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Responses of photosynthetic characteristics and growth in rice and winter wheat to different elevated CO_2 concentrations

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Abstract

This study investigated the effects of different elevated CO_2 concentrations [ambient CO_2 concentration (CK), CK plus 40 µmol mol^{-1} (T_1), CK plus 200 µmol mol^{-1} (T_2)] on photosynthetic characteristics and growth of rice (*Oryza sativa* L.) and winter wheat (*Triticum aestivum* L.). The results showed that T_2 treatment decreased the net photosynthetic rate and leaf nitrogen content (LNC) but increased the light-saturated net photosynthetic rate of rice. Additionally, T_2 treatment increased biomass accumulation and yield in both rice and winter wheat to some extent. T_1 treatment, however, had little effect on photosynthetic parameters, LNC, biomass, and yield during the rice and winter wheat growing seasons. The above results suggest that the photosynthesis and growth responses of rice and winter wheat to different CO_2 concentrations differed, in general, the increase of CO_2 concentrations influenced more photosynthetic performance and growth of C_3 plants than lower CO_2 concentrations.

Keywords: climate change; crop; gas exchange; open-top chamber; photosynthetic acclimation.

Introduction

Elevated carbon dioxide (eCO_2) concentrations, mainly due to the burning of fossil fuels and human land-use activities, have been shown to have a profound impact on global climate change (Tausz-Posch *et al*. 2020). The atmospheric CO_2 concentration has risen from a preindustrial level of approximately 280 µmol mol^{-1} to the current level of 410 µmol mol^{-1} (Shabbir *et al*. 2019), and it is expected to reach 700 µmol mol^{-1} by the end of the 21st century (Srinivasarao *et al*. 2016). As a necessary substrate for photosynthesis, the changing CO_2 concentrations directly or indirectly affect the morphological and physiological characteristics of plants and then affect agricultural and natural ecosystems (Tausz *et al*. 2013).

Rice (*Oryza sativa* L.) and wheat (*Triticum aestivum* L.) are the most important food crops in Asia, providing food grains for more than 20% of the population worldwide (Guo *et al*. 2016). With the growth of world population, global food demand is estimated to increase by 100–110% from 2005 to 2050 (Tilman *et al*. 2011). However, the rising atmospheric CO_2 concentrations are coincident with the increase in temperature, altered precipitation, and intense extreme events, which may have opposite effects on sustainable food production (Bencke-Malato *et al*. 2019). Therefore, it is a challenge to improve crop productivity to meet the growing human food demand on the background of global climate change (Saha *et al*. 2015). With the rising atmospheric CO_2 concentrations, many scholars pay extensive attention to the 'CO_2 fertilization effect', that is, the promotion of plant growth or productivity by the increase of atmospheric CO_2 concentrations, in the hope that it will compensate for the crop yield reduction caused by climate change to a certain extent (Lv *et al*. 2020).

Over the last three decades, the simulation of plant growth responses to eCO_2 concentrations has been conducted using growth chambers, closed-top chambers, open-top chambers (OTC), and free air carbon dioxide enrichment (FACE) experiment (Uprety *et al*. 2006, Reddy *et al*. 2010, Dusenge *et al*. 2019). Numerous studies have

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Abbreviations: AQY – apparent quantum yield; C_a – atmospheric CO_2 concentration; CE – carboxylation efficiency; C_i – intercellular CO_2 concentration; C_i/C_a – the ratio of intercellular CO_2 concentration to ambient CO_2; eCO_2 – elevated carbon dioxide; g_s – stomatal conductance; LNC – leaf nitrogen content; P_g – gross photosynthetic rate; P_N – net photosynthetic rate; P_{Nmax} – light-saturated net photosynthetic rate; PNUE – photosynthetic nitrogen-use efficiency; R_D – dark-respiration rate; R_P – photorespiration rate; TGM – thousand-grain mass.
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shown that the rising CO_2 concentrations could stimulate the net photosynthetic rate (Nowak *et al*. 2004, Ainsworth and Rogers 2007) and increase dry matter production and yield, particularly in C_3 plants (Liu *et al*. 2008, Bishop *et al*. 2014). Besides, CO_2 enrichment could induce partial stomatal closure, increase stomatal resistance, decrease stomatal conductance, and improve water-use efficiency (Leakey *et al*. 2009, Kimball 2016, Pan *et al*. 2020).

After long-term exposure to high eCO_2 concentrations, however, the initial stimulation on photosynthetic rate will not increase continuously, and sometimes it will be lower than that in plants grown under ambient conditions (Seneweera 2011, Warren *et al*. 2015, Pastore *et al*. 2019). This phenomenon is commonly called photosynthetic acclimation or downregulation and has been extensively reported in the literature (Yong *et al*. 2007, Alonso *et al*. 2009, Salazar-Parra *et al*. 2015). Furthermore, as CO_2 concentrations increase, these positive eCO_2 concentrations effects are often accompanied by the changed nutrient contents in plant tissues, such as the decrease of tissue nitrogen (N) concentration (Seneweera *et al*. 2002, Dier *et al*. 2019). The leaf nitrogen content (LNC) is one of the key factors that determine photosynthetic capacity and photosynthetic nitrogen-use efficiency (PNUE) (Moon *et al*. 2015). The CO_2 enrichment has been reported to promote the accumulation of photoassimilates and therefore dilute plant tissue nitrogen content such that LNC is decreased (Gifford *et al*. 2000). Ainsworth and Long (2005) examined the literature on the effects of eCO_2 concentrations on LNC of plants using meta-analysis and showed that CO_2 enrichment decreased LNC by an average of 13% under FACE experiments.

