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Full Length Research Paper

Yield components and its conformation responded to elevated atmospheric CO_2 in three rice (*Oryza sativa* L.) generations

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During three rice generations in Asominori (*Japonica*) and IR24 (*Indica*), the yield and its components — namely grain yield per plant, fertile tillers, 1000-grain weight, grain number per panicle — were greater under Free Air CO_2 Enrichment (FACE, 200 μmol $CO_2 \cdot mol^{-1}$ above current levels) than those under current CO_2 concentration (Ambient, about 370 μmol $CO_2 \cdot mol^{-1}$). And significant difference in generations, varieties, and CO_2 concentrations existed in the yield and its components of Asominori and IR24. For the third generation planted under FACE, the dry matter weight of a single main stem and its components in Asominori and IR24 were higher under FACE than those under Ambient from the date of anthesis to maturation. As compared with that under Ambient, dry weight per day, filling power and remobilized C reserve under FACE increased in Asominori and IR24, but the transfer ratio of assimilate and harvest index (HI) declined under FACE. The degree of response to FACE in Asominori and IR24 showed that a positive response to long term treatment of elevated CO_2.

Key words: CO_2 concentration, *Indica* rice, *Japonica* rice, yield, yield components.

INTRODUCTION

Globally, rice is the most important crop for humans in terms of direct consumption (Horie et al., 1997). The need for greater rice production is particularly urgent because the population of traditional rice producing countries will require 70% more rice by the year 2025 (International Rice Research Institute, 1993). Because of rice's importance, effects of ongoing regional and global environmental changes on rice yield (grain mass at maturity) need to be better understood. As an example, the energy production from fossil fuels has increased the CO_2 concentration of Earth's atmosphere from about 275 – 280 $\mu mol \cdot mol^{-1}$ to 370 $\mu mol \cdot mol^{-1}$ since 1750 and may reach 550 $\mu mol \cdot mol^{-1}$ by the middle of 21st century (Kobayashi, 2001). CO_2 is needed for plant photosynthesis. The increase in atmospheric CO_2 stimulates photosynthesis and has the potential to enhance the growth and yield of many agricultural crop species, including that of rice (Kimball et al., 2002). So, there is a need to determine how the predicted increase in the levels of atmospheric CO_2 will affect rice yield.

Over the last thirty years, in order to understand the effects of CO_2 enrichment on rice production, many studies have been carried out (Baker et al., 1990; Ziska et al., 1996; Moya et al., 1998; Nakagawa and Horie, 2000; Kim et al., 2001, 2003; Huang et al., 2002; Uprety et al., 2003; Baker, 2004; Yang et al., 2006 and 2007). Across all these studies, the increase in yield due to CO_2 enrichment (570 – 700 $\mu mol \cdot mol^{-1}$) ranged from 5 to 60%. The variation in increase was induced not only by environments (Ziska et al., 1996; Kim et al., 2001, 2003; Baker, 2004) but also by cultivar grown (Moya et al., 1998; Uprety et al., 2003; Baker, 2004). For instance, among the cultivars tested in Moya experiment, N-22 showed the greatest relative response of both yield and biomass to increasing CO_2, while NPT2 showed no response and IR72 was intermediate.

The above studies were conducted on rice grown for

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only a single generation or more frequently - less. There is little information on the extent to which plants show intergenerational differences in their response to elevated CO_2. A few studies with C_3 annuals indicated that elevated CO_2 may differentially affect growth across generations (Bezemer et al., 1998; Huxman et al., 1998; Ward et al., 2000) with potentially no further increases in plant biomass relative to first generational responses (Ward et al., 2000; Derner et al., 2004).

How about the rice yield if they were continued planted under increasing CO_2 concentration for several generations? The objective of this study was to determine responses of three generations of two genotypes of rice yield to CO_2 enrichment under FACE and dry matter accumulation and transformation during grain filling on third generation.

