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The impact of free-air CO_2 enrichment (FACE) and N supply on growth, yield and quality of rice crops with large panicle

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Abstract

Because CO_2 is needed for plant photosynthesis, the increase in atmospheric [CO_2] has the potential to enhance the growth and development of plant. However, the resultant effects on growth, yield and quality of field-grown rice remain unclear, especially under differing nitrogen (N) availability and/or using cultivars with large panicles. To investigate these, a Free-Air CO_2 Enrichment (FACE) experiment was performed at Wuxi, Jiangsu, China, in 2001-03. A japonica cultivar with large panicle was exposed to two [CO_2] (ambient, ambient+200 μmol mol^{-1}) at three levels of N supply (15, 25, 35 g N m^{-2}). FACE accelerates phenology significantly, with 3-5 days earlier in heading and 6-9 days earlier in maturity across 3 years. FACE significantly increased the grain yield by 12.8%, which was mainly due to substantially increased panicle number per square meter (+19%) as result of significant increases in tillering occurrence speed. However the spikelet number per panicle was greatly reduced (-8%), which was due mainly to the significant increase in degenerated spikelets per panicle (+52%) while differentiated spikelets per panicle showed no change. Overall DM accumulation at harvest was stimulated somewhat more (+16%) by FACE, compared to grain yield, by an average of 13% by FACE, thus resulting in 3% reduction in harvest index. FACE caused significant reduction in shoot N concentration (-7%) and significant increase in P concentration (+14%) at grain maturity, resulting in significant increase in N use efficiency and significant reduction in P use efficiency. Both shoot N uptake (+9%) and P uptake (+33%) showed significant increase at harvest, which was mainly due to significant enhanced N and P uptake during early growth stage. On a per plant basis, FACE significantly increased cumulative root volume, root dry weight, adventitious root length and adventitious root number at heading, which was mainly associated with significant increases in root growth rate during early growth period, while total surface area, active adsorption area and root oxidation activity per unit root dry weight showed significant reduction. As for grain quality, FACE cause deterioration of processing suitability and appearance quality drastically, the nutritive value of grain was also negatively influenced by FACE due to a reduction in grain protein and Cu concentration. By contrast, FACE resulted in better eating/cooking quality. For most cases, no [CO_2]×N interaction was detected for the growth, yield and quality parameters. Data from this study has important implications for fertilizer (e.g. N, P) management and variety selection in rice production systems under future elevated [CO_2] conditions.

1. Introduction

Empirical records provide incontestable evidence of global changes; Foremost among these changes is the increasing atmospheric CO_2 concentration ([CO_2]), which, as is predicted, will double the concentration of the pre-industrial era around the mid 21st century (IPCC, 2001). Atmospheric carbon dioxide is the substrate for photosynthesis for all terrestrial higher plants, hence, its enrichment must have profound impact on plant growth and development. Rice (*Oryza sativa* L.) is one of the most leading crops in the world and the first staple food in Asia, providing nutrition to a large proportion of the world's population. The improvement of grain yield and quality are the two most important objectives in rice production in most of the rice-producing areas of the world. Hence, it is very important to determine how the predicted increase in the levels of atmospheric [CO_2] will affect growth, yield and quality of rice.

Over the last a decade, many studies have been carried out to determine the effects of elevated [CO_2] on growth, yield and quality of rice crops (Baker and Allen, 1993; Horie et al., 1995, 2000; Ziska et al., 1997; Seneweera et al., 1996, 1997; Kim et al., 1996, 2001, 2003a, b; Tomio et al., 2005). Studies with cereal crops other than rice suggest that nitrogen (N) availability can have a large effect on the responses of agricultural crops to elevated [CO_2] (Kimball et al., 1995, 2002). However, as for the interactive effects of elevated [CO_2] and N availability on the growth and yield of rice crops, we know only a single study conducted for three cropping seasons (1998-2000) using a japonica cultivar with small panicle (average ca. 80 spikelets per panicle) under differing low N levels (from 4 to 15 g N m^{-2}) (Kim et al., 2001, 2003a b; Lieffering et al., 2004; Tomio et al., 2005). To date, there is no information on the combined effect of these factors on growth, yield and quality of rice cultivar with large panicles or under differing high N supply. However, over the last several decades, the consumption of N fertilizer increased dramatically with the increase in rice yield in developing countries. For example, the average rate of N application for rice production in China is about 75% higher than the world average (FAO, 2001). At present, in Tai Lake region in China, N application has reached 27-30 g m^{-2} and even exceeded 35 g m^{-2}. On the other hand, the presence of large panicles of high-yielding rice cultivars ensures that a sufficient spikelet number per unit area can be obtained, leading to the increase of the grain yield potential (Ling et al., 1994; Peng et al., 1999). So there is a need to reveal out [CO_2]-response on the rice growth, yield and quality of large panicle cultivar under high N application.

The effects of elevated [CO_2] on rice growth and development were studied mostly based on the experiments conducted using chambers or enclosures with elevated [CO_2] (Baker and Allen, 1993; Horie et al., 1995, 2000; Ziska et al., 1997; Seneweera et al., 1996, 1997; Kim et al., 1996). In both situations, the environment experienced by the crops can be markedly different from that under field conditions, which have been shown to influence the response of plants to elevated [CO_2] (McLeod and Long, 1999). Also, because of their limited size, use of these facilities prevents intensive destructive sampling. However, the free-air CO_2 enrichment (FACE) technique can avoid these limitations of enclosure methods (McLeod and Long, 1999), as a result, it is presumed to be the most ideal method to study the response of crop ecosystem to elevated [CO_2]. The China Rice FACE platform, which is also the second Rice FACE system in the world, have been set up and operated in June 2001, with the objective of investigating the effects of elevated [CO_2] on rice growth, yield, quality, soil change in microbiology, nutrients supply, competition among crop and herbs, canopy micro-meteorology, trace gas emission and consumption under field conditions.

In the study reported here, as in the Japanese Rice FACE project (also first rice FACE facility in the world), rice crops were grown from seedling to grain maturity under two levels of [CO_2] (ambient and ambient plus 200 μmol mol^{-1}) (Kim et al., 2001, 2003a b). In contrast, however, according to the actual Chinese rice production, a cultivar with larger panicle (ca 155 spikelets per panicle) that has been used in large-scale production in China was tested and three higher N levels (15, 25, 35 g N m^{-2}) were supplied. The objective of the present work was to elucidate the effects of elevated [CO_2] in combination with differing high N availability on growth, yield and quality of rice with large panicle. The results obtained here should provide important implications with respect to adaptation strategies of rice under future elevated CO_2 conditions.