To our knowledge, most of the previous studies on this subject have focused on the effects of high eCO_2 concentrations (*i.e.*, a doubled CO_2 concentration or elevated by 200 μmol mol^{-1} more than the ambient level) on growth, development, and yield of plants (Kim *et al*. 2003, Singh *et al*. 2017). The increase of atmospheric CO_2 concentration is a gradual process and will not increase to a very high concentration in a short period of time. Even if atmospheric CO_2 concentrations had increased at a rate of 2.11 μmol mol^{-1} $year^{-1}$ over the last decade (IPCC 2014), it would take approximately 100 years to result in an elevation of 200 μmol mol^{-1} over the ambient concentration. To the best of our knowledge, little is studied about how the photosynthetic characteristics and growth of plant response to low eCO_2 concentrations.

In this study, an *in situ* field experiment in which rice (*Oryza sativa* L.) and winter wheat (*Triticum aestivum* L.) was exposed to three different concentrations of CO_2 (ambient, ambient + 40 μmol mol^{-1}, and ambient + 200 μmol mol^{-1}) was performed using OTC from 2016 to 2017. The objectives of this study were to determine the potential effects of different eCO_2 concentrations on the photosynthetic performance, biomass accumulation, and yield of rice and winter wheat, under the hypothesis that high eCO_2 concentrations could induce a stress response in vegetation that could result in a high sensitivity to changes of these growth parameters, while low eCO_2 concentrations are closer to the ambient levels and plants might be insensitive to them.

Materials and methods

Site description: The field experiment was conducted at the Agricultural Meteorology and Ecology Experimental Station of Nanjing University of Information Science and Technology (32°16'N, 118°86'E) in eastern China from 2016 to 2017. This site belongs to the subtropical humid climate. The average annual precipitation and temperature are approximately 1,100 mm and 15.6°C, respectively. The total annual sunshine time exceeds 1,900 h, and the frostless period is more than 237 d. Rice (*Oryza sativa* L. 'Nanjing 9108') and winter wheat (*Triticum aestivum* L. 'Yangmai 22') rotation system prevails in this region, and the soil (0–20 cm depth) is classified as yellow-brown soil (26.1% clay) with an organic C of 11.95 g kg^{-1}, total N of 1.45 g kg^{-1}, and pH 6.3 (1:2, soil:water suspension).

Experimental design: The field experiment consisted of three treatments: ambient CO_2 concentration (CK), ambient plus 40 μmol mol^{-1} (T_1), and ambient plus 200 μmol mol^{-1} (T_2). Each treatment was replicated four times. In total, the field experiment contained 12 independent OTC, which were arranged in the field at equal spacing.

Locally prevalent Japonica rice cultivar (Nanjing 9108) was sown under ambient field conditions on May 20 in 2016 and transplanted (30-d old) manually into each OTC, with three seedlings per hill and 30 hills per square meter. Fertilizer was applied at a rate of 176 kg(N) ha^{-1} in three split doses during the rice growing season. The percentage of nitrogen fertilizer applied was at the ratio of transplant (basal fertilizer): tillering: heading = 40:30:30%. The basal fertilizer was compound fertilizer ($N:P_2O_5:K_2O$ = 15:15:15%), the tillering and heading stages fertilizer was urea (nitrogen content 46.7%). Winter wheat cultivar (Yangmai 22) was hand sown with a density of 320 kernels per square meter on 15 November in 2016. Fertilizer was applied at a rate of 220 kg(N) ha^{-1} in two split doses during the winter wheat growing season. The ratio of the nitrogen fertilizer applied was seeding (basal fertilizer): turning green = 70:30%. Other crop management measures were conducted according to local practices. The detailed information related to the main growth stages and fertilization schedules is shown in the text table below.

OTC facilities: The field experiment was conducted using OTC, each of which was a regular octagonal prism constructed using an aluminum alloy frame (12 m^2 bottom area and 3 m in height) with a highly transparent glass covering (3 mm thickness and 90% light transmittance). The vertical beams of the frame were bent inward with a length of 0.9 m and a 45° tilt. The top of each OTC had a tapered opening to facilitate top air exchange and kept the temperature and humidity inside of the chambers closer to the natural environment. Each OTC was equipped with a CO_2 sensor (*GMM222*, *Vaisala Inc*., Helsinki, Finland) with

Date	Rice	Date	Winter wheat
20 May 2016	Seeding	15 November 2016	Seeding, 15.4 g(N) m^{-2}, 15.4 g(P) m^{-2}, 15.4 g(K) m^{-2}
21 June 2016	Transplanting, 7.04 g(N) m^{-2}, 7.04 g(P) m^{-2} ,7.04 g(K) m^{-2}	1 December 2016	Seedling
5 July 2016	Tillering, 5.28 g(N) m^{-2}	6 February 2017	Turning green, 6.6 g(N) m^{-2}
18 July 2016	Jointing	7 March 2017	Jointing
28 August 2016	Heading, 5.28 g(N) m^{-2}	1 April 2017	Heading
9 November 2016	Maturity	18 May 2017	Maturity

a range of 0–2,000 µmol mol^{-1} to detect CO_2 concentrations in real time. Circular polyvinyl chloride tubes (15 mm in diameter) with small holes (2 mm in diameter) were fixed around the T_1 and T_2 treatments wall approximately 1.4 m above the ground. Using the CO_2 cylinder as the air source (high-pressure liquid CO_2 with a purity of 99%), the CO_2 gas vaporized by the heater was sprayed into the T_1 and T_2 treatments through the blower. Solenoid valves linked a computer programmed automatic CO_2 concentration control system. When the CO_2 concentration of the T_1 and T_2 treatments was lower than the target concentration, the solenoid valves would open for supplementing CO_2. The automatic control system operated for 24 h per day and adjusted the supply of CO_2 gas every two seconds to maintain the target CO_2 concentration of the T_1 and T_2 treatments. Additionally, each OTC had two fans installed inside to evenly mix the internal gases.

