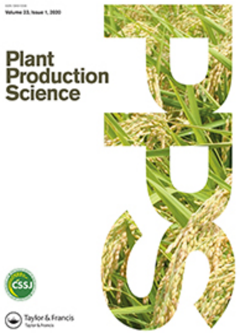

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Analysis of factors related to varietal differences in the yield of rice (*Oryza sativa* L.) under Free-Air CO_2 Enrichment (FACE) conditions

Satoshi Yoshinaga[a], Takeshi Tokida[b], Yasuhiro Usui[b], Hidemitsu Sakai[b], Hirofumi Nakamura[c], Toshihiro Hasegawa[b], Hiroshi Nakano[a], Yumiko Arai-Sanoh[a], Tsutomu Ishimaru[a], Toshiyuki Takai[a] and Motohiko Kondo[a]

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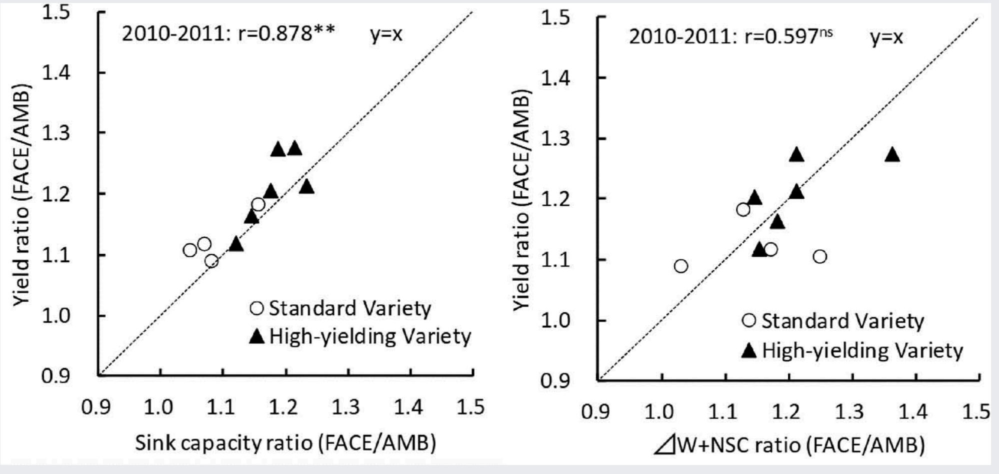
ABSTRACT

Enhancing crop traits that increase grain yield under elevated CO_2 concentrations is an important option for increasing the future productivity of rice. Here, we compared the growth and yield of five varieties with different genetic background under Free-Air CO_2 Enrichment (FACE) conditions to identify traits responsible for varietal differences in yield increase under elevated CO_2. Three high-yielding and two standard rice varieties grown under FACE conditions commonly had (1) shorter growth periods, (2) higher dry matter production, (3) higher numbers of spikelets (sink capacity) and panicles; and (4) higher yield than those grown under ambient CO_2. Yield enhancement by elevated CO_2 (FACE/Ambient), however, differed significantly among varieties, ranging from 1.10 to 1.25. The greater response of the sink capacity, defined as the product of spikelet number and single grain mass, was the main factor involved in yield increase. Three high-yielding varieties (Momiroman, Takanari, and Hokuriku 193) had greater sink capacity than two standard varieties and the sink capacity of these varieties significantly increased under FACE condition. However, yield enhancement in elevated CO_2 was lower in Hokuriku 193 than in Momiroman and Takanari. In Hokuriku 193, sink production was relatively low while dry matter production was similar to the others. Therefore, larger increase in sink production efficiency per unit of dry matter production under FACE was found to be a particularly important varietal trait, suggesting that efforts to develop varieties suited to the predicted elevated CO_2 condition should focus on this and the related traits.



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1. Introduction

Atmospheric CO_2 concentration, which stood at 280 ppm 200 years ago, has risen constantly in recent years; it currently stands at approximately 400 ppm, and is expected to rise further to 550 ppm around 2050 unless strict mitigation measures are implemented (Meinshausen et al., 2011). The rise in CO_2 concentration not only increases temperatures but is also expected to seriously affect food production. Increase in dry matter production, as a result of enhanced photosynthesis has been reported as an effect of rising CO_2 levels on crop yield, but the degree of this increase differs

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among crop species (Ainsworth & Rogers, 2007; Ziska et al., 2012). To increase food production while addressing climate change and population growth, we need to pinpoint characteristics of crops adapted to future environments.