2.Materials and Methods

The rice FACE experimental system was located at Wuxi city, Jiangsu province, China (31°37'N, 120° 28'E), which has eight rings located in different paddies having similar soils and agronomic histories. Three replicate plots were randomly allocated for the elevated CO_2 treatments (hereinafter called FACE plots) and five for the ambient treatments (hereinafter referred to as ambient plots). Each replicate plot was ca. 80 m^2. In the FACE plots, crops were grown within 12.5 m diameter 'rings' which sprayed pure CO_2 both day and night throughout the growing season except for a few days during transplantation towards the plot centre from eight peripheral emission tubes (5 m long) located about 50-60 cm above the canopy. In the ambient plots, plants were grown under ambient [CO_2] without ring structures. The target [CO_2] in the FACE plots throughout the season was controlled to 200 μmol mol^{-1} above that of ambient by computer system platform. Details of the design, rationale, operation, and performance of the CO_2 exposure system used in this study are provided by Okada et al. (2000) and Liu et al. (2002).

A japonica cv. Wuxiangging 14 tested in the experiment was a major local cultivar with large panicle (ca 155 spikelets per panicle) and a high-yielding potential. Standard cultivation practices as commonly performed in the area were followed in all experimental plots. Rice seeds were sown on 18 May. The seedlings for the ambient plots were grown under ambient [CO_2] conditions, while those for the FACE plots were grown under elevated [CO_2] conditions. On 13 June, the seedlings were manually transplanted at a density of 3 seedlings per hill into the FACE and ambient plots. Spacing of the hills was 16.7 by 25 cm (equivalent to 24 hills m^{-2}). Each of the eight circular rings (main plots) was further spit into three subplots to test the effect of three different N levels: low (LN, 15 g N m^{-2}), medium (MN, 25 g N m^{-2}) and high N (HN, 35 g N m^{-2}). The more detailed description of soil properties and cropping history was provided in the previously published reports (Yang et al., 2006a, b, 2007a, b, c, d).

Areas of the crop were destructively sampled at different times over the season. Sampling dates were fixed so as to coincide as much as possible with the early-tillering, mid-tillering, panicle initiation (PI), booting, heading (50% of plant headed) and grain maturity stages of the plants. In 2001, Plants were sampled at 28 and 51 days after transplanting (DAT), heading stage, and grain maturity. In 2002, plants were sampled at 16, 27, 47 and 58 DAT, heading stage and grain maturity. In 2003, sampled at 12, 28 and 45 DAT, heading stage and grain maturity. In order to ensure representativeness of the sampling, the number of stems in 100 hills was counted at different places in each subplot, and then five plants with the mean stem number were selected. To maintain canopy conditions, the vacant spaces left after sampling were replanted with hills taken from the borders and these replanted hills were not subject to sampling any more. The samples were separated into living and dead leaf tissues, stem (including leaf sheath), root, and panicle (when applicable). For two of the five hills green leaf areas were measured. All the plant parts were oven-dried at 80°C for 72 h or until dry weights were constant for subsequent measurements. Grain yield and quality was determined of all the plants from a 2 m^2 patch (excluding plants in the borders) in each subplot. The details of measurements for nutrient concentrations, root characteristics, yield formation, and grain quality properties as well as statistical analysis all can be found in previous reports (Yang et al., 2006a, b, 2007a, b, c, d).

3. Results

3.1. Effects of CO_2 and N on phenology

The duration from sowing to heading, from heading to maturity and the whole growth duration of rice shrank 3-5 (mean value 3.4, Fig. 1a), 1-5 (mean value 2.4, Fig. 2a), 4-9 (mean value 5.8) days, respectively, in the FACE vs ambient plots. Increment of N application rate could weaken the effect of FACE on growth duration. For the most part, the year effects were significant for the whole growth duration; however, interactions between all treatment variables (Year×CO_2, Year×N, CO_2×N, Year×CO_2×N) were hardly detected.

3.2. Effects of CO_2 and N on biomass, yield and yield components

On average, compared to ambient [CO_2], FACE significantly increased shoot biomass and grain yield

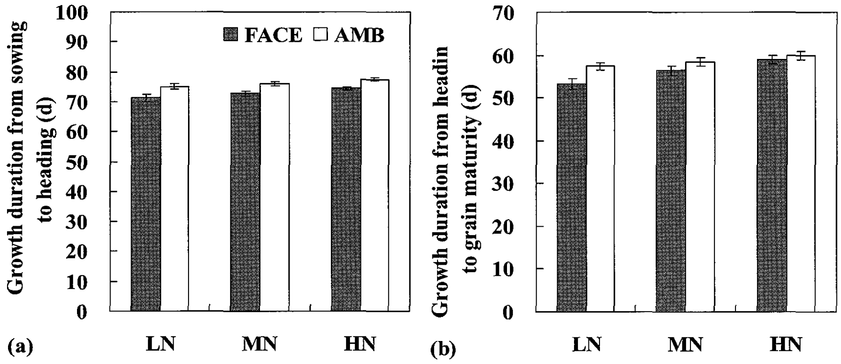

Fig. 1. Effect of elevated [CO_2] of growth duration from transplanting to heading (a) and from heading to grain maturity (b) of rice plants under three levels of N application (15, 25, 35 g m^{-2}) over three cropping seasons (2001-03). Data are average values across three years with ± one standard error (vertical bars).