MATERIALS AND METHODS

Study site and experimental layout

The Chinese rice FACE (Free Air CO_2 Enrichment) facilities were located at Anzhen village (120°27' 51'' E, 31°37' 24'' N), Wuxi city during 2002 - 2003 and were transferred to Xiaoji village (119° 42' 0'' E, 32°35' 5'' N), Yangzhou city in 2004, in Jiangsu Province, East China. Both sites are on a typical region for rice production in China. In Anzhen village, soil was classified as Stagnic Anthrosols (local name: huangni soil), annual precipitation 1100 - 1200 mm, annual average temperature 16°C, annual sunshine time 2000 h and frostless days 230 d. Though in Xiaoji village the soil was also Stagnic Anthrosols (local name: xiajiang soil), the local conditions are slightly different: annual precipitation 1000 - 1100 mm, annual average temperature 14.6°C, annual sunshine time 2000 h and frostless days 230 d.

There were three ambient rings and three FACE rings (ambients + 200 $\mu mol \cdot mol^{-1}$). The distance between FACE and ambient rings were more than 90 m to minimize FACE's influence on ambient plots. Pure CO_2 was sprayed on the FACE rings through laser-drilled holes in tubes 50 cm higher than rice canopy. CO_2 concentration in the FACE rings was automatically controlled at 200 $\mu mol \cdot mol^{-1}$ above ambient CO_2 concentration.

Crop history

Asominori (*Japonica,* a local Japanese variety) and IR24 (*Indica,* a variety from the International Rice Research Institute) were the parents of chromosome segment substitution lines for quantitative trait loci in our experimental group. We understood their agronomic traits and genetic background; hence, we chose these two cultivars as research materials.

25d rice seedlings grown under ambient air were transplanted by hand to the plot from the year 2003 to 2005. Though nearly all local farmers use machines for planting, we used hand transplanting to ensure an even number of seedlings per hill and regular hill spacing. Plantation density was 24 hills m^{-2} with each hill 3 seedlings. The seedlings under FACE in 2004 and 2005 were planted from the seeds harvested from the previous year's FACE.

During three field years, the same amount of fertilizer was added. N was supplied as urea (NH_2CONH_2) (85%) and $(NH_4)_2HPO_4$ (15%) at 250 kg N ha^{-1} (normal N supply for local rice fields) with 40% of N supplied as a basal dressing -20% on the fifth day after transplanting and 40% at the panicle initiation stage. Phosphorus was applied at 75 kg P_2O_5–ha^{-1}. The soil was flooded before transplanting and the water layer of 5 cm above soil level was maintained except when the field was drained several times.

With the exception of using hand transplanting to establish the crops, all other agronomic techniques including cultivation, hill spacing, fertilizer application and pest management were similar to those used by the local farmers.

Sampling, harvesting and yield determination

80 panicles on the main stem were tagged on the same flowing day for each treatment. Fifteen tagged main stems were sampled every 15 d from anthesis to maturity. Panicle, straw and leaves on each main stem were separated to dry at 80°C to constant weight and weight. The main stem sampled at flowering day was also used to analyze the content of nonstructural carbohydrate as described by Yang (2003).

To determine yield, 12 hillers of rice were harvested when grain matured (45 d after heading). After air drying for one month, panicle number per plant was counted and the grain threshed carefully. Fertile spikelets were selected based on weight using an airflow method and counted. The dry weight of fertile spikelets was determined by every thousandth grain. Grain yield per plant was the product in number of fertile tiller per plant × average grain number per panicle × single grain weight (calculated from 1000-grain weight). Harvest Index (HI) was calculated based on grain mass divided by aboveground biomass at harvest.

Statistical analysis

ANOVA was used to determine differences between FACE and Ambient. Hypotheses about the effects of generations in addition to levels of CO_2 and cultivars were tested using the GLM procedure provided by the SAS Institute in our university. All results reported as significant had a $P < 0.05$.