During the rice growing season, the CO_2 exposure treatments were performed from 21 June to 9 November in 2016. The average CO_2 concentrations in the CK, T_1, and T_2 treatments were 413 ± 13, 439 ± 16, and 596 ± 35 µmol mol^{-1}, respectively. During the winter wheat growing season, the CO_2 fumigation was initiated from 20 February to 12 May in 2017, and the average CO_2 concentrations of the CK, T_1, and T_2 treatments were 412 ± 8, 447 ± 13, and 602 ± 30 µmol mol^{-1}, respectively.

Gas exchange: Light-response curve was measured using a *Li-6400* portable photosynthesis system (*Li-Cor Inc*., Lincoln, NE, USA) during the main growth stages of the rice and winter wheat. The fully expanded, healthy, functional leaf was selected for the gas-exchange measurement under the sunny and cloudless conditions. PAR was sequentially set to 2,000; 1,500; 1,000; 800, 600, 400, 200, 100, 50, 20, 0 µmol(photon) m^{-2} s^{-1} with a red-blue LED light source. The leaf temperature was set according to the plant growth environment temperature, and the relative humidity was controlled at 60%. Gas-exchange properties were logged after the photosynthesis system parameters achieved stability. Gas-exchange parameters were calculated according to Thornley (1976):

$$P_N = \frac{\mathrm{PAR} \times \mathrm{AQY} + P_{Nmax} - \sqrt{(\mathrm{PAR} \times \mathrm{AQY} + P_{Nmax})^2 - 4\theta \mathrm{PAR} \times \mathrm{AQY} \times P_{Nmax}}}{2\theta} - R_D$$

where P_N is net photosynthetic rate [µmol(CO_2) m^{-2} s^{-1}], PAR is photosynthetically active radiation [µmol(photon) m^{-2} s^{-1}], AQY is apparent quantum yield [µmol(CO_2) m^{-2} s^{-1}], P_{Nmax} is light-saturated net photosynthetic rate [µmol(CO_2) m^{-2} s^{-1}], R_D is dark respiration [µmol(CO_2) m^{-2} s^{-1}], and θ is curvature of light-response curve (dimensionless).

The CO_2-response curves were determined after light-response curve measurement, and P_N was measured at 13 CO_2 concentrations (400, 300, 200, 100, 50, 20, 400, 600, 800; 1,000; 1,200; 1,500; 2,000 µmol mol^{-1}). The saturating light was set at 1,200 µmol(photon) m^{-2} s^{-1}. The CO_2-injection system maintained constant CO_2 concentrations in the sample chamber. The CO_2-response parameters were calculated according to the method proposed by Watling *et al*. (2000). The formula is as follows: $A = a\,(1 - e^{-bx}) + c$. Where A is the net photosynthetic rate (P_N) [µmol(CO_2) m^{-2} s^{-1}], a is CO_2-saturated net photosynthetic rate [µmol(CO_2) m^{-2} s^{-1}], b is carboxylation rate, x is intercellular CO_2 concentration (C_i) [µmol(CO_2) mol^{-1}], and c is photorespiration rate (R_P), [µmol(CO_2) m^{-2} s^{-1}]. Using this equation, the carboxylation efficiency (CE) was calculated as $b\,(a + c)$.

LNC: After measuring the photosynthesis, the leaf was removed and placed in an oven at 105°C for 30 min and then dried at 65°C for 48 h. The LNC was measured using a *CHNOS Elemental Analyzer* (*Vario EL III*, *Elementar Analysensystem GmBH*, Hanau, Germany).

Biomass and yield: The rice and winter wheat were harvested at the jointing and heading stages. Samples were divided into root, stem, leaf, and ear; all parts were dried in an oven at 65°C for 48 h and weighed. After the crop matured, the 1 m^2 crop samples of each OTC were harvested for yield analysis.

Statistical analysis: All statistical analyses were performed by one-way analysis of variance (*ANOVA*) using *SPSS 21.0* software (*SPSS Inc*., Chicago, IL, USA), and comparisons between the mean values were accomplished by the least significant difference (*LSD*) at $p<0.05$. Linear regression analysis was performed on the relationship between the P_g and the LNC. All graphs were created using *Origin 8.0* software (*Origin Lab*, Northampton, MA, USA).

Results

Photosynthetic parameters: As shown in Fig. 1*A*, at the jointing, heading, and milky maturity stages of rice, compared with the CK and T_1 treatments, the P_N of the T_2 treatment significantly decreased by 10 and 8%, 20 and 14%, and 18 and 18%, respectively. During the winter wheat growing season, the T_2 treatments had no significant effect on P_N at the two different stages (Fig. 1*B*). The T_1 treatment, however, had no significant effect on P_N in both rice and winter wheat. In general, the CO_2 concentration did not have a significant effect on the g_s, C_i, and C_i/C_a in any of the growth stages during the rice (Fig. 1*C*,*E*,*G*) and winter wheat growing seasons (Fig. 1*D*,*F*,*H*).

The light and CO_2-response parameters are shown in Table 1. Compared with the CK and T_1 treatments, the P_{Nmax} of the T_2 treatment significantly increased by 43 and 42%, and 41 and 39%, at the jointing and heading of rice, respectively. Meanwhile, no significant difference in any other index (AQY, R_D, and R_P) was found between the different treatments. During the winter wheat growing season, the T_1 and T_2 treatments did not significantly influence P_{Nmax}, AQY, R_D, CE, and R_P. Besides, the T_1 treatment had no significant effect on photosynthetic response parameters in both rice and winter wheat.

