Effects of Elevated CO2 Concentration and Leaf Clipping and Spikelet Thinning on Yield Formation in Rice 'Y Liangyou 2' Postprint

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Abstract

Using a paddy field FACE (Free Air CO2 Enrichment) platform, with the super rice hybrid 'Y Liangyou 2' that holds the world record for high yield as experimental material, CO2 treatments were set at two levels: ambient CO2 concentration [(382.5$±$2.0) mol · mol 1] and elevated CO2 concentration (increased by 200 mol · mol 1). At the full heading stage, source-sink manipulations were established as control, flag leaf removal (removing 1 leaf), removal of all functional leaves (removing 3 leaves), and alternate removal of primary branches (spikelet thinning), to investigate the effects of elevated CO2 concentration on rice yield and its components under open-field conditions with different source-sink treatments. The results showed that for rice without leaf removal or spikelet thinning treatment (i.e., the control), elevated CO2 concentration increased the grain yield of 'Y Liangyou 2' by an average of 12%, which was mainly associated with slight increases in both spikelets per panicle and seed-setting ability. Elevated CO2 concentration increased the yield of rice under the remove-1-leaf and remove-3-leaves treatments by 26% and 57%, respectively, which was mainly associated with substantial increases in both filled grain percentage and average grain weight of all grains. For rice subjected to spikelet thinning treatment at the full heading stage, the yield increase caused by elevated CO2 concentration was similar to that of the control rice. Compared with the control, the remove-1-leaf and remove-3-leaves treatments at the full heading stage reduced rice grain yield by 17% and 52%, respectively, both reaching highly significant levels, which was mainly associated with significant decreases in both filled grain percentage and average grain weight of all grains; although spikelet thinning treatment at the full heading stage significantly increased rice seed-setting ability, the yield decreased substantially (29%) due to halved spikelets per panicle. The response of final grain yield to elevated CO2 concentration was significantly positively correlated with the responses of filled grain percentage and average grain weight of all grains. These results indicate that artificial alteration of the source-sink ratio at the rice full heading stage (particularly leaf removal) can modify the responses of grain filling ability and final yield to elevated CO2 concentration.

Full Text

Effect of Elevated CO_2 Concentration and Source-Sink Manipulation at Heading on Grain Yield Formation in Rice 'Y Liangyou 2'

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Abstract

Using a Free Air CO_2 Enrichment (FACE) platform in paddy fields, we investigated how elevated CO_2 affects rice yield and its components under different source-sink manipulations in the super hybrid rice combination 'Y Liangyou 2' , which holds the world record for high yield. Two CO_2 concentrations were established: ambient $[(382.5\$\pm2.0)\mu mol \cdot mol^{\{-1\}]andelevated(ambient+200\mu mol\cdot mol}\{-1\}).Attheheadingstage,foursource-sinktreatmentswereimposed:control(nomanipulation),flagleafremoval(LC1),removalofallfunctionallea$ increased grain yield by 12% in 'Y Liangyou 2' , primarily due to slight increases in both spikelet number per panicle and grain filling capacity. For LC1 and LC3 treatments, elevated CO_2 enhanced yields by 26% and 57%, respectively, which was mainly attributed to substantial increases in filled grain percentage and average grain weight across all grains. In spikelet-thinned plants, the yield increase under elevated CO_2 was similar to that observed in control plants. Compared with the control, leaf removal at heading reduced grain yield by 17% (LC1) and 52% (LC3), both highly significant, primarily due to significant declines in filled grain percentage and average grain weight. Although spikelet thinning significantly improved grain filling capacity, yield decreased dramatically (-29%) because total spikelet number was halved. The response of final grain yield to elevated CO_2 showed significant positive correlations with the responses of filled grain percentage and average grain weight. These findings indicate that artificial alteration of source-sink ratios at heading, particularly through leaf removal, can modify the response of grain filling capacity and final yield to elevated CO_2 concentration.