RESULTS

FACE had positive effects on yield per plant, fertile tillers, grain number per panicle and 1000-grain weight in Asominori and IR24 during three generations (Figure 1 and Table1). FACE significantly increased yield per plant in Asominori and IR24 during three generations but the increased ranges varied. The increased ranges of Asominori showed the first generation (42.48%) > the second generation (21.52%) ≈ the third generation (23.45%). However, IR24 showed the first generation (43.66%) > the second generation (38.38%) > the third generation (33.21%).

For the first generation, FACE significantly enhanced fertile tillers in Asominori and IR24 but for the other two generations, only Asominori significantly increased on the third generation. The increased ranges in Asominori showed the first generation (23.33%) > the third generation (10.57%) > the second generation (5.58%). For IR24, the ranges showed the first generation (41.42%) > the second generation (6.05%) ≈ the third generation (5.35%).

FACE significantly increased grain number per panicle in Asominori and IR24 during three generations, contributing most to the yield increase due to FACE

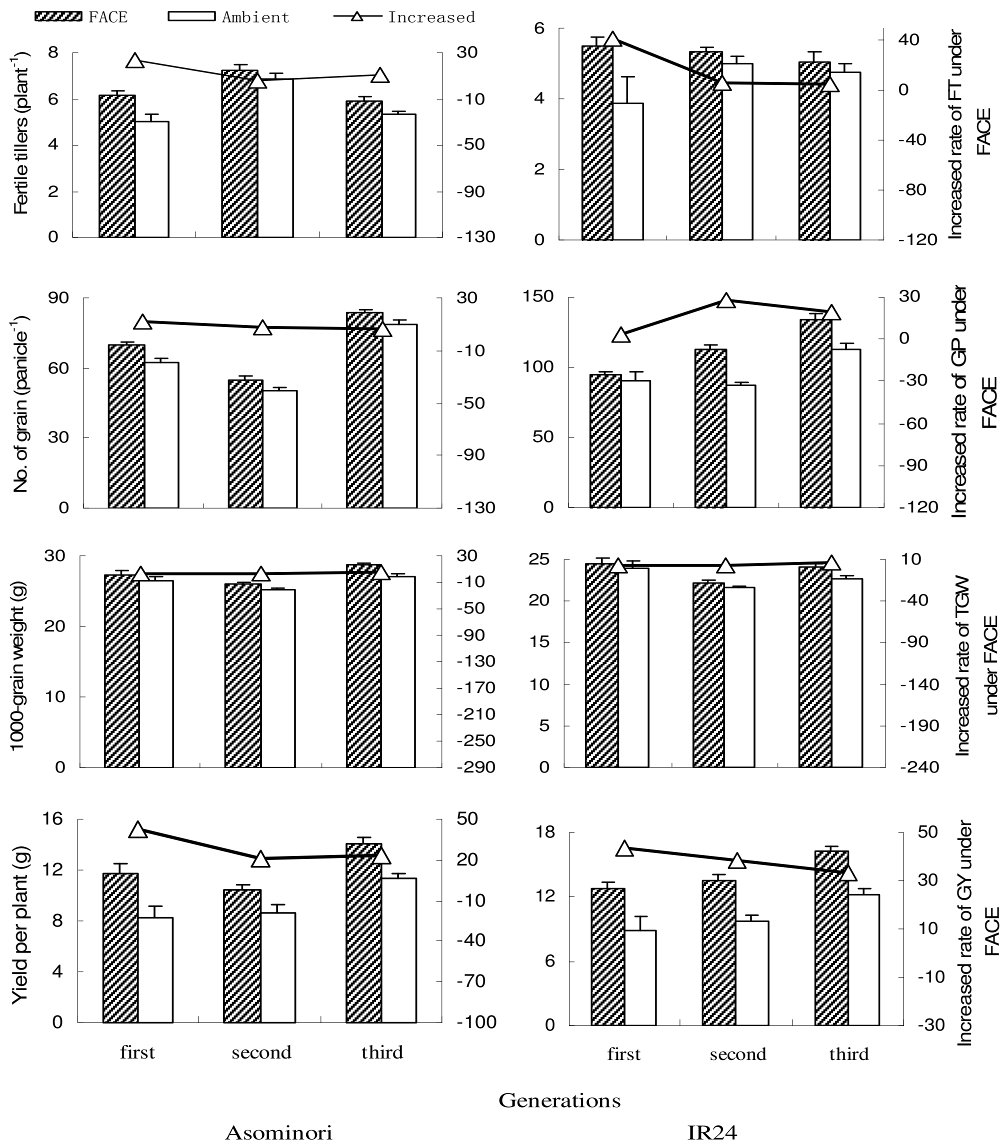

Figure 1. Effect of FACE to yield and its components in Asominori and IR24. FACE: 570 μmol·mol^{-1} in CO_2 concentration; Ambient: 370 μmol·mol^{-1} in CO_2 concentration. Note: First generation was the rice planted under the first year FACE. Second or third generation was the rice from the previous year's FACE seeds.

except for IR24 in the first generation. The increased ranges of Asominori showed the first generation (11.75%) > the second generation (8.18%) > the third generation (6.05%); However, IR24 showed the first generation (3.76%) < the second generation (28.39%) > the third generation (19.57%) and the third generation > the first generation.