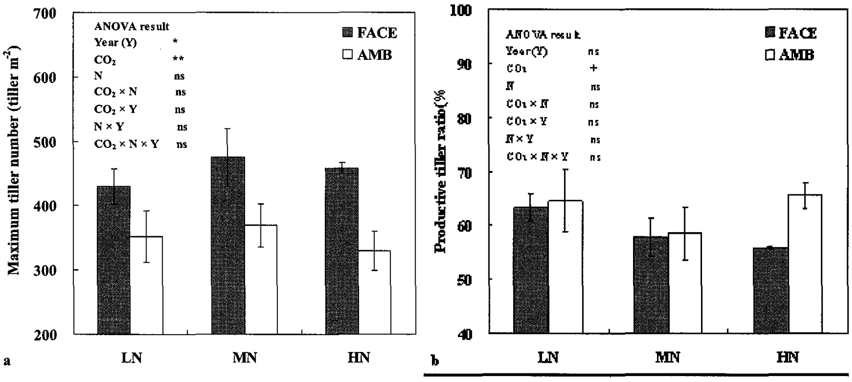

Fig. 2. Effect of elevated [CO_2] on maximum tiller number per square meter (m^2) (a) and productive tiller ratio (%) under three levels of N application (15, 25, 35 g m^{-2}). Data averaged aross 2001 and 2002. Vertical bars indicated one standard error. ANOVA results are shown with ns, +, * and ** indicating no significance, $P < 0.1$, $P < 0.05$ and $P < 0.01$, respectively.

of rice crops at maturity, with an average increase of 16% (data not shown) and 12.8% (Table 1) across the three years, respectively. Across [CO_2] levels, biomass and grain yield increased significantly with N supply from 15 to 25 g N m^2, but further increases in N supply to 35 g m^{-2} resulted in significant decline.

FACE significantly increased panicle number per square meter, showing an average increase of 18.8% across three years (Table 1). Across [CO_2] levels, the panicle number per square meter increased significantly with increasing N level from 15 to 25 g N m^2, but higher N (e.g. 35 g N m^{-2}) levels showed the reverse. Panicle number per square meter is determined by maximum tiller number (MTN) per square meter and productive tiller ratio (PTR). FACE significantly increased MTN per square meter (+30.0%, Fig. 2a), while PTR was reduced with FACE (-7.7%, Fig. 2b), indicating greater panicle number per square meter was mainly due to the substantial increases in tiller occurrence with FACE.

FACE significantly reduced spikelet number per panicle (SNPP), averaging 7.6% across the three seasons (Table 2). N had no significant effect on SNPP. SNPP is represented by the difference in the number of differentiated and degenerated spikelets. Our results indicated that FACE had no effect on the number of differentiated spikelets per panicle (Fig. 3a), while it significantly increased the number of degenerated spikelets per panicle, averaging 97.3% and 38.6% in 2001 and 2002, respectively (Fig. 3b).

Filled spikelet percentage and grain weight all responded positively to FACE but negatively to N (Table 1). Though the degree of stimulation due to FACE was less overall, averaging 4.9% for filled spikelet percentage and 1.3% (0.4 mg) for grain weight across three years, both of them reached significant level ($P < 0.01$).

For the most part, the year effects were all significant for final biomass, grain yield and yield components (Table 1); however, interactions between all treatment variables were hardly detected.

3.3. Effects of CO_2 and N on N uptake and utilization

Averaged across all N levels and years, FACE significantly increased shoot N uptake by 9% at grain maturity (Fig. 4a). The whole growth season of rice plants is consisted of different growth periods. On average, shoot N uptake in FACE plots was increased significantly by 46, 38, 6 and 16% during the growth periods from transplanting to early-tillering (Period 1), early-tillering to mid-tillering (Period 2), mid-tillering to panicle initiation (PI) (Period 3) and heading to grain maturity (Period 5), respectively, while it was reduced by 2% in the period from PI to heading (Period 4), the responses showing a progressive decrease with time during the season up to heading and then a slightly increase at grain maturity (Fig. 5a). The similar trend applied to shoot N uptake ratio (the ratio of shoot N uptake during a given growth period to final shoot N acquisition at maturity): on average, the response of shoot N uptake ratio to FACE was 33, 26, -3, -11 and 10% in Periods 1, 2, 3, 4 and 5 of the growth period, respectively (figure not shown).

As a result of the greater increase in shoot DM production at maturity, relative to the increase in N up-

Table 1. Effect of elevated [CO_2] on yield and its components of rice crops under three levels of N application (15, 25, 35 g m^{-2}) over three cropping seasons (2001-03)

Year	N	CO_2	Panicle number (m^{-2})	Spikelet number ($panicle^{-1}$)	Total spikelets (m^{-2})	Spikelet fertility (%)	Grain weight (mg)	Yield (g m^{-2})
2001	LN	FACE	347.2	128.8	44719	76.3	30.0	1149
		AMB	284.8	144.7	41211	67.1	30.5	1040
	MN	FACE	364.8	143.7	52422	68.5	30.3	1217
		AMB	315.2	153.0	48226	63.0	30.0	1095
2002	LN	FACE	324.0	137.5	44550	72.0	28.5	1064
		AMB	284.4	149.6	42546	62.9	27.9	980
	MN	FACE	346.0	136.5	47229	63.5	27.6	1167
		AMB	291.6	151.2	44090	63.2	27.9	992
	HN	FACE	328.0	147.2	48282	61.7	27.9	1081
		AMB	288.0	152.8	44006	61.0	27.7	932
2003	LN	FACE	303.6	148.8	45176	73.2	28.2	1003
		AMB	253.0	154.0	38962	74.6	27.1	880
	MN	FACE	318.1	145.0	46125	71.3	27.3	976
		AMB	269.6	159.4	42974	71.8	26.3	903
	HN	FACE	330.7	141.5	46794	66.9	26.8	936
		AMB	257.1	156.3	40185	70.0	26.2	783
				ANOVA results				
	Year (Y)		**	*	**	**	**	**
	CO_2		**	**	**	*	*	**
	N		**	ns	**	**	**	**
	CO_2×N		ns	ns	ns	ns	ns	ns
	CO_2×Y		ns	ns	ns	*	**	ns
	N×Y		ns	ns	ns	ns	ns	ns
	CO_2×N×Y		ns	ns	ns	ns	ns	ns

ns, * and ** indicating no significance, $P < 0.05$ and $P < 0.01$, respectively.

Table 2. Effect of elevated [CO_2] on total surface area (TSA), active adsorption area (AAA) and amount of α-NA oxidation per unit root dry weight (RDW) under three levels of N application [15, 25, 35 g m^{-2}] in 2003 rice season

N	CO_2	TSA per unit RDW (m^2 g^{-1})	AAA per unit RDW (m^2 g^{-1})	Amount of α-NA oxidation per unit RDW (μg g^{-1} h^{-1})
	FACE	8.12	2.32	120.88
	AMB	10.74	2.89	147.89
MN	FACE	7.06	2.35	137.45
	AMB	9.16	3.18	170.03
LN	FACE	6.87	2.32	134.03
	AMB	9.99	3.07	245.13
CO_2		**	*	**
N		*	n.s.	**
CO_2×N		n.s.	n.s.	**

ns, * and ** indicating no significance, $P < 0.05$ and $P < 0.01$, respectively.