Keywords: Rice; Free Air CO_2 Enrichment (FACE); Sink-source manipulation; Leaf cutting; Spikelet thinning; Grain yield; Yield components

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Introduction

The continuous increase in atmospheric carbon dioxide (CO_2) concentration represents one of the most prominent phenomena of global climate change. Atmospheric CO_2 has risen from 280 mol · mol^{-1} in pre-industrial times to the current level of 400 mol · mol^{-1}, with the rate of increase accelerating. Projections indicate that concentrations will reach at least 550 mol · mol^{-1} by 2050 and could rise as high as 936 mol · mol^{-1} by the end of this century. Elevated atmospheric CO_2 directly and indirectly affects metabolic processes in major food crops, altering crop productivity and consequently impacting food security.

Rice (*Oryza sativa*) is one of the world’ s most important crops, serving as the staple food for over half of the global population. With continuous population growth and decreasing arable land, demand for rice will continue to increase in coming decades. Therefore, quantitatively assessing the impacts of elevated atmospheric CO_2 on rice is crucial for ensuring long-term global food security. Due to its importance, research on CO_2 and rice began 40 years ago using various fumigation systems, including greenhouses, Soil-Plant-Atmosphere Research (SPAR) units, Temperature Gradient Chambers (TGCs), Open-Top Chambers (OTCs), and later, Free Air CO_2 Enrichment (FACE) platforms in paddy fields. Extensive literature indicates that yield increases under elevated CO_2 vary widely, reaching up to 400%, and are significantly influenced by cultivar, cultivation practices, and environmental factors. In terms of yield components, CO_2-induced yield increases are typically associated with increases in panicle number per unit area, spikelet number per panicle, or both, while grain filling capacity usually shows minimal response.

Source-sink interactions play a crucial regulatory role in crop yield formation. Previous research has extensively investigated how source-sink manipulation affects rice yield, with general consensus that high-yielding rice populations are characterized by high sink-source ratios (grain-leaf ratio). However, few studies have analyzed the effects of elevated CO_2 on rice yield formation from a source-sink balance perspective. Recent large-scale FACE studies in paddy fields have shown that rice cultivars with greater yield responses to elevated CO_2 are typically those that maintain strong responsiveness during the mid-to-late growth stages, which is often closely related to larger sink capacity. Therefore, we hypothesized that altering the source-sink balance could change the response of a given cultivar’ s final yield to CO_2.

Developing high-yielding crop varieties that are also responsive to elevated CO_2

represents an essential adaptation strategy. China's super rice breeding program, initiated in 1966, has achieved remarkable progress, reaching its first through fourth phase targets for single-season rice yield (10.5–15.0 $t \cdot ha^{-1}$) in 2000, 2004, 2011, and 2014, respectively. This study selected the phase-3 super rice pioneer combination 'Y Liangyou 2' as experimental material. Using a large-scale paddy FACE platform to simulate mid-21st century atmospheric CO_2 concentrations, we investigated how leaf and spikelet manipulation at heading affects rice yield response under elevated CO_2, aiming to provide insights for adaptation strategies in rice production under future climate scenarios.

Materials and Methods

1.1 Experimental Platform The field experiment was conducted in 2014 at the China FACE research platform located in Jiangdu District, Yangzhou City, Jiangsu Province (119°42 0 E, 32°35 5 N). The experimental field soil is classified as Qingnitu (a type of paddy soil). The region has an average annual precipitation of approximately 980 mm, annual evaporation exceeding 1,100 mm, mean annual temperature of 14.9°C, annual sunshine hours exceeding 2,100 h, and an average frost-free period of 220 days. The cropping system is single-season rice followed by winter fallow. Soil physicochemical properties were: organic carbon 18.4 $g \cdot kg^{-1}$, total nitrogen 1.45 $g \cdot kg^{-1}$, total phosphorus 0.63 $g \cdot kg^{-1}$, total potassium 14.0 $g \cdot kg^{-1}$, available phosphorus 10.1 $mg \cdot kg^{-1}$, available potassium 70.5 $mg \cdot kg^{-1}$, sand particles (2–0.02 mm) 578.4 $g \cdot kg^{-1}$, silt particles (0.02–0.002 mm) 285.1 $g \cdot kg^{-1}$, clay particles (<0.002 mm) 136.5 $g \cdot kg^{-1}$, bulk density 1.16 $g \cdot cm^{-3}$, and pH 7.2.

