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Enhanced rice phosphorus use efficiency under elevated atmospheric CO_2 and its drivers

Haiwei Zhang [a], Ting Xiao [a], Zihua Shi [a], Rui Ren [a], Yu Jiang [a,b], Yanfeng Ding [a,b], Songhan Wang [a,b,*]

[a] *Jiangsu Collaborative Innovation Center for Modern Crop Production, Key Laboratory of Crop Physiology and Ecology in Southern China, Nanjing Agricultural University, Nanjing, Jiangsu 210095, China*
[b] *Sanya Research Institute of Nanjing Agriculture University, Sanya, Hainan 572024, China*

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ABSTRACT

Soil phosphorus (P) is the second most important nutrient for rice growth and development, but its use efficiency (PUE) is still very low. Meanwhile, the elevated atmospheric carbon dioxide (CO_2) concentration during recent decades has increased the biomass and rice yield globally, but its impact on the PUE of rice is still not well understood. Therefore, this study aims to explore the effect of elevated CO_2 on PUE of rice and its underlying mechanisms, based on the evidence from two-years field free-air CO_2 enhancement (FACE) experiment and the results from a global meta-analysis, we use the open-top chamber (OTC) to explore its underlying mechanism. Results showed that compared to atmospheric CO_2 (ACO_2), elevated CO_2 (ECO_2) has significantly increased the PUE of rice, with a magnitude of 16.6 %. The effects of elevated CO_2 on PUE was higher for Japonica rice than that for Indica rice. These findings were also confirmed by the results from a global meta-analysis. Results based on OTC experiments showed that the aboveground biomass (AGB) of rice increased by 27.8 % and the soil available P increased by 20.3 % with elevated CO_2., two possible drivers accounting for the positive CO_2 effect on rice PUE were investigated, of which one was the enhanced aboveground biomass and the other one was the enhanced soil phosphatase and available P content, both could increase the P accumulation of rice under elevated CO_2 conditions. Further analysis showed that these two factors jointly controlled the elevated PUE at elevated CO_2 conditions, of which the contribution from enhanced aboveground biomass was larger. These findings thus suggested that elevated CO_2 will promote the absorption of P and accelerate the P cycles in rice soils. Our results also could provide important benefits for forming management strategies to balance the contradiction between increasing demand for food and limited P fertilizer resources in the context of climate change.

1. Introduction

Rice is a staple food crop worldwide and the main source of energy for Asian population (Seck et al., 2012; Tang et al., 2022). Therefore, rice yield plays a crucial role for ensuring global food security (Bandumula, 2018). Phosphorus (P) is the second most important nutrient for rice growth and development, involving in various physiological and biochemical processes (Li et al., 2021; Takahashi and Katoh, 2024), including plant cell formation (Li et al., 2021; Takahashi and Katoh, 2024), photosynthesis (Conroy et al., 1986), material transport (Alewell et al., 2020), regulation of cell osmotic pressure and soil pH, and the enhancement of stress resistance (Fu et al., 2014). In addition, soil P can also promote the root development of rice, increase the grain yield by enhancing tillers and branches (Chen et al., 2019). Insufficient supply of P will lead to reduced growth of rice, decreased stress resistance, reduced number of tillers, and ultimately result in the decline of grain yield (Vandamme et al., 2016; Zhang et al., 2021a, 2021b).

Although a large amount of P fertilizer have entered into the agricultural ecosystem, soil P is still one of the important factors limiting crop growth (Bhat et al., 2017; Hou et al., 2018a, 2018b; Hou et al., 2021). Approximately 67 % of the world's land area still lacks available soil P (Hou et al., 2018a, 2018b; Pereira et al., 2020), and 30 % of the

* Corresponding author at: Jiangsu Collaborative Innovation Center for Modern Crop Production, Key Laboratory of Crop Physiology and Ecology in Southern China, Nanjing Agricultural University, Nanjing, Jiangsu 210095, China.
E-mail address: wangsonghan@njau.edu.cn (S. Wang).

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world's crop yield is largely affected by P deficiency (Ali et al., 2019). For traditional agricultural practices, mineral P fertilizers were widely used to improve crop yield (Wang et al., 2015). However, the use efficiency of P fertilizer is still very low (Dodd et al., 2015; Wu et al., 2020), with only 10 %-30 % of the P fertilizer applied to soil can be absorbed and finally utilized by crops (He et al., 2019; Gagnon et al., 2020). At the same time, the remaining 70–90 % of the P fertilizer has been adsorbed and precipitated by the mineral surface as fixed P that cannot be used by crops (Hinsinger, 2001; Gypser and Freese, 2020). More importantly, approximately 90 % of the world's mineral P fertilizer used for agricultural production were originated from non-renewable phosphate rock, which was estimated to be depleted by about 2050 (Bera et al., 2018). Therefore, the contradiction between the growing demand for crop yield and limited P fertilizer resources has become increasingly prominent. Enhancing the use efficiency of P fertilizer is becoming critical important to ensure the sustainability of global food supply.