Rice is one of the world's most important crops, and its consumption is growing, notably in low-income countries (GRiSP, 2013). However, the current rate of yield increase in rice will be insufficient to meet the growing food demand (Ray, Mueller, West & Foley, 2013). Our ability to maintain stable food production will depend on the development of production techniques for ensuring stable rice production and the breeding of varieties that produce high yields under elevated CO_2 concentrations. This in turn urgently requires the identification of traits related to yield stabilization under elevated CO_2 conditions.

Precise evaluation of crop growth response to elevated CO_2 concentrations requires field experiments with crop communities. Free-air carbon dioxide enrichment (FACE) is an evaluation method developed in the late 1980s that involves elevating CO_2 levels in open-air plant communities (Kobayashi, 2001). The method has since been used to conduct experiments on rice and many other crop species (Long, Ainsworth, Rogers & Ort, 2004). Examples of FACE experiments include studies conducted on rice in cool northern regions of Japan from the late 1990s up to 2008 and later resumed in the Kanto region (central Japan) in 2010. Similar studies have also been carried out in China since 2000 (Yang et al., 2007).

Numerous researches have been conducted in recent years on rice growth and yield under elevated CO_2 conditions, and shown that rice biomass and yield increase under FACE (Kim et al., 2003; Yang et al., 2006, 2007; Liu et al., 2008; Shimono et al., 2009; Hasegawa et al., 2013, 2015; Usui et al., 2016) and growth chambers (Baker, 2004; Kim, Horie, Nakagawa & Wada, 1996b; Moya, Ziska, Namuco & Olszyk, 1998; Sasaki et al., 2005; Yoshida, Horie, Nakazono, Ohno & Nakagawa, 2011; Ziska, Manalo & Ordonez, 1996). Most of the reports showed that the yield increase was mainly due to an increase in the number of spikelets (Kim et al., 2003; Yang et al., 2006; Liu et al., 2008; Hasegawa et al., 2013, 2015; Usui et al., 2016; Yoshida et al., 2011). The magnitude of yield increase reportedly differs significantly among varieties. Ziska et al. (1996) showed that yield increase under elevated CO_2 levels ranged from −7% to 76% in their growth chamber experiments. FACE studies have demonstrated yield increases from 3% to 18% for four varieties (Shimono et al., 2009), 3% to 36% for eight varieties (Hasegawa et al., 2013), 3% to 30% for four varieties (Sakai, Tokida, Usui, Nakamura & Hasegawa, 2019) and equaling 34% for an F_1 hybrid *Indica* variety (Liu et al., 2008).

The yield response to elevated CO_2 was found to be greater for varieties that had greater responses in biomass and nitrogen uptake (Sakai et al., 2019; Shimono et al., 2009) or in sink capacity often represented by the number of spikelets (Hasegawa et al., 2013, 2015; Yoshida et al., 2011). The number of spikelets is strongly influenced by both nitrogen nutrition and dry matter accumulation during the reproductive growth phase (Kobayasi & Horie, 1994), but the genetic variability of these traits in response to elevated CO_2 remains poorly understood. Thus, in order to determine the factors related to varietal differences in the yield response to elevated CO_2, the evaluations of the interactions between yield and 1) biomass production, 2) nitrogen uptake, 3) sink production is important, using diverse varieties differing in these characteristics are necessary.

In recent years, various high-yielding varieties including *japonica-indica* hybrids have started to be cultivated in Japan for use as animal feed or rice flour (Yoshinaga, Takai, Arai-Sanoh, Ishimaru & Kondo, 2013). Given that the photosynthetic ability, biomass and sink production potentials of these varieties are considerably greater than those of standard varieties (Yoshinaga et al., 2013), they may well possess traits that are also advantageous for boosting yields under elevated CO_2 levels.

Therefore, in this study, we compared the growth under elevated CO_2 conditions of both standard and recent developed high-yielding varieties in Japan to identify traits responsible for differences in rice yield, with the eventual aim of developing cultivation techniques and varieties suited to the predicted elevated CO_2 conditions.

