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Yield responses to elevated CO$_2$ concentration among Japanese rice cultivars released since 1882

Hidemitsu Sakai[a], Takeshi Tokida [a], Yasuhiro Usui[b], Hirofumi Nakamura[c] and Toshihiro Hasegawa [d]

[a]Institute for Agro-Environmental Sciences, National Agriculture and Food Research Organization (NARO), Tsukuba, Ibaraki, Japan; [b]Hokkaido Agricultural Research Center, NARO, Memuro, Hokkaido, Japan; [c]Taiyo Keiki Co. Ltd., Toda, Saitama, Japan; [d]Tohoku Agricultural Research Center, NARO, Morioka, Iwate, Japan

ABSTRACT

Atmospheric CO$_2$ concentrations ([CO$_2$]) have increased by more than 100 μmol mol^{-1} over the last century and are projected to rise further. Breeding cultivars with a greater response to elevated [CO$_2$] (E-[CO$_2$]) can be an effective adaptation to global climate change. We wondered whether E-[CO$_2$]-responsive cultivars have been unintentionally selected through empirical breeding as [CO$_2$] has increased. If so, modern cultivars may respond better to E-[CO$_2$] than old ones. We conducted free-air CO$_2$ enrichment (FACE) experiments in 2 years to examine whether rice cultivars bred in different eras differ in response to E-[CO$_2$] and to determine any associated traits. We tested five Japanese cultivars: Aikoku (released in 1882), Norin 8 (1934), Koshihikari (1956), Akihikari (1976) and Akidawara (2009). The yields of Aikoku and Norin 8 increased by 19.3% and 30.3%, respectively, under E-[CO$_2$], while those of Koshihikari and Akihikari increased by 15.9% and 3.4%, respectively. However, that of Akidawara, the newest cultivar, also increased by 19.0%. Norin 8's strong response to E-[CO$_2$] was associated with increases in both spikelet density and percentage of ripened grains, both of which were closely related to nitrogen uptake. These results suggest that breeding has not necessarily improved cultivars' response to E-[CO$_2$], and that selection for traits such as sink capacity and nitrogen uptake can be effective to improve rice productivity under E-[CO$_2$].
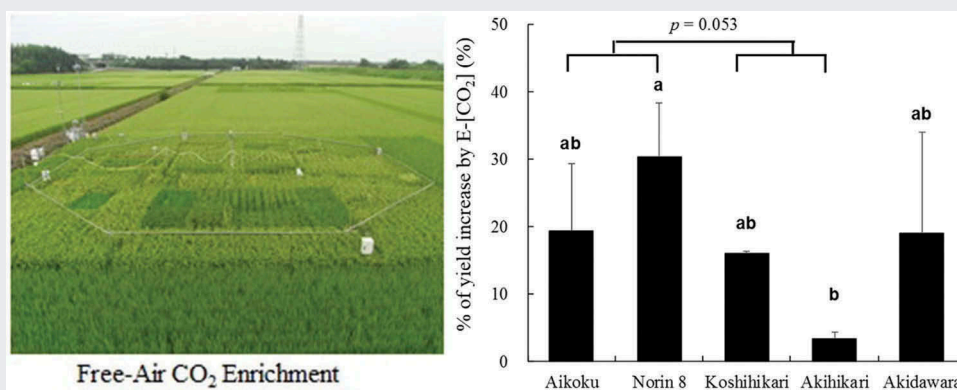
Introduction

Atmospheric CO$_2$ concentrations ([CO$_2$]) have increased by more than 100 μmol mol^{-1} from approximately 280 μmol mol^{-1} in pre-industrial times mainly through anthropogenic CO$_2$ emissions and are projected to reach as high as 936 μmol mol^{-1} by the end of this century (IPCC, 2013). Global warming and change of precipitation patterns resulting from this rise will have mainly negative effects on

crop production (Semenov & Porter, 1995; Zhao et al., 2017). However, increasing [CO$_2$] will offer opportunities to increase crop productivity because CO$_2$ is a substrate for photosynthesis and increases photosynthesis rates. Significant intraspecific variation in the yield response to elevated [CO$_2$] (E-[CO$_2$]) was found in major food crops (Ziska, Manalo & Ordonez, 1996; Shimono et al., 2009; Hasegawa et al., 2013 for rice; Seneweera et al., 2010 for wheat; Bishop et al., 2015 for soybean). Therefore, screening

for or breeding E-[CO_2]-responsive cultivars offers an effective way to adapt crops to global climate change (Ziska et al., 2012).