Meanwhile, atmospheric carbon dioxide (CO_2) concentration has increased from 280 ppm during the pre-industrial revolution age to 419.3 ppm in 2023 (NOAA, 2023). Under different climate scenarios, it is expected that atmospheric CO_2 concentration will reach to 550 ppm and 730 ppm by 2050 and 2100 respectively (Masson-Delmotte et al., 2021). Elevated CO_2 concentration generally will promote the growth of crop, and thereby increase the biomass and crop yield, referring as the 'CO_2 fertilization effect (CFE)' (Kolby Smith et al., 2016; Wang et al., 2020). The effect of CFE is more remarkable for C_3 crops such as rice, since that current CO_2 concentrations still do not reach the saturation point of photosynthesis for C_3 plants (Tausz Posch et al., 2020). The availability of soil nutrients can significantly influence crop responses to elevated CO_2, while simultaneously, elevated CO_2 may alter plants nutrient acquisition and utilization patterns. As the second most essential plant nutrient, P is essential nutrients that are required for multiple biochemical processes such as plant photosynthesis, growth and physiology(Wang et al., 2023), P dynamics under elevated CO_2 have been extensively investigated. Previous studies demonstrated that elevated CO_2 stimulated root system development (Benlloch-Gonzalez et al., 2014), enhanced carbon allocation to roots, and ultimately boosted phosphatase enzyme activity (Souza et al., 2017). These physiological changes collectively could accelerate mineralization of soil organic P, thereby improving P uptake efficiency in crops (Pandey et al., 2015a, 2015b; An et al., 2018). However, some studies have shown that elevated CO_2 concentration has no significant effect on P uptake (Jena et al., 2018). These inconsistent results may be related to the differences in plant species, soil types, phosphate fertilizer treatments, and the magnitude of elevated CO2 concentration.

With the ever-increasing concentration of CO_2, improving the utilization efficiency of P fertilizer in rice may be a feasible solution to solve the contradiction between the increasing demand for food and the limited P fertilizer resources. However, the effect of elevated CO_2 on P use efficiency (PUE) for rice and its underlying mechanism are still not fully investigated. Therefore, this study aims to investigated the response of PUE to elevated CO_2 and its underlying mechanisms, relying on the evidence from field controlled experiments and a global compilation result from meta-analysis. To this aim, we first quantified the impacts of elevated CO_2 on PUE of rice, using the field measurements from two-years free-air CO_2 enhancement (FACE) experiments. We also investigated the difference of the response in PUE to elevated CO_2 among two main rice-subspecies (Japonica and Indica). We then verified our findings based on a global compilation result based on meta-analysis. Finally, we comprehensively investigated the underlying mechanism of the PUE response to elevated CO_2, using the measurements from pot experiments with various P fertilizer application gradients. We assume that elevated CO_2 increases soil available phosphorus content and promotes phosphorus uptake by rice; on the other hand, aboveground biomass promoted phosphorus accumulation, thereby improving the PUE under elevated CO_2.

2. Materials and methods

2.1. Field FACE experiment

The FACE platform was established in 2020. The FACE experiments were conducted for 2022–2023 at the Danyang Experimental Station (119°28′E, 31°54′N), Danyang City, Jiangsu Province. The site is located in the Yangtze River Delta region with a subtropical monsoon climate. This area is the main rice producing regions in China, with an average annual temperature of about 22℃. The basic physical and chemical properties of soil are shown in Table S1.

The FACE system consists of six identical octagonal rings with a diameter of 8 m, of which three rings are treated with atmospheric CO_2 concentration (aCO_2) and the other three rings are treated with elevated atmospheric CO_2 concentration (eCO_2). The FACE system consists of three systems, including the gas supply system, the monitoring system and the control system. A circle of poly vinyl chloride (PVC) pipes with small holes was installed at a distance of 50 cm from the rice canopy to form a gas supply system. Eight sensors were evenly distributed in a 4-meter circle centered at the center of each circle to form a detection system. The CO_2 concentration, wind speed and air temperature were then detected and recorded. The control system can adjust the CO_2 concentration in real time at a frequency of 30 s. During the day, CO_2 is sprayed into the eCO_2 loop through the ventilation system, and the CO_2 concentration in the loop is maintained at about 550 ppm by the control system.

We used the rice varieties following the local farmer's conventional recommendation, i.e., a Japonica rice variety (Wuyunjing 23) and an Indica rice variety (Yangdao 6). The transplanting date was June 20. The row spacing was 25 × 15 cm, of which Yangdao 6 had 2 seedlings per hole, and Wuyunjing 23 had 3 seedlings per hole. Urea, superphosphate (P_2O_5) and potassium sulfate (K_2O) were applied as nitrogen (N), P and potassium (K) fertilizers respectively. The amount of N fertilizer was 225 kg/ha, the amount of P fertilizer (P_2O_5) was 120 kg/ha, and the amount of K fertilizer (K_2O) was 160 kg/ha. N fertilizer was applied in three times: 40 % at the transplanting stage, 30 % at the tillering stage, and 30 % at the young spike differentiation stage. P fertilizer was applied at the soil tillage stage, while K fertilizer was split equally between the soil tillage and jointing stages. All other field practices followed local recommendations.

2.2. Meta-analysis

We collected data from previous studies to validate our findings about the response of PUE to elevated CO_2. Literatures used for this meta-analysis were mainly collected through academic resource search platform "Google Scholar" and "Web of Science ", using "elevated CO_2", "rice" and "phosphate fertilizer" as keywords. The selected literatures must meet the following criteria: (1) experiments must be carried out under field conditions, using open top chambers (OTC) or FACE facilities; (2) the data must come from the control experiment, and the increase of CO_2 was determined; (3) the mean value and sample size of the treatment and control groups for each variable were reported either numerically or graphically, or original data could be obtained from the author; (4) the experiment must spanned at least one growing season, and the utilization rate of P fertilizer can be calculated directly or indirectly; (5) to ensure that the observed differences were solely attributed to CO_2 variations, it is imperative that all other environmental conditions and treatments remain consistent across the experimental groups, thereby eliminating the potential influence of confounding factors on PUE. Following the above criteria, we collected data from 11 experimental sites and used GetData Graph Digitizer 2.25 to obtain 23 site-years of observations (16 for Japonica rice and 7 for Indica rice).