Leaf nitrogen content: During the rice growing season, compared with the CK treatment, the T_2 treatment significantly decreased the LNC by 8% at the jointing stage and 9% at the heading stage, and no significant difference was observed at the milky maturity stage. The T_1 treatment, however, had no significant effect on LNC compared with the CK treatment in any of the three different stages of

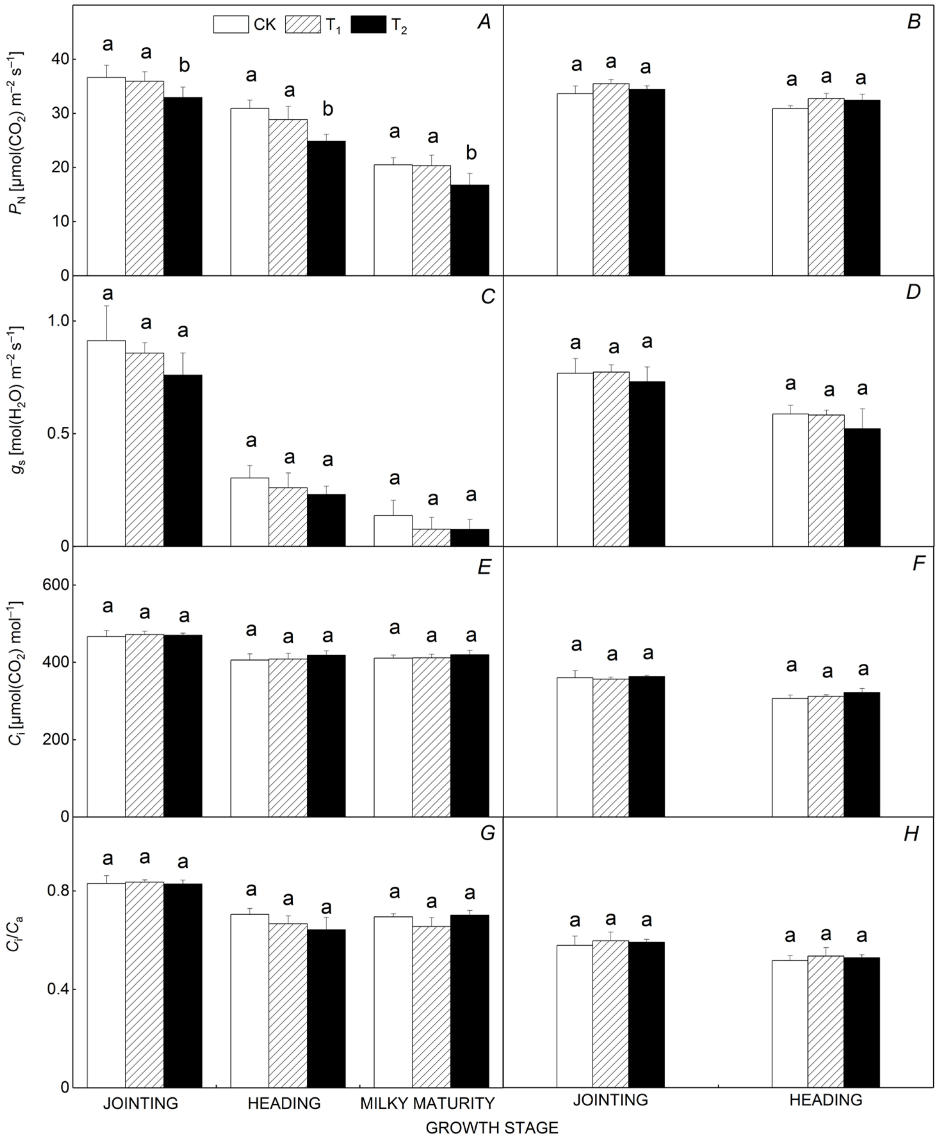

Fig. 1. Effects of different elevated carbon dioxide (eCO_2) concentrations on the net photosynthetic rate (P_N), stomatal conductance (g_s), intercellular CO_2 concentration (C_i), and the ratio of intercellular CO_2 concentration to ambient CO_2 (C_i/C_a) of rice (*A*,*C*,*E*,*G*) and winter wheat (*B*,*D*,*F*,*H*) under the same CO_2 concentration [600 μmol(CO_2) mol^{-1}]. CK – ambient CO_2 concentration; T_1 – ambient plus 40 μmol mol^{-1}; T_2 – ambient plus 200 μmol mol^{-1}. Data are the mean values ± SE ($n = 4$). *Different lowercase letters* indicate a significant difference between different treatments at $p<0.05$.

Table 1. Effects of different elevated carbon dioxide (eCO_2) concentrations on light and CO_2-response parameters of rice and winter wheat. P_{Nmax} – light-saturated net photosynthetic rate; AQY – apparent quantum yield; CE – carboxylation efficiency; R_D – dark-respiration rate; R_P – photorespiration rate. CK – ambient CO_2 concentration; T_1 – ambient plus 40 μmol mol^{-1}; T_2 – ambient plus 200 μmol mol^{-1}. Data are the mean values ± SE (n = 4). *Different lowercase letters* indicate a significant difference between different treatments at p<0.05.

Parameter	Treatment	Rice Jointing	Heading	Milky maturity	Winter wheat Jointing
P_{Nmax} [μmol(CO_2) m^{-2} s^{-1}]	CK	35.6 ± 2.3^b	28.6 ± 2.6^b	20.4 ± 2.4^a	40.48 ± 2.73^a
	T_1	36.0 ± 2.5^b	28.9 ± 2.1^b	25.5 ± 3.0^a	44.65 ± 3.42^a
	T_2	51.0 ± 1.5^a	40.2 ± 2.9^a	22.4 ± 3.1^a	48.00 ± 3.81^a
AQY [μmol(CO_2) m^{-2} s^{-1}]	CK	0.058 ± 0.003^a	0.043 ± 0.007^a	0.056 ± 0.004^a	0.067 ± 0.002^a
	T_1	0.062 ± 0.002^a	0.047 ± 0.005^a	0.068 ± 0.011^a	0.068 ± 0.002^a
	T_2	0.062 ± 0.006^a	0.058 ± 0.010^a	0.061 ± 0.002^a	0.071 ± 0.004^a
R_D [μmol(CO_2) m^{-2} s^{-1}]	CK	2.57 ± 0.06^a	1.34 ± 0.23^a	0.93 ± 0.41^a	2.25 ± 0.89^a
	T_1	2.36 ± 0.16^a	1.49 ± 0.27^a	0.88 ± 0.11^a	1.20 ± 0.17^a
	T_2	2.41 ± 0.13^a	1.70 ± 0.35^a	0.44 ± 0.11^a	3.52 ± 0.94^a
CE	CK	0.195 ± 0.026^a	0.167 ± 0.009^a	0.099 ± 0.015^{ab}	0.207 ± 0.021^a
	T_1	0.161 ± 0.007^a	0.157 ± 0.018^a	0.127 ± 0.012^a	0.204 ± 0.005^a
	T_2	0.142 ± 0.012^a	0.129 ± 0.018^a	0.090 ± 0.007^b	0.209 ± 0.003^a
R_P [μmol(CO_2) m^{-2} s^{-1}]	CK	15.4 ± 1.9^a	13.4 ± 1.1^a	7.7 ± 1.7^a	12.58 ± 2.59^a
	T_1	12.6 ± 0.2^a	12.6 ± 2.0^a	10.0 ± 0.7^a	13.64 ± 0.38^a
	T_2	12.7 ± 1.9^a	11.3 ± 1.6^a	8.2 ± 0.5^a	13.70 ± 0.34^a