The platform consisted of three FACE plots and three ambient control plots (Ambient). FACE plots were spaced >90 m apart from each other and from control plots to minimize CO_2 cross-contamination. Each FACE plot was designed as a regular octagon with a diameter of 12 m and area of 102 m^2. During operation, pure CO_2 gas was released through peripheral pipes toward the plot center. A computer network system monitored and controlled CO_2 concentration, automatically adjusting release rate and direction based on ambient CO_2 concentration, wind direction, wind speed, and CO_2 concentration at canopy height, maintaining CO_2 concentration 200 $mol \cdot mol^{-1}$ above ambient throughout the main growth stages. Control plots had no FACE pipes and remained under natural conditions.

1.2 Plant Material and Cultivation The super rice variety 'Y Liangyou 2', which set the world high-yield record in 2011, was used as experimental material. This two-line indica hybrid combination was developed by the Hunan Hybrid Rice Research Center, using 'Y58S' as the female parent and 'Yuanhui 2' as the male parent. Rice seedlings were raised in dry nursery beds, sown on May 20, and transplanted on June 21 at one seedling per hill with row spacing of 25 cm and hill spacing of 16.7 cm (24 hills per m^2). Total nitrogen application was 22.5 g $\cdot$ m^{-2}, with 40% applied as basal fertilizer (June 20), 30% as tillering fertilizer (June 28), and 30% as panicle fertilizer (July 25). Phosphorus and potassium were each applied at 9 g $\cdot$ m^{-2} as basal fertilizer (June 20). Water management consisted of: maintaining a water layer (~3 cm) from June 21 to July 20; multiple mild drying cycles from July 21 to August 10 (natural drainage followed by 3 days dry → 1 day flooded → 4 days dry → 1 day flooded, repeated); intermittent irrigation from August 11 to 10 days before harvest (3 days flooded, 2 days dry), followed by drainage until harvest. Pests, diseases, and weeds were controlled promptly to ensure normal rice growth and development.

1.3 Experimental Treatments A split-plot design was employed with CO$_2$ concentration as the main plot factor and source-sink manipulation as the subplot factor. CO$_2$ treatments consisted of ambient CO$_2$ concentration [Ambient, (382.5$±2.0)*μmol · mol*^{-1}]*andelevatedCO{2}$ concentration (FACE, Ambient + 200 mol · mol*$^{-1}$*). Source-sink treatments were imposed at heading stage (when 80% of plants had headed, September 6). Based on average tiller numbers from plot surveys, uniformly growing plants were selected and tagged for four treatments: (1) LC1: removal of the entire flag leaf; (2) LC3: removal of the top three functional leaves; (3) SR: removal of alternate primary panicle branches (spikelet removal); and (4) CK: control (no leaf or spikelet removal). Each treatment comprised 10 hills with three replications, with all other conditions held constant. CO*$_2$ *fumigation ran from June 28 to October 26, daily from sunrise to sunset. During the fumigation period, the average CO*$_2$ *concentration in control plots was (382.5$*±2.0)*μmol · mol*^{-1}*, whiletheactualaverageCO*{2}$ concentration in FACE plots was (581.9$±0.3)*μmol · mol*^{-1}$.