Rice (*Oryza sativa* L.), one of the most important staple food crops, feeds about half of the world's population (Maclean et al., 2002). Genetic improvement was one of the major technological advances in the last century. In Japan, nationally organized rice breeding started in 1893. Rice improvement had initially been based on the separation of pure lines from landraces until cross-breeding started in 1904. The major targets of the rice breeding programs were high yield and resistance to pests, diseases and cold injury. Continuing efforts in breeding, along with intensification of culture, resulted in rapid increases in yield (Chen, 2018; Horie et al., 2005) until the 1970s, when Japan achieved rice self-sufficiency. Since then, the main breeding objectives have shifted to high-eating quality (Horie et al., 2005). In the last few decades, breeders have returned their attention to productivity to reduce costs and have developed high-yielding cultivars by introducing *indica* genes (Yoshinaga et al., 2018).

Because the increase in [CO_2] over the last century has been steady, E-[CO_2]-responsive cultivars may have been selected unintentionally (Ziska et al., 2012). If so, modern cultivars may respond better to E-[CO_2]. Some crops have been evaluated for this response in glasshouses or open-top chambers. Old wheat cultivars showed greater yield responses to E-[CO_2] than modern cultivars, mainly owing to their inherent ability to form tillers and panicles (Manderscheid & Weigel, 1997; Ziska, 2008; Ziska, Morris & Goins, 2004). Oats showed similar results (Ziska & Blumenthal, 2007). But old and recent cultivars of barley showed no significant difference (Schmid et al., 2016). Thus, modern cultivars do not necessarily show a better response to E-[CO_2].

We previously reported that the yield response of rice to E-[CO_2] varied widely among cultivars including some old and new cultivars in a free-air CO_2 enrichment (FACE) experiment under open-field conditions in a single season (Hasegawa et al., 2013). In that study, we showed the intraspecific variation in the yield responses to E-[CO_2] from a single-season, but detailed analyses of the associated yield traits particularly with regard to the time cultivars developed remain undone. In this study, we repeated the experiment to compare Japanese cultivars released since 1882 with additional measurements of key growth traits. The objectives were to examine the effects of breeding era on yield sensitivity to [CO_2] and associated yield traits.

Materials and methods

Study sites

FACE experiments were conducted in farmers' fields in Tsukubamirai City, Ibaraki Prefecture, Japan (35°58′N, 139°60′E, 10 m a.s.l.), during the 2010 and 2011 growing seasons. The soil is a Fluvisol, which is typical of alluvial areas with 23% clay and 40% silt contents. The total carbon and nitrogen concentrations were 21.4 and 1.97 mg g^{-1}, respectively.

CO_2 treatments

Four blocks (replicates) were established in paddy fields, each consisting of two octagonal plots (240 m^2, 17 m across): an ambient [CO_2] (A-[CO_2]) plot and an elevated [CO_2] (E-[CO_2]) plot. The E-[CO_2] plots were equipped with emission tubes on the perimeter, where pure CO_2 was released from the windward side to keep the [CO_2] measured at the central point at 200 µmol mol^{-1} above ambient, as described by Nakamura et al. (2012). The season-long daytime average [CO_2] ± day-to-day standard deviation was 385 ± 11.0 (2010) and 379 ± 13.9 (2011) µmol mol^{-1} in the A-[CO_2] plots and 585 ± 15.9 (2010) and 560 ± 26.3 (2011) µmol mol^{-1} in the E-[CO_2] plots.

