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ORIGINAL PAPER

An Elevated CO_2 Concentration Improves the Photosynthetic Efficiency and Grain Yield of Rice Plants but Concurrently Increases the Nitrogen Fertilizer

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Abstract

Elevated atmospheric CO_2 concentrations (e[CO_2]) have a profound impact on crop production. However, within the e[CO_2] trend, the influence of different nitrogen (N) application rates on the photosynthetic efficiency of rice leaves, as well as the resulting changes in grain yield, remains poorly understood. Open-top chambers (OTCs) were utilized as the research platform; there were three [CO_2] treatments, i.e., ambient [CO_2] treatment as the control group (CG, 400 ± 10 mmol mol–1); C1 (560 ± 10 mmol mol^{-1}); and C2 (600 ± 10 mmol mol^{-1}); and three levels of nitrogen fertilizer, N1, N2, and N3 (100, 200, and 300 kg ha^{-1}). Chlorophyll fluorescence (ChlF) technology was used to study the variations in photosynthetic parameters during the crucial growth stage of rice and to analyze yield composition disparities. The findings demonstrated that the level of e[CO_2] and nitrogen fertilizer dose significantly influenced the chlorophyll content and photosynthetic efficiency of rice leaves throughout the growth period, ultimately impacting yield composition. Moreover, a notable positive interaction effect between these two factors was observed. Compared with CGN1, N2 and N3 had greater leaf maximum photochemical quantum efficiency (F_v/F_m) and energy transformation potential (F_v/F_o). Relatively speaking, nitrogen fertilizer had a more significant effect than e[CO_2]. Overall, e[CO_2] can undeniably enhance rice photosynthesis and ultimately lead to increased yield, but it is imperative to also focus on augmenting the application of nitrogen fertilizer.

Keywords Elevated carbon dioxide · Nitrogen level · Rice · Chlorophyll fluorescence · Grain yield

1 Introduction

Anthropogenic activities, such as land-use changes, deforestation, and the combustion of fossil fuels, release substantial quantities of greenhouse gases (GHGs) into the atmosphere, and carbon dioxide (CO_2) is widely recognized as the most significant contributor to greenhouse effects (Cui et al. 2023; Ou et al. 2021). The global atmospheric CO_2 concentration ([CO_2]) increased from 310 ppm to 415 ppm between 1960 and 2021, with projections indicating a potential increase

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to around 600 and 800 ppm by the middle and end of the century, respectively (Baldwin et al. 2019). Atmospheric elevated CO_2 concentrations (e[CO_2]) will have a profound impact on agricultural planting ecology and production systems (Cui et al. 2023). The significance of rice as a staple food worldwide cannot be overstated, with approximately 45–50% of the global population relying on rice food (Bailey-Serres et al. 2019; Zhu et al. 2018). Food production has undergone a remarkable increase in recent years; however, the efficiency of photosynthesis has stagnated, and the potential for enhancing photosynthetic efficiency has the capacity to boost yields by up to 40% (Miglani et al. 2021; Simkin et al. 2019). Analyzing crop photosynthetic responses to e[CO_2] and maximizing the "fertilizer effect" induced by elevated [CO_2] will contribute to mitigating the adverse impacts of climate change on crop production (Faye et al. 2023; Wang et al. 2021).

Chlorophyll fluorescence (ChlF) technology is a convenient, time-efficient, and nondestructive practice for clarifying photosynthetic physiology and has been applied to crops such as rice, wheat, maize, and tomato (Buareal et al. 2023; Dechant et al. 2020; Li et al. 2023; Zhang et al. 2023). The results of these studies can help determine the laws governing light energy absorption and the photosystem II (PSII) electron transfer rate in the leaves of plants, as well as elucidate the mechanisms underlying light adaptation, suppression, and protection in the photosynthetic system of plants (Dechant et al. 2020). After being excited by light, PSII electrons are transported to chlorophyll and subsequently to two quinone molecules, QA and QB, for power. Alterations in the parameters of light capture, electron transport, and energy conversion activity are important for exploring photosynthetic metabolism (Lv et al. 2022). CO_2 serves as a substrate for plant photosynthesis, possessing both infrared absorption characteristics and providing the necessary carbon for plant growth and photosynthesis (Wang et al. 2018). An e[CO_2] enhances the conversion rate and activity of PSII, thereby augmenting primary photoenergy and ultimately elevating photosynthetic capacity (Buareal et al. 2023; Javaid et al. 2022). As a typical C_3 crop, rice exhibits sensitivity to potential alterations in environmental CO_2 levels (AbdElgawad et al. 2021; Faye et al. 2023). Cai et al. (2020) reported that e[CO_2] enhanced nitrogen utilization, the electron transport rate, and ChlF efficiency in rice leaves; Wang et al. (2020) revealed that the impact of e[CO_2] on crop photosynthesis varied across different growth stages. Moreover, e[CO_2] exposure after the rice panicle stage accelerated leaf senescence, decreased the chlorophyll content (SPAD), and impaired the regulation of photosynthetic processes. Furthermore, some related findings have shown that prolonged exposure to high CO_2 concentrations does not significantly impact fluorescence parameters, even inhibiting plant photosynthetic rates, disrupting the central structure of PSII reactions, or reducing the leaf photosynthetic capacity (Leakey et al. 2012; Wang et al. 2015b).

Excessive nitrogen use can cause nitrogen loss and environmental pollution, and proper nitrogen management, such as adjusting fertilization rates and timing and implementing precision agriculture, can reduce nitrogen losses and environmental risks (Saiki et al. 2020; Yin et al. 2023). Promoting the use of crop varieties with high nitrogen use efficiency and optimizing nitrogen fertilizer sources can also help reduce nitrogen pollution (Saiki et al. 2020; Waqas et al. 2023). In addition to aboveground variables, light, temperature, and CO_2 are the primary regulatory factors for photosynthetic capacity (Dong et al. 2022; Waring et al. 2023). The availability of nitrogen (N) significantly impacts the levels of leaf photosynthetic pigments, thylakoid membrane proteins, and Calvin cycle-related enzymes, consequently affecting the capacity for photosynthetic CO_2 fixation (Andrews et al. 2018; Dong et al. 2022; Liu et al. 2023). The application of nitrogen can maintain carbon storage in terrestrial ecosystems under e[CO_2], mitigate the adverse effects of potentially high e[CO_2] on plants, and increase crop photosynthesis and electron transport capacity (Kumar et al. 2023; Xu et al. 2020). It has been reported that increasing the nitrogen application rate results in elevated ChlF parameter values, such as initial fluorescence (F_o), potential photochemical efficiency (F_v/F_o), and maximum photochemical efficiency (F_v/F_m) of PSII (Lin et al. 2013; Yin et al. 2023). Research on the difference between the effect of e[CO_2] and nitrogen application rates on crop photosynthesis has progressed (Feng et al. 2015; Snider et al. 2021; Wang et al. 2022). One can hypothesize that there exists a threshold for nitrogen fertilizer application under specific e[CO_2] conditions, which may reach the optimal level to enhance crop photosynthesis and the formation of the final yield. The underlying mechanism linking these factors has yet to be elucidated.

Current studies on the response of crops to e[CO_2] primarily focus on fixed CO_2 concentrations, where there is a sudden increase in CO_2 levels followed by a sustained high concentration. The increase in [CO_2] is a gradual process (Ainsworth and Long 2021; Wang et al. 2015a, 2019). This study utilized an automatic control system and open-top chambers (OTCs) to investigate the impact of varying CO_2 concentrations and nitrogen application levels on SPAD values, chlorophyll fluorescence induction kinetic curves, and parameter characteristics at different growth stages of rice over a two-year period. The determination of grain yield was conducted after the rice plants reached maturity. The anticipated outcomes of this study will offer technical support and establish a theoretical foundation for the application of ChlF technology in investigating the mechanisms of crop photosynthetic adaptation under e[CO_2] conditions. Furthermore, these findings will contribute to the development of strategies for optimizing nitrogen fertilizer application in crop production.