FACE had insignificant increase in 1000-grain weight of Asominori and IR24 for the first and second generation, but FACE had significant increase in Asominori and IR24 on the third generation. The increased ranges in Asominori were the first generation (3.38%) ≈ the second generation (3.30%) < the third generation (6.12%), IR24 was the first generation (2.52%) < the second generation (3.16%) < the third generation (5.88%).

During three generations, we found yield per plant and its components had the significant difference existing for two rice cultivars (Cul), three generations (Gen) and two levels of atmospheric CO_2 ([CO_2]). The only exceptions are for the 1000-grain weight on generations. However, the difference between Cul × [CO_2], Cul × Gen, [CO_2] × Gen and Cul × [CO_2] × Gen were different in yield and its components. Yield per plant was not influenced by the interaction of Cul, Gen and [CO_2] but grain number per panicle was completely influenced by the interaction of Cul, Gen and [CO_2]. Fertile tiller was influenced by Cul ×

Table 1. Analysis of variance on rice yield per plant and its components under FACE and Ambient.

Trait	Grain Yield ($GY, plant^{-1}$) (g)	Fertile tillers ($FT, plant^{-1}$)	Grain number ($GP, panicle^{-1}$)	1000-grain weight (TGW, g)
Cultivar (Cul)	**	**	**	**
Level of CO_2 ([CO_2])	**	**	**	**
Generation (Gen)	**	**	**	ns
Cul × [CO_2]	ns	ns	**	ns
Cul × Gen	ns	**	**	**
[CO_2] × Gen	ns	*	**	ns
Cul × [CO_2] × Gen	ns	ns	**	ns

Note: ** and * indicated significant variation at level of $p \leq 0.01$ and $p \leq 0.05$；ns refer to non-significance.

Gen and [CO_2] × Gen while 1000-grain weight only was influenced by Cul × Gen.

Accumulation, translocation and transformation rate of dry matter during grain filling