2. Materials and methods

2.1. Field experimental details

Field experiments were conducted in the Tsukuba FACE site which was established in farmers' rice fields in Tsukubamirai City, Ibaraki prefecture in Japan (35°58′N, 139°60′E) from 2010 to 2011. The soil is a Fluvisol, which is typical of alluvial areas. Five Japanese rice (*Oryza sativa* L.) genotypes with different genetic background, Koshihikari, Nipponbare, Momiroman, Takanari, and Hokuriku193 were grown under irrigated conditions. Nipponbare and Koshihikari are previous and current representative conventional *japonica* varieties which are popular for the consumption eaten as boiled rice in Japan. The cultivated areas of Nipponbare had been largest in the 1970s and those of Koshihikari have been largest from the late 1970s to the present. The others are multipurpose varieties which were developed as high-yielding, and used for flour and/or animal feed. In this report, Takanari and

Hokuriku 193 were defined as *indica*-dominant varieties, Momiroman were defined as *japonica*-dominant varieties, based on the results in Yamamoto et al. (2010).

Seeds were sown in a seedling nursery box, and 30-day-old seedlings were transplanted, with three seedlings per hill, on 26 May in 2010 and 25 May in 2011. The planting density was 22.2 hills m^{-2}, with 30-cm row spacing and 15-cm intra-row spacing. Nitrogen fertilizers were supplied with urea and controlled release fertilizers (Type LP40, LP100 and LP140 polyolefin-coated urea, JCAM AGRI Co. Ltd., Japan Tokyo). The LP40, LP100, and LP140 fertilizers release 80% of their total nitrogen content at a uniform rate until 100 and 140 days after application, respectively, at temperatures between 20°C and 30°C. For all the varieties, the basal application contained 12 g N m^{-2} (3 g from urea, 6 g from LP100 and 3 g from LP140). The top-dressing provided 4 g N m^{-2} (from LP40) with the exception of Koshihikari due to its lower lodging resistance. Basal fertilizers were applied about 1 week before transplanting, and plots were top-dressed about 30 days before heading at the neck-node differentiation stage. Phosphorus and potassium (10.0 g P_2O_5 m^{-2} and 10.0 g K_2O m^{-2} as fused fertilizer) were applied to all plots before puddling. Weeds, insects, and diseases were controlled by using standard herbicides and pesticides as required to avoid yield loss. The experimental plots were arranged in a split-plot design (main and subplots were CO_2 concentration and variety, respectively) with four replicates. The size of each plot was 3.4 m^2.

2.2. CO_2 treatment

Atmospheric CO_2 concentration in FACE experiment were controlled as described by Nakamura et al. (2012). Average atmospheric CO_2 concentration during growth duration in FACE plots were 584 μmol mol^{-1} in 2010 and 560 μmol mol^{-1} in 2011 and that in ambient plots was 386 μmol mol^{-1} in 2010 and 379 μmol mol^{-1} in 2011.

2.3. Measurement of dry matter production, nitrogen uptake, and NSC contents

Plants were sampled at the full-heading stage and the maturity. The full-heading date was defined as the date when about 80% of panicles in a canopy had emerged. Nine and 6 hills were sampled at full-heading and matured stage from each plot. Among them, two representative hills with average number of panicles, were selected and separated into four parts: leaf blades, leaf sheaths and culms, panicles, and dead parts. The weights of each part and of the entire plants were measured after drying for 72 h at 80°C.

Each dried sample was ground to a powder with a vibrating sample mill (TI-1001, CMT Co., Tokyo, Japan) for measuring nitrogen and non-structural carbohydrates (NSC) contents. The nitrogen content was measured by the Dumas combustion method (NCH analyzer, Sumika Chemical Analysis Service, Tokyo, Japan). The NSC contents of the stems and leaf sheaths were measured by the gravimetric method (Ohnishi & Horie, 1999).

2.4. Yield and yield components

At maturity, plants from 12 hills (0.72 m^2) of each plot were harvested for the determination of yield and yield components. After the panicle number was counted, the panicles were threshed and the unhulled and hulled rice were weighed to measure the rough grain and hulled grain yields. Then, grains were screened by a grain sorter; the sieve size of the sorter was changed depending on the grain shape and size of each variety, namely 1.7 mm for Koshihikari, Takanari, and Hokuriku 193 with relatively longer grains, 1.8 mm for Nipponbare and Momiroman with medium grains. The 1000-grain weight was calculated using screened hulled grain. The rough grain yield, hulled grain yield, and 1000-grain weight were adjusted to 14% moisture content.

Forty to 80 g of subsample was selected from rough grain, using Sample Divider (Fujikinzoku, Tokyo, Japan). The number of spikelets per unit area was calculated as the number of spikelets of the subsample divided by the subsample weight and multiplied by the weight of the total amount of unhulled grain per unit area. The number of spikelets per panicle was calculated as the number of spikelets per area divided by the number of panicles per area. Sink capacity was defined as single grain weight multiplied by the number of spikelets per area. The sink-filling rate was calculated as the hulled grain yield divided by sink capacity.