Plant materials

We tested five *japonica* cultivars (Fig. S1): 'Aikoku' (released in 1882), 'Norin 8' (1934), 'Koshihikari' (1956), 'Akihikari' (1976) and 'Akidawara' (2009). All except for Akidawara were selected because those were or are widely planted, especially in the Kanto region, and were or are within the top five in annual planted area in Japan. Akidawara, the newest cultivar, has been planted increasingly more widely for its high-yielding trait (Yoshinaga et al., 2018), which was introduced from the parent cultivar 'Akenohoshi' (*indica/japonica*) (Ando et al., 2011).

Cultural practices

Germinated seeds were sown in seedling trays on 26 April 2010 and 25 April 2011. After emergence, seedlings were raised in puddled open fields, with a tunnel cloche for the first 2 weeks. They were then transplanted by hand at a spacing of 30 cm × 15 cm (22.2 hills m^{-2}), with three seedlings per hill, on 26 May 2010 and 25 May 2011.

Equal amounts of phosphorus (P) and potassium (K) were given to all the plots in early April, before plowing; compound P-K fertilizer was applied at a rate of 4.36 g P

m^{-2} and 8.30 g K m^{-2}. Fields were kept submerged after late April. Three kinds of nitrogen (N) fertilizer were applied just before puddling: 2 g N m^{-2} as urea, 4 g N m^{-2} as another coated controlled-release fertilizer (LP100, JCAM Agri. Co. Ltd., Tokyo, Japan), and 2 g N m^{-2} as another type of controlled-release fertilizer (LP140). The two types of coated urea differ in the rate of release: LP100 releases 80% of its total N over 100 days at 25°C and LP140 does so over 140 days.

The field was kept flooded until late August, when the surface water was drained for harvesting. We applied flush irrigations on several occasions to keep the soil moist. Each cultivar was harvested at maturity in mid-to-late September.

Growth and yield measurements

In each plot, we monitored panicle emergence of at least four hills of each cultivar every other day and defined the heading date as the date when 50% of the productive tillers reached panicle-tip emergence.

At heading and maturity, four hills of each cultivar (six hills of Koshihikari) per plot were sampled. We also dug up a block of soil 30 cm wide, 15 cm long and 15 cm deep around one of those hills (two of Koshihikari) and carefully washed the soil from the roots with running water. We separated plants into living and dead leaf blades, stems (including leaf sheaths), roots and panicles, and measured the living leaf area with a leaf area meter (AAM-8; Hayashi denko, Tokyo, Japan). The plant parts were then oven-dried at 80°C for 72 h and weighed. The samples were ground, and the N concentrations were determined by NC analyzer (Sumigraph NC-22F, Sumika Chemical Analysis Service, Tokyo, Japan). Total N contents were calculated from dry weight and N concentration of each organ. Here, we regarded the total N contents as the amount of N uptake till then.

At physiological maturity, eight hills per cultivar (21 of Koshihikari) were sampled to measure grain yield and yield components. After the plants were air-dried under a rain shelter, we counted panicles. After threshing, we measured the total weight of the spikelets. Each spikelet sample was then split into three subsamples. One sub-sample (half of the spikelets) was dehulled to determine the brown rice weight. We measured the moisture con-tent of the grains with a grain moisture tester (Riceter f, Kett Electric Laboratory, Tokyo, Japan). Brown rice yield and single-grain mass were expressed on a 15% moisture content basis. Another subsample (a quarter of the spike-lets) was used to determine the proportion of ripened spikelets by sorting in an ammonium sulfate solution with specific gravity of 1.06. The third subsample was stored for future chemical analyses.