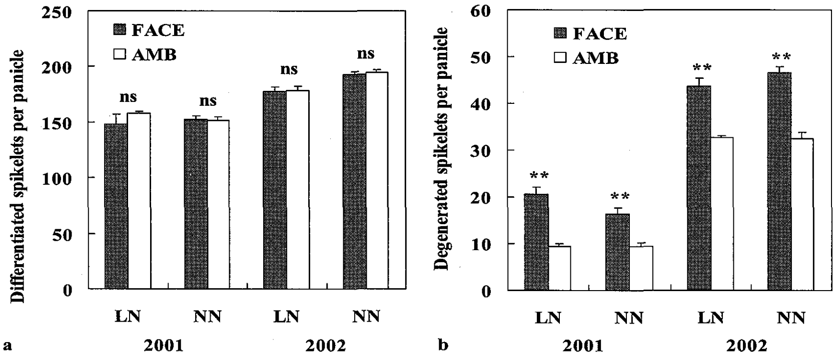

Fig. 3. Effect of elevated [CO$_2$] on number of differentiated spikelets (a) and degenerated spikelets (b) per panicle under three levels of N application (15, 25, 35 g m^{-2}) over two cropping seasons (2001-02). Vertical bars indicated one standard error. ANOVA results are shown with ns, ** indicating no significance, $P < 0.01$, respectively.

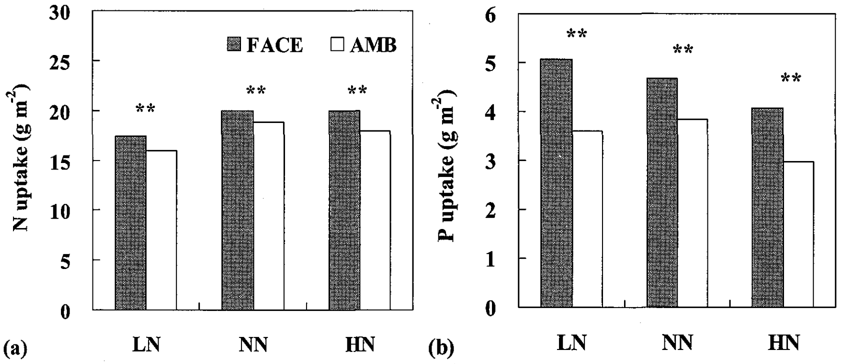

Fig. 4. Effects of elevated [CO$_2$] on shoot N (a) and P (b) uptake at maturity under three different levels of N application (15, 25, 35 g m^{-2}) over three cropping seasons (2001-03). Bars represent ± stardard error (n = 3 or 5) when it exceeds the size of the symbol.

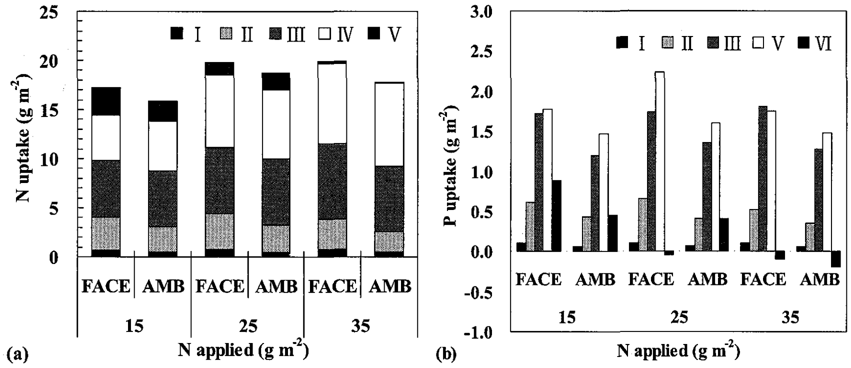

Fig. 5. Effect of elevated [CO$_2$] on shoot N (a) and P (b) uptake during five successive growth periods of rice under three different levels of N application (15, 25, 35 g m^{-2}) over three cropping seasons (2001-03). A, B, C, D and E indicate different growth periods: from transplanting to early-tillering, early-tillering to mid-tillering, mid-tillering to panicle initiation (PI), PI to heading, heading to grain maturity, respectively. For each N level, data are average values across three years (2001-03).

take, N use efficiency (NUE) increased significantly, whereas the reverse was true for shoot N concentration at maturity. Averaged across all N levels and years, shoot N concentration was lower under FACE by 7% at maturity. As for NUE at maturity, N use efficiency for biomass (NUEp), N use efficiency for grain (NUEg) and N harvest index (NHI) increased by an average of 7 ($P < 0.05$), 5.7 ($P < 0.05$) and 2.0% ($P > 0.05$) with FACE, respectively.

Across [CO_2] levels, shoot N concentration and uptake increased apparently with increasing N supply, while NUE showed an opposite trend. For the most part, interactions between all treatments variables were not detected although there was obvious variation between different years with regards to N nutrient parameters.

3.4. Effects of CO_2 and N on P uptake and utilization

Shoot P accumulation showed significant and substantial increase under FACE irrespective of N application (Fig. 4b). Averaged across all N levels and years, the shoot P uptake was greater under FACE by 33% at maturity. The whole growth season of rice plants is consisted of different growth periods. Averaged over all N levels and seasons, shoot P uptake in the FACE plots was increased significantly by 57, 51, 37, 26 and 11%, in Periods 1, 2, 3, 4 and 5 of the growth periods, respectively, showing a progressive decrease with time across the season (Fig. 5b). The similar trend applied to shoot P uptake ratio (i.e., the ratio of P uptake during a given growth period to final P acquisition at maturity): on average, the response of shoot P uptake ratio to FACE was 19, 14, 3, -5 and -16% in Periods 1, 2, 3, 4 and 5 of the growth period, respectively (figure not shown).

