Effects of Elevated CO2 on Diurnal Variation of Photosynthesis in Hybrid Rice: A FACE Study Postprint

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Abstract

Elevated atmospheric carbon dioxide (CO2) concentration causes global warming, but as a photosynthetic substrate, it promotes photosynthesis in green crops. To clarify the effects of elevated CO2 concentration on the diurnal variation of photosynthesis in hybrid rice during the grain filling stage, in 2014, a paddy field FACE (Free Air CO2 Enrichment) platform was utilized with two new hybrid rice combinations that had previously set high-yield records in production, Yongyou 2640 and Y Liangyou 2, as test materials. Two levels were established: ambient CO2 and elevated CO2 concentration (increased by 200 mol/mol), and the diurnal variation of photosynthesis at the heading stage and mid-grain filling stage, as well as biomass at maturity, were measured. The results showed that under elevated CO2 concentration, the leaf net photosynthetic rate of both combinations at the heading stage increased significantly (52% average increase over the whole day), but the average increase was halved at the mid-grain filling stage, with this photosynthetic down-regulation being more pronounced in Y Liangyou 2. Elevated atmospheric CO2 concentration caused a substantial decrease in leaf stomatal conductance of both hybrid rice combinations at the heading and mid-grain filling stages, leading to decreased transpiration rate and substantially increased water use efficiency. The response of stomatal conductance and transpiration rate to CO2 in Y Liangyou 2 was greater in the morning than in the afternoon, while Yongyou 2640 showed the opposite pattern. Although elevated atmospheric CO2 concentration significantly increased intercellular CO2 concentration at different times during the grain filling stage of hybrid rice, it mostly had no significant effect on stomatal limitation value, particularly the ratio of intercellular to ambient CO2 concentration, with consistent trends between the two varieties. Elevated atmospheric CO2 concentration had a significantly greater effect on aboveground biomass and its components in Yongyou 2640 than in Y Liangyou 2, and there were

mostly interaction effects between CO2 and variety. These results indicate that compared with Yongyou 2640, Y Liangyou 2 benefited less from the elevated CO2 concentration environment in terms of final productivity, which may be related to obvious photosynthetic acclimation in this variety during the late growth stage, but this photosynthetic acclimation does not appear to be caused by stomatal limitation.

Full Text

Preamble

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Effect of Increasing Atmospheric CO_2 Concentration on Photosynthetic Diurnal Variation Characteristics of Hybrid Rice: A FACE Study

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Abstract

Rising atmospheric carbon dioxide (CO_2) concentration has been implicated in global warming, yet as the primary substrate for photosynthesis, it also enhances photosynthetic activity in green plants. To clarify the effects of elevated CO_2 on diurnal photosynthetic variation in hybrid rice during grain filling, a paddy field experiment was conducted in 2014 using Free Air CO_2 Enrichment (FACE) technology with two high-yielding hybrid combinations: Yongyou 2640 (YY2640) and YLiangyou No.2 (YLY2). Plants were grown from transplanting to grain maturity under ambient CO_2 and elevated CO_2 (200 mol/mol above ambient). Elevated CO_2 significantly increased flag leaf net photosynthetic rate (P) at heading by an average of 52% for both combinations, but this enhancement was halved at mid-grain filling. This photosynthetic acclimation was more pronounced in YLY2. Stomatal conductance (G) decreased substantially at both growth stages under elevated CO_2, leading to reduced transpiration rate and significantly increased water use efficiency. The CO_2 response of G and transpiration was greater in the morning for YLY2, while YY2640 showed stronger responses in the afternoon. Elevated CO_2 markedly increased intercellular CO_2 concentration (C) at all times, but had no significant effect on the ratio of intercellular to ambient CO_2 concentration or stomatal limitation value, with both varieties showing similar trends. Significant CO_2 × variety interactions were observed for aboveground biomass and its components, with greater responses in YY2640 than YLY2. These results indicate that compared with YY2640, the lower CO_2 gain in final productivity of YLY2 may result from photosynthetic acclimation at late growth stages, and this down-regulation of leaf photosynthesis was not caused by stomatal limitation.