1.4 Measurements and Calculations At maturity (when 80% of plants reached full maturity, defined as >95% of grain husks turning yellow or >95% of spikelets and secondary glumes turning yellow), panicles from each treatment were harvested in the field, bagged, and the number of harvested hills and total panicles were recorded. Panicles were manually threshed and dried in mesh bags to constant weight. Filled and unfilled grains were separated using an FX-winnower (Hangzhou Huier Company) at an air flow rate of 1.2 m^3 $\cdot$ min^{-1} and air pressure of 400 Pa (approximately 100 g per winnowing, 90 s duration), followed by manual inspection and tactile separation of any remaining unfilled grains. Empty grains were separated similarly. Filled grains were counted using a seed counter, while unfilled and empty grains were counted manually. The following secondary parameters were calculated:

- Panicle number per m^2 = (Number of harvested panicles / Number of hills) × 24 hills $\cdot$ m^{-2} (1)
- Spikelet number per panicle = Total grain number of sample / Number of panicles (2)
- Filled grain rate (%) = (Number of filled grains in sample / Total grain number) × 100 (3)

- Filled grain weight (mg) = (Weight of filled grains in sample (g) / Number of filled grains) × 1,000 (4)
- Average grain weight (mg) = (Total grain weight of sample (g) / Total grain number) × 1,000 (5)
- Grain yield per panicle (g) = Weight of filled grains in sample / Number of sampled panicles (6)
- Grain yield ($g \cdot m^{-2}$) = Panicle number per m^2 × Spikelet number per panicle × Filled grain rate × Filled grain weight (7)

1.5 Statistical Analysis All data were processed and graphed using Microsoft Excel 2013. Split-plot ANOVA was performed using SPSS 19.0 with the general linear model, treating CO_2 and source-sink treatments as fixed factors and plot replication as a random factor. Treatment comparisons were made using the Least Significant Difference (LSD) test. Differences exceeding $LSD_{0\cdot01}$, $LSD_{0\cdot05}$, and $LSD_{0\cdot1}$ were considered highly significant (or significant at $P<0.01$), significant (or significant at $P<0.05$), and marginally significant (or significant at $P<0.1$), respectively.

Results

2.1 Effects of Elevated CO_2 and Source-Sink Treatments at Heading on Grain Yield of 'Y Liangyou 2' The effects of FACE, leaf cutting, and spikelet thinning on grain yield per unit area of super rice 'Y Liangyou 2' are shown in Figure 1a [Figure 1: see original paper]. Compared with Ambient, elevated CO_2 increased average grain yield by 173 $g \cdot m^{-2}$, representing a 23% increase ($P<0.01$). Specifically, yield increases under CK (no leaf or spikelet removal), LC1, LC3, and SR treatments were 131 $g \cdot m^{-2}$, 215 $g \cdot m^{-2}$, 238 $g \cdot m^{-2}$, and 108 $g \cdot m^{-2}$, corresponding to increases of 12%, 26%, 57%, and 15%, respectively, all reaching significant levels ($P<0.01$). Compared with CK, leaf removal at heading reduced grain yield per unit area by 192 $g \cdot m^{-2}$ (17%), 579 $g \cdot m^{-2}$ (52%), and spikelet thinning reduced yield by 324 $g \cdot m^{-2}$ (29%), all highly significant. ANOVA indicated no significant interactions between CO_2 concentration and leaf or spikelet removal treatments for grain yield per unit area.

Dividing grain yield per unit area by panicle number per unit area yielded grain yield per panicle. Figure 1b shows that elevated CO_2 increased average grain yield per panicle by 0.8 g, a 22% increase ($P<0.01$). Under CK, LC1, LC3, and SR conditions, increases were 0.8 g, 0.8 g, 1.1 g, and 0.6 g, corresponding to 15%, 21%, 55%, and 16% increases, respectively, all significant at $P<0.1$. Compared with CK, LC1, LC3, and SR treatments reduced grain yield per panicle by 0.9 g (18%), 2.9 g (53%), and 1.7 g (31%), respectively, all highly significant. No interaction effects were observed between CO_2 and leaf or spikelet removal treatments.