Gas exchange measurements

To measure leaf gas exchange at heading, we measured light-saturated net photosynthesis rate (A_{sat}) of the uppermost fully expanded leaf of one plant of each cultivar per replicate with a portable photosynthesis system (LI-6400, Li-Cor, Lincoln, NE, USA). During mea-surements, the photosynthetic photon flux density was maintained at 1800 µmol m^{-2} s^{-1}, the leaf temperature at 32°C, $[CO_2]$ at the growth $[CO_2]$ (380 µmol mol^{-1} for the A-$[CO_2]$ plots, 580 µmol mol^{-1} for the E-$[CO_2]$ plots) and relative humidity at >60%.

Statistical analyses

We conducted an analysis of variance (ANOVA), using a split-split-plot design, with year as the whole factor, $[CO_2]$ as the split-plot factor and cultivar as the split-split-plot factor; we used the general linear model pro-cedure of SPSS 17.0 for Windows (SPSS Japan Inc.; now IBM, Tokyo, Japan). We tested the significance of the response ratio (E-$[CO_2]$: A-$[CO_2]$) by ANOVA after nat-ural-logarithm (ln) transformation to avoid heterogene-ity in the error variance (Hedges, Gurevitch & Curtis, 1999). We examined the relative importance of yield components by multiple regression analysis based on the response ratio after ln transformation because the relationships between yield and its components were multiplicative. For simplicity, we used the three compo-nents for the analysis: spikelet density (panicle number × spikelets per panicle), percentage of ripened grain, and single grain mass.

Results

Meteorological conditions

Meteorological conditions in the 2 years were shown in Table 1. The mean air temperature over the growing season was 25.0°C in 2010 and 24.1°C in 2011, higher than that of the long-term (1980–2009) average of ~23°C, and was nearly the same among the cultivars. During 30 days before heading (DBH) and after heading (DAH), which correspond to panicle formation and grain-filling periods, respectively, the mean air temperature differed among the cultivars by up to 1.1°C and 0.9°C, respec-tively. The mean solar radiation showed the similar trend as the air temperature, with a lager difference among the cultivars.

Growth and development

E-$[CO_2]$ shortened days to heading (DTH) by 1 day, when averaged across the years and cultivars ($P < 0.001$, Table 2).

Table 1. Meteorological conditions over the growing season, during 30 days before heading (DBH) and after heading (DAH) in 2010 and 2011.

Year	Cultivar	Days from TP to harvest	Mean air temperature (°C)	Mean air temperature during 30 DBH (°C)		Mean air temperature during 30 DAH (°C)		Mean solar radiation (MJ m^{-2} day^{-1})	Mean solar radiation during 30 DBH (MJ m^{-2} day^{-1})		Mean solar radiation during 30 DAH (MJ m^{-2} day^{-1})	
				A-[CO$_2$]	E-[CO$_2$]	A-[CO$_2$]	E-[CO$_2$]		A-[CO$_2$]	E-[CO$_2$]	A-[CO$_2$]	E-[CO$_2$]
2010	Aikoku	107	25.1	26.0	26.0	27.6	27.6	18.7	18.4	18.4	18.5	18.5
	Norin 8	119	24.9	27.5	27.2	27.5	27.6	18.3	20.5	19.7	18.8	18.7
	Koshihikari	104	25.0	26.2	26.1	27.8	27.7	18.9	18.5	18.6	19.2	18.9
	Akihikari	97	24.8	25.2	25.2	27.7	27.7	18.8	16.4	16.4	19.6	19.6
	Akidawara	111	25.1	27.1	27.2	27.8	27.7	18.6	19.9	19.8	18.9	19.1
	Mean	108	25.0	26.4	26.4	27.7	27.7	18.6	18.7	18.6	19.0	19.0
2011	Aikoku	106	24.1	25.8	25.9	25.8	25.8	17.0	19.0	19.5	17.2	16.6
	Norin 8	119	24.2	25.7	25.7	25.2	25.2	17.0	17.5	17.5	15.5	15.5
	Koshihikari	112	24.1	25.5	25.6	26.1	26.0	17.0	18.6	19.0	17.0	16.9
	Akihikari	97	23.9	26.4	26.3	25.7	25.8	17.1	20.1	20.4	17.6	17.8
	Akidawara	119	24.2	25.6	25.6	25.4	25.5	17.0	18.1	18.2	16.2	16.2
	Mean	111	24.1	25.8	25.8	25.7	25.6	17.0	18.7	18.9	16.7	16.6

A-[CO$_2$], ambient CO$_2$ concentration; E-[CO$_2$], elevated CO$_2$ concentration (ambient + 200 μmol mol^{-1}).