As a result of the greater increase in P uptake, relative to the increase in DM production at maturity, P use efficiency (PUE) decreased significantly, whereas the reverse was true for shoot P concentration. Averaged across all N levels and years, shoot P concentration increased by 14% in FACE vs. ambient plants at maturity. As for PUE, P use efficiency for biomass (PUEp), P use efficiency for grain (PUEg) and P harvest index (PHI) were all decreased significantly with FACE by an average of 12, 13 and 7%, respectively.

N fertilization had little effect on all the observed P nutrient parameters. For the most part, interactions between all treatments variables were not detected although there was obvious variation between different years with regards to P nutrient parameters mentioned above.

3.5. Effects of CO_2 and N on root growth and development

On a per hill basis, cumulative adventitious root number (ARN), adventitious root length (ARL), root volume (RV) and root dry weight (RDW) per hill were consistently high at elevated relative to ambient [CO_2] ($P < 0.01$) (Fig. 6): Averaged across all N levels and two years, cumulative ARN, ARL, RV and RDW per hill was greater under FACE by 29.0, 24.6, 34.7 and 35.5% at heading stage, respectively. N treatment had no effect on these parameters except for ARL per hill. The year effects were all significant ($P < 0.01$ or $P < 0.05$) for the four parameters, with the absolute values being markedly higher in 2003 than in 2002 growth season; however, interactions between all treatments variables were generally, but not always, nonsignificant for these parameters.

In contrast to root accumulation, FACE treatments exerted negative effects on total surface area (TSA), active adsorption area (AAA) and root oxidation activity (as measured by amount of α-NA oxidation) per unit root dry weight (RDW) at heading independently of N fertilization (Table 2): Averaged over three N levels, TSA, AAA and root oxidation activity per unit RDW were reduced by 26.3%, 23.6% and 30.3%, respectively. ANOVA showed that the differences between two [CO_2] levels were significant for the three parameters ($P < 0.01$). N treatments had no influence on AAA per unit RDW but significant impacts on the other two parameters. And no interactions between [CO_2] and N supply were observed except for amount of α-NA per unit RDW.

3.6. Effects of CO_2 and N on grain quality

In general, the processing quality are evaluated by three milling traits, namely, brown rice percentage (BRP), milled rice percentage (MRP), head rice percentage (HRP). BRP showed small but significant increase (0.3%, Fig. 7a) with FACE, while, FACE significantly reduced MRP, HRP by 2.0 and 23.4% across the three seasons (Fig. 7b, c), respectively. Across both [CO_2] levels, BRP, MRP and HRP all increased apparently with increasing N supply.

Figs 7c, d, e summarizes three main appearance quality traits, including of chalky grain percentage

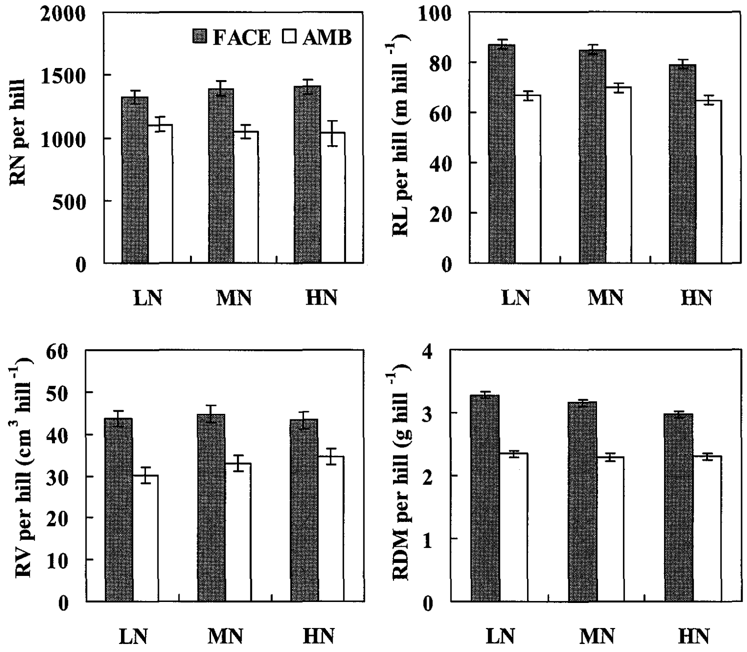

Fig. 6. Effect of elevated [CO_2] on adventitious root number (ARN, a), adventitious root length (ARL, b), root volume (RV, c), root dry weight (RDW, d) per hole under three different levels of N application (15, 25, 35 g m^{-2}) over two cropping seasons (2002-03). Data averaged for 2002 and 2003. Bars represent ± stardard error when it exceeds the size of the symbol.