2.2 Effects of Elevated CO_2 and Source-Sink Treatments at Heading on Yield Components of 'Y Liangyou 2'

2.2.1 Panicle Number per Unit Area and Spikelet Number per Panicle The responses of panicle number per unit area and spikelet number per panicle in 'Y Liangyou 2' are shown in Figure 2 [Figure 2: see original paper]. Elevated CO_2 had no significant effect on panicle number per unit area but increased spikelet number per panicle by an average of 17 spikelets, an 8% increase (P=0.02). The range across different source-sink treatments was 4-14%, though none reached individual significance. Compared with CK, leaf removal or spikelet thinning had no significant effect on panicle number per unit area. LC1 and LC3 treatments did not significantly affect spikelet number per panicle, but SR treatment reduced spikelet number by 103, a 37% decrease, highly significant. No interactive effects were detected between CO_2 concentration and source-sink treatments for these two parameters.

2.2.2 Filled Grain Rate, Filled Grain Weight, and Average Grain Weight Results for filled grain rate showed that elevated CO_2 increased the average filled grain rate by 9% (P<0.01) compared with Ambient (Figure 3a [Figure 3: see original paper]). The increase under leaf removal conditions (>10%) was substantially greater than under CK or SR treatments (~3%). Compared with CK, LC1 and LC3 treatments reduced filled grain rate by 14% and 47%, respectively, while SR treatment increased it by 5%, all highly significant.

For filled grain weight (Figure 3b), elevated CO_2 increased the average filled grain weight by 0.5 mg, a 2% increase (P<0.05). Across different source-sink treatments, the increase ranged from 0.4-0.8 mg, equivalent to 1.4-3.4%, with CK and LC1 reaching highly significant or significant levels. Compared with CK, LC1 and SR treatments increased filled grain weight by 0.7 mg (3.1%) and 1.7 mg (7.4%), respectively, both highly significant, while LC3 had no significant effect.

Figure 3c shows that elevated CO_2 increased average grain weight (including all filled, unfilled, and empty grains) by 1.9 mg, a 10.1% increase (P<0.01). By treatment, FACE increased average grain weight by 1.3 mg (6.3%), 2.1 mg (11.1%), 2.9 mg (24.1%), and 1.2 mg (5.4%) under CK, LC1, LC3, and SR conditions, respectively, all significant at P<0.1. Compared with CK, LC1 and LC3 reduced average grain weight by 1.8 mg (8.2%) and 8.3 mg (38.3%), respectively, while SR increased it by 1.8 mg (8.6%), all highly significant. Despite substantial effects of elevated CO_2, LC1, LC3, and SR on filled grain rate, filled grain weight, and average grain weight, no significant interactive effects were observed among treatments (Figure 3a-c).

2.3 Relationship Between Yield Component Responses to CO_2 and Final Yield Response Correlation analysis between grain yield and its component responses to elevated CO_2 under different conditions is presented in

Table 1 . The response of grain yield per unit area to elevated CO_2 was not significantly correlated with responses of panicle number per unit area, spikelet number per panicle, or filled grain weight, but showed highly significant positive linear correlations with responses of filled grain rate (Figure 4a [Figure 4: see original paper]) and average grain weight (Figure 4c). Similarly, the response of grain yield per panicle to elevated CO_2 was significantly positively correlated with responses of filled grain rate (Figure 4b) and average grain weight (Figure 4d), but not with the other three yield components.

Discussion and Conclusion

Previous rice studies have shown that elevated CO_2 typically affects panicle number more than spikelet number per panicle. However, our results indicate that spikelet number per panicle responded slightly more to CO_2 than did panicle number, primarily because panicle number showed almost no response. Panicle number is the product of maximum tiller number and tiller survival rate. Observations of tiller dynamics revealed that elevated CO_2 had no significant effect on either maximum tiller number or tiller survival rate in this variety, indicating weak tiller responsiveness to CO_2, which differs from previous reports on hybrid rice. We also found that source-sink manipulation at heading did not alter the responses of panicle number and spikelet number per panicle to FACE, because both tillering and spikelet formation processes were complete by the time of manipulation. This confirms that the samples selected for source-sink treatments at heading were representative.