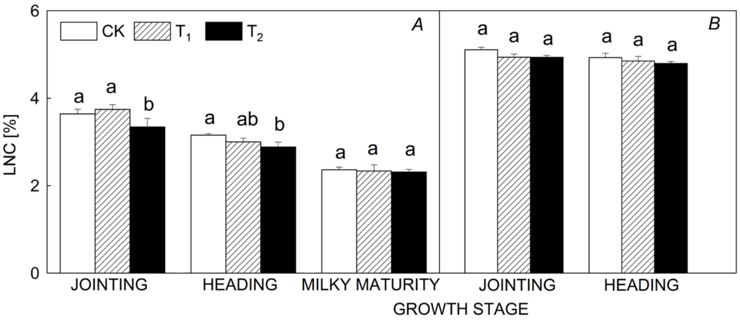

Fig. 2. Effects of different elevated carbon dioxide (eCO_2) concentrations on leaf nitrogen content (LNC) of rice (*A*) and winter wheat (*B*). CK – ambient CO_2 concentration; T_1 – ambient plus 40 μmol mol^{-1}; T_2 – ambient plus 200 μmol mol^{-1}. Data are the mean values ± SE (n = 4). *Different lowercase letters* indicate a significant difference between different treatments at p<0.05.

rice (Fig. 2*A*). During the winter wheat growing season, the LNC of the T_1 and T_2 treatments showed a downward trend, although this difference did not reach statistical significance (Fig. 2*B*).

The relationship between the total photosynthetic rate and the LNC is presented in Fig. 3. During the rice growing season, there was a significant positive correlation between the P_g and LNC. The R^2 of the CK, T_1, and T_2 treatments was 0.81, 0.67, and 0.61, respectively (Fig. 3*A*). In contrast, no correlation was found between the P_g and the LNC in winter wheat. The R^2 of the CK, T_1, and T_2 treatments was 0.01, 0.38, and 0.11, respectively (Fig. 3*B*).

Biomass: The effects of different eCO_2 concentrations on the biomass of rice and winter wheat are shown in Table 2. During the rice growing season, the T_1 and T_2 treatments had no significant effect on the leaf, ear, root, aboveground, or total biomass accumulation. However, the T_1 and T_2 treatments generally tended to promote biomass accumulation in all parts of the plants (except for the leaves), and the biomass of the T_2 treatment was higher than that in the T_1 treatment. At the jointing stage, compared with the CK treatment, the T_2 treatment significantly increased the stem biomass by 49%. During the winter wheat growing season, at the heading stage, compared with the CK treatment, the T_2 treatment significantly increased the leaf, stem, and aboveground biomass by 40, 38, and 40%, respectively.

Yield composition: As shown in Table 3, different eCO_2 concentrations had no significant effect on grain number, TGM, and the unfilled grain number of rice. Compared with the CK treatment, the T_2 treatment increased the grain number, TWG, and unfilled grain number to some extent, with an increase of 3.3, 1.3, and 22.9%, respectively. For winter wheat, CO_2 enrichment tended to increase the number of grains but had no significant effect on the TGM. Compared with the CK treatment, the T_1 and T_2 treatments increased the grain number by 1.5 and 6.1%, respectively.

Different eCO_2 concentrations, in general, could in-

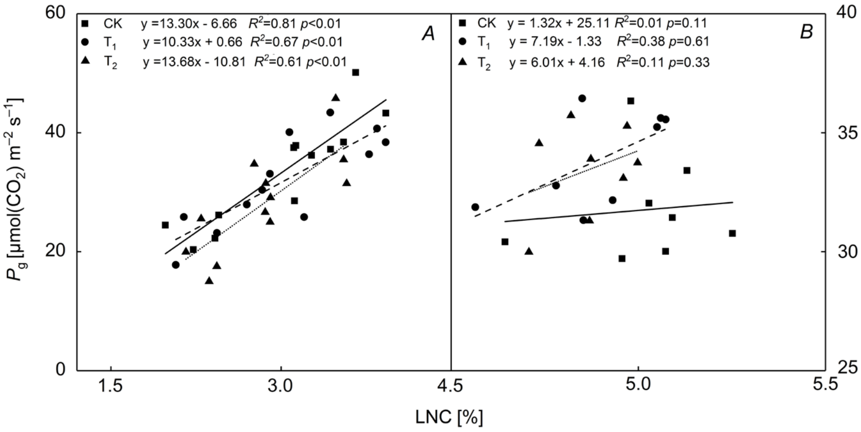

Fig. 3. Relationship between the gross photosynthetic rate (P_g) and leaf nitrogen content (LNC) of rice (*A*) and winter wheat (*B*). CK – ambient CO_2 concentration; T_1 – ambient plus 40 µmol mol^{-1}; T_2 – ambient plus 200 µmol mol^{-1}.