2.3. OTC experiment

In order to investigate the possible mechanism accounting for the variation in PUE under elevated CO_2, we conducted a pot experiment using OTC facilities at the same location with FACE experiment. The OTC facility includes eight open-top chambers, We set the CO_2 concentration in four OTCs at 400 ppm as ACO_2 treatment, and in the other four OTCs, we set CO_2 concentration at 600 ppm as ECO_2 treatment. Each OTC platform was a regular hexagonal prism. The frame was structured of aluminum alloy and was surrounded by toughened glass with extremely high light transmittance. The total height is 2.5 m and the bottom area is 11.5 m^2.

The experiment consisted of two CO_2 levels, two rice sub-species and four P application levels. Two rice sub-species were Wuyunjing 23 (Japonica rice) and Yangdao 6 (Indica rice) respectively, same to the varieties used at FACE experiment. Four P application levels were no P fertilizer (CK), low P (LP, 60 kg/ha P_2O_5), medium P (MP, 120 kg/ha P_2O_5), and high P (HP, 180 kg/ha P_2O_5). The application time of N, P and K fertilizers were the same to the FACE experiment. In the OTC experiment, CO_2 concentrations were continuously enhanced throughout the whole growing-season from the tillering stage (June 25) to the harvest (October 25). Pots were planted in small plastic pots (20 ×15 ×25 cm) with 4 kg soil per pot. The soils were collected from the FACE experiment and the basic physical and chemical properties of soil are the same to FACE experiment. All other field practices followed local recommendations.

2.4. Sampling and measurement methods

2.4.1. Measurement of net photosynthetic rate for rice leaves

The net foliar photosynthetic rate of rice leaves was measured at three critical growth stages: the jointing stage, heading stage, and flowering stage. The net foliar photosynthetic rate was measured at a sunny morning (between 9:00 and 11:00 AM) using the LiC-6800 photosynthesis measurement system (LI-COR Inc., Lincoln, USA). For the jointing stage, the second top leaf was measured, while flag leaves were measured during heading and flowering stages. Measurements were taken at leaf midpoints, the light intensity is set at 1500 $\mu mol \cdot m^{-2}$ s^{-1} and the CO_2 concentration was maintained at a level consistent with the experimental design.

2.4.2. Measurement of aboveground dry matter

According to the number of tillers (jointing stage and heading stage) and the number of spikes (maturity stage), three representative plants were selected from each treatment, and the plants were divided into three parts: stems, leaves and spikes. The plants were killed at 105℃ for 30 min, and dried at 75℃ until the quality was constant and weighed.

2.4.3. Measurement of P accumulation by rice plants

The stems, leaves and spikes (only for mature stage) at jointing stage, heading stage and mature stage were crushed and extracted by concentrated H_2SO_4-H_2O_2 digestion method (Soon and Kalra, 1995). Briefly, dry samples (0.1–0.5 g, ±0.0001 g) were mixed with 5–10 water drops in a 100 mL digestion tube. After adding 5.00 mL concentrated H_2SO_4 and covering with a funnel, the mixture underwent overnight cold digestion, followed by high-temperature digestion. Gradual H_2O_2 additions (decreasing amounts) were applied until the solution turned colorless/clear, then heated for 20–30 min to eliminate excess H_2O_2. After cooling, the digestate was diluted to 100 mL, shaken, and clarified (via standing or P-free filtration). The volume fraction of sulfuric acid in the test solution is about 5 %. The P content was determined by German seal Auto Analyzer AA_3 continuous flow analyzer (Chen et al., 2025).

The P accumulation by rice plants was determined by multiplying the dry matter and the P concentration in different organs. The PUE (%) was then calculated as follows (Su et al., 2023):

$$PUE = \frac{U - U_0}{F}$$

where U and U_0 were the P accumulation by rice plants at harvest stage with and without P fertilizer application; F was the P fertilizer application rate.

2.4.4. Collection and determination of soil samples

Soil samples were collected at the jointing stage, heading stage and maturity stage for the OTC experiment. The whole pot of soil was poured out and broken, and the soil near the rice roots was collected. The soil was dried naturally for the determination of soil available P content, phosphatase activity and other indicators.

The Olsen method (Olsen, 1954) was used to determine soil available phosphorus (P) content. A 5.00 g (±0.01 g) air-dried, 20-mesh sieved soil sample was mixed with 100 mL 0.5 M $NaHCO_3$ in a 250 mL flask, shaken (180 rpm, 30 min, 20–25°C), and filtered (P-free paper). A 10.00 mL filtrate aliquot was mixed with 5.00 mL color-developing agent, diluted to 25 mL, incubated (30 min, >20°C), and absorbance at 700 nm was measured. Results were calculated against a P standard curve. Soil neutral phosphatase (S-ACP) activity was measured using a soil neutral phosphatase (S-ACP) activity assay kit (Shanghai Enzyme Linked Biology, micromethod 100 T/96S). Neutral phosphatase activity Using 1umol phenol released per gram of soil per day at 37℃ as an enzyme activity unit, and the unit is umol d^{-1} g^{-1}.

2.5. Statistical analysis

The data processing was conducted using SPSS 26.0, and Origin 2022 was utilized for generating figures. For the significance analysis of the individual and interactive effects of CO_2 concentration and fertilization treatment, SPSS 26.0 was employed. Comparisons between each treatment were carried out through the Least Significant Difference (LSD) method, where results exceeding the LSD0.05 threshold were deemed statistically significant, and those surpassing the LSD 0.01 threshold were considered extremely significant.