Keywords: hybrid rice; FACE (Free Air CO_2 Enrichment); carbon dioxide (CO_2); photosynthetic; diurnal variation; adaptation

Introduction

Atmospheric carbon dioxide (CO_2) concentration has been increasing continuously and at an accelerating rate, representing one of the most prominent and certain phenomena of global climate change [1]. Since the pre-industrial era (280 mol/mol), atmospheric CO_2 has now exceeded 400 mol/mol and is projected to reach 470-570 mol/mol by 2100 [2-3]. Despite various mitigation measures, CO_2 enrichment remains one of the few global change factors with positive effects on crop productivity [4-5]. As the substrate for photosynthesis, elevated CO_2 can enhance photosynthesis in C_3 crops. Rice, which feeds half of the world' s population, is the third most important crop globally and the most valuable in many regions. Since its large-scale promotion in the 1970s, hybrid rice has played an irreplaceable role in ensuring China' s food security. Studies have shown that hybrid rice growth and yield respond more strongly to elevated CO_2 than conventional rice [6-8], offering promising prospects for future rice production. However, the universality of this high responsiveness and its underlying mechanisms remain unclear, as research has been limited and often focused on single varieties [9-12].

Photosynthesis is a key biochemical process highly sensitive to environmental factors, and its response and acclimation to elevated CO_2 largely determine final yield potential. While numerous studies have reported effects of elevated CO_2 on conventional rice photosynthesis [7,13-14], few parameters have been examined in hybrid rice. To our knowledge, no studies have investigated diurnal photosynthetic responses of hybrid rice under elevated CO_2. Although short-term CO_2 enrichment enhances rice photosynthesis, long-term exposure can lead to photosynthetic acclimation or down-regulation [7,13]. Whether such acclimation occurs in hybrid rice during late field growth stages and whether varietal differences exist are important questions for improving predictive modeling and developing adaptation strategies for future rice production.

Unlike chamber studies, FACE (Free Air CO_2 Enrichment) technology enables research under standard crop management practices with natural air flow in open fields, providing realistic simulation of future crop environments [17]. Since its first application in rice ecosystems by Japanese scientists in 1998 [19], FACE technology has been widely adopted in climate change research [4,17-18]. China established its rice FACE platform in 2001 through international cooperation [20], which has operated continuously and yielded important advances [6,7]. This study utilized this open-field system to simulate mid-century atmospheric CO_2 levels, investigating effects on photosynthetic diurnal variation and biomass accumulation in high-yielding hybrid rice to provide new theoretical insights for maximizing hybrid rice productivity in future CO_2-enriched environments.

1. Experimental Site and Platform

The experiment was conducted in 2014 at the China Rice FACE platform located in the Liangzhongchang Experimental Field, Xiaji Town, Yangzhou City, Jiangsu Province (119°42 0 E, 32°35 5 N). The region has a subtropical monsoon climate with mean annual temperature of 14.9°C, annual precipitation of 1100 mm, annual evaporation exceeding 980 mm, frost-free period of 220 days, and annual sunshine duration >2100 hours. The soil is classified as Qingnitu (hydromorphic paddy soil) with the following properties: organic matter 18.4 g/kg, total nitrogen 1.45 g/kg, total phosphorus 0.63 g/kg, total potassium 14.0 g/kg, available nitrogen 70.5 mg/kg, available phosphorus 10.1 mg/kg, available potassium 110 mg/kg, pH 7.2, sand content (2–0.02 mm) 578.4 g/kg, silt content (0.02–0.002 mm) 285.1 g/kg, and clay content (<0.002 mm) 136.5 g/kg. The cropping system is single-season rice with winter fallow.

The FACE system consisted of octagonal rings 12 m in diameter with >90 m spacing between rings to prevent CO_2 cross-contamination. During operation, pure CO_2 was injected through peripheral pipes toward the ring center. A computer network monitored and regulated CO_2 concentration and canopy temperature, automatically adjusting CO_2 release speed and direction based on ambient CO_2 levels at canopy height. During key growth stages, CO_2 concentration in FACE rings was maintained at 200 mol/mol above ambient from sunrise to sunset. Throughout the experiment, the control rings averaged (371.9$±2.0)μmol/mol, whileFACEringsaveraged(571.9±0.3)μmol/mol, representinga(199.2±$1.9) mol/mol increase. Temperature and photosynthetic photon flux density (PPFD) during the rice growth period are shown in [Figure 1: see original paper].

2. Experimental Design and Materials

A split-plot design was employed with CO_2 treatment as the main plot (ambient vs. elevated at 200 mol/mol above ambient) and hybrid variety as the subplot. Two newly developed high-yielding combinations were tested: Yongyou 2640 (YY2640), an indica-japonica hybrid designated as a super rice variety by the Ministry of Agriculture in 2013, and YLiangyou No.2 (YLY2), an indica hybrid. Seeds were sown on May 28 and transplanted on June 23 at a density of three seedlings per hill with 20 cm × 20 cm spacing. Total nitrogen application was

22.5 g/m^2 using compound fertilizer ($N:P_2O_5:K_2O$ = 15:15:15). Basal fertilizer accounted for 40% (applied on June 22), tillering fertilizer 30% (July 5), and panicle fertilizer 30% (August 13). A 3 cm water layer was maintained until 7 days before harvest, with multiple light drying periods during tillering. Other management practices followed high-yielding field standards.