2.5. Statistical analysis

Analysis of variance (ANOVA) was performed using 'Statistix 9' (Analytical Software, FL, USA), according to the split-plot design (main plot CO_2 concentration, subplot variety) to assess varietal differences, the effects of CO_2 concentration and of varieties X CO_2 concentration interactions. The significance of mean values was analyzed using Tukey's test (0.05).

3. Results

3.1. Climate conditions and growth duration

The climate conditions in standard variety Nipponbare control plots during the growing seasons are shown in Table 1. In both years, mean temperatures and solar radiation were higher than climatic normals during the period from transplanting to heading and during the grain-filling period (heading to maturity). This trend was particularly conspicuous during the grain-filling period in 2010, when mean temperature was 3.3°C and solar radiation was 3.6 MJ m^{-2} d^{-1} above climatic normals. Heading occurred earlier under FACE conditions than under ambient conditions (AMB), with the full-heading stage being reached 1 to 3 days earlier and growth period for all five varieties being an average of 2 days shorter in FACE plots than AMB plots (Table 2).

Table 1. Climate condition of Nipponbare with ambient in experiment years.

	Mean temperature (°C)		Solar radiation (MJ m^{-2} d^{-1})	
Year	T-H	H-M	T-H	H-M
2010	24.0 (+1.9)	27.1 (+3.3)	18.7 (+2.5)	18.3 (+3.6)
2011	23.7 (+1.6)	24.7 (+0.9)	17.2 (+1.0)	15.8 (+1.1)

T: transplanting time, H: heading stage, M: maturity. Values in the parenthesis are the difference from the average of 1981–2010.

3.2. Dry matter production and nitrogen uptake

Data for dry matter production and nitrogen uptake for each variety in both experimental years are shown in Table 2. Aboveground dry weight was found to differ among varieties at full-heading and at maturity and was found to significant increase in FACE plots relative to the AMB plots. The 2 years mean FACE/AMB ratio of aboveground dry weight for all five varieties combined was 1.11 at full-heading and 1.15 at maturity, with no interaction being evident between CO_2 concentration and variety. Means for aboveground dry weight increase during grain-filling period (ΔW), accumulated NSC at full-heading, and the sum of these (ΔW+NSC) for all five varieties combined were also found to be significantly greater in FACE plots than in AMB plots, again with no evident interaction between CO_2 concentration and variety. ΔW+NSC in Takanari out of five varieties were found to be significantly larger in FACE plots than in AMB plots. In the case of nitrogen uptake, although those at maturity was found to increase significantly in FACE relative to AMB plots (FACE/AMB ratio 1.04) at a $P < 0.05$ level, the magnitudes of increase were less than those for aboveground dry weight. Significant differences in harvest index were found among varieties but not between FACE and AMB plots.

Table 2. Growth parameters of five rice varieties grown under ambient (AMB) and FACE.