3. Results

3.1. Elevated CO_2 enhanced rice PUE

Based on the measurements from two-years of field FACE experiments, we found that elevated CO_2 concentration could significantly improve the PUE of rice, with an averaged magnitude of 16.6 % (Fig. 1). This phenomenon was confirmed for the results of individual year 2022 and 2023. In addition, although the PUE was both significantly or marginally significantly increased with elevated CO_2 for Japonica rice and Indica rice, the response of PUE to elevated CO_2 seemed to be higher for Japonica rice (WYJ23, 17.8 %, Fig. 1) than that for Indica rice (YD6, 15.4 %, Fig. 1).

In order to validate our finding of the enhanced PUE under elevated CO_2, we also conducted two additional analyses. First, we collected the results from previous field experiments and used meta-analysis to verify the effect of elevated CO_2 on PUE. Among a wide range of environmental and experimental factors, elevated CO_2 was the first most important predictor for PUE in rice, and cultivar type was the second (Fig. 2a). More importantly, results also showed that the elevated CO_2 concentration could significantly increase the PUE of rice (26.6 %, Fig. 2b). Moreover, the enhancement of PUE for Japonica rice (46.2 %, Fig. 2c) was significantly higher than that for indica rice (7.0 %, Fig. 2c).

Second, we also used pot experiments at the same site with the FACE experiments to verify the response of rice PUE to elevated CO_2. The pot experiments were conducted for different rice sub-species and for various amount of field P fertilizers. We again found that the elevated CO_2 concentration could significantly improve the PUE for rice, with an

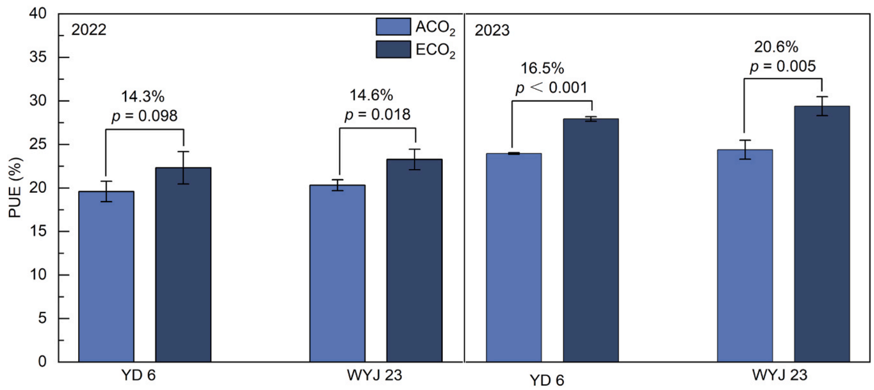

Fig. 1. Response of PUE to elevated CO_2 based on FACE experiment. Bars and error-bars represent the mean values and their standard errors respectively. The relative differences in PUE (with a unit of %) between ACO_2 and ECO_2 were calculated and marked atop of the bars. YD6, Yangdao6 (Indica rice); WYJ23, Wuyunjing23 (Japonica rice). ACO_2 and ECO_2 indicates ambient CO_2 treatment and elevated CO_2 treatment respectively. The significance of the difference in PUE was calculated using the two-sample *t*-test.

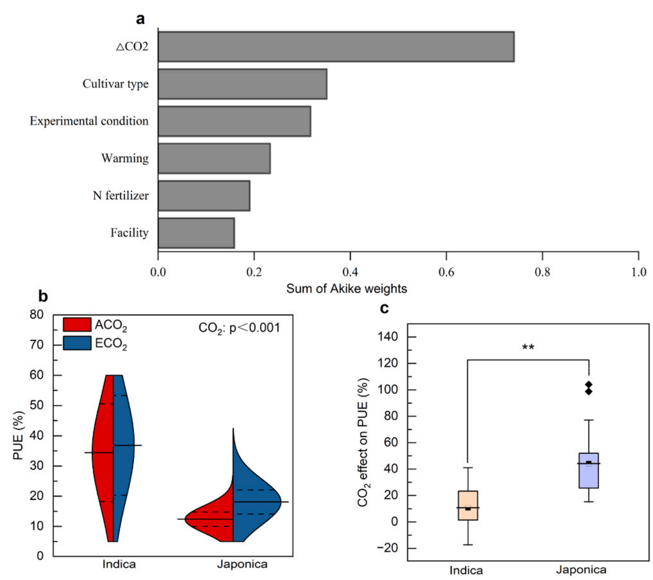

Fig. 2. Response of PUE to elevated CO_2 based on Meta-analysis. a, Importance of the environmental predictors that affecting PUE. The importance was calculated based on the sum of Akaike weights derived from model selection using AICc (Akaike's Information Criteria corrected for small samples). $\triangle CO_2$, the degree of CO_2 enhancement. **b,** Comparisons of PUE under ACO_2 and ECO_2. ACO_2 and ECO_2 indicates ambient CO_2 treatment and elevated CO_2 treatment respectively. The statistical significance (*p*-value) between the PUE of ACO_2 and ECO_2 was estimated using a two-sample *t*-test. Solid black lines represent the mean value of PUE for each cultivar type and the dotted line represents the 95 confidence interval. **c,** The CO_2 effect on PUE for Indica and Japonica rice. **: a significantly different CO_2 effect on PUE between Indica and Japonica rice using a two-sample *t*-test at $p < 0.01$.