Accumulation of dry matter during grain filling

FACE enhanced accumulation of dry weight in single straw, panicle and main stem of Asomonori and IR24 during heading date to maturation (Figure 2). However, the rate of increased dry weight was different for the part of the plant, cultivars and the date of grain filling. In the straws of Asomonori and IR24, the rate of increased dry weight was as such: on heading date (36.66%, 34.06%) > 30 d after heading (34.54%, 33.56%) > 45 d after heading (31.56%, 28.31%) > 15 d after heading (8.41%, 25.52%). In the panicles of Asominori, the rate of increased dry weight was as such: 15 d after heading (30.51%) ≈ 45 d after heading (30.60%) > 30 d after heading (16.66%) > heading date (4.85%). But for IR24, it was: 45 d after heading (40.76%) > heading date (37.09%) > 30 d after heading (31.84%) > 15 d after heading (18.12%). The main stem of Asominori had these results: 45 d after heading (28.19%) ≈ heading date (27.83%) > 30 d after heading (24.74%) > 15 d after heading (18.08%), IR24 was 45 d after heading (37.55%) > 30 d after heading (32.22%) > 15 d after heading (19.47%) > heading date (16.20%).

Translocation and transformation of dry matter during grain filling

FACE had positive effects on flag leaf area, the soluble carbohydrate of straw and sheath on heading date (NSC), dry weight per day, filling power, and remobilized C reserve but negative effects on transfer ratio of assimilation and harvest index in Asominori and IR24 (Table 2). FACE significantly increased flag leaf area in Asominori (14.33%) and IR24 (33.38%). The degree of increase in IR24 was greater than that for Asominori. These indicated IR24 had bigger sources to synthesize photosynthesis production than that of Asominori under FACE.

For Asominori and IR24, FACE significantly improved dry weight per day (28.74%, 76.17%) and filling power (37.93%, 41.44%), but had insignificant increase in remobilized C reserve (10.78%, 24.78%). The degree of increase in IR24 was also greater than that for Asominori. These showed that accumulation and translation of assimilation in IR24 were higher than that of Asominori under FACE.

FACE had insignificant reduction in transfer ratio of assimilation (-11.55%, -10.83%) and harvest index (-6.19%, 4.69%) in both Asominori and IR24 though the reduction is less for IR24. These indicated economic transformation was not improved with higher accumulation of assimilation but rather was worsened.

DISCUSSION

Three generational yield components in rice responded to elevated CO_2 by exhibiting intriguing trends. There was substantial variation in the absolute values of yield per plant and its components. This variation was most likely caused not only by year-to-year differences in weather variables such as air temperature and incident solar radiation but also importantly by the seed harvested from previous year's FACE. Because the significant interaction between generations existed in yield components except for the 1000-grain weight.

Derner (2004)'s research in wheat showed CO_2 enrichment on seed created a compositional change (higher C:N ratio) that contributed to greater seedling growth in generations. However, greater seedling growth in generations did not result in greater plant production for either ambient or elevated CO_2 concentrations, but instead reduced the plant size and production from the first to third generation. Our results in three generational yield per plant of Asominori and IR24 at maturation were in lines with Derner's research in wheat, namely the