3. Measurements and Methods

Photosynthetic Parameters: At heading, uniform plants were marked for measurements conducted at heading and 24 days after heading. Using a LI-6400xt portable photosynthesis system (LI-COR, USA) with a red-blue light source, net photosynthetic rate (P), stomatal conductance (G), transpiration rate (T), intercellular CO_2 concentration (C), and the ratio of intercellular to ambient CO_2 concentration were measured on flag leaves between 9:30–17:30 at 2-hour intervals. Light quantum flux was set at 1200 mol m^{-2} s^{-1}, with leaf chamber CO_2 concentration set at 380 mol/mol for ambient and 580 mol/mol for elevated CO_2 treatments. Measurements were taken on the upper surface of the middle-upper portion of flag leaves, with three plants measured per plot and values averaged.

Biomass: At maturity (when plants reached yellow ripeness), representative plants were sampled from each plot based on average tiller numbers from field surveys. Plants were separated into leaves, stem-sheaths, and panicles, oven-dried at 105°C for 30 minutes, then at 70°C to constant weight, and weighed (g/m^2). Care was taken to protect fragile organs during sampling.

4. Statistical Analysis

All data were processed using Excel 2013 and analyzed with SPSS 22.0 using General Linear Model procedures. Significance levels were set at $P \leq 0.01$, ≤ 0.05, ≤ 0.1, and > 0.1, denoted by **, *, +, and ns respectively. Duncan' s method was used for multiple comparisons, following previously reported protocols [22].

2. Results and Analysis

2.1 Effects of CO_2 Concentration on Net Photosynthetic Rate

Both control and elevated CO_2 treatments showed single-peak diurnal P curves, with maximum values at 13:30. Elevated CO_2 significantly increased P at all measurement times during both growth stages. At heading, P increased by an average of 52% across both varieties, but this enhancement was reduced by half at mid-grain filling. This photosynthetic acclimation was more pronounced in YLY2. Variety comparisons revealed that YY2640 showed greater P responsiveness than YLY2 at heading, though this difference diminished at mid-grain filling. The CO_2 × variety interaction was significant at both stages ($P < 0.01$) [FIGURE:2, TABLE:1].

2.2 Effects of CO_2 Concentration on Stomatal Conductance

Stomatal conductance (G) showed single-peak diurnal patterns similar to P . Elevated CO_2 significantly reduced G at all measurement times during both stages, with greater reductions at mid-grain filling than at heading. The two varieties exhibited contrasting response patterns, particularly at 24 days after heading, where YLY2 showed significantly greater morning responses than YY2640. The CO_2 × variety interaction was significant for G at multiple time points [FIGURE:3, TABLE:1].

2.3 Effects of CO_2 Concentration on Transpiration Rate

Transpiration rate (T) also displayed single-peak diurnal curves peaking at 11:00–13:30. Elevated CO_2 reduced T at most measurement times in both stages, though reductions were smaller than for G . Variety differences in response timing were evident, with YLY2 showing smaller morning responses but larger afternoon responses compared to YY2640. Average daily T decreased by 8–16% at heading and 9–14% at mid-grain filling. The CO_2 × variety interaction was significant at 24 days after heading [FIGURE:4, TABLE:1].

2.4 Effects of CO_2 Concentration on Water Use Efficiency

Water use efficiency (WUE = P /T) showed no consistent diurnal patterns. Elevated CO_2 significantly increased WUE at all times during both stages, with greater enhancements at heading (86% average increase) than at mid-grain filling (49%). Variety differences were minimal, though YLY2 tended to show slightly greater responses. The CO_2 × variety interaction was significant at multiple time points [FIGURE:5, TABLE:1].

2.5 Effects of CO_2 Concentration on Intercellular CO_2 Concentration

Elevated CO_2 significantly increased intercellular CO_2 concentration (C) at all measurement times during both stages, with average increases of 43% at heading and 50% at mid-grain filling ($P < 0.01$). No significant differences were observed between varieties, and the CO_2 × variety interaction was not significant [FIGURE:6, TABLE:1].

2.6 Effects of CO_2 Concentration on Ci/Ca Ratio and Stomatal Limitation

The ratio of intercellular to ambient CO_2 concentration (C /C) and stomatal limitation value (L = 1 - C /C) showed minimal variation across measurement times. Elevated CO_2 had no significant effect on C /C ratio or L at most time points, with consistent trends between varieties. The CO_2 × variety interaction was not significant for either parameter .