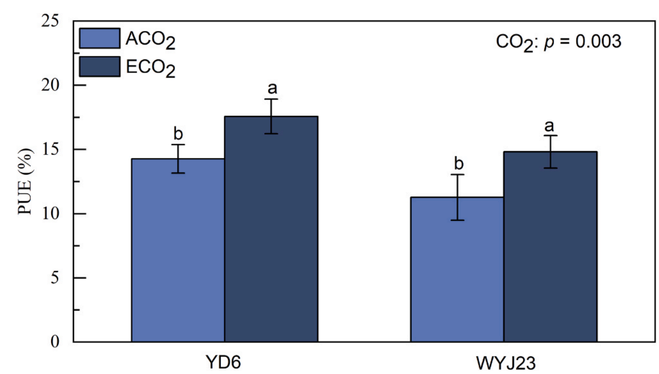

Fig. 3. Response of PUE to elevated CO_2 based on OTC experiment. ACO_2 and ECO_2 indicates ambient CO_2 treatment and elevated CO_2 treatment respectively. The statistical significance between the PUE of ACO_2 and ECO_2 was estimated using a two-sample *t*-test, and different lowercase letters indicate significant differences at $p < 0.05$. YD6, Yangdao6 (Indica rice); WYJ23, Wuyunjing23 (Japonica rice).

average value of 26.8 % (Fig. 3a). Also, the CO_2 effect on PUE for Japonica rice (WYJ23) was about 31.4 %, significantly greater than that for Indica rice (YD6, 23.1 %, Fig. 3b). Overall, the results based on FACE experiment, meta-analysis and OTC experiment together suggest that elevated CO_2 can significantly improve the PUE of rice and the CO_2 effect on PUE has notable difference between rice sub-species.

3.2. Possible mechanisms

We then investigated the possible mechanisms accounting for the CO_2 effects on rice PUE. Two hypotheses have been proposed, of which the first is that elevated CO_2 generally will promote the photosynthetic rate and increase the accumulation of aboveground dry matter, leading to a large need of P need and finally increasing the PUE. The other hypothesis is that elevated CO_2 concentration will promote the soil phosphatase activity, increase the level of soil P supply, and finally leading to the increase in PUE.

(1) Enhanced aboveground biomass with elevated CO_2

We verified the first hypothesis based on the measurements from FACE and OTC experiments. Averaging the results from the FACE experiment, elevated CO_2 has significantly increased the aboveground biomass (AGB) at maturity (11.9 %, Fig. 4). The responses of AGB to elevated CO_2 also had significant difference between rice sub-species: the increase of AGB for Indica rice (16.5 %) was significantly higher than that for Japonica rice (7.7 %, Fig. 4). This finding was also observed for the pot experiment, which we observed that elevated CO_2 concentration significantly increased the AGB of rice at most of growing stages (Fig. S1c). In addition, at the maturity stage, the response of AGB to elevated CO_2 for Indica rice was also higher than that for Japonica rice (Fig. S1).

We further investigated the response of net photosynthetic rate (An) to elevated CO_2, since An is the key parameter affecting the aboveground dry matter accumulation. Elevated CO_2 concentration generally significantly enhanced the An of rice at the leaf level throughout the growth period (Fig. 5). However, the response of An to elevated CO_2 also

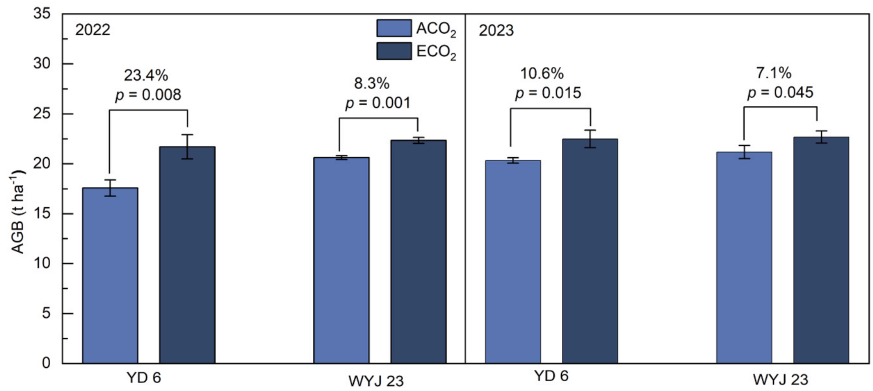

Fig. 4. Response of AGB to elevated CO_2 based on FACE experiment. Bars and error-bars represent the mean values and their standard errors respectively. The relative differences in AGB (with a unit of %) between ACO_2 and ECO_2 were calculated and marked atop of the bars. YD6, Yangdao6 (Indica rice); WYJ23, Wuyunjing23 (Japonica rice). ACO_2 and ECO_2 indicates ambient CO_2 treatment and elevated CO_2 treatment respectively. The significance of the difference in AGB was calculated using the two-sample *t*-test.

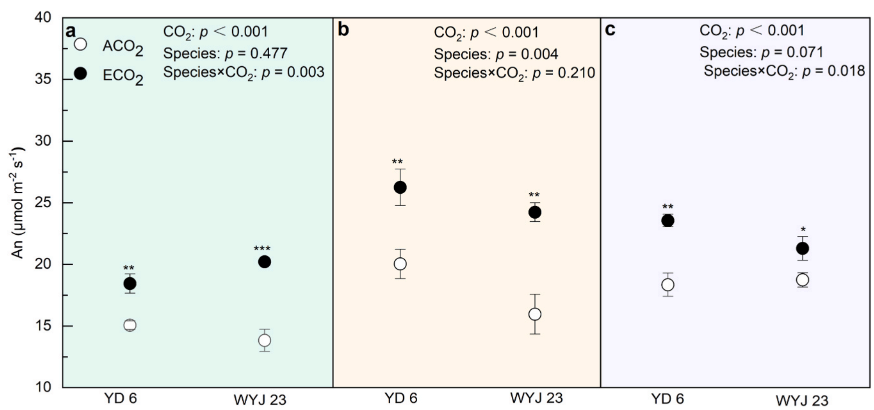

Fig. 5. Response of An to elevated CO_2 at Jointing stage (a), heading stage (b) and flowering stage (c) based on OTC experiment. Error-bars represent the standard errors. YD6, Yangdao6 (Indica rice); WYJ23, Wuyunjing23 (Japonica rice). ACO_2 and ECO_2 indicates ambient CO_2 treatment and elevated CO_2 treatment respectively. The significance of the CO_2 and rice sub-species impacts on AGB were assessed using the two-way analysis of variance (ANOVA) test.