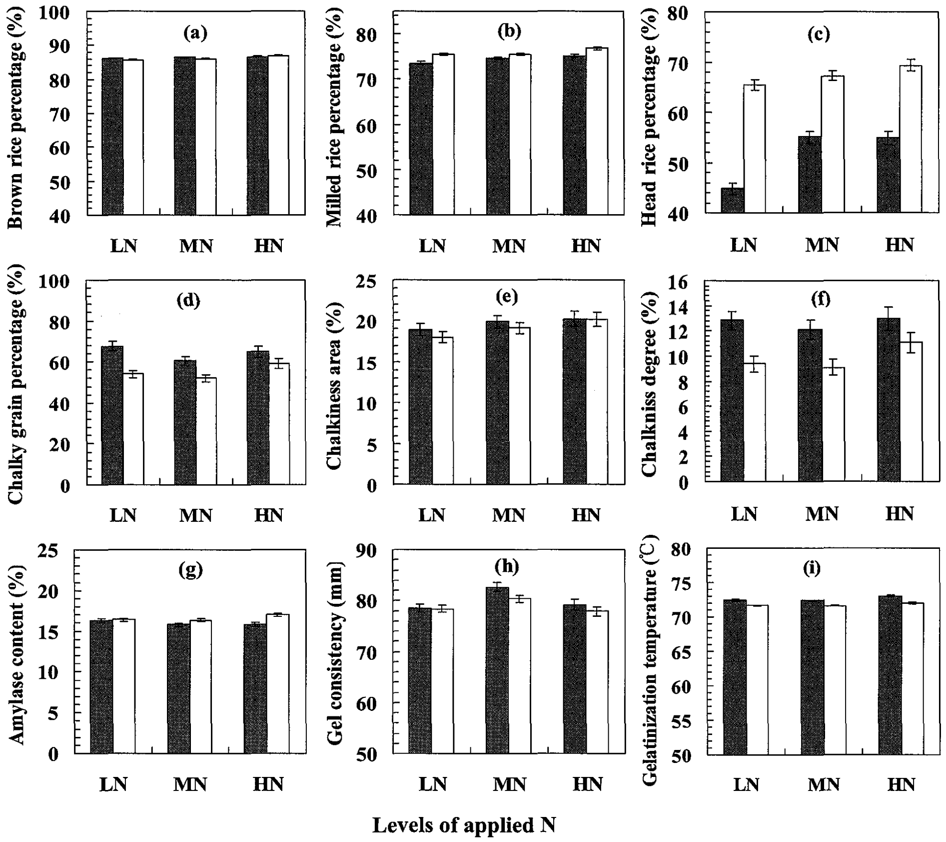

Fig. 7. Effect of elevated [CO_2] on brown rice percentage (BRP, a), milling rice percentage (MRP, b) and head rice percentage (HRP, c), chalky grain percentage (CGP, d), chalkiness area (CA, e), chalkiness degree (CD, f), amylose content (AC, g), gel consistency (GC, h) and gelatinization temperature (GT, i) of rice plants under three different levels of N application (15, 25, 35 g m^{-2}). Data are average values across three years with ± one stardard error (vertical bars).

(CGP), chalkiness area (CA), chalkiness degree (CD) of brown rice. CGP, CA and CD were consistently higher at the elevated relative to the ambient [CO_2] regardless of the N treatment ($P < 0.01$), showing an average increase of 16.9, 3.1 and 28.3% across three years, respectively. By contrast to [CO_2], N had relatively minor effects on appearance quality properties.

The cooking/eating quality of rice is largely determined by three primary physical and chemical characteristics of the starch in the endosperm: amylose content (AC), gel consistency (GC) and gelatinization temperature (GT). When averaged over all N levels and years, FACE significantly decreased AC in milled rice by 3.8% (Fig. 7g). Although not statistically, the trend was for lower N application to decrease AC in milled rice. As for GC, it showed only a weak increase in FACE grains compared to ambient ones (Fig. 7h). Across [CO_2] levels, varying the supply of N significantly influenced GC with greatest GC occurring at MN rather than LN or HN. With respect to GT, FACE grains showed an average increase of 0.8°C (relative increases 1.2%) across three years (Fig. 7i), while no influence of N fertilization was observed.

Regardless of N application rate, FACE significantly reduced protein concentration (PC) in milled rice, while protein yield per square meter exhibited opposite trend (Figs 8a, b): averaged across two [CO_2] levels and three years, PC in milled rice was lower under FACE by 6.2%, while significant 6.0% increase was found for protein yield. Across [CO_2] levels, PC increased apparently with increasing N supply. Unlike PC, the yield of protein increased with increasing N supply, but luxury N application (35 g m^{-2}) resulted in significant reduction.

The ANOVA results consistently showed that the year effects were all significant for all the grain quality properties; however, for the most part, interactions between all treatments variables were not detected.

4. Discussion

4.1. Phenology

Concerning effects of FACE on phenology, there is only one report to date by Kobayashi et al. (2000), finding that the FACE grown plants exhibited ca 2 days earlier in heading compared with the ambient grown plants. Our trial indicated that FACE accelerates phenology significantly, with 3-5 days earlier in heading and 6-9 days earlier in grain maturity. In addition to the increased daytime canopy temperature and inside canopy air temperature due to FACE (Luo et al., 2002), we speculate that a significant decrease in N concentration and significant increases in concentrations of both P and soluble carbohydrate of plants contributed to the accelerated phenology.

4.2. Grain yield formation

As for the interactive effects of elevated [CO_2] and N supply on grain yield of rice, there is only one study to date conducted using Japanese Rice FACE facility (Kim et al., 2003a). In our present experiment, the low nitrogen (LN, 15 g N m^2) was actually higher or equal to the high nitrogen (HN, 12 or 15 g N m^2) in Japanese Rice FACE experiment (Kim et al., 2003a). We detected an average response of 13% to FACE in rice yields which is similar to the result by Kim et al. (2003a). However, unlike their results, we found no significant [CO_2]×N interaction with respect to grain yield, suggesting that the positive effects of

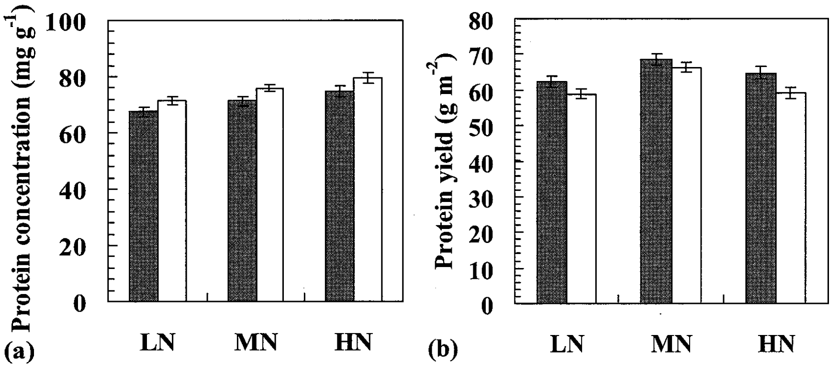

Fig. 8. Effect of elevated [CO_2] on protein concentration (a) and protein yield (b) in milled rice under three different levels of N application (15, 25, 35 g m^{-2}). Data are average values across three years with ± one standard error (vertical bars).

N availability on the responses of rice yield to elevated [CO_2] would reduce or even disappear under higher levels of fertilizer N (as in this trial). Regardless of CO_2 treatment, the absolute values of yield increased significantly with N supply from 15 to 25 g N m^2, but further increases in N supply to 35 g m^{-2} resulted in significant reduction, which were also different from the result by Kim et al. (2003a), suggesting that, as under ambient condition, the absolute grain yield under elevated [CO_2] will also approach a ceiling at a given N level.

The grain yield of rice is a function of panicle number per square meter, SNPP, filled grain percentage and grain mass. Our results indicated that the main reason for the increases in yield with FACE were due mainly to the increased panicle number per square meter (+19%), while SNPP showed significant reduction due to FACE.