Table 2. Effects of different elevated carbon dioxide (eCO_2) concentrations on the biomass of rice and winter wheat. CK – ambient CO_2 concentration; T_1 – ambient plus 40 µmol mol^{-1}; T_2 – ambient plus 200 µmol mol^{-1}. Data are the mean values ± SE (n = 4). *Different lowercase letters* indicate a significant difference between different treatments at $p<0.05$.

Biomass [g per 5 plants]	Treatment	Rice Jointing	Rice Heading	Winter wheat Jointing	Winter wheat Heading
Leaf	CK	11.99 ± 1.12^a	18.05 ± 1.43^a	11.55 ± 2.07^a	11.26 ± 0.42^b
	T_1	12.94 ± 1.00^a	19.65 ± 2.00^a	11.88 ± 0.80^a	12.59 ± 0.74^{ab}
	T_2	12.31 ± 1.18^a	16.49 ± 1.28^a	13.31 ± 0.73^a	15.75 ± 2.22^a
Stem	CK	12.43 ± 1.38^b	32.90 ± 4.43^a	10.90 ± 2.65^a	22.71 ± 1.43^b
	T_1	16.46 ± 2.02^{ab}	35.89 ± 4.52^a	11.75 ± 0.92^a	24.65 ± 1.79^{ab}
	T_2	18.52 ± 2.44^a	38.49 ± 5.36^a	13.58 ± 1.23^a	31.28 ± 3.65^a
Ear	CK	-	10.25 ± 1.15^a	-	2.43 ± 0.89^a
	T_1	-	10.75 ± 0.86^a	-	3.75 ± 0.60^a
	T_2	-	11.52 ± 1.07^a	-	3.98 ± 0.27^a
Root	CK	4.43 ± 0.39^a	7.47 ± 1.15^a	-	-
	T_1	4.84 ± 0.01^a	8.52 ± 1.01^a	-	-
	T_2	4.87 ± 0.53^a	10.06 ± 1.81^a	-	-
Aboveground	CK	24.42 ± 2.50^a	63.39 ± 7.18^a	22.45 ± 4.70^a	36.40 ± 2.07^b
	T_1	29.40 ± 3.02^a	68.26 ± 7.42^a	23.60 ± 1.62^a	41.00 ± 2.65^{ab}
	T_2	30.83 ± 3.62^a	68.54 ± 7.60^a	26.89 ± 1.82^a	51.01 ± 5.71^a
Total	CK	28.84 ± 2.89^a	70.87 ± 8.29^a	-	-
	T_1	34.24 ± 3.31^a	76.77 ± 8.26^a	-	-
	T_2	35.60 ± 4.15^a	78.60 ± 8.95^a	-	-

Table 3. Effects of different elevated carbon dioxide (eCO_2) concentrations on yield composition of rice and winter wheat. CK – ambient CO_2 concentration; T_1 – ambient plus 40 µmol mol^{-1}; T_2 – ambient plus 200 µmol mol^{-1}; TGM – thousand-grain mass. Data are the mean values ± SE (n = 4). *Different lowercase letters* indicate a significant difference between different treatments at $p<0.05$.

Treatment	Rice [15 plants] Grain number	Rice TGM [g]	Rice Unfilled grain number	Winter wheat [20 plants] Grain number	Winter wheat TGM [g]
CK	2,902 ± 61^a	21.72 ± 0.30^a	310 ± 32^a	962 ± 43^a	40.07 ± 0.37^a
T_1	2,845 ± 57^a	21.76 ± 0.19^a	305 ± 36^a	976 ± 53^a	40.16 ± 0.31^a
T_2	2,997 ± 87^a	22.00 ± 0.19^a	381 ± 27^a	1,021 ± 35^a	40.12 ± 0.24^a

crease the yield of rice and winter wheat to a certain extent (Fig. 4). For rice, the T_1 and T_2 treatments tended to increase the yield, although this difference did not reach statistical significance (Fig. 4*A*). Compared with the CK treatment, the T_1 and T_2 treatments increased the yield of rice by 37.37 g m^{-2} and 167.10 g m^{-2}, with an increase of 3.0 and 13.5%, respectively. Compared with the T_1 treatment, the T_2 treatment increased yield by

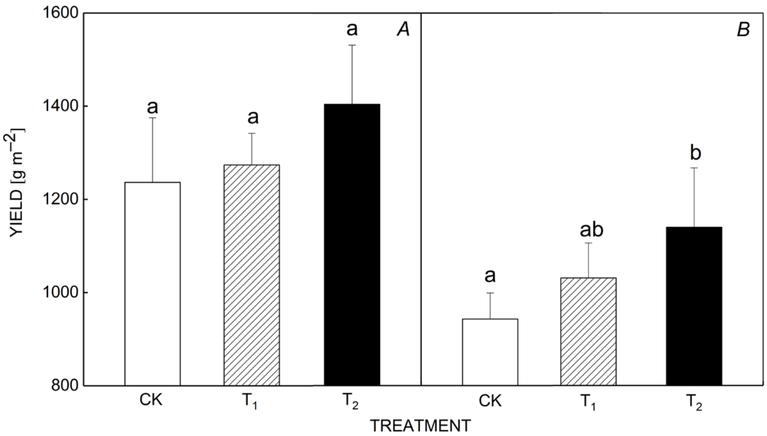

Fig. 4. Effects of different elevated carbon dioxide (eCO_2) concentrations on the yield of rice (*A*) and winter wheat (*B*). CK – ambient CO_2 concentration; T_1 – ambient plus 40 µmol mol^{-1}; T_2 – ambient plus 200 µmol mol^{-1}. Data are the mean values ± SE (n = 4). *Different lowercase letters* indicate a significant difference between different treatments at $p<0.05$.