has significantly divergences between Japonica rice and Indica rice for the heading and maturity stages (Fig. 5), possibly explaining the different responses of AGB to elevated CO_2 between Japonica rice and Indica rice (Fig. 5).

(2) Accelerated soil P activity with elevated CO_2

We next verified the second hypothesis related to soil P activity. There are many forms of P in soil, of which available P can be directly absorbed and utilized by rice. According to the results from our pot

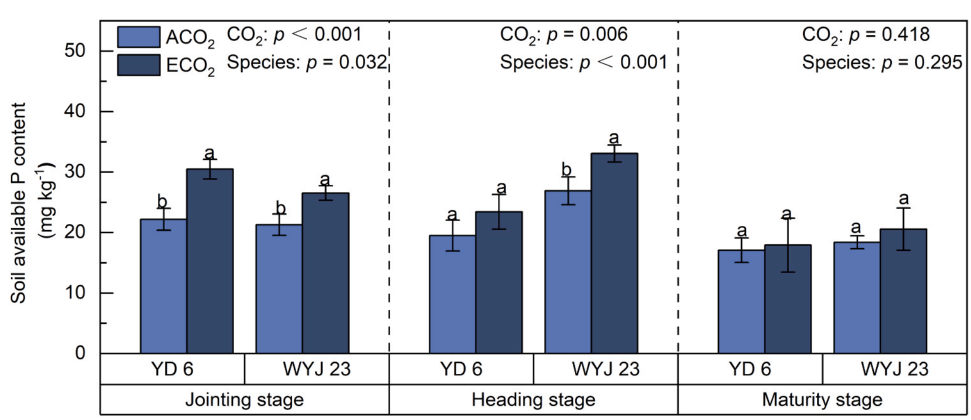

Fig. 6. Response of soil available P content to elevated CO_2 and rice sub-species at Jointing stage, Heading stage and Maturity stage, based on OTC platform. Bars and error-bars represent the mean values and their standard errors respectively. YD6, Yangdao6 (Indica rice); WYJ23, Wuyunjing23 (Japonica rice). ACO_2 and ECO_2 indicates ambient CO_2 treatment and elevated CO_2 treatment respectively. The significance of the CO_2 and rice sub-species impacts on soil available P content were assessed using the two-way analysis of variance (ANOVA) test. Different lowercase letters indicate a significant different soil available P content between ACO_2 and ECO_2 at the $p < 0.05$ levels.

experiment, elevated CO_2 concentration could increase the soil available P content during the whole growth period, but the increased magnitude was the largest at the jointing stage. In addition, the response of soil available P content to elevated CO_2 was also different for different rice sub-species, i.e., the response for Japonica rice was stronger than that for Indica rice throughout the growing seasons (Fig. 6).

To investigate why elevated CO_2 increased the soil available P content, we also estimated the key parameter of soil P transformation, i.e., soil neutral phosphatase activity. Base on the results from the pot experiment, we found that elevated CO_2 generally significantly increased soil neutral phosphatase for all of the growing stages (Fig. 7). Besides, the response of soil neutral phosphatase activity to elevated CO_2 generally was larger for Japonica rice compared to that for Indica rice (Fig. 7).

3.3. *Joint control of improved biomass and soil P activity on the enhanced PUE*

Finally, based on the above analysis, we investigated the drivers accounting for the enhanced PUE under elevated CO_2 using the structural equation modeling (SEM) analysis. Results showed that elevated CO_2 concentration could directly and indirectly affect the PUE of rice by changing the photosynthetic rate, the supply of P in soil and the absorption of P by rice. On one hand, elevated CO_2 had a positive effect on rice photosynthetic rate and AGB, and thus led to the enhanced P need and accumulation, which finally resulted in the enhanced PUE (Fig. 8a). On the other hand, elevated CO_2 could stimulate the soil neutral phosphatase activity, enhanced the soil available P concentration, and thus finally led to the increased aboveground P uptake and PUE of rice (Fig. 8a). Moreover, when comparing these two possible mechanisms accounting for the enhanced PUE, the effect from increased AGB was larger than that from the enhanced soil neutral phosphatase activity (Fig. 8b).