				Aboveground dry weight (g m^{-2})		ΔW	NSC FH	ΔW+NSC	ΔW+NSC	Nitrogen uptake (g m^{-2})		
CO_2	Variety	Days to FH (days)	Growth duration (days)	FH	M	(g m^{-2})	(g m^{-2})	(g m^{-2})	ratio	FH	M	Harvest Index
AMB	Koshihikari	69 f	105 g	1070 e	1614 f	544 b	233 f	777 c		10.2 c	12.6 c	0.36 bc
	Nipponbare	78 b	117 d	1137 de	1703 ef	566 b	242 ef	808 bc		11.8 abc	14.3 abc	0.31 c
	Momiroman	77 b	124 a	1199 cde	1741 def	542 b	287 cd	828 bc		12.2 abc	13.9 abc	0.30 c
	Takanari	72 d	113 e	1120 de	1732 def	612 ab	267 def	879 bc		11.7 abc	14.5 abc	0.37 ab
	Hokuriku193	80 a	122 b	1523 b	2118 b	595 b	408 b	1003 ab		14.1 a	15.5 a	0.33 bc
FACE	Koshihikari	66 g	102 h	1214 cde	1806 de	617 ab	267 def	885 bc	(1.14)	10.3 bc	12.9 bc	0.35 bc
	Nipponbare	75 c	113 e	1251 cd	1899 cd	648 ab	282 cde	930 bc	(1.15)	12.3 abc	14.7 ab	0.31 c
	Momiroman	75 c	122 b	1338 c	1996 bc	658 ab	319 c	977 ab	(1.18)	12.7 ab	14.6 ab	0.32 bc
	Takanari	70 e	111 f	1236 cd	2062 bc	826 a	304 cd	1130 a	(1.29)	11.8 abc	15.9 a	0.38 a
	Hokuriku193	79 a	121 c	1687 a	2403 a	716 ab	456 a	1172 a	(1.17)	13.8 a	15.7 a	0.33 bc
AMB	Mean	75	116	1210	1781	572	287	859		12.0	14.1	0.33
FACE	Mean	73	114	1345	2033	693	326	1019		12.2	14.8	0.34
	ratio	(0.97)	(0.98)	(1.11)	(1.14)	(1.21)	(1.13)	(1.19)		(1.02)	(1.04)	(1.02)
ANOVA	Year (A)	**	**	**	ns	ns	**	ns		**	**	ns
	CO_2 (B)	**	**	**	**	**	**	**		ns	*	ns
	Variety (C)	**	**	**	**	*	**	**		**	**	**
	A X B	ns	ns	ns	ns	ns	**	ns		ns	ns	ns
	B X C	ns	ns	ns	ns	ns	ns	ns		ns	ns	ns
	C X A	**	**	**	**	ns	**	ns		ns	ns	**
	A X B X C	ns	ns	ns	ns	ns	ns	ns		ns	ns	ns

Data indicate the mean of 2 years with four replications. Days to FH: days from transplanting to the full-heading stage. Growth duration: days from transplanting to the maturity. ΔW: Increase of aboveground dry weight at grain-filling period. NSC: non-structural carbohydrates. Values in parentheses represent the ratio of FACE/AMB. Values within a column followed by the same letter are not significantly different at the 0.05 probability level by Tukey's test. * and **: significant at the 0.05 and the 0.01 level. ns: not significant by ANOVA. FH: full-heading. M: maturity.

3.3. Yield and relevant traits

Yields and yield components are shown in Table 3. The mean FACE/AMB ratio for rough grain and hulled grain yields for all five varieties combined under FACE conditions was 1.18 and 1.17. Rough grain and hulled grain yields in four out of five varieties were found to be significantly greater in FACE plots than in AMB plots. Interaction between variety and CO_2 concentration was also observed, with the FACE/AMB ratio for Takanari and Momiroman under FACE conditions being larger (>1.2) than those for the three other varieties. In yield components for all five varieties combined, the number of panicles and spikelets, sink capacity and sink filling rate all increased significantly in FACE plots. The number of spikelets and sink capacity of three high-yielding varieties were greater than those of standard varieties and significantly increased under FACE condition as evidenced by a significant interaction between CO_2 concentration and variety ($P < 0.01$). As with yield, the FACE/AMB ratio in sink capacity for Momiroman and Takanari were much larger compared with the three other varieties (Table 3).

To compare the effects of sink formation and source supply potential during grain-filling as factors responsible for boosting yield under FACE conditions, we analyzed the relationship between FACE/AMB ratios for yield and sink capacity, and the relationship between FACE/AMB ratios for yield and the sum of usable carbohydrates (ΔW + NSC) (Figure 1). Our results showed a very strong significant positive correlation between FACE/AMB ratios for yield and sink capacity, but no such correlation between yield and ΔW+NSC.

As described above, both dry matter production and sink capacity increased under FACE conditions. Whereas an interaction between CO_2 concentration and variety was observed for sink capacity, no such interaction was found for dry matter production and nitrogen uptake. Varietal differences for the effects of FACE on aboveground dry weight and sink capacity are shown in Table 4. While no significant varietal differences were found in actual increase of dry matter at full-heading under FACE conditions compared with those of AMB, clear varietal differences between varieties were observed in the actual sink capacity increase under FACE conditions compared with those of AMB, with significantly higher increases in the high-yielding varieties Takanari and Momiroman than in the standard varieties Koshihikari and Nipponbare. Takanari and Momiroman also showed higher sink production efficiency per unit of dry matter production (Sink capacity/Aboveground dry weight) than did the other varieties; in both high-yielding varieties, this measure significantly increased under FACE conditions compared to AMB. On the other hand, the sink production efficiency per absorbed nitrogen (Sink capacity/Nitrogen uptake) in Takanari and Momiroman didn't show significant difference compared with that of Koshihikari under both AMB and FACE condition.

