-3040.2010.02129.x

Mundia, C. W., Secchi, S., Akamani, K., and Wang, G. (2019). A regional comparison of factors affecting global sorghum production: The case of north America, Asia and Africa's Sahel. *Sustainability* 11, 2135. doi: 10.3390/su11072135

Prasad, V. B. R., Govindaraj, M., Djanaguiraman, M., Djalovic, I., Shailani, A., Rawat, N., et al. (2021). Drought and high temperature stress in sorghum: physiological, genetic, and molecular insights and breeding approaches. *Int. J. Mol. Sci.* 22, 9826. doi: 10.3390/ijms22189826

Prasad, P. V. V., Vu, J. C. V., Boote, K. J., and Allen, L. H. (2009). Enhancement in leaf photosynthesis and upregulation of Rubisco in the C_4 sorghum plant at elevated growth carbon dioxide and temperature occur at early stages of leaf ontogeny. *Funct. Plant Biol.* 36, 761–769. doi: 10.1071/FP09043

Sales, C. R. G., Wang, Y., Evers, J. B., and Kromdijk, J. (2021). Improving C_4 photosynthesis to increase productivity under optimal and suboptimal conditions. *J. Exp. Bot.* 72, 5942–5960. doi: 10.1093/jxb/erab327

Scafaro, A. P., Von Caemmerer, S., Evans, J. R., and Atwell, B. J. (2011). Temperature response of mesophyll conductance in cultivated and wild *Oryza* species with contrasting mesophyll cell wall thickness. *Plant Cell Environ.* 34, 1999–2008. doi: 10.1111/j.1365-3040.2011.02398.x

Silva, R. G. D., Alves, R. C., and Zingaretti, S. M. (2020). Increased [CO_2] causes changes in physiological and genetic responses in C_4 crops: A brief review. *Plants* 9, 1567. doi: 10.3390/plants9111567

Soltani, S., Mosavi, S. H., Saghaian, S. H., Azhdari, S., Alamdarlo, H. N., and Khalilian, S. (2023). Climate change and energy use efficiency in arid and semiarid agricultural areas: A case study of Hamadan-Bahar plain in Iran. *Energy* 268, 126553. doi: 10.1016/j.energy.2022.126553

Thornley, J. H. M. (1976). *Mathematical Models in Plant Physiology* (London, UK: Academic Press), 86–110.

Thornley, J. H. M. (1998). Dynamic model of leaf photosynthesis with acclimation to light and nitrogen. *Ann. Bot-London.* 81, 421–430. doi: 10.1006/anbo.1997.0575

Urban, J., Ingwers, M. W., McGuire, M. A., and Teskey, R. O. (2017). Increase in leaf temperature opens stomata and decouples net photosynthesis from stomatal conductance in *Pinus taeda* and *Populus deltoides* × *nigra*. *J. Exp. Bot.* 68, 1757–1767. doi: 10.1093/jxb/erx052

von Caemmerer, S. (2013). Steady-state models of photosynthesis. *Plant Cell Environ.* 36, 1617–1630. doi: 10.1111/pce.12098

von Caemmerer, S., and Farquhar, G. D. (1981). Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. *Planta* 153, 376–387. doi: 10.1007/BF00384257

Wall, G. W., Brooks, T. J., Adam, N. R., Cousins, A. B., Kimball, B. A., Pinter, P. J.Jr., et al. (2001). Elevated atmospheric CO_2 improved sorghum plant water status by ameliorating the adverse effects of drought. *New Phytol.* 152, 231–248. doi: 10.1046/j.0028-646X.2001.00260.x

Wassenaar, M. L. J., van Ieperen, W., and Driever, S. M. (2022). Low red to far-red ratio increases resistance to CO_2 diffusion and reduces photosynthetic efficiency in low light grown tomato plants. *Environ. Exp. Bot.* 200, 104918. doi: 10.1016/j.envexpbot.2022.104918