2 Materials and Methods

2.1 Study Site

The experimental field site was located at the Agrometeorological and Ecological Experimental Station (32.21°N, 118.71°E; 18 m above sea level), which is affiliated with Nanjing University of Information Science and Technology in Jiangsu Province, China. Located in the middle and lower reaches of the Yangtze River, this region features a subtropical monsoon climate and serves as one of China's primary grain production bases. The predominant rice–wheat rotation and double-season rice cropping planting modes were adopted in this area. The average annual precipitation in the area is 1100 mm, while the temperature is 15.6 °C. The soil type at the station was characterized as silty loam, with a sand content of 5.2%, a silt content of 85.1%, a pH of 6.1, a bulk density of 1.51 g cm^{-3}, a soil organic carbon concentration of 9.52 g kg^{-1}, a total nitrogen concentration of 1.18 g kg^{-1}, a total phosphorus concentration of 0.85 g kg^{-1}, and a total potassium concentration of 18.17 g kg^{-1} in the depth range of 0–20 cm.

2.2 Field Experiment

The main local cultivar "Nanjing 9108" (japonica-rice) was used as the research object; it grew for 149–153 days, and the rice was cultivated in both 2019 and 2020. We aimed to investigate the effects of elevated CO_2 levels on rice growth and yield under field conditions, and the CO_2 concentrations used were based on realistic scenarios of future CO_2 levels that are projected to occur due to climate change. The study consisted of three [CO_2] treatments: ambient [CO_2] as a control (CG, 400 ± 10 mmol mol^{-1}), and a gradual increase in [CO_2] of 160 µmol mol^{-1} (C1, 560 ± 10 mmol mol^{-1}) and 200 µmol mol^{-1} (C2, 600 ± 10 mmol mol^{-1}) compared to that in CG; the CO_2 concentration gradually increased from seedling transplantation until maturity. Each [CO_2] treatment consisted of 4 replicates, resulting in a total of 12 OTCs. In each OTC, different rice growing areas were divided, and three levels of nitrogen fertilizer were also applied: low nitrogen (N1, 100 kg ha^{-1}), medium nitrogen (N2, 200 kg ha^{-1}), and high nitrogen (N3, 300 kg ha^{-1}). During the experiment, plastic or glass barriers were installed between different plots to prevent the movement of nitrogen across the areas. In addition to relying on natural rainfall, artificial irrigation was also carried out to ensure that nitrogen would not flow into other plots. Therefore, this study included a total of 9 treatments: CGN1, CGN2, CGN3, C1N1, C1N2, C1N3, C2N1, C2N2, and C2N3. The OTCs were octagonal prisms made from aluminum alloy frames with a height of 3 m, opposite side diameter of 3.75 mm, and base area of 10 m^2, as shown in Fig. S1. The glass had top openings inclined inward at a 45-degree angle, and high light transmittance ordinary glass was installed. Each OTC was equipped with a temperature and humidity automatic recorder and CO_2 sensor (GMM222, Vaisala, Finland), which had a range of 0-2000 µmol mol^{-1} and a response time of 30 s. A round PVC pipe, equipped with small apertures, was securely mounted 1 m above the floor to serve as an indoor gas delivery system. The CO_2 gas supply originated from a high-purity cylinder (40 L) containing 99% pure CO_2. One fan was placed in each OTC to ensure a uniform CO_2 concentration, and the computer program automatically monitored and adjusted the CO_2 concentration in each OTC. A schematic diagram of the composition of the CO_2 automatic control system is shown in Fig. S2.

Urea, potassium superphosphate, and potassium chloride were utilized as nitrogen, phosphate, and potassium fertilizers, respectively. The nitrogen fertilizer was divided into a basal fertilizer and top dressing. For rice, the basal fertilizer used was compound fertilizer composed of 15% nitrogen, phosphorus, and potassium (N: P: K = 15%: 15%: 15%). Urea with a nitrogen content of 46.7% was applied as the top dressing. The nitrogen fertilizer application ratio for the N1 treatment was 3:1:1 for basal fertilizer, tillering fertilizer, and ear fertilizer, and the ratio for the N2 and N3 treatments was 2:2:1. The same rice cultivation pattern was consistently maintained throughout the study period. The flooding-midterm drainage-flooding irrigation model was adopted during the rice season, and regular pest control and weed removal were implemented during the rice planting period to ensure optimal crop growth. The specific division of the critical growth stages and the fertilization schedules used for rice are shown in Table S1.

2.3 Measurements of the Leaf Chlorophyll Content

The SPAD value can indicate the chlorophyll content because there is a correlation between the light absorption capacity of chlorophyll and the SPAD value. In this study, leaf SPAD values were determined using a chlorophyll meter (SPAD-502, Konica Minolta, Inc., Japan). Before use, the chlorophyll meter was calibrated by turning on the power switch and entering the main menu. The measurement probe was pressed and held until the display screen indicated "calibration successful" and the buzzer emitted a "beep" sound. During the measurement, a plant was placed in the measurement position, and the measurement probe was pressed for 2–3 s. The buzzer emitted a "beep" sound. The measurement probe was released, and the display screen automatically showed the SPAD value. Measurements were conducted during the critical growth period of rice, specifically between 7:00 and 11:00 under sunny weather conditions. Four randomly selected inverted leaves with similar growth were chosen from the first fully unfolded leaf at the top. After the heading stage, all sword leaves were measured. The middle section of the entire leaf was selected, avoiding the main leaf vein. The SPAD value of the leaf was determined by measuring the main leaf vein three times on both sides and calculating the average value.

2.4 Determination of Leaf Chlorophyll Fluorescence Parameters

The leaf fluorescence parameters were measured using a continuous excitation chlorophyll fluorescence meter (Handy PEA, Norfolk, UK), and the date of determination was approximately the same as that for the chlorophyll content determination. All transient fluorescence from 10 µs to a maximum of 300 s can be recorded at one time. The instrument was equipped with a dark adaptation clip to ensure complete adaptation of the blade. After 20 min of dark adaptation, the fluorescence probe was placed in the circular groove of the clip to ensure close contact and prevent any light from entering. The metal shading sheet was removed from the dark adaptation clip, after which the fast chlorophyll fluorescence induction kinetic curve (OJIP) was measured. Referring to Srivastava et al. (1997), the following ChlF parameters were calculated: initial fluorescence (F_o), maximum fluorescence (F_m), and variable fluorescence (F_v) for the leaves after dark adaptation. The above parameters were calculated to obtain the maximum photochemical quantum efficiency (F_v/F_m) and energy transformation potential (F_v/F_o) of PSII.

2.5 Measurements of Grain Yield Composition

The grain yield was measured after the rice plants reached maturity. Three plots with a sample area of 1 m^2 were selected per treatment. The rice ears were harvested, dried in an oven at 35 °C until they reached a constant weight, and subsequently threshed to obtain solid grains, which were subsequently weighed to determine the grain yield (GY). Once the rice plants reached maturity, samples of leaves, stem sheaths, ears, and roots were randomly selected from each treatment of 40 plants per plot. These samples were then heated in an oven at a temperature of 105 °C for thirty minutes, followed by drying at 65 °C until a constant weight was achieved, after which the average weight was calculated to obtain the aboveground biomass (AGB). Moreover, the seed setting rate (SST), spike number (SN), and kernels per spike (KPS) were determined. The SST was represented as a percentage, indicating the ratio of the number of filled grains to the total number of grains per rice panicle (including filled and empty grains). The 1,000-grain weight (TGW) was calculated by randomly selecting 1000 seeds from the yield determination samples, and the moisture content of the rice was determined to be 13%.

2.6 Data Analysis

The statistical analysis in this study utilized Microsoft Excel 2021 and SPSS 22.0 software (SPSS, Inc., Chicago, IL, USA). A two-way analysis of variance (ANOVA) was conducted to study the effects of different CO_2 concentrations, nitrogen fertilizer treatments, and their interaction on the SPAD values of rice leaves. To determine the significance of the variations in chlorophyll fluorescence parameters and grain yield components under different CO_2 concentrations and nitrogen applications, the least significant difference (LSD) method was used ($P < 0.05$). The statistical significance level was set at $P = 0.05$ or 0.01. Origin 2021 software (OriginLab Corp., Wellesley Hills, USA) was used to generate the figures in this study.