4. Discussion

The absorption capacity of P is an important factor affecting crop growth and yield formation, and the PUE is an important indicator of fertilizer absorption and utilization. Based on field FACE and OTC experiments, and the results from meta-analysis, this study found that elevated CO_2 could significantly increase the PUE of rice. The PUE of rice is directly affected by the accumulation of P in the aboveground part of rice plant (Fig. S3). These results are partly consistent with several previous studies, of which showed that elevated CO_2 had increased the P uptake in the aboveground part of plant (Owensby et al., 1993), while some other studies showed there were generally no effect (LI and KANG, 2002). Similarly, for the natural ecosystems, vegetation generally will adapt to the low concentration of P in the soils by increasing root clusters(Hodge, 2004; Haling et al., 2013), developing mycorrhizal associations(Shen et al., 2011; Brown et al., 2013), and changing the rhizosphere environment(Zhang et al., 2010; Richardson and Simpson, 2011), in order to meet the demand for P under elevated CO_2 situations, thereby increasing the absorption of P. However, the deficiency of P from soils will reduce the response of plants to elevated CO_2, reduce P absorption, and weaken the enhance of PUE by elevated CO_2(Körner, 2006; Jin et al., 2015). In summary, elevated CO_2 can improve the PUE, whether in natural ecosystems or agricultural systems, but P limitation will reduce the enhance in PUE by elevated CO_2. In addition, we found elevated CO_2 generally can promote the soil P uptake, and this effect in the early growth stage was larger than that in the late growth stage (Fig. S3), consistent with the results of a previous study (Yang et al., 2005). The underlying reason might be that the elevated CO_2 can induce great changes in the roots of rice at the early growth stage (Fig. S4).

The aboveground phosphorus accumulation of plants is determined by the aboveground biomass and the phosphorus concentration of each part. The mechanism of elevated CO_2 to increase the aboveground phosphorus accumulation of plants was different, some crops (such as mung bean) increased biomass, but the phosphorus concentration did not change significantly(Li et al., 2015); other crops(such as rice) showed a simultaneous increase in biomass and phosphorus concentration(Yang et al., 2007). The biomass production of rice is determined by the balance between net photosynthetic rate and respiration (Sakai et al., 2001). Previous studies have shown that elevated CO_2 increases biomass by promoting photosynthesis (Long et al., 2004), this is consistent with our findings (Fig. 4 & S2). Our results confirm the previous findings that the biomass of different rice varieties respond differently to elevated CO_2 (Tao and Wang, 2021). In the early growth stage, the response of aboveground biomass of Wuyunjing 23 to the elevated CO_2 was higher than that of Yangdao 6, and the response of Wuyunjing 23 to the elevated CO_{22} was lower than that of Yangdao 6 in the late growth stage, the reason is that photosynthetic adaptation appeared in the late stage of Wuyunjing 23 (Fig. 5). The increase of soil available P content can increase the P concentration of rice. The reason may be that the increase of soil available P can increase the carbon fixation of rice. P is the main component of protein and nucleic acid, and under elevated CO_2, crops need more P to support their higher protein turnover and metabolic rate, and to increase Rubisco activation, RuBP regeneration and total energy demand(Pandey et al., 2015a, 2015b).

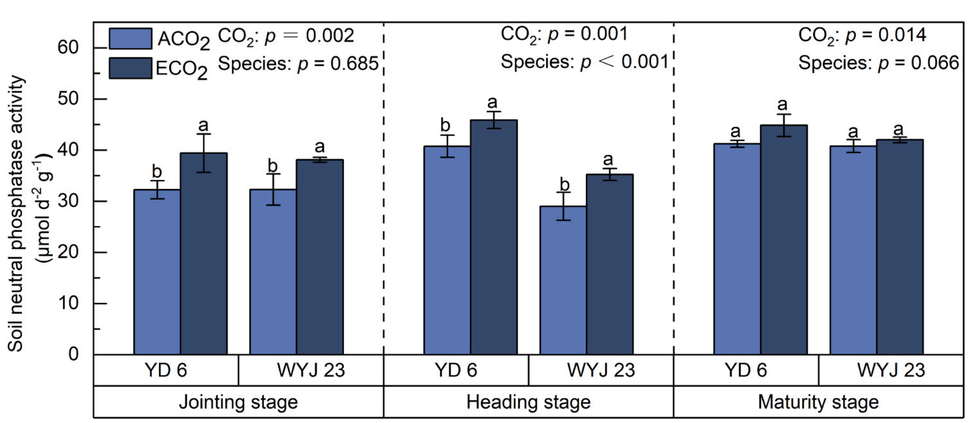

Fig. 7. Response of soil neutral phosphatase activity to elevated CO_2 and rice sub-species at Jointing stage, Heading stage and Maturity stage, based on OTC platform. Bars and error-bars represent the mean values and their standard errors respectively. YD6, Yangdao6 (Indica rice); WYJ23, Wuyunjing23 (Japonica rice). ACO_2 and ECO_2 indicates ambient CO_2 treatment and elevated CO_2 treatment respectively. The significance of the CO_2 and rice sub-species impacts on soil neutral phosphatase activity were assessed using the two-way analysis of variance (ANOVA) test. Different lowercase letters indicate a significant different soil neutral phosphatase activity between ACO_2 and ECO_2 at the $p < 0.05$ levels.