Table 3. Yield and yield components of five rice varieties grown under ambient (AMB) and FACE.

CO_2	Variety	Rough grain yield (g m^{-2})	Hulled grain yield (g m^{-2})	Hulled grain yield ratio	Panicles (m^{-2})	no. of spikelet /panicle	no. of spikelet (X 10^3 m^{-2})	1000-grain weight (g)	Sink capacity (g m^{-2})	Sink capacity ratio	Sink filling (%)
AMB	Koshihikari	859 de	679 de		400 b	93 b	37.1 fg	22.3 cd	829 e		82.5 abc
	Nipponbare	813 e	634 e		413 b	85 b	34.8 g	22.7 bc	790 e		80.3 c
	Momiroman	878 de	655 de		238 e	178 a	42.4 cde	23.7 a	1004 bc		65.2 d
	Takanari	1004 bc	778 bc		282 d	167 a	46.5 bc	20.6 e	956 cd		81.4 bc
	Hokuriku193	1090 b	840 b		258 de	170 a	43.3 cd	22.8 bc	986 cd		85.4 a
FACE	Koshihikari	942 cd	745 cd	(1.10)	425 ab	93 b	39.8 def	22.2 d	885 de	(1.07)	85.0 ab
	Nipponbare	932 cd	729 cd	(1.15)	452 a	85 b	38.2 efg	23.1 b	882 de	(1.12)	82.7 abc
	Momiroman	1085 b	810 bc	(1.24)	276 d	183 a	50.2 b	23.6 a	1188 a	(1.18)	68.7 d
	Takanari	1266 a	970 a	(1.25)	321 c	179 a	57.0 a	20.5 e	1170 a	(1.22)	82.9 abc
	Hokuriku193	1244 a	958 a	(1.14)	283 d	174 a	49.0 b	22.8 b	1117 ab	(1.13)	85.9 a
AMB	Mean	929	717		318	139	40.8	22.4	913		78.9
FACE	Mean	1094	842		351	143	46.8	22.4	1048		81.0
	ratio	(1.18)	(1.17)		(1.10)	(1.03)	(1.15)	(1.00)	(1.15)		(1.03)
ANOVA	Year (A)	ns	ns		**	**	**	**	**		**
	CO_2 (B)	**	**		**	ns	**	ns	**		**
	Variety (C)	**	**		**	**	**	**	**		**
	A X B	ns	ns		ns	ns	ns	ns	ns		ns
	B X C	**	**		ns	ns	**	ns	**		ns
	C X A	**	**		**	**	**	**	**		**
	A X B X C	ns	ns		ns	ns	ns	*	ns		ns

Data indicate the mean of 2 years with four replications. Values within a column followed by the same letter are not significantly different at the 0.05 probability level by Tukey's test. Values in parentheses represent the ratio of FACE/AMB. * and **: significant at the 0.05 and the 0.01 level. ns: not significant by ANOVA. Sink capacity (g m^{-2}) = No. of spikelets (m^{-2}) × 1000-grain weight (g)/1000. Sink filling rate (%) = 100 × Hulled grain yield (g m^{-2})/Sink capacity (g m^{-2}).