3 Results

3.1 Leaf Chlorophyll (SPAD) Content

The leaf SPAD values of the rice plants were observed to decrease consistently during the growth period according to the data presented in Table 1. C1N1 and C3N1 presented an increase in SPAD values during some stages (tillering and booting) compared to those of CGN1, but a decrease was observed during other stages (ranging from 0.89 to 12.87%). In the context of e[CO_2], increasing nitrogen fertilizer can increase SPAD values, and high concentrations of $CO_{2,}$ along with high nitrogen application rates, have the most significant impact on increasing SPAD values, particularly during the rice pregrowth stage. Compared to CGN2 and CGN3, C1N2 and C1N3 exhibited increases of 4.58% and 9.32%, respectively, during the tillering stage and 4.58% and 9.32%, respectively, during the booting stage, while C2N2 and C2N3 increased by 7.17% and 2.86%, respectively, during the tillering stage and by 9.63% and 11.40%, respectively, during the booting stage.

Except during the filling period, changes in the CO_2 concentration had a significant impact on the SPAD values of the rice leaves during growth ($P < 0.05$). Moreover, nitrogen

Table 1 Effects of elevated CO_2 concentrations and nitrogen fertilization levels on the SPAD value of rice (two-year average)

Treatments		Growth stage							
CO_2	N	Tillering	Jointing	Booting	Heading	Flowering	Filling	Maturity	Average
CG	N_1	40.81 ± 0.3bB	41.90 ± 0.8bA	39.64 ± 1.1bB	39.14 ± 0.7bA	37.99 ± 1.0bAB	41.12 ± 2.2aA	20.28 ± 1.6bA	37.27 ± 1.2bA
	N_2	44.76 ± 0.4aB	44.81 ± 0.5aB	44.20 ± 2.4aA	42.18 ± 0.4aA	41.25 ± 0.8aB	41.51 ± 1.1aA	21.91 ± 1.9bB	39.93 ± 1.3aA
	N_3	42.17 ± 0.9abB	42.37 ± 0.8bB	40.16 ± 2.4bB	44.23 ± 0.8aA	41.09 ± 0.5aB	44.92 ± 2.1aA	26.34 ± 1.2aA	40.18 ± 1.1aB
C1	N_1	43.72 ± 0.1bA	41.37 ± 1.0bA	41.92 ± 1.5bA	38.79 ± 0.5bA	39.22 ± 0.4bA	37.65 ± 0.2cA	17.67 ± 0.8cB	37.19 ± 1.0bA
	N_2	45.68 ± 0.6aAB	45.93 ± 0.7aAB	43.10 ± 1.8aB	41.43 ± 0.7abA	40.91 ± 0.7abB	40.57 ± 0.6bA	23.64 ± 1.1aA	40.18 ± 1.1aA
	N_3	46.10 ± 0.3aA	45.99 ± 0.9aA	41.09 ± 1.0bB	44.14 ± 1.9aA	42.36 ± 0.7aA	43.64 ± 0.4aA	20.12 ± 0.6bB	40.49 ± 1.0aB
C2	N_1	43.37 ± 0.5bA	38.78 ± 1.0bB	41.47 ± 1.2bA	37.08 ± 0.6bB	36.97 ± 0.2bB	38.59 ± 1.2bA	18.50 ± 0.5bB	36.39 ± 1.0cB
	N_2	46.81 ± 0.4aA	46.09 ± 0.8aA	44.76 ± 1.3aA	42.33 ± 0.6aA	43.04 ± 0.1aA	41.45 ± 1.7abA	18.56 ± 0.6bC	40.43 ± 0.8bA
	N_3	46.23 ± 0.5aA	47.20 ± 1.0aA	44.36 ± 1.3aA	44.08 ± 1.4aA	42.99 ± 0.2aA	45.37 ± 1.4aA	24.88 ± 0.7aA	42.16 ± 0.9aA
ANOVA									
CO_2		**	**	*	*	*	ns	*	*
N		**	**	**	**	**	**	**	**
CO_2×N		**	**	*	*	*	ns	*	*

Note CG, C1, and C2 represent ambient $[CO_2]$ and a gradual increase in $[CO_2]$ by 160 μmol mol^{-1} and 200 μmol mol^{-1}, respectively, and N1, N2, and N3 represent low nitrogen (100 kg ha^{-1}), medium nitrogen (200 kg ha^{-1}), and high nitrogen (300 kg ha^{-1}), respectively. The same lowercase and uppercase letters in the columns reveal significant differences among the nitrogen fertilizer treatments at the same CO_2 concentration and among the nitrogen fertilizer treatments at different CO_2 concentrations ($P < 0.05$); values following ± are the standard errors ($n = 4$) of the replicates. * and ** indicate that ANOVA was significant at the 0.05 and 0.01 levels, respectively, and ns indicates not significant

fertilizer application exhibited an even stronger correlation with SPAD values across all growth stages ($P < 0.01$). Overall, the effect of nitrogen fertilizer on the leaf SPAD values was significantly greater than that of the CO_2 concentration changes. Furthermore, the combination of N level and CO_2 concentration had a significant impact on the leaf SPAD values ($P < 0.05$).

3.2 Chlorophyll Fluorescence Induction Kinetic Curve

The OJIP kinetic curves of the rice leaves treated with different CO_2 concentrations exhibited a characteristic “S” shape, encompassing distinct phases, including the O, J, I, and P phases (Fig. 1). Compared to the CG, the C1 and C2 treatments significantly decreased the fluorescence intensity of the OJIP curve in the rice leaves during the tillering stage, specifically from phase J to phase I. However, no significant changes were observed during the jointing-mature stage. The fluorescence values at the J phase point ($t = 2$ ms) in the filling stage were ranked as C2 > CG > C1. Furthermore, during the jointing and booting stages, the fluorescence values in the CG treatment surpassed those in the C1 and C2 treatments. However, in the other stages, the fluorescence values in the CG treatment group were lower than those in the C1 and C2 groups. The fluorescence value under the C2 treatment exhibited a significant increase of 18.0% ($P = 0.009$) at the mature stage, while no statistically significant differences were observed in the other growth stages. The fluorescence intensity values in the tillering, booting, filling, and milk ripening stages were greater than those in C1 and C2 in the I phase ($t = 30$ ms), while they were lower than those in C1 and C2 in the other stages. However, there were no significant differences in the fluorescence in the I phase across the growth stages.

3.3 Chlorophyll Fluorescence Parameters

With the growth of rice, there was a gradual decrease in the leaf maximum photochemical quantum efficiency (F_v/F_m) and energy transformation potential (F_v/F_o) of PSII, as depicted in Figs. 2 and 3. During the rice growth period, the leaf F_v/F_m exhibited an overall upward trend with increasing $[CO_2]$ or nitrogen application rate. Compared to CGN1 treatment, CGN2, C1N2 and C2N2 showed significant increases of 7.01–11.10%; and CGN3, C1N3 and C2N3 showed significant increases of 8.38–12.15% ($P < 0.05$), respectively. Notably, the increase in F_v/F_m in rice leaves induced by $e[CO_2]$ was contingent upon specific nitrogen fertilizer levels at certain growth stages. For example, under C2, the leaf F_v/F_m of N3 reached its highest value, and the leaf F_v/F_m of N2, rather than N3, reached its maximum