Panicle number per square meter is determined by MTN per square meter and PTR. Our results indicated that greater panicle number per square meter was clearly due to the increases in maximum tiller number (+30%) with FACE being substantially more than the decreases in PTR (-8%). As the ratio of the number of panicle-bearing tillers to that of total tillers was lower with FACE across all N levels, so in this study we also found a small but significant 3% reduction in harvest index (HI, data not shown). Similar trends in MTN, PTR and HI with FACE have also been reported by Kim et al. (2003a, b). The variations of MTN and PTR are determined by the changes of tillering speed during different growth stages. Further analysis indicated that FACE-induced increase in MTN was related to significant increases in tillering occurrence speed at early growth stage (ca. from 10 to 30 DAT), while FACE-induced reduction in PTR was linked with increased tillering extinction speed at middle growth stage (ca. from 45 DAT to heading) (data not shown).

With respect to SNPP, some researchers reported significant increases due to elevated [CO_2] (Kim et al., 1996, 2003a), while others reported no change (Baker and Allen, 1993). In this study, FACE significantly reduced SNPP by 8%. The above results indicated that the responses of SNPP to elevated [CO_2] depended on the cultivars grown or experimental conditions. SNPP is represented by the difference in the number of differentiated and degenerated spikelets. Our results for the first time indicated the negative effect of CO_2-enrichmant on SNPP was not due to spikelet differentiation per panicle but mainly due to the enhancement of spikelet degeneration per panicle. Based on other parameter responses, we hypothesized that greater degenerated spikelets per panicle due to FACE may be mainly attributed to dissonance between carbon and nitrogen metabolisms during the phases of spikelet formation.

4.3. N uptake and utilization

The present study showed the final shoot N uptake at maturity was increased significantly by 9% due to FACE, and this is in contrast to those with rice from a OTC study (Ziska et al., 1996) and a FACE study (Kim et al., 2001, 2003b) which demonstrated that the total amount of N taken up was similar for both elevated and ambient [CO_2] crops by the end of the experiments. In addition to the difference in test cultivar and environmental conditions, one possibility for this contrast may be due to the different levels of N supplied. The N application rate in this trial was 15-35 g N m^{-2}, while it was 0-20 g N m^{-2} in the two experiments cited above (Ziska et al., 1996; Kim et al., 2001, 2003a). A result with cotton by Rogers et al. (1996) indicated that there was no CO_2 effects on N accumulation at low level to moderate level of N supply, while apparent [CO_2]-induced increases in N accumulation were observed at high level of N supply. Thus, there appears to be a fairly wide range in the effects of elevated [CO_2] on N yield depending on soil N availability.

The final shoot N acquisition of rice at maturity is related to dynamics of shoot N uptake during various growth periods. To date, there is no information on effects of elevated [CO_2] on seasonal changes in shoot N uptake of rice. Our study indicated that the response in shoot N uptake declined gradually with crop development before heading, while it showed a slight increasing trend again after heading, with average responses of 46, 38, 6, -2 and 16% during the Period 1, 2, 3, 4 and 5. With respect to shoot N uptake ratio, the average responses to FACE were 33, 26, -3, -11 and 10%, respectively, during the respective growth periods, similar to what occurred with shoot N uptake. Such seasonal responses in shoot N uptake (ratio) are mainly regulated by soil N availaility, plant N uptake ability and also related to plant phenology: Overall, because of plentiful N supply in the soil together with a greater relative N uptake capacity during early development, FACE plants showed the largest N uptake increase over the season as compared with ambient plants. As soil N availability and plant N uptake ability decreased during MGP, together with accelerated crop phenology, relative stimulation of N uptake by FACE either disappeared or even slightly reversed. Contrary to seasonal trend in N uptake response to elevated [CO_2] before heading, FACE crops showed again enhanced N uptake during LGP. Such a phenomenon could primarily be attributed to N fertilization in this trial (40% of the total N was applied at about 20 days before heading) which induced higher soil N availability again during LGP, though mean duration from heading to grain maturity shrank 2.4 days on average in FACE crops.

4.4. P uptake and utilization

The present study indicated that the total shoot P uptake over the whole season was increased substantially by 33% under FACE, which is similar to most of previous reports (Fangmeier et al., 1997; Barrett and Gifford, 1999). The final P accumulation of plant is related to dynamics of P uptake during various growth periods. Our results indicated that there were clear seasonal trends in shoot P uptake response: the relative stimulation due to FACE declined gradually with crop development, with average responses of 57, 51, 37, 26 and 11% during the Period 1, 2, 3, 4 and 5. With respect to shoot P uptake ratio, the average responses to FACE were 19, 14, 3, -5 and -16%, respectively, during the respective growth periods, similar to what occurred with shoot P uptake. Considering the seasonal changes in other parameters, we conclude that P uptake of rice before PI appeared to be mainly determined by P uptake ability (or P demand) as showed by stronger rice root system and relatively lower soil P availability under FACE condition, while shoot P uptake after PI seemed to be mainly regulated by soil P availability, which was reflected in the inability of rice root systems and increased soil extractable P in the FACE plots.

As for CO_2 response of P concentration in plants or leaves, a variety of observations have been made under different experimental conditions, most of which have shown negative response (Manderscheid et al., 1995) or zero response (Manderscheid et al., 1995; Seneweera and Conroy, 1997; Fangmeier et al., 1999), less of which have showed positive response (Rouhier and Read, 1998). In this experiment, because there was an increase in the amount of P taken up relative to the biomass across the season, the significant and sustained increase in P concentration was observed due to elevated [CO_2]. These inconsistencies showed the potentially complex nature of the CO_2 effect on P concentration, which could be attributed to complex interactions between the uptake of P and other elements at different availability and mobility under varied experimental conditions (include soil type, weather and species).

4.5. Root growth and development

Because of the greater inaccessibility of belowground system, only a fraction of rice studies have examined root responses to elevated [CO_2], of such limited studies, almost all of them just focused on root biomass (Baker *et al.*, 1990; Ziska *et al.*, 1996; Moya *et al.*, 1998; Weerakoon *et al.*, 1999; Kim *et al.*, 2001, 2003 b). In this FACE trial, four root parameters on a per hill basis were examined at heading: RV, RDW, ARL and ARN. These parameters all showed prominent increases (25-33%) under FACE. The root accumulation at heading is related to root growth rate during different growth periods. Further study indicated that larger root standing crop at heading stage was mainly associated with significant increases in root growth rate during early growth period, while a slight inhibition of root growth rate (except ARN-growth rate) occurred during middle growth period.