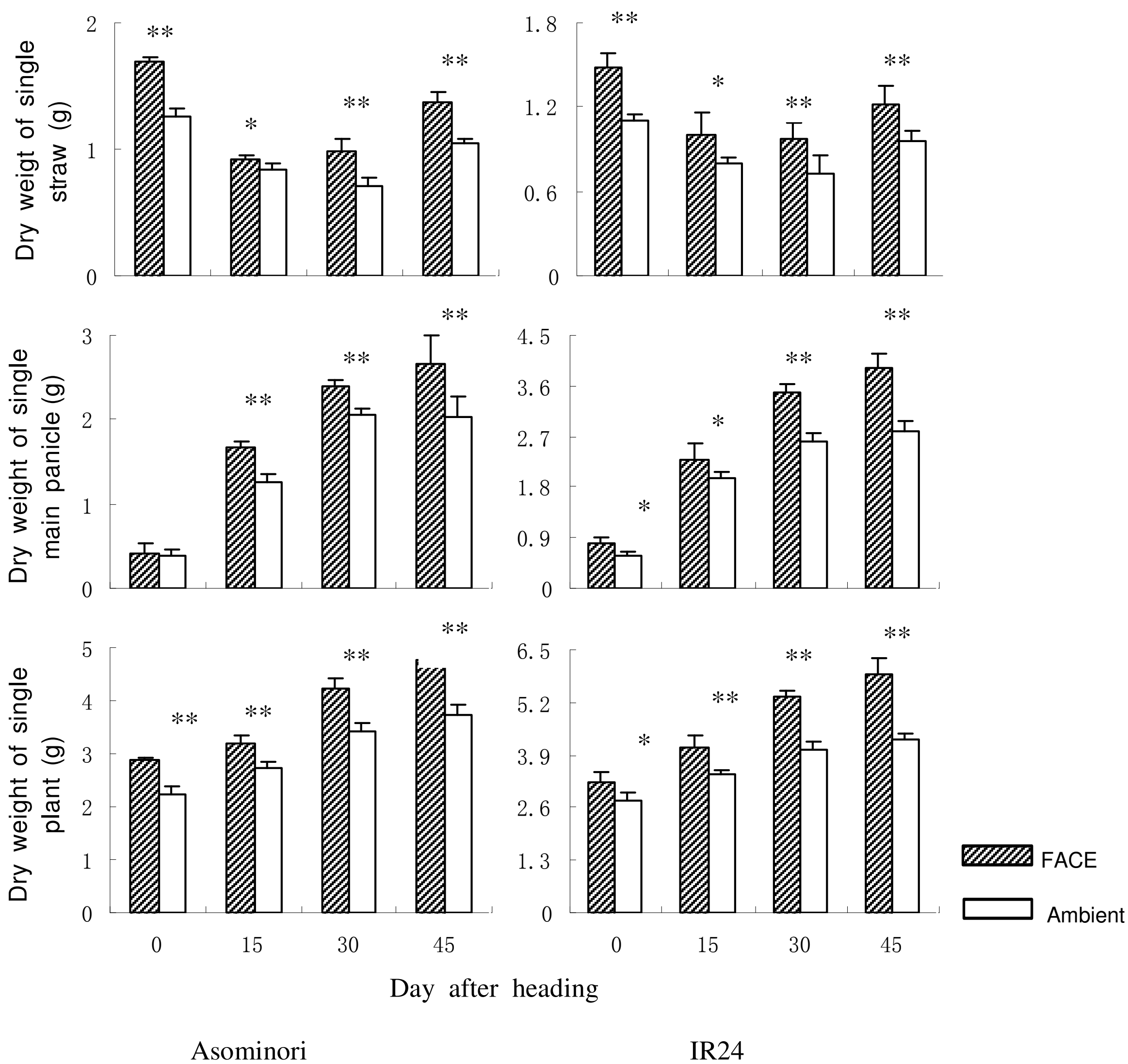

Figure 2. Effect of FACE to dry weight of Asominori and IR24 from heading date to maturity. Note: 0 indicates heading date. 15, 30 and 45 indicates the days after heading date. Symbol ** and symbol * indicates significant variation between FACE and Ambient at level of p ≤ 0.01 and p ≤ 0.05, respectively.

increasing rate of yield per plant under FACE in second and third generation were lower than that of the first generation (Figure 1). This result may be attributable to a compensatory response to limited growing conditions such as the relatively nutrient-poor soil used. Because the fertilizer was the same during three experimental years, greater seedling growth in generations must need more nutrition to satisfy their growth. When nutrition was poor the growth was limited. Studies about the relation of yield, nutrition and CO_2 enrichment further explained our hypothesis (Kobayashi and Horie, 1994; McKee and Woodward, 1994; Ziska et al., 1996; Kim et al., 2003; Yang et al., 2006).