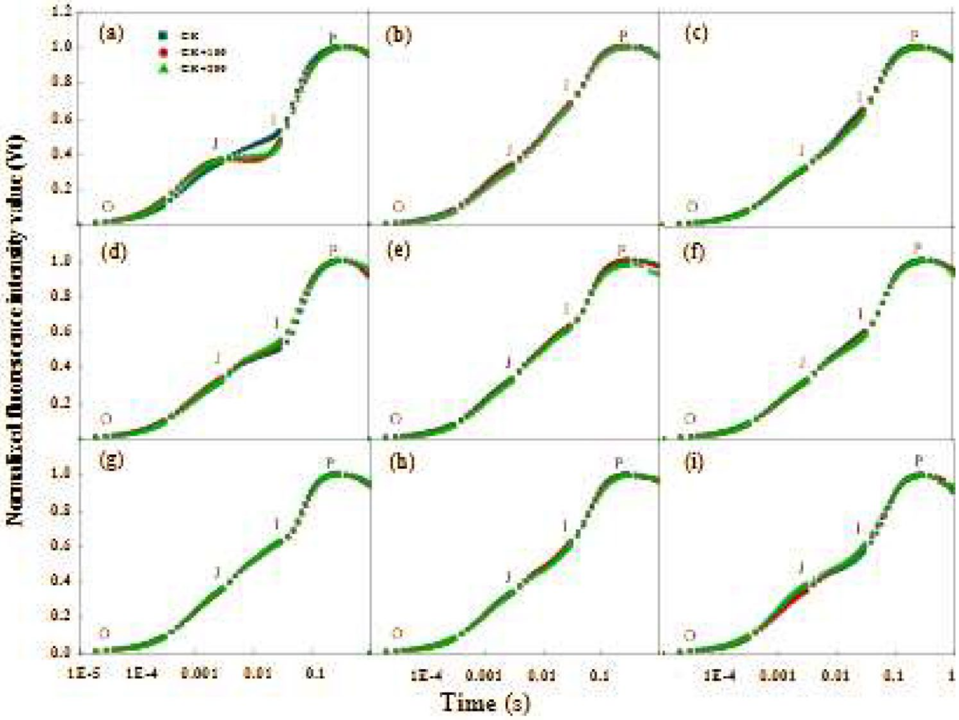

Fig. 1 Impact of varying CO_2 concentrations on the kinetic curves of chlorophyll fluorescence in leaves at key growth stages of rice: (**a**) tillering, (**b**) jointing, (**c**) booting, (**d**) heading, (**e**) flowering, (**f**) filling, (**g**) milky ripening, (**h**) waxy ripening, and (**i**) maturity. The fluorescence kinetic curves were acquired from 20 independent replicates

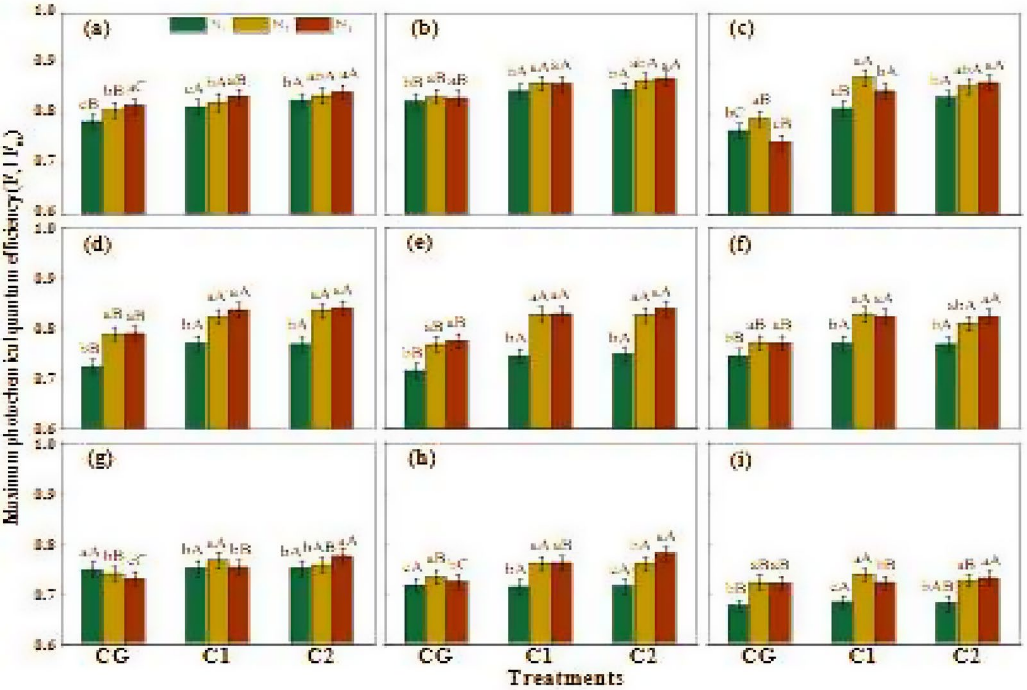

Fig. 2 Impact of varying CO_2 concentrations and nitrogen fertilizer levels on the PSII maximum photochemical quantum efficiency (F_v/F_m) of leaves in key growth stages of rice: (**a**) tillering, (**b**) jointing, (**c**) booting, (**d**) heading, (**e**) flowering, (**f**) filling, (**g**) milky ripening, (**h**) waxy ripening, and (**i**) maturity. The same lowercase and uppercase letters in columns reveal significant differences among nitrogen fertilizer treatments at the same CO_2 concentration and among nitrogen fertilizer treatments at different CO_2 concentrations ($P < 0.05$); values following ± are the standard errors ($n = 4$) of the replicates