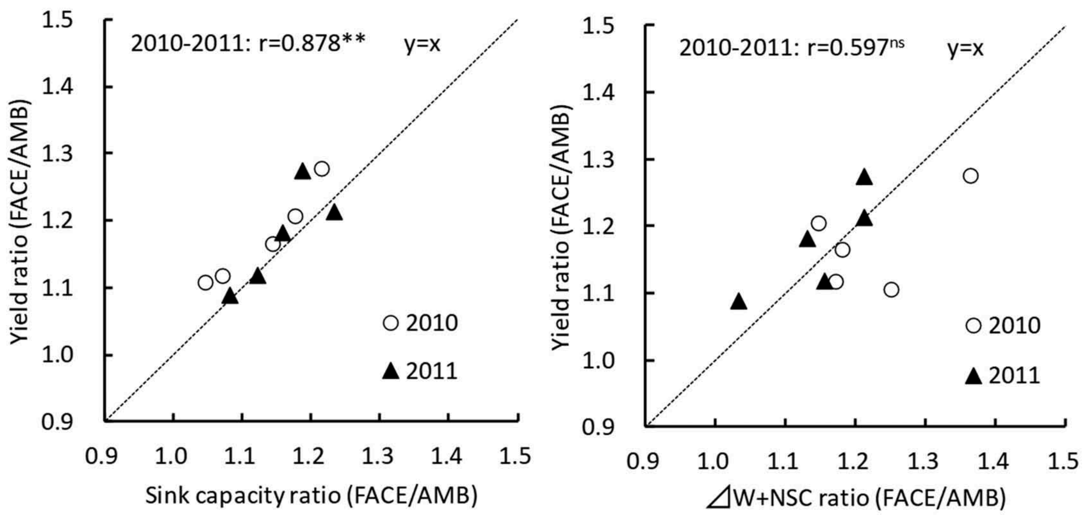

Figure 1. Effects of sink capacity and source accumulation on the change of yield under FACE condition.

Notes: Sink capacity (g m^{-2}) = No. of spikelet (m^{-2}) × 1000 grain weight (g)/1000. ΔW: Increase of aboveground dry weight at grain-filling period. NSC: non-structural carbohydrates at full-heading stage.

Table 4. Increase of aboveground dry weight and sink capacity in FACE, and sink production efficiency.

			Sink production efficiency			
	Difference (FACE-AMB)		Sink capacity/Aboveground dry weight (g g^{-1})		Sink capacity/Nitrogen uptake (g g^{-1})	
Variety	Aboveground dry weight (g m^{-2})	Sink capacity (g m^{-2})	AMB	FACE	AMB	FACE
Koshihikari	120	56 d	0.77 ab	0.73 b	81.4 a	85.7 abc
Nipponbare	114	91 cd	0.70 bc	0.71 b	67.2 b	71.9 c
Momiroman	114	184 ab	0.82 a	0.89 a	82.1 a	93.1 ab
Takanari	116	214 a	0.85 a	0.95 a	81.9 a	99.9 a
Hokuriku193	164	131 bc	0.65 c	0.67 b	70.1 ab	81.0 bc
Mean	126	135	0.76	0.79	76.5	86.3
CO_2 (A)	-	-	ns		**	
Variety (B)	ns	**	**		**	
A × B	-	-	*		ns	

Data indicate the mean of 2 years with four replications. Values of aboveground dry weight and nitrogen uptake are those at full-heading. Values within a column followed by the same letter are not significantly different at the 0.05 probability level by Tukey's test. * and **: significant at the 0.05 and the 0.01 level. ns: not significant by ANOVA. Values with underline are significantly larger sink production efficiency in FACE than AMB at the 0.05 probability level by t-test.

4. Discussion

In this study, rice plants grown under FACE conditions had (1) shorter growth periods, (2) higher dry matter production, (3) higher numbers of spikelets (sink capacity) and panicles; and (4) higher yield. Among these traits, interactions between CO_2 concentration and variety were significant for sink capacity and yield.

4.1. Changes in the growth

As with the results of previous reports (Hasegawa et al., 2013; Kim, Horie, Nakagawa & Wada, 1996a), FACE induced earlier heading and reduced the growth period by an average of 2 days. In general, a shorter growth period results in lower dry matter production. However, in this study, aboveground dry weight in FACE plots exceeded that in AMB plots at the same growth stage, compensating for the effects of shorter growth period.

As shown in Table 2, no interaction was observed between CO_2 concentration and variety for aboveground dry weight under FACE conditions, and as shown in Table 4, no differences were observed between varieties for increase of aboveground dry weight in FACE. Dry matter increase was also the main growth response reported in previous FACE studies (Hasegawa et al., 2015; Kim, Lieffering, Miura, Kobayashi & Okada, 2001; Usui et al., 2016; Yamakawa, Saigusa, Okada & Kobayashi, 2004; Yang et al., 2009; Yoshimoto, Oue & Kobayashi, 2005) and was attributed to accelerated single leaf photosynthetic rate under elevated CO_2 conditions. In a study comparing Koshihikari, Nipponbare, and Takanari (Ohsumi et al., 2007), Takanari showed high stomatal conductance, suggesting high single leaf photosynthetic rate. In our study, the fact that we did not observe significant interaction between CO_2 concentration and variety in aboveground dry weight (Table 2) suggests that high stomatal conductance in Takanari (Chen et al., 2014; Ikawa et al., 2017) have little impact on the response in dry matter productivity to FACE conditions. Also, ΔW and NSC at the full-heading stage, both traits that are directly involved in grain-filling, increased under FACE conditions. The increase of aboveground dry weight at full-heading was largely due to the increase in the dry weight of culm and leaf sheath (data not shown). It might contribute to the increase in NSC accumulated at full-heading (Table 2).