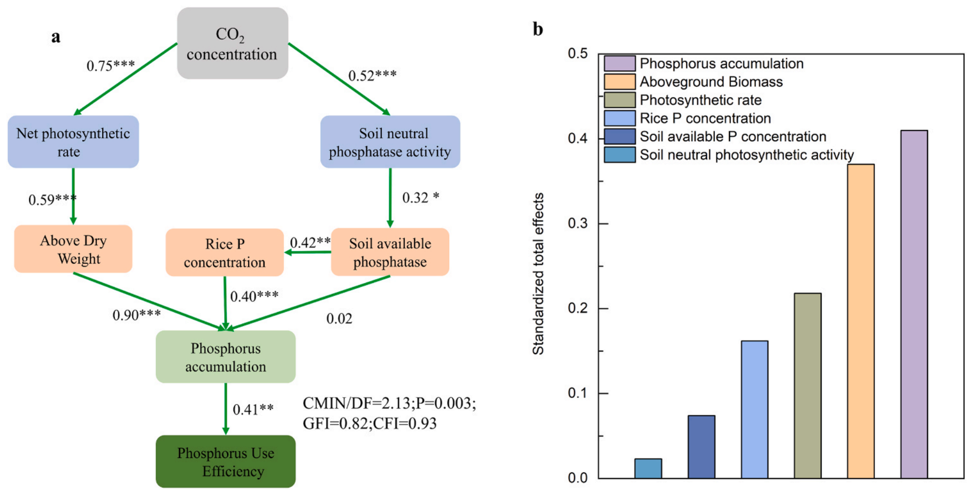

Fig. 8. Possible drivers accounting for the enhanced PUE under elevated CO_2. a, Direct and indirect effects of elevated CO_2 on PUE of rice based on SEM. The green arrow indicates a significant positive effect ($p < 0.05$), whereas dashed arrow indicates nonsignificant relationship. Values adjacent to arrows represent the standardized path coefficients. *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$. **b,** Standardized total effect of each individual driving factor on the PUE of rice.

The effect of elevated CO_2 on plant P uptake may be the combined effect of plant P absorption capacity, plant phenology and soil P availability (Yang et al., 2007). The P necessary for plant growth primarily originated from soils, where it exists in numerous forms and undergoes complex transformations (Hou et al., 2016). In general, soil P can be broadly classified into two categories: inorganic P and organic P. The transformation of P in soil is influenced by many factors, including geochemical processes, biological effects, human activities, and climate change (Yang et al., 2019). From the results in this study, elevated CO_2 has promoted the shoot P uptake and soil available P content (Fig. 7), indicating that elevated CO_2 promoted soil P mineralization. Consistently to our findings, previous studies have reported that elevated atmospheric CO_2 concentration would significantly increase the available P content for a rice-wheat rotation system (Ma et al., 2007) (Zhang et al., 2014). Likewise, based on OTC experiment, a previous study has also suggested that an increase of 100 ppm in atmospheric CO_2 concentration would lead to an enhancement in the available P content in rice soils (Satapathy et al., 2015). In addition, under elevated CO_2, crops allocate more photosynthetic carbon to the underground part, promote root growth, and increase crop P uptake (O Sullivan et al., 2020).

Soil phosphatase activity was significantly positively correlated with soil available P content (Zhan et al., 2015). The change of soil enzyme activity will affect the release process of P, and then affect the available P pool in soil. Phosphatase plays a vital important role in the process of soil organic P activation. Phosphatase can convert the organic P to inorganic P, and then can be utilized by plants as available P nutrients. Previous studies have shown that elevated CO_2 can promote the mineralization of organic P in soil by increasing the content of organic acids in crop root exudates and the phosphatase activity secreted by soil (Jin et al., 2014; Souza et al., 2017). Besides, the soil phosphatase activity in 0–10 cm soil layer was significantly increased by elevated CO_2 concentration (Chen et al., 2002). The increase of soil phosphatase activity is thus closely related to the increase of CO_2, which can promote the growth and development of plant roots. Elevated CO_2 also can promote the root growth and metabolism, increase phosphatase secretion and accelerate soil organic P mineralization by increasing root carbon content (Dhillion et al., 1995; Khan et al., 2008). These evidence from previous studies well supported our finding in this study, i.e., elevated CO_2 promoted the increase of soil phosphatase activity and soil available P content. Besides, the positive effect of CO_2 on soil phosphatase activity is more pronounced in the early growing stage, consistent to the observation of a significant increase in soil available P in the early growth stage (Fig. 7). On the contrary, in the late growing stage, the effect of elevated CO_2 on root exudates may be reduced due to root senescence (Fig. S4).

In summary, the mechanism underlying the improved the PUE under elevated CO_2 conditions for rice includes two aspects. On one hand, elevated CO_2 increased photosynthesis and aboveground dry matter accumulation (Ainsworth and Long, 2005).On the other hand, under elevated CO_2, crops allocated more photosynthetic carbon to roots, promoted root growth (Cotrufo and Gorissen, 1997), changing the root environment, and increased soil available P content(Wang et al., 2025). Then the enhancement of root system possibly promoted P activity, which in turn increased soil p activation (Wang et al., 2023; Rocabruna et al., 2024). At the same time, the increase of roots improved the ability of crops to obtain P from soil (Yang et al., 2008; Tao et al., 2024).

5. Conclusions

To conclude, based on two-years of FACE experiment, OTC experiment and meta-analysis, we found that elevated CO_2 can significantly improve the PUE in rice. The positive effect of elevated CO_2 on rice PUE had clear divergences between different rice sub-species, with a higher magnitude for Japonica rice than that of Indica rice. The enhanced aboveground biomass through increased photosynthetic rate, and the enhanced soil available P content through the increased soil phosphatase activity possibly jointly contributed to the enhanced PUE of rice under elevated CO_2 conditions, of which the contribution from the former seems to be larger than that from the later. These findings suggest that elevated CO_2 will promote the absorption of P by rice and accelerate the P cycle in cropland soils. Our results also are beneficial for forming management strategies to balance the contradiction between increasing demand for food and limited P fertilizer resources in the context of climate change.

CRediT authorship contribution statement

Rui Ren: Investigation. **Zihua Shi:** Investigation. **Yanfeng Ding:** Supervision. **Yu Jiang:** Supervision. **wang songhan:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Funding acquisition, Formal analysis, Data curation. **Ting Xiao:** Investigation. **Haiwei Zhang:** Writing – original draft.

Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2025.109827.

Data availability

Data will be made available on request.

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