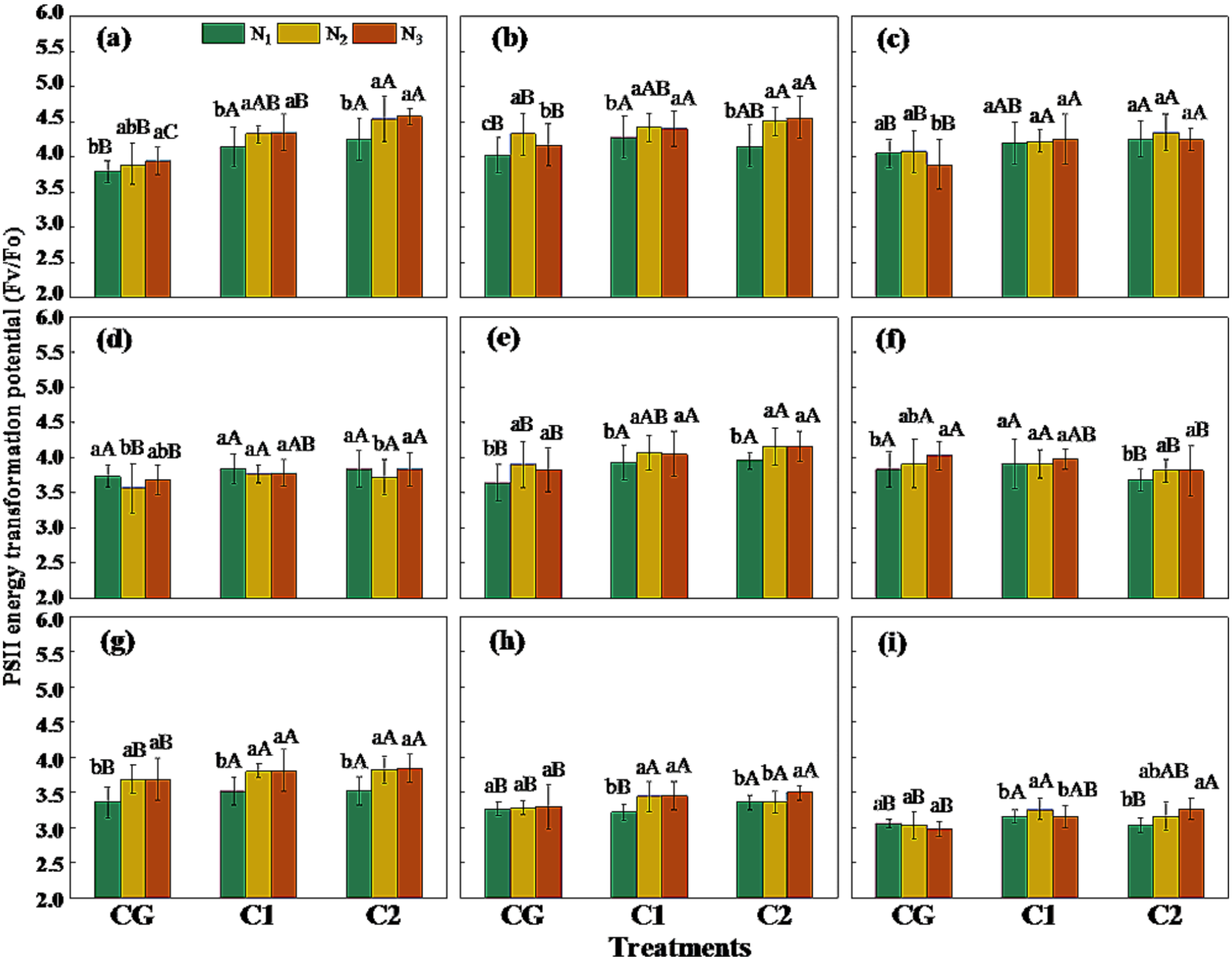

Fig. 3 Impact of varying CO_2 concentrations and nitrogen fertilizer levels on the PSII energy transformation potential (F_v/F_o) of leaves in key growth stages of rice: (**a**) tillering, (**b**) jointing, (**c**) booting, (**d**) heading, (**e**) flowering, (**f**) filling, (**g**) milky ripening, (**h**) waxy ripening, and (**i**) maturity. The same lowercase and uppercase letters in columns indicate significant differences among nitrogen fertilizer treatments at the same CO_2 concentration and among nitrogen fertilizer treatments at different CO_2 concentrations ($P < 0.05$); values following ± are the standard errors ($n = 4$) of the replicates

under the CG and C1 conditions during the booting, milky ripening, and maturity stages. The PSII energy transformation potential (F_v/F_o) of the rice leaves exhibited a similar trend. The F_v/F_o reached its peak during the tillering and jointing stages, and under C2 conditions, there was a significant increase in the F_v/F_o of N2 and N3 by 6.79% and 7.73%, respectively, in the tillering stage ($P < 0.05$), with additional increases of 8.54% and 9.80%, respectively, in the jointing stage. In general, the effects of nitrogen fertilizer on F_v/F_m and F_v/F_o of rice leaves were more significant than those of e[CO_2].

3.4 Grain Yield and Composition

The grain yield of the rice plants exhibited an upward trend with increasing nitrogen fertilizer levels under fixed [CO_2] conditions, and this trend became more pronounced as the [CO_2] increased (Fig. 4). In the CG treatment, each yield component increased significantly with increasing nitrogen application, but the SST, SN, and KPS were greater at the N2 level than at the N3 level. The yield components exhibited a significant growth pattern with the application of nitrogen fertilizer under both C1 and C2, and the increase was most pronounced under C2. Notably, the interaction between e[CO_2] and nitrogen fertilizer had a significantly greater impact on rice ears (including SN and KPS) than on grains (including SST and TGW). Compared to CGN1, all other treatments exhibited an increase in grain yield. However, C2N1 had the lowest growth rate (0.94%), but this was not statistically significant. On the other hand, C2N3 demonstrated a substantial increase of 14.45%. Similarly, e[CO_2] increased the AGB of rice plants by 9.25–23.61%

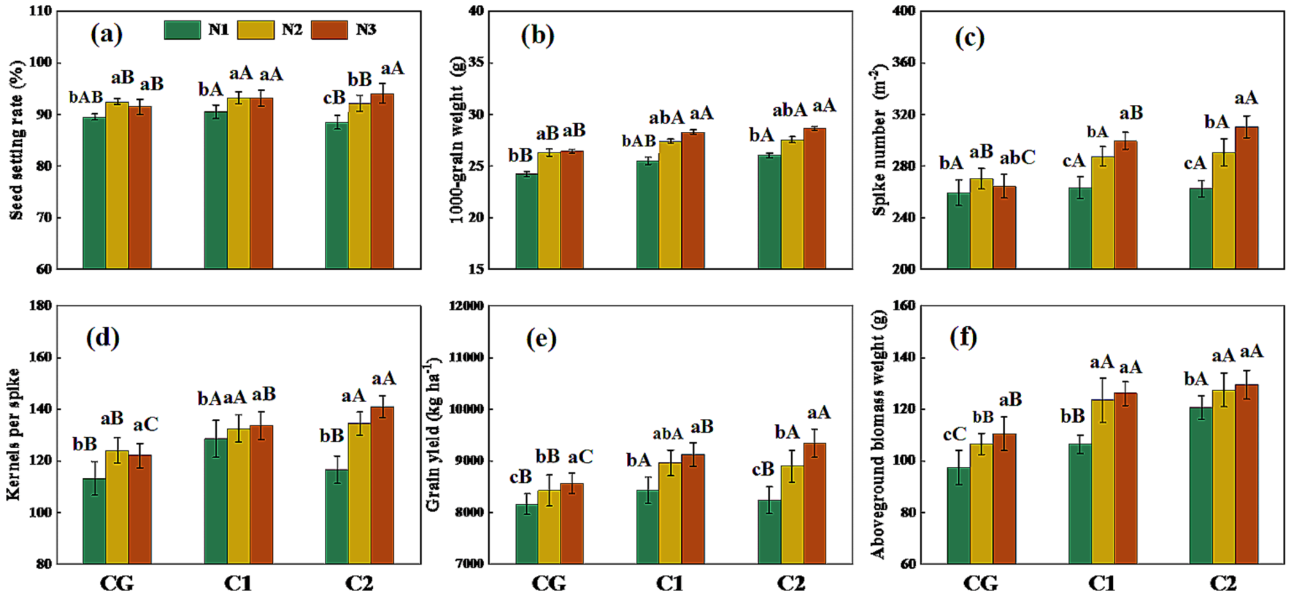

Fig. 4 Impact of varying CO_2 concentrations and nitrogen fertilizer levels on the rice seed setting rate (**a**), 1000-grain weight (**b**), spike number (**c**), kernels per spike (**d**), grain yield (**e**), and aboveground biomass (**f**). The same lowercase and uppercase letters in a column reveal significant differences among nitrogen fertilizer treatments at the same CO_2 concentration and among nitrogen fertilizer treatments at different CO_2 concentrations ($P < 0.05$); values following ± are the standard errors ($n = 4$) of the replicates

at the different nitrogen levels. Compared to those in CG, the increases in N2 and N1 were the greatest, reaching 15.95% and 23.61%, respectively, under the conditions of C1 and C2. Generally, the presence of elevated levels of CO_2 enhanced the rice grain yield, and this trend was further promoted by nitrogen fertilizer application, with C2N3 exhibiting the highest efficacy.

4 Discussion

An increase in the atmospheric CO_2 concentration significantly enhanced the chlorophyll content of the rice leaves, especially during the early growth period. Numerous studies have indicated that e[CO_2] leads to a reduction in the photorespiration rate of C_3 plants, an increase in the carboxylation rate of rubisco, and a subsequent increase in the net photosynthesis of leaves (Chen et al. 2022; Sage and Kubien 2007). After the rice booting stage, due to nutrient absorption by the panicle and inadequate nutrient supply, there is a shift in plant physiological metabolism, leading to pronounced leaf senescence and a reduced chlorophyll content (Shi et al. 2022; Wang et al. 2015b). Consequently, the impact of e[CO_2] on photosynthesis was significantly attenuated during the middle and late stages of rice growth, and the current focus should be on implementing rational fertilization practices to increase the nutrient supply level of plants and optimize the nutrients required for photosynthesis (Makino 2021; Yin et al. 2023). Notably, the impact of nitrogen fertilizer on the SPAD value of leaves was significantly greater than that of e[CO_2] throughout the entire rice growth period. This can be attributed primarily to the fact that nitrogen is a constituent of chlorophyll, which itself is a nitrogenous compound. The essence of photosynthesis lies in converting light energy into chemical energy, with CO_2 serving as one of the raw materials, and a deficiency in nitrogen consequently weakens the overall photosynthetic process (Lin et al. 2013; Makino 2021; Skinner 2013). Lenka et al. (2019) used 15 N-labeled nitrogen fertilizer and reported that, under e[CO_2], soybean nitrogen fixation significantly increased, requiring the application of more nitrogen fertilizer; in addition, in wheat cultivation, e[CO_2] accelerated the uptake of nitrogen from the soil by crops, resulting in the need for higher nitrogen fertilization rates (Lenka et al. 2021). According to our observations under e[CO_2], additional nitrogen fertilizer may be necessary to ensure leaf photosynthetic efficiency and promote growth. While increased CO_2 availability enhances the raw materials for photosynthesis, once photosynthetic efficiency reaches saturation and nitrogen becomes limited, plant respiration can be impeded, consequently weakening the overall photosynthetic activity (Bhardwaj et al. 2020; Ye et al. 2022). In general, simultaneous increases in the atmospheric CO_2 concentration and nitrogen application rate had synergistic effects on enhancing the chlorophyll content in rice.