Meanwhile, insignificant increase in nitrogen uptake was observed at full-heading despite the fact that aboveground dry weight increased under FACE conditions. Although a significant increase in nitrogen uptake under FACE conditions was observed at maturity, the magnitude of this increase was small compared with the increase in aboveground dry weight (Table 2). This imbalance between dry weight and nitrogen uptake is consistent with the results of previous studies (Ma et al., 2007; Yamakawa et al., 2004), but it effectively means that the nitrogen content of rice plants and hulled grains are reduced. Because a decrease in the nitrogen content of rice plants and hulled grains can cause reduction in grain quality especially at the high-temperature conditions (Usui et al., 2016; Yang et al., 2007), fertilizing regimens will likely need to be reviewed to ensure stable quality under FACE conditions.

4.2. *Factors behind varietal differences in yield increases under FACE conditions*

Many studies have reported yield increases under FACE conditions (Kim et al., 2003; Yang et al., 2006, 2007; Liu et al., 2008; Shimono et al., 2009; Hasegawa et al., 2013, 2015; Usui et al., 2016) and have attributed this increase to an increase in the number of spikelets. This study also showed that yield increase is closely related to an increase in sink capacity compared with the increase in source amounts (ΔW and NSC) (Figure 1). Although sink capacity increase generally contributes to yield increase, sink capacity increase on its own cannot ensure sufficient yield increase because sink capacity increase is accompanied by a decline in sink filling (Ohsumi et al., 2011). In this regard, we believe that sink filling rates did not decline in conjunction with sink capacity increase, because the usable dry matter during maturation (ΔW + NSC) mostly exceeded the increase in sink capacity under FACE conditions (Tables 2 and 3).

In this study, FACE/AMB ratio of hulled grain yield varied between 1.10 and 1.25 depending on variety, and Momiroman and Takanari showed a consistent increase and exceeded 1.20 (Table 3). Although Shimono et al. (2009) have suggested that differences in yield may reflect differences in biomass and nitrogen uptake up to the heading stage, biomass and nitrogen uptake of Momiroman and Takanari, the two varieties that showed relatively large yield increases under FACE conditions in this study, did not differ markedly from those of the other varieties. Regarding this discrepancy in results, it should be noted that the Shimono et al. (2009) study was conducted under cool conditions (under 20°C) that would facilitate the translation of dry matter production into yield increase. Studies carried out by Yoshida et al. (2011) and Hasegawa et al. (2013) also demonstrated a strong positive correlation between sink capacity and the magnitude of yield increase under FACE conditions, suggesting that varieties with large sink capacities are better equipped to produce increased yields under FACE conditions. Nakano et al. (2017) also indicated quantitative trait loci for large sink capacity stimulate yield increase under FACE. Similarly, in a study by Liu et al. (2008) in which the yield of F_1 hybrids increased markedly under FACE conditions, the authors speculated that large sink capacity was involved in yield increase. The Momiroman, Takanari and Hokuriku 193 varieties used in this study have all been designated as high-yielding varieties (Yoshinaga et al., 2013) with high sink capacities. Although those three varieties showed a significant increase of sink production efficiency per unit of absorbed nitrogen under FACE condition (Table 4), the increase of sink capacity and yield under FACE in Hokuriku 193 was lower than those in Momiroman and Takanari (Table 3). As shown in Table 4, sink production efficiency per unit of dry matter production for Hokuriku 193 was low under both AMB and FACE conditions. And the value did not increase under FACE condition compared with AMB, although those of other two high-yielding varieties significantly increased. Thus, the lower sink production efficiency per unit of dry matter production may be the reason for this variety's relative lower yield increase, and this can be the critical trait for the selection of favourable varieties for the increase in yield under high CO_2 conditions.

4.3. *Significance for future research*

This study has revealed that sink production efficiency per unit of dry matter production is an important trait contributing to increased yield under FACE conditions. Since several quantitative trait loci (QTL), including *GN1* and *APO1* (Nakano et al., 2017) have been identified as contributing to sink capacity increase and have already been introgressed into multiple varieties, these QTLs should be actively utilized in the breeding of varieties suited to elevated CO_2 levels. Ensuring stable high-yielding cultivation under high CO_2 conditions will also require an examination of cultivation management methods, using sink production efficiency per unit of fertilizer nitrogen as an indicator to determine the most effective timing and quantity of top dressing to increase spikelet number.

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Disclosure statement

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