1000-grain weight in Asominori and IR24 in addition to grain number per panicle in IR24 showed the increasing rate under FACE in second or third generation was greater than that of the first generation. This phenomenon is mostly likely the result of acclimation to CO_2 enrichment. Under FACE, leaf areas were enlarged and more carbohydrate was accumulated in organs of rice such as leaf and stem (Table 2). Because the plant has the ability to regulate between source and sink, the sink (grain number and weight) will broaden with enlarged source (leaf) (Paul and Foyer, 2001). In spite of enlarged source and sink, yield per plant in second and third generation was still lower than that of first generation. Aside from the above poor nutrition, when further analysis of accumulation and transfer in dry weight were done, we found FACE improved dry weight per day, filling power and remobilized C reserve. However, it also reduced the transfer ratio of assimilation and harvest index. Clearly, FACE enhanced the accumulation of assimilation

Table 2. Translocation and transformation rate of dry matter production in rice under FACE.

Trait	Asominori			IR24		
	FACE	Ambient	Increased	FACE	Ambient	Increased
Flag leaf area (cm^{-2})	31.70±2.59	27.16±3.09	14.33%**[a]	46.77±5.08	30.92±3.44	33.88%**
NSC (mg/g)=	256.38±21.45	218.97±20.72	17.08%*	259.42±29.78	204.16±20.72	27.06%*
Dry weight per day ($mg \cdot stem^{-1} \cdot d^{-1}$) (45 d)	47.6	37.0	28.74%**	59.8	34.0	76.17%*
Filling power ($mg \cdot stem^{-1}$)	56.2	40.8	37.93%**	73.1	51.7	41.44%*
Remobilized C reserve (%)	18.85%	17.02%	10.78%	17.07%	13.68%	24.78%
Transfer ratio of assimilation (%)	30.14%	41.69%	-11.55 %	54.64%	65.43%	-10.83%
Harvest index (%)	0.52±0.03	0.55±0.02	-6.19%	0.61±0.03	0.64±0.05	-4.69%

Note: Symbol **and symbol * indicates significant variation at level of $p \le 0.01$ and $p \le 0.05$, respectively. Symbol = indicates the soluble carbohydrate of straw and sheaths on heading date (NSC). Some clarifications of abbreviations: dry weight per day($mg \cdot stem^{-1} \cdot d^{-1}$) = (Dry weight at mature –Dry weight at heading)/days after heading, filling power ($mg \cdot stem^{-1}$) = (Dry weight of panicle at maturity—Dry weight of panicle at heading)/ days after heading, remobilized C reserve (%) = (dry weight of stems and sheaths at anthesis —dry weight of stems and sheaths at maturity)/ dry weight of stems and sheaths at anthesis, and transfer ratio of assimilation (%) = (panicle weight at maturity —panicle weight at anthesis)/ [NSC in straw and sheaths at anthesis × dry weight of single stem + (dry weight of plant at maturity —dry weight of plant at anthesis)] ×100.

and the translocation from source (leaf or stem) to sink (panicle). Similar findings were also reported for rice (Sasaki et al., 2005). However, economic transformation was not improved with higher accumulation and translocation of assimilation. The reason for ineffective transfer may be the obstacle in structure of transport tissue, especially at node of panicle or the grain had the lower ability to "absorb and transfer" assimilation from photosynthesis (Yang et al., 1997). A similar reduction in HI with elevated CO_2 has also been reported for wheat (Hakala, 1998) and rice (Kim et al., 2003).

Additionally, there is genetic variation within species that results in different responses to elevated CO_2 (Yelle, 1989; Moyer et al., 1998; Batts et al., 1998; Uprety et al., 2003; Baker, 2004). In our study, we found the genetic variation between Asominori and IR24 in responses to elevated CO_2, most notably in the third generation. There were significant interactions between two cultivars in yield per plant and its components during three generations. The increased yield per plant in IR24 was mainly induced by grain number per panicle but for Asominori it was mainly induced by fertile tillers. In increasing rate of yield per plant, the degree of IR24 response to FACE was greater than that of Asominori. It indicated IR24 had a greater potential to increase yield under future CO_2 enrichment environment.

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