The F_v/F_m value is utilized to indicate the maximum efficiency of chlorophyll molecules in absorbing and utilizing light energy under conditions of light saturation, and F_v/F_o

represents the magnitude of the chlorophyll fluorescence signal and is frequently employed to characterize photosynthetic efficiency and plant physiological status (Banks 2018; Ogaya et al. 2011; Sharma et al. 2015). This study revealed that the change trends of F_v/F_m and F_v/F_o were roughly the same under each treatment. During photosynthesis, higher values of F_v/F_m and F_v/F_o signify the enhanced conversion of light energy into chemical energy by chlorophyll molecules, thereby indicating the improved utilization of photosynthetically generated light energy by plants (Banks 2018; Sharma et al. 2015). There is no doubt that both e[CO_2] and nitrogen fertilizer levels can improve the photosynthetic efficiency of rice leaves, as these substances are essential substrates for photosynthesis (Makino 2021; Yin et al. 2023). However, the promotion effects of these two factors exhibited certain differences similar to the changes in the SPAD values in the leaves. In the rice booting-filling stage, the variation in nitrogen fertilizer significantly influenced the F_v/F_m. Previous studies have indicated that nitrogen fertilizer application plays a crucial role in enhancing tiller consolidation and stem thickening during the panicle and grain development stages of rice, which are essential for ensuring optimal rice growth (Bhardwaj et al. 2020; Jin-wen et al. 2022). These findings provide theoretical support for the promotion of plant photosynthesis, which aligns with our own research.

With an increase in the atmospheric CO_2 concentration and at medium- and high-nitrogen fertilizer levels, the photosynthetic efficiency of the rice leaves exhibited greater enhancement than that at low nitrogen levels. It can be inferred that under appropriate nitrogen application conditions, increasing the rate of nitrogen application positively influences the promotion of photosynthetic efficiency under high CO_2 concentrations. In other words, as the atmospheric CO_2 concentration increases, the crop nitrogen demand also increases. The nitrogen content in plant leaves is reduced by an increase in the CO_2 concentration, while the application of an appropriate amount of nitrogen fertilizer can increase the leaf nitrogen content and facilitate photosynthesis (Taylaran et al. 2011). In fact, the regulation of nitrogen fertilizer application under e[CO_2] has been documented in related reports. Xu et al. (2020) revealed that future increases in CO_2 concentrations are projected to result in a substantial decline in the availability of nitrogen, particularly ammonium nitrogen, within rice ecosystems; Jin et al. (2017) reported that as the concentration of CO_2 increases, the aboveground nitrogen content of plants decreases, which leads to an increased demand for photosynthetic nitrogen requirements in leaves. In summary, we conclude that under the general trend of e[CO_2], to maintain the productivity of photosynthetic systems in paddy fields, a large amount of nitrogen may be needed.

CO_2 serves as a crucial substrate for determining plant biomass and crop yield. In theory, e[CO_2] will stimulate plant biomass and yield, potentially inducing alterations in various processes involved in dry matter production from source to sink, as well as in plant equilibrium and direction (Dutta et al. 2022; Gong et al. 2021). The interaction between e[CO_2] and nitrogen fertilizer significantly enhanced rice grain yield, with both factors exhibiting mutual reinforcement. Notably, the increase in yield attributed to nitrogen fertilizer was more pronounced than that attributed to e[CO_2], particularly under high CO_2 concentrations. However, the aforementioned factors may not exert a significant impact on the accumulation of dry matter or the yield of aboveground parts of maize and sorghum, nor may their constituent elements (Andrews et al. 2018; Triggs et al. 2004; Twine et al. 2013). Unlike C_4 crops, which can utilize low concentrations of CO_2, C_3 crops (including rice, wheat and others) are particularly sensitive to e[CO_2]. In terms of the photosynthetic rate, the photosynthesis of C_3 crops is enhanced under increasing atmospheric CO_2 concentrations, ultimately resulting in improved yield performance (Lv et al. 2022). Additionally, nitrogen is the primary nutrient among the three essential nutrients for crop yield and various physiological activities. The manipulation or alteration of e[CO_2] carbon metabolism impacts crop nitrogen uptake and regulates the carbon-to-nitrogen ratio in crops (Dong et al. 2022; Dutta et al. 2022; Skinner 2013). We propose that there exists a threshold for CO_2 concentration and nitrogen fertilizer application that can optimize the enhancement of photosynthetic efficiency and yield composition. Furthermore, additional research may be required to determine whether increasing the nitrogen application rate in response to future continuous increases in [CO_2] would be beneficial.

5 Conclusions

A rice field ecosystem was subjected to two years of continuous observation utilizing a research platform that simulated an increase in free atmospheric concentration. Elevated CO_2 levels and increased nitrogen fertilizer application significantly enhanced both the photosynthetic efficiency and grain yield composition of rice, with notable interactions between these two factors. Since nitrogen availability limits leaf photosynthesis, the effects of nitrogen fertilizer on the yield of light and the efficiency of rice are relatively more significant. Notably, as the CO_2 concentration increases, there may be a dilution in the aboveground nitrogen content of plants, leading to an increased demand for nitrogen fertilizer by crops. Therefore, while an increase in the CO_2 concentration can significantly enhance photosynthesis and crop yield, and this effect can be observed under conditions of high nitrogen fertilizer application. The findings of this study offer crucial theoretical support for the development of rational nitrogen fertilization strategies for crops in light of the projected increase in CO_2 concentration in the future.

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Declarations

Competing Interests The authors declare that they have no known competing financial interests that could have appeared to influence the work reported in this paper.

References

AbdElgawad H, de Soua A, Alotaibi MO, Mohammed AE, Schoenaers S, Selim S, Saleh AM (2021) The differential tolerance of C3 and C4 cereals to aluminum toxicity is faded under future CO_2 climate. Plant Physiol Bioch 169:249–258. https://doi.org/10.1016/j.plaphy.2021.11.018

Ainsworth EA, Long SP (2021) 30 years of free-air carbon dioxide enrichment (FACE): what have we learned about future crop productivity and its potential for adaptation? Global Change Biol 27:27–49. https://doi.org/10.1111/gcb.15375

Andrews M, Condron LM, Kemp PD, Topping JF, Lindsey K, Hodge S, Raven JA (2018) Elevated CO_2 effects on nitrogen assimilation and growth of C3 vascular plants are similar regardless of N-form assimilated. J Exp Bot 70:683–690. https://doi.org/10.1093/jxb/ery371

Bailey-Serres J, Parker JE, Ainsworth EA, Oldroyd GED, Schroeder JI (2019) Genetic strategies for improving crop yields. Nature 575:109–118. https://doi.org/10.1038/s41586-019-1679-0

Baldwin JW, Dessy JB, Vecchi GA, Oppenheimer M (2019) Temporally compound heat Wave events and global warming: an emerging hazard. Earths Future 7:411–427. https://doi.org/10.1029/2018EF000989

Banks JM (2018) Chlorophyll fluorescence as a tool to identify drought stress in Acer genotypes. Environ Exp Bot 155:118–127. https://doi.org/10.1016/j.envexpbot.2018.06.022

Bhardwaj AK, Rajwar D, Basak N, Bhardwaj N, Chaudhari SK, Bhaskar S, Sharma PC (2020) Nitrogen mineralization and availability at critical stages ofRice (Oryza sativa) crop, and its relation to SoilBiological Activity and Crop Productivity under Major Nutrient ManagementSystems. J Soil Sci Plant Nut 20:1238–1248. https://doi.org/10.1007/s42729-020-00208-y