129.73 g m^{-2}, with an increase of 10.2%. It can be seen from Fig 4*B*, compared with the CK and T_1 treatments, that the T_2 treatment increased the yield of winter wheat by 196.75 g m^{-2} and 108.82 g m^{-2}, with an increase of 20.9 and 10.6%; the T_1 treatment increased the yield by 87.93 g m^{-2}, with an increase of 9.3%.

Discussion

Photosynthesis provides energy for biomass accumulation and is one of the important factors for plant growth and development (Lu *et al*. 2017). It has been well documented that short-term (a period of min to hours) eCO_2 concentrations stimulate photosynthesis, while the initial stimulation of photosynthesis gradually decreases after long-term (a period of weeks to months) eCO_2 concentration exposure (Bloom *et al*. 2002, Seneweera *et al*. 2011). In this study, the photosynthetic characteristics showed different trends of rice and winter wheat in response to eCO_2 concentrations. In rice, we observed that the T_2 treatment significantly decreased the photosynthetic capacity of leaves compared to the CK and T_1 treatments (Fig. 1*A*). This demonstrates that the rice appeared to have undergone photosynthetic downregulation to the high eCO_2 concentrations. The reasons for the photosynthetic downregulation mainly include stomatal limitation and nonstomatal factors (Farquhar and Sharkey 1982). In our study, although the g_s under the T_2 treatment showed a downward trend (Fig. 1*C*), the C_i values among different treatments were similar during the rice growing season (Fig. 1*E*). Besides, no significant difference in C_i/C_a was found under different treatments (Fig. 1*G*). Therefore, in our study, this eliminates the phenomenon of photosynthetic acclimation due to reduced stomatal limitation (Chen *et al*. 2005). Rubisco enzyme plays an important role in the photosynthesis of plants (Vicente *et al*. 2015), accounting for 15–35% of total LNC in C_3 plants (Evans 1989, Makino and Osmond 1991). Some studies have reported that the decreased amount and activity of Rubisco may be related to a decrease in LNC (Aranjuelo *et al*. 2011, Wang *et al*. 2013). In our study, a significant decrease in LNC was observed under the T_2 treatment in rice (Fig. 2*A*), which might partly explain why the photosynthetic acclimation appeared under the high CO_2 concentration. It is noteworthy that, although rice and wheat are C_3 plants, our study found that there was no significant effect on P_N under different treatments, and high CO_2 concentration did not lead to photosynthesis downregulation phenomenon during the winter wheat growing season (Fig. 1*B*). The possible reason is that, on the one hand, the photosynthesis of plants will have different responses due to different species, and even the same plant will have different responses to CO_2 at different growth and development stages. Also, the differences in photosynthetic characteristics are usually detected, and a significant intraspecific variation in responses to eCO_2 has been found in rice and wheat (Woodrow 1994). On the other hand, wheat grown under the high CO_2 enrichment environment only showed a decrease in photosynthetic capacity when the nitrogen supply is low, and no photosynthesis downregulation occurred under appropriate fertilization conditions (Gutiérrez *et al*. 2013).

Photosynthesis characteristic parameters reflect the ability of plants to benefit from light energy and CO_2 and can be used to evaluate photosynthetic physiological and ecological characteristics of plants (Pan *et al*. 2020). The P_{Nmax} is the key index to measure the maximum photosynthetic capacity of leaves. As can be seen from Table 1, the T2 treatment significantly increased the P_{Nmax} of rice. However, although the P_{Nmax} of winter wheat showed an increasing trend under eCO_2 conditions, it did not reach statistical significance. The results indicated that high CO_2 enrichment could improve the maximum photosynthetic capacity of rice and winter wheat to some extent. The values of AQY and CE are the initial slopes of light-response and CO_2-response curves, respectively, which can reflect the ability of plants to utilize low light energy and low CO_2 concentration. In our study, AQY increased with the rising CO_2 concentrations, although this difference did not reach statistical significance. The results showed that CO_2 enrichment is beneficial to improve AQY, which may increase the P_{Nmax} of rice and winter wheat. During the rice growing season, the CE was marginally reduced under the T_2 treatment, which may be related to the decrease of LNC due to high CO_2 concentration. This indicates that high CO_2 concentration further reduces the utilization ability of rice at low concentrations of CO_2. Besides, we also found that, compared with high CO_2 concentration, low eCO_2 concentration did not affect the photosynthetic characteristics, such as P_N, g_s, C_i, C_i/C_a, P_{Nmax}, R_D, CE, and R_p, during the whole rice and winter wheat growing seasons (Fig. 1, Table 1). The possible reason is that, in our experiment, the set low eCO_2 concentration (ambient plus 40 μmol mol^{-1}) is closer to the natural environment, and the influence of CO_2 concentration on plants' physiology and ecology may not be as obvious as that of high eCO_2 concentration (ambient plus 200 μmol mol^{-1}). On the other hand, due to the adaptability of plants, the low eCO_2 concentration is close to the plant's natural growth environment, it may adapt to the increase of lower CO_2 concentration in a short time. Therefore, photosynthetic characteristics of low eCO_2 concentrations are close to the control treatment.