2.7 Effects of CO_2 Concentration on Biomass at Maturity

Elevated CO_2 significantly increased aboveground biomass at maturity by an average of 12.6% across both varieties. However, significant CO_2 × variety interactions were observed ($P < 0.01$). YY2640 showed a 24.9% increase in total aboveground biomass ($P < 0.01$), while YLY2 increased by only 9.0% ($P = 0.15$). Stem-sheath and panicle biomass increased significantly in YY2640 (16–29% increases, $P < 0.05$ to $P < 0.01$), whereas YLY2 showed only slight, non-significant increases. Leaf dry weight tended to decrease slightly under elevated CO_2 [Figure 7: see original paper].

3. Conclusion and Discussion

Breeding varieties with strong CO_2 responsiveness but low yield potential has limited practical value. Therefore, understanding whether currently cultivated high-yielding varieties maintain high responsiveness is crucial. This study selected super high-yielding hybrid rice YY2640 and YLY2, conducting the first investigation of diurnal photosynthetic responses in hybrid rice using FACE technology. Maturity measurements showed that control-grown YY2640 achieved panicle dry weights of 770–855 g/m^2, substantially exceeding average rice yields in Jiangsu Province [23] and national averages [24–25].

Photosynthetic acclimation under long-term elevated CO_2 has been widely reported [7,13–14]. In this study, while elevated CO_2 increased flag leaf P by 52% at heading, this enhancement was halved at mid-grain filling, indicating clear photosynthetic down-regulation. This acclimation was more pronounced in YLY2. At heading, both varieties showed similar absolute and relative P responses, but significant differences emerged at mid-grain filling, with YY2640 maintaining stronger responsiveness. This difference may relate to variation in spikelet number responses; a companion study on the same platform found that elevated CO_2 increased total spikelet number by 17.3% in YY2640 ($P < 0.01$) but only 7.7% in YLY2 ($P = 0.06$). Greater sink capacity increases demand for photosynthates, potentially alleviating feedback inhibition of photosynthesis [16,18], which may explain YY2640’ s sustained responsiveness.

Stomatal responses to elevated CO_2 are well documented, with plants reducing G to adapt to high CO_2 environments [15]. Under well-watered and nitrogen-sufficient conditions, rice G typically decreases by about 20% under elevated CO_2 [26]. This study observed larger reductions: average G decreased by 36% and 37% at heading and mid-grain filling, respectively. YLY2 exhibited more pronounced responses, particularly in the morning, while YY2640 showed stronger afternoon responses. This diurnal variation in G responsiveness contributed to significant CO_2 × variety interactions and highlights the importance of consistent measurement timing in photosynthesis studies.

The photosynthetic down-regulation observed in YLY2 was likely not caused by stomatal limitation. Although G was significantly reduced, intercellular CO_2 concentrations increased substantially, and stomatal limitation values remained unchanged. The lack of significant CO_2 × variety interactions for C and L further indicates that stomatal limitation was not the primary determinant of photosynthetic acclimation in these hybrids. Non-stomatal factors, such as reduced enzyme activity and photosynthetic component content, may be responsible. Measurements of leaf nitrogen concentration revealed that YLY2 showed significant declines at both heading (11% decrease) and mid-grain filling (14% decrease) under elevated CO_2, whereas YY2640 showed only slight, non-significant decreases. Reduced nitrogen levels can diminish the activity and concentration of photosynthetic enzymes like Rubisco, which is considered a primary cause of photosynthetic down-regulation under elevated CO_2 [27–29].

Elevated CO_2 effects on water relations were evident through increased WUE. Despite higher canopy temperatures (data not shown), reduced G increased stomatal resistance, lowering transpiration intensity per leaf area [4]. This study showed T decreased by 8–16% while WUE increased by 49–86%, with consistent trends across varieties and growth stages. These results demonstrate that elevated CO_2 significantly enhances drought resistance in hybrid rice.

CO_2 effects on final productivity showed clear genotypic differences, with significant CO_2 × variety interactions for aboveground biomass. YY2640 exhibited greater responsiveness than YLY2, consistent with its weaker photosynthetic acclimation. The differential responses among biomass components (leaf, stem-sheath, panicle) suggest that varietal differences in CO_2 responsiveness may stem from non-stomatal factors related to photosynthetic biochemistry rather than stomatal limitations. The underlying biological mechanisms and regulatory pathways require further investigation.

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