Wu, C., Chen, D., Xia, G., Sun, X., and Zhang, S. (2023). Response characteristics of photosynthetic productivity of the canopy spatial distribution pattern of *Larix kaempferi*. *Forests* 14, 1171. doi: 10.3390/f14061171

Xu, Z., Yin, H., Xiong, P., Wan, C., and Liu, Q. (2012). Short-term responses of *Picea asperata* seedlings of different ages grown in two contrasting forest ecosystems to experimental warming. *Environ. Exp. Bot.* 77, 1–11. doi: 10.1016/j.envexpbot.2011.10.011

Xue, W., Nay-Htoon, B., Lindner, S., Dubbert, M., Otieno, D., Ko, J., et al. (2016). Soil water availability and capacity of nitrogen accumulation influence variations of intrinsic water use efficiency in rice. *J. Plant Physiol.* 193, 26–36. doi: 10.1016/j.jplph.2016.02.003

Yan, Z., He, D., Niu, G., and Zhai, H. (2019). Evaluation of growth and quality of hydroponic lettuce at harvest as affected by the light intensity, photoperiod and light quality at seedling stage. *Sci. Hortic-Amsterdam* 248, 138–144. doi: 10.1016/j.scienta.2019.01.002

Yang, X., Bi, Y., Ma, X., Dong, W., Wang, X., and Wang, S. (2022). Transcriptomic analysis dissects the regulatory strategy of toxic cyanobacterium *Microcystis aeruginosa* under differential nitrogen forms. *J. Hazard. Mater.* 428, 128276. doi: 10.1016/j.jhazmat.2022.128276

Yang, X. L., Dong, W., Liu, L. H., Bi, Y. H., Xu, W. Y., and Wang, X. (2023). Uncovering the differential growth of *Microcystis aeruginosa* cultivated under nitrate and ammonium from a photophysiological perspective. *ACS ES&T Water* 3, 1161–1171. doi: 10.1021/acsestwater.2c00624

Yang, X. L., Liu, L. H., Yin, Z. K., Wang, X. Y., Wang, S. B., and Ye, Z. P. (2020). Quantifying photosynthetic performance of phytoplankton based on photosynthesis–irradiance response models. *Environ. Sci. Eur.* 32, 24. doi: 10.1186/s12302-020-00306-9

Ye, Z. P., Duan, S. H., Chen, X. M., Duan, H. L., Gao, C. P., Kang, H. J., et al. (2021). Quantifying light response of photosynthesis: Addressing the long-standing limitations of non-rectangular hyperbolic model. *Photosynthetica* 59, 185–191. doi: 10.32615/ps.2021.009

Ye, Z. P., Ling, Y., Yu, Q., Duan, H. L., Kang, H. J., Huang, G. M., et al. (2020). Quantifying light response of leaf-scale water-use efficiency and its interrelationships with photosynthesis and stomatal conductance in C_3 and C_4 species. *Front. Plant Sci.* 11. doi: 10.3389/fpls.2020.00374

Ye, Z. P., Suggett, J. D., Robakowski, P., and Kang, H. J. (2013). A mechanistic model for the photosynthesis-light response based on the photosynthetic electron transport of photosystem II in C_3 and C_4 species. *New Phytol.* 199, 110–120. doi: 10.1111/nph.12242

Ye, Z. P., and Yu, Q. (2008). A coupled model of stomatal conductance and photosynthesis for winter wheat. *Photosynthetica* 46, 637–640. doi: 10.1007/s11099-008-0110-0

Yin, X., Busch, F. A., Struik, P. C., and Sharkey, T. D. (2021). Evolution of a biochemical model of steady-state photosynthesis. *Plant Cell Environ.* 44, 1–27. doi: 10.1111/pce.14070

Yu, Q., Zhang, Y. Q., Liu, Y. F., and Shi, P. L. (2004). Simulation of the stomatal conductance of winter wheat in response to light, temperature and CO_2 changes. *Ann. Bot-London.* 93, 435–441. doi: 10.1093/aob/mch023