Table 2. Effects of elevated [CO$_2$] on days to heading, plant height, maximum tiller number and leaf area index (LAI) of five cultivars tested under FACE conditions in 2 years.

Year	Cultivar	Days to heading		Plant height (cm)		Maximum tiller number (m^{-2})		LAI at heading stage	
		A-[CO$_2$][1]	E-[CO$_2$]	A-[CO$_2$]	E-[CO$_2$]	A-[CO$_2$]	E-[CO$_2$]	A-[CO$_2$]	E-[CO$_2$]
2010	Aikoku	64	63	87.3	86.0	439	502	3.52	3.89
	Norin 8	79	77	86.7	85.7	565	643	4.83	4.88
	Koshihikari	67	65	94.8	96.2	516	535	4.12	3.71
	Akihikari	57	56	81.3	82.8	500	531	3.43	3.24
	Akidawara	74	73	85.3	84.8	439	443	4.28	4.14
	Mean	68	67	87.1	87.1	492	531	4.04	3.97
2011	Aikoku	68	67	108.0	107.7	481	479	3.97	3.89
	Norin 8	84	83	97.8	95.6	524	589	4.83	5.20
	Koshihikari	71	70	102.8	106.4	490	563	4.56	4.87
	Akihikari	57	56	81.0	83.4	433	457	3.55	3.63
	Akidawara	80	79	95.4	95.6	426	435	4.40	4.55
	Mean	72	71	97.0	97.7	471	505	4.26	4.43
2y-mean	Aikoku	66	65	97.7	96.9	460	491	3.75	3.89
	Norin 8	82	80	92.3	90.7	545	616	4.83	5.04
	Koshihikari	69	68	98.8	101.3	503	549	4.34	4.29
	Akihikari	57	56	81.2	83.1	467	494	3.49	3.44
	Akidawara	77	76	90.4	90.2	433	439	4.34	4.35
	Mean	70	69	92.0	92.4	481	518	4.15	4.20
ANOVA results[2]									
Year		***		*		ns		**	
CO$_2$		***		ns		ns		ns	
Year×CO$_2$		ns		ns		ns		ns	
Cultivar		***		ns		*		***	
Cultivar×Year		***		***		ns		ns	
Cultivar×CO$_2$		ns		*		ns		ns	
Cultivar×Year×CO$_2$		ns		ns		ns		ns	

1) A-[CO$_2$], ambient CO$_2$ concentration; E-[CO$_2$], elevated CO$_2$ concentration. 2) ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; ns, not significant.

Since the mean temperature during the growing season was higher in 2010 than in 2011, the average DTH across the cultivars was 4 days shorter in 2010 than in 2011 ($P < 0.001$). DTH differed significantly among the cultivars ($P < 0.001$), ranging from an average across the years, [CO_2] of 57 days for Akihikari to 82 days for Norin 8. DTH of the earliest maturing cultivar, Akihikari, did not differ between years, resulting in a significant year × cultivar interaction ($P < 0.001$).

Neither plant height nor leaf area index (LAI) at heading was affected by E-[CO_2], when averaged across the years and cultivars (Table 2). Maximum tiller number was marginally greater in E-[CO_2] ($P > 0.05$). Plant height and LAI averaged across the cultivars were greater in 2011 than in 2010 ($P < 0.05$). Maximum tiller number and LAI differed significantly among cultivars ($P < 0.05$). Averaged across the years, they were highest in Norin 8 and lowest in Akidawara and Akihikari. Plant height showed a significant year × cultivar and CO_2 × cultivar interaction ($P < 0.05$).

Total dry weight across the years and