The growth of plants at atmospheric CO_2 concentrations greater than the ambient levels could greatly influence plant tissue chemistry (Loladze 2002, Taub and Wang 2008). Nitrogen is an important component of plant synthesis of chlorophyll and various enzymes, and approximately 75% of the nitrogen in plant leaves occurs in chloroplasts, most of which are used to construct photosynthetic apparatus (Takashima *et al*. 2004). It has been reported that the long-term response to CO_2 concentrations is mainly due to the limitation of nitrogen supply (Seneweera 2011). Many experiments have also detected a decrease in plant tissue nitrogen concentration under CO_2 enrichment conditions (Ainsworth and Long 2005, Norby *et al.* 2010), particularly in leaf tissues (Seneweera 2011). For example, Xie *et al*. (2002) found that the LNC of rice decreased by 8.4, 9.7, 10.2, and 3.2% at the tillering, jointing, heading, and maturity stages, respectively, under the FACE experiment. In the FACE study in Arizona, it was found that under severe N deficiency, the increase of CO_2 concentration reduced the LNC by 25% in the first year and by 19% in the second year on average, but the LNC of wheat was not affected under optimum conditions in a 4-year FACE experiment (Sinclair *et al*. 2000). In our present study, high CO_2 concentration significantly reduced LNC of rice (Fig. 2*A*), and the LNC of winter wheat was slightly but insignificantly reduced under different eCO_2 concentrations (Fig. 2*B*). This is consistent with the previous research results. Moreover, the low eCO_2 concentration had no significant effect on the LNC of rice and winter wheat. It has been predicted that increased photoassimilate accumulation in plants as a result of eCO_2 concentrations will result in a dilution of plant N such that the N concentration in the leaves will decrease (Gifford *et al*. 2000). As shown by our results, in general, the different CO_2 treatments stimulated the biomass accumulation and diluted N content in plant tissues to a certain extent (Table 2), which may account for the decrease in LNC. Studies have shown that there is a strong and significant positive correlation between photosynthetic capacity and LNC (Zhang *et al*. 2010). Some studies, however, have indicated that photosynthetic capacity is either negatively or insignificantly correlated with LNC among species (Takashima *et al*. 2004). In the present study, we found that there was a significant positive correlation between the P_g and LNC during the rice growing season (Fig. 3*A*), while no correlation was found during the winter wheat growing season (Fig. 3*B*). This may be due to the differences in N partitioning between thylakoid and soluble proteins, electron transport capacity, and specific activities of Rubisco, which caused that the relationship between LNC and photosynthetic capacity varied among different plants (Evans 1989). The ratio of photosynthetic capacity to LNC can be used as an indicator to evaluate the photosynthetic efficiency of nitrogen input, which is PNUE, which can be used to express the instantaneous measure of the relationship between nitrogen-use efficiency and fixed CO_2 (Takashima *et al*. 2004). As shown in Fig. 3*A*, different eCO_2 concentrations did not affect the PNUE, demonstrating that the increase of CO_2 concentrations did not affect the physiological utilization rate of nitrogen in rice leaves. In contrast, there was no correlation in winter wheat; it may be that each species has a different N allocation to various components, which leads to the difference of photosynthesis–N relationship and PNUE between different species (Pierce *et al*. 2003, Novriyanti *et al*. 2012).

The concentration of eCO_2 affects plant photosynthesis, which in turn may impact the potential growth and development of roots, stems, leaves, and other organs (Srivastava *et al*. 2001). Biomass increases in rice and winter wheat under eCO_2 concentrations have been widely reported (Dijkstra *et al.* 1999, Kim *et al*. 2003, Yang *et al.* 2006). Here, we assessed the effects of different eCO_2 concentrations on the biomass of rice and winter wheat. No significant change in biomass was found during the rice growing stages (Table 2). We did, however, observed that high CO_2 concentration significantly increased the biomass of leaf, stem, and aboveground mass at the heading stage in winter wheat. Furthermore, we also found the biomass accumulation was greater in the T_2 treatment as compared to the T_1 treatment. This suggested that plants have higher photosynthetic capacity under high CO_2 conditions, which inevitably promoted fixation and transformation of carbon, thus increasing the accumulation of more biomass. As can be seen from Table 1, in general, the P_{Nmax} of the T_2 treatment was greater than that grown under the CK and T_1 treatments, which may be beneficial to promote the biomass accumulation of rice and wheat to a certain extent.

Material production and accumulation are the basis of crop yield formation. Using meta-analysis techniques, it was indicated that the average crop yield increased by 17% under eCO_2 conditions (Ainsworth and Long 2005), among which the yield of rice and wheat increased by 20% (Wang *et al*. 2015) and 24% (Wang *et al.* 2013), respectively. In this study, we found that the yield of rice and winter wheat increased with the rising CO_2 concentrations to some extent (Fig. 4), and high eCO_2 concentration significantly increased the yield of winter wheat (Fig. 4*B*). The results are in agreement with former studies, although the magnitude of increase varies depending upon location and cultivar. Furthermore, in general, the T_2 treatment showed a higher yield of rice and winter wheat than those grown in the T_1 treatment. This is probably because high CO_2 concentrations promoted a greater increase in grain number and TGM of rice and winter wheat (Table 3). According to regression analysis, the fitting equations of rice and winter wheat yield and different eCO_2 concentrations were: $y = 0.83x + 906.9$ ($R^2 = 0.99$) and $y = 0.90x + 607.1$ ($R^2 = 0.97$), respectively, which indicated that there was a positive correlation between the yield of rice and winter wheat and CO_2 concentration within a certain range. Similar results have been reported by Long *et al.* (2006), using a meta-analysis of crop yield response to the CO_2 enrichment, showing that crop yield responded linearly to the increase of CO_2 concentrations.

Conclusions: In summary, our results showed that photosynthetic acclimation was observed under high eCO_2 concentration. Besides, the high eCO_2 concentration significantly increased P_{Nmax} but decreased the LNC during the rice growing season. Moreover, high eCO_2 concentration promoted higher biomass accumulation and yield than the low eCO_2 concentration in rice and winter wheat. In contrast, the low eCO_2 concentration had little effect on photosynthetic characteristics, LNC, biomass accumulation, and yield during the rice and winter wheat growing seasons. This study, therefore, indicated that the photosynthesis and growth of rice and winter wheat have different responses to high and low eCO_2 concentrations. As the low eCO_2 concentrations are closer to the natural growth environment of plants, in general, the photosynthetic performance and growth of plants, especially for C_3 plants, are relatively insensitive to low eCO_2 concentrations compared to high eCO_2 concentrations. It is noteworthy that atmospheric CO_2 concentrations change gradually, and our experiment was only conducted for one year. It is not clear whether plants grown under low eCO_2 concentrations have a 'memory effect', and therefore the effects of gradually increasing CO_2 concentrations on the progeny of the rice and winter wheat should be further studied.

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