Buareal K, Kato T, Morozumi T, Ono K, Nakashima N (2023) Red solar-induced chlorophyll fluorescence as a robust proxy for ecosystem-level photosynthesis in a rice field. Agr for Meteorol 336:109473. https://doi.org/10.1016/j.agrformet.2023.109473

Cai C, Li G, Di L, Ding Y, Fu L, Guo X, Struik PC, Pan G, Li H, Chen W, Luo W, Yin X (2020) The acclimation of leaf photosynthesis of wheat and rice to seasonal temperature changes in T-FACE environments. Global Change Biol 26:539–556. https://doi.org/10.1111/gcb.14830

Chen R, Liu X, Chen J, Du S, Liu L (2022) Solar-induced chlorophyll fluorescence imperfectly tracks the temperature response of photosynthesis in winter wheat. J Exp Bot 73:7596–7610. https://doi.org/10.1093/jxb/erac388

Cui J, Zhang X, Reis S, Wang C, Wang S, He P, Chen H, van Grinsven HJM, Gu B (2023) Nitrogen cycles in global croplands altered by elevated CO_2. Nat Sustain. https://doi.org/10.1038/s41893-023-01154-0

Dechant B, Ryu Y, Badgley G, Zeng Y, Berry JA, Zhang Y, Goulas Y, Li Z, Zhang Q, Kang M, Li J, Moya I (2020) Canopy structure explains the relationship between photosynthesis and sun-induced chlorophyll fluorescence in crops. Remote Sens Environ 241:111733. https://doi.org/10.1016/j.rse.2020.111733

Dong N, Wright IJ, Chen JM, Luo X, Wang H, Keenan TF, Smith NG, Prentice IC (2022) Rising CO_2 and warming reduce global canopy demand for nitrogen. New Phytol 235:1692–1700. https://doi.org/10.1111/nph.18076

Dutta A, Lenka NK, Praharaj CS, Hazra KK (2022) Impact of elevated CO_2 on soil–plant Phosphorus Dynamics, Growth, and yield of Chickpea (Cicer arietinum L.) in an Alkaline Vertisol of Central India. J Soil Sci Plant Nut 22:1904–1914. https://doi.org/10.1007/s42729-022-00781-4

Faye B, Webber H, Gaiser T, Müller C, Zhang Y, Stella T, Latka C, Reckling M, Heckelei T, Helming K, Ewert F (2023) Climate change impacts on European arable crop yields: sensitivity to assumptions about rotations and residue management. Eur J Agron 142:126670. https://doi.org/10.1016/j.eja.2022.126670

Feng W, He L, Zhang H-Y, Guo B-B, Zhu Y-J, Wang C-Y, Guo T-C (2015) Assessment of plant nitrogen status using chlorophyll fluorescence parameters of the upper leaves in winter wheat. Eur J Agron 64:78–87. https://doi.org/10.1016/j.eja.2014.12.013

Gong Z, Dong L, Lam S, Zhang D, Zong Y, Hao X, Li P (2021) Nutritional quality in response to elevated CO_2 concentration in foxtail millet (Setaria italica). J Cereal Sci 102:103318. https://doi.org/10.1016/j.jcs.2021.103318

Javaid MM, Florentine SK, Ashraf M, Mahmood A, Sattar A, Wasaya A, Li F-M (2022) Photosynthetic activity and water use efficiency of Salvia verbenaca L. under elevated CO_2 and water-deficit conditions. J Agron Crop Sci 208:536–551. https://doi.org/10.1111/jac.12613

Jin J, Li Y, Liu X, Wang G, Tang C, Yu Z, Wang X, Herbert SJ (2017) Elevated CO_2 alters distribution of nodal leaf area and enhances nitrogen uptake contributing to yield increase of soybean cultivars grown in Mollisols. PLoS ONE 12:e0176688. https://doi.org/10.1371/journal.pone.0176688

Jin-wen H, Jia-yi WU, Hong-fei C, Zhi-xing Z, Chang-xun F, Cai-hong S, Wei-wei LIN, Pei-ying W, Khan MU, Wen-xiong LIN (2022) Optimal management of nitrogen fertilizer in the main rice crop and its carrying-over effect on ratoon rice under mechanized cultivation in Southeast China. J Integr Agr 21:351–364. https://doi.org/10.1016/S2095-3119(21)63668-7

Kumar G, Basak N, Priyadarsani S, Bagchi TB, Kumar A, Pradhan SK, Sanghamitra P (2023) Alteration in the physico-chemical traits and nutritional quality of rice under anticipated rise in atmospheric CO_2 concentration: a review. J Food Compos Anal 121:105332. https://doi.org/10.1016/j.jfca.2023.105332

Leakey ADB, Ainsworth EA, Bernacchi CJ, Zhu X, Long SP, Ort DR (2012) Photosynthesis in a CO_2-Rich atmosphere. In: Eaton-Rye JJ, Tripathy BC, Sharkey TD (eds) Photosynthesis: Plastid Biology, Energy Conversion and Carbon Assimilation. Springer Netherlands, Dordrecht, pp 733–768

Lenka NK, Lenka S, Mahapatra P, Sharma N, Kumar S, Aher SB, Yashona DS (2019) The fate of 15 N labeled urea in a soybean-wheat cropping sequence under elevated CO_2 and/or temperature.

Agr Ecosyst Environ 282:23–29. https://doi.org/10.1016/j.agee.2019.04.033

Lenka NK, Lenka S, Yashona DS, Shukla AK, Elanchezhian R, Dey P, Agrawal PK, Biswas AK, Patra AK (2021) Carbon dioxide and/or temperature elevation effect on yield response, nutrient partitioning and use efficiency of applied nitrogen in wheat crop in central India. Field Crop Res 264:108084. https://doi.org/10.1016/j.fcr.2021.108084

Li Y, Gu X, Li Y, Fang H, Chen P (2023) Ridge-Furrow mulching combined with appropriate nitrogen rate for enhancing photosynthetic efficiency, yield and water use efficiency of summer maize in a semi-arid region of China. Agr Water Manage 287:108450. https://doi.org/10.1016/j.agwat.2023.108450

Lin Y-c, Hu Y-g, Ren C-z, Guo L-c, Wang C-l, Jiang Y, Wang X-j, Phendukani H, Zeng Z-h (2013) Effects of Nitrogen Application on Chlorophyll fluorescence parameters and Leaf Gas Exchange in Naked Oat. J Integr Agr 12:2164–2171. https://doi.org/10.1016/S2095-3119(13)60346-9

Liu C, Bol R, Ju X, Tian J, Wu D (2023) Trade-offs on carbon and nitrogen availability lead to only a minor effect of elevated CO_2 on potential denitrification in soil. Soil Biol Biochem 176:108888. https://doi.org/10.1016/j.soilbio.2022.108888

Lv C, Huang Y, Yang K, Yang J, Cao P, Hu Z, Sun W, Yu L (2022) Multiyear CO_2 elevation improves PSII efficiency in a japonica rice cultivar. Crop Sci 62:346–357. https://doi.org/10.1002/csc2.20642

Makino A (2021) Photosynthesis improvement for enhancing productivity in rice. Soil Sci Plant Nutr 67:513–519. https://doi.org/10.1080/00380768.2021.1966290

Miglani GS, Kaur R, Sharma P, Gupta N (2021) Leveraging photosynthetic efficiency toward improving crop yields. J Crop Improv 35:361–402. https://doi.org/10.1080/15427528.2020.1824168

Ogaya R, Peñuelas J, Asensio D, Llusià J (2011) Chlorophyll fluorescence responses to temperature and water availability in two co-dominant Mediterranean shrub and tree species in a long-term field experiment simulating climate change. Environ Exp Bot 71:123–127. https://doi.org/10.1016/j.envexpbot.2010.10.016

Ou Y, Roney C, Alsalam J, Calvin K, Creason J, Edmonds J, Fawcett AA, Kyle P, Narayan K, O'Rourke P, Patel P, Ragnauth S, Smith SJ, McJeon H (2021) Deep mitigation of CO_2 and non-CO_2 greenhouse gases toward 1.5°C and 2°C futures. Nat Commun 12:6245. https://doi.org/10.1038/s41467-021-26509-z

Sage RF, Kubien DS (2007) The temperature response of C3 and C4 photosynthesis. Plant Cell Environ 30:1086–1106. https://doi.org/10.1111/j.1365-3040.2007.01682.x

Saiki M, Nguyen TPM, Shindo J, Nishida K (2020) Nitrogen balance in paddy fields under flowing-irrigation condition. Nutr Cycl Agroecosys 116:19–30. https://doi.org/10.1007/s10705-019-10019-y

Sharma DK, Andersen SB, Ottosen C-O, Rosenqvist E (2015) Wheat cultivars selected for high Fv/Fm under heat stress maintain high photosynthesis, total chlorophyll, stomatal conductance, transpiration and dry matter. Physiol Plant 153:284–298. https://doi.org/10.1111/ppl.12245

Shi Y, Guo E, Cheng X, Wang L, Jiang S, Yang X, Ma H, Zhang T, Li T, Yang X (2022) Effects of chilling at different growth stages on rice photosynthesis, plant growth, and yield. Environ Exp Bot 203:105045. https://doi.org/10.1016/j.envexpbot.2022.105045

Simkin AJ, López-Calcagno PE, Raines CA (2019) Feeding the world: improving photosynthetic efficiency for sustainable crop production. J Exp Bot 70:1119–1140. https://doi.org/10.1093/jxb/ery445

Skinner RH (2013) Nitrogen fertilization effects on pasture photosynthesis, respiration, and ecosystem carbon content. Agr Ecosyst Environ 172:35–41. https://doi.org/10.1016/j.agee.2013.04.005

Snider J, Harris G, Roberts P, Meeks C, Chastain D, Bange M, Virk G (2021) Cotton physiological and agronomic response to nitrogen application rate. Field Crop Res 270:108194. https://doi.org/10.1016/j.fcr.2021.108194

Srivastava A, Guissé B, Greppin H, Strasser RJ (1997) Regulation of antenna structure and electron transport in Photosystem II of Pisum sativum under elevated temperature probed by the fast polyphasic chlorophyll a fluorescence transient: OKJIP. BBA-Bioenergetics 1320:95–106. https://doi.org/10.1016/S0005-2728(97)00017-0

Taylaran RD, Adachi S, Ookawa T, Usuda H, Hirasawa T (2011) Hydraulic conductance as well as nitrogen accumulation plays a role in the higher rate of leaf photosynthesis of the most productive variety of rice in Japan. J Exp Bot 62:4067–4077. https://doi.org/10.1093/jxb/err126

Triggs JM, Kimball BA, Pinter PJ, Wall GW, Conley MM, Brooks TJ, LaMorte RL, Adam NR, Ottman MJ, Matthias AD, Leavitt SW, Cerveny RS (2004) Free-air CO_2 enrichment effects on the energy balance and evapotranspiration of sorghum. Agr for Meteorol 124:63–79. https://doi.org/10.1016/j.agrformet.2004.01.005

Twine TE, Bryant JJ, Richter T, Bernacchi K, McConnaughay CJ, Morris KD, Leakey SJ, A.D.B (2013) Impacts of elevated CO_2 concentration on the productivity and surface energy budget of the soybean and maize agroecosystem in the Midwest USA. Global Change Biol 19:2838–2852. https://doi.org/10.1111/gcb.12270

Wang J, Wang C, Chen N, Xiong Z, Wolfe D, Zou J (2015a) Response of rice production to elevated [CO_2] and its interaction with rising temperature or nitrogen supply: a meta-analysis. Clim Change 130:529–543. https://doi.org/10.1007/s10584-015-1374-6

Wang M, Xie B, Fu Y, Dong C, Hui L, Guanghui L, Liu H (2015b) Effects of different elevated CO_2 concentrations on chlorophyll contents, gas exchange, water use efficiency, and PSII activity on C3 and C4 cereal crops in a closed artificial ecosystem. Photosynth Res 126:351–362. https://doi.org/10.1007/s11120-015-0134-9

Wang J, Li L, Lam SK, Zhang X, Liu X, Pan G (2018) Changes in nutrient uptake and utilization by rice under simulated climate change conditions: a 2-year experiment in a paddy field. Agr for Meteorol 250–251:202–208. https://doi.org/10.1016/j.agrformet.2017.12.254

Wang J, Hasegawa T, Li L, Lam SK, Zhang X, Liu X, Pan G (2019) Changes in grain protein and amino acids composition of wheat and rice under short-term increased [CO_2] and temperature of canopy air in a paddy from East China. New Phytol 222:726–734. https://doi.org/10.1111/nph.15661

Wang B, Cai W, Li J, Wan Y, Li Ye, Guo C, Wilkes A, You S, Qin X, Gao Q, Liu K (2020) Leaf photosynthesis and stomatal conductance acclimate to elevated [CO_2] and temperature thus increasing dry matter productivity in a double rice cropping system. Field Crop Res 248:107735. https://doi.org/10.1016/j.fcr.2020.107735

Wang W, He J, Wang Z, Gu J, Liu L, Zhang W, Ziska LH, Zhu J (2021) Leaf characteristics of rice cultivars with a stronger yield response to projected increases in CO_2 concentration. Physiol Plant 171:416–423. https://doi.org/10.1111/ppl.13246

Wang X, Zou J, Qi X, Li Q, Ma L, Li Y, Li X, Wang L (2022) High concentration of CO_2 improve the Pb Resistance of Oryza sativa L. Seedlings by enhancing photosynthesis and regulating plant endogenous hormones. J Plant Growth Regul 41:3556–3567. https://doi.org/10.1007/s00344-021-10533-w

Waqas M, Hawkesford MJ, Geilfus C-M (2023) Feeding the world sustainably: efficient nitrogen use. Trends Plant Sci 28:505–508. https://doi.org/10.1016/j.tplants.2023.02.010

Waring EF, Perkowski EA, Smith NG (2023) Soil nitrogen fertilization reduces relative leaf nitrogen allocation to photosynthesis. J Exp Bot erad195. https://doi.org/10.1093/jxb/erad195

Xu C, Zhang K, Zhu W, Xiao J, Zhu C, Zhang N, Yu F, Li S, Zhu C, Tu Q, Chen X, Zhu J, Hu S, Koide RT, Firestone MK, Cheng L (2020) Large losses of ammonium-nitrogen from a rice ecosystem under elevated CO_2. Sci Adv 6:eabb7433. https://doi.org/10.1126/sciadv.abb7433

Ye C, Ma H, Huang X, Xu C, Chen S, Chu G, Zhang X, Wang D (2022) Effects of increasing panicle-stage N on yield and N use efficiency of indica rice and its relationship with soil fertility. Crop J 10:1784–1797. https://doi.org/10.1016/j.cj.2022.02.003

Yin Y, Zhu J, Xu X, Jia M, Warner TA, Wang X, Li T, Cheng T, Zhu Y, Cao W, Yao X (2023) Tracing the nitrogen nutrient status of crop based on solar-induced chlorophyll fluorescence. Eur J Agron 149:126924. https://doi.org/10.1016/j.eja.2023.126924

Zhang Z, Liu X, Li N, Cao B, Huang T, Li P, Liu S, Zhang Y, Xu K (2023) Effect of ofloxacin levels on growth, photosynthesis and chlorophyll fluorescence kinetics in tomato. Plant Physiol Bioch 194:374–382. https://doi.org/10.1016/j.plaphy.2022.11.029

Zhu C, Kobayashi K, Loladze I, Zhu J, Jiang Q, Xu X, Liu G, Seneweera S, Ebi KL, Drewnowski A, Fukagawa NK, Ziska LH (2018) Carbon dioxide (CO_2) levels this century will alter the protein, micronutrients, and vitamin content of rice grains with potential health consequences for the poorest rice-dependent countries. Sci Adv 4:eaaq1012. https://doi.org/10.1126/sciadv.aaq1012