The root physiological response is an important component of the root response to rising CO_2. For rice, there is no relevant information on root activity responses. Our data indicated that specific root activity of rice (i.e., TAA, AAA and amount of α-NA oxidation per unit RDW) all dropped sharply with FACE. We concluded that the CO_2-induced decreases in specific root activities were associated with a larger amount of root accumulation during early growth period and lower N concentration and higher C/N ratio in roots in FACE vs. ambient plants.

4.6. Grain quality

Milling quality of rice is one of the most important traits in rice as it is directly related to market value and thus influences income of both rice producers and processor. To date, however, little is known regarding the impact of elevated [CO_2] on processing quality of rice. One of the prominent phenomenons observed in this study was the significant decreases in milling traits (i.e., MRR and HRP), indicating a higher fraction of removed outer layer (i.e., pericarp and aleurone) and broken (or damaged) rice during milling (i.e., higher degree of milling). Because the milling conditions were identical for FACE and ambient plants, the grains in the FACE plots were supposed to be lower hardness or more easily ground than those in the ambient plots. The dramatic 24% reduction in MHP needs requisite attention in future research because most rice is consumed in the whole grain form.

Appearance is influenced by grain size and shape. The latter is mainly composed of CGP, CA and CD. Our results indicated that FACE significantly increased CGP (+16%) and CD (+28%). The higher extent of chalkiness implies that rice grains grown under higher [CO_2] condition have a lower density of starch granules and are therefore more prone to breakage during milling, as indicated by a close negative correlation in this study between CGP ($r = -0.757^{**}$), CA ($r = -0.393^{**}$), CD ($r = -0.544^{**}$) and HRP when plotted for each combination of years, CO_2, N and blocks. Similar relationship between appearance and milling quality has also been reported in the literatures (Nakatat and Jackson, 1973). These are two possible reasons for the observed deleterious effects of elevated [CO_2] in chalkiness and milling quality. First, from the point of view of internal causes, such results appeared to be associated with the changes in grain-filling characteristics (include rate and duration of grain filling) due to FACE. As for grain-filling rate, our results indicated that the FACE plants showed a significant increase during the early grain-filling stage, whereas an adverse trend was displayed during the late grain-filling stage (data not shown). Additionally, our data of this study also demonstrated that, the FACE plants matured and senesced about 6 to 9 days earlier than the ambient plants. Because of the acceleration of senescence, there was a shortening of grain-filling duration, and consequently influencing final physical qualities of grains. Second, in term of external causes, it is well documented that temperature during grain-filling is one of the most important environmental factors that significantly affects the rice quality (Resurreccion et al., 1977). Using the same FACE platform, Ruo et al. (2002) reported FACE significantly increased daytime canopy temperature and inside canopy air temperature during the filling stage. We speculate that this temperature rise also contributed to the increased grain-filling rate at early ripening stage and the earlier maturity, which resulted in incomplete filling of the grain thereby leading to an increase in chalky appearance but a decrease in milling rate.

The cooking/eating quality is a very important aspect of the grain quality. AC is considered to be the most important trait closely related to the eating/cooking quality of rice. In general, higher contents of amylose relative to amylopectin increase the hardness of the cooked grain (Mohapatra and Bal, 2006). In this study, AC in starch was significantly reduced by FACE, suggesting that [CO_2] enrichment is likely to reduce the hardness of the cooked grain. Our observation is in contrast to the results of Seneweera et al. (1996) and Terao et al. (2005). From a growth chamber experiment with rice, Seneweera et al. (1996) reported significant increase in AC with elevated [CO_2], while in Japanese rice FACE experiment no change in AC was detected (Terao et al., 2005). The explanation for this inconsistency probably resides in varietal differences.

Rice is a major source of dietary protein for most of the Asian rice-growing countries. Our results indicated that, although the FACE treatment caused decreases (-6%) in grain PC, the significant increase in grain yield due to FACE resulted in greater harvests of protein (+6%). This result is basically in agreement with previous results reported in the literature (Seneweera et al., 1996, 1997; Terao et al., 2005). The observed decrease in PC under FACE directly reduced the nutritional value of rice, but at the same time, increased the palatability of cooked rice: generally, low PC in the grains is closely associated with the improvement of taste properties (Ishima et al., 1974; Matsue et al., 1997). Our measurements of viscosity properties indicated that, corresponding to the change in AC, FACE grown plants showed a significant increase in peak viscosity (+5%) and breakdown (+3%), but a 28% significant decrease was recorded in setback (data not shown), all these effects on the three RVA pasting properties being considered to be a favorable changes for enhancing the sensory acceptability of cooked rice (Allahgholipour et al., 2006). Based on PC response to FACE, together with responses of AC and three RVA pasting properties (i.e. PV, MV and BD) mentioned above which are also involved in the sensory acceptability of cooked rice, we could therefore assume that the palatability should be improved in rice grown under elevated [CO_2]. Such a hypothesis needs to be confirmed by sensory evaluation.

4.7. Implications

The results of this study have important implications for formulating adaptation strategies of rice to achieve maximum productivity while maintaining desirable quality characteristics in a future high CO_2 word, at least for the similar conditions of this experiment. First, the current recommended rates of N fertilization (ca. 25 g N m^2 in China) for rice production systems should not be modified as the [CO_2] rises. Excessive N supply would not only reduce the rice yield and quality (Matsue *et al.*, 1997), but also induce bad environmental pollution (Ling et al., 1994). Secondly, it is likely that the rice cultivation technologies may need to be focused on regulations during the middle and late growth stages (e.g. increase N fertilizer proportion after PI, enhance irrigation management during MGS and use relevant plant growth regulator) in order to (1) enhance root growth and activities during middle growth stage, (2) facilitate nutrient (i.e., N, P) uptake after PI, and (3) increase the PTR and HI, but reduce the number of degenerated spikelets per panicle. However, additional experiments with different cultivars would be needed to develop N fertilizer strategies for high-yield cultivation under future elevated [CO_2] conditions.

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