Numerous studies have reported on the effects of elevated CO_2 on filled grain rate and filled grain weight, but few have addressed average grain weight. These metrics reflect grain filling capacity from different perspectives. Both chamber and FACE studies have shown that elevated atmospheric CO_2 generally increases rice grain filling capacity, though the magnitude is typically small. Under control conditions, we found that elevated CO_2 significantly increased filled grain rate, filled grain weight, and average grain weight in 'Y Liangyou 2' , with filled grain weight and average grain weight reaching significant levels, consistent with previous FACE studies. Under leaf removal conditions, however, the increases in filled grain rate and average grain weight induced by elevated CO_2 were 2–4 times greater than in control plants. Heading-stage leaf removal did not change total spikelet number but reduced photosynthetic leaf area, thereby increasing the sink-source ratio. This change may help sink organs (grains) actively extract photosynthates from source organs (leaves), creating a "pull" that enhances the CO_2 response in leaf-removal treatments. In contrast, spikelet removal drastically reduced sink capacity, resulting in minimal CO_2 response for filled grain rate (Figure 3a) and filled grain weight (Figure 3b).

A meta-analysis by Ainsworth showed that increasing CO_2 concentration from 365 to 627 $\mathrm{mol \cdot mol^{-1}}$ increased rice grain yield by an average of 23% (n=97), with only a 13% increase under FACE conditions (n=20). Our experiment demonstrated that under natural growth conditions, elevated CO_2 increased grain yield by 12%, nearly identical to the meta-analysis results but substantially lower than previously reported CO_2 responses for hybrid rice. This discrepancy may be related to the minimal panicle response to CO_2 in this hybrid combination. Further source-sink manipulation revealed that leaf removal significantly enhanced the yield response to elevated CO_2 compared with non-manipulated plants, with greater leaf removal producing larger responses, while spikelet removal had no significant effect on the CO_2 fertilization effect. These responses were largely consistent with trends in grain filling parameters, particularly filled grain rate and average grain weight. Correlation analysis confirmed that the response of final grain yield to CO_2 was primarily related to responses of these two parameters. Average grain weight, which includes all filled, unfilled, and empty grains, largely reflects grain filling capacity and thus showed similar response patterns to filled grain rate. Grain yield per panicle excludes pre-treatment differences in panicle number among samples, more accurately reflecting how source-sink manipulation modulates the CO_2 fertilization effect. Similar to yield per unit area, the response of grain yield per panicle to elevated CO_2 was substantially greater in leaf-removal treatments than in control or spikelet-removal treatments.

Artificial source-sink manipulation at heading had no significant effect on panicle number or spikelet number per panicle, but profoundly affected grain filling capacity. LC1 and LC3 treatments significantly reduced filled grain rate and average grain weight, ultimately decreasing yield per unit area by 17% and 52%, respectively, with greater reductions following more extensive leaf removal, consistent with previous studies. In contrast, spikelet thinning significantly improved grain filling parameters, but final yield decreased substantially due to halved spikelet number, a finding also reported in earlier studies.

The super rice combination ‘Y Liangyou 2’ selected for this study achieved an average yield of 1,049 $g \cdot m^{-2}$ (approximately 700 kg per 667 m^2) under control conditions. A 200 $mol \cdot mol^{-1}$ increase in atmospheric CO_2 concentration had no effect on panicle number but increased other yield components, thereby enhancing final yield by 12%. We also found that artificially reducing the source-sink ratio at heading (e.g., through leaf removal) could enhance the CO_2 fertilization effect, primarily through enhanced responses of grain filling parameters. Rice cultivars exhibit various source-sink types, such as source-limited, sink-limited, and source-sink interactive types. Therefore, further research is needed to investigate differences in CO_2 responses among different source-sink type rice cultivars and their underlying physiological mechanisms.

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Note: Figure translations are in progress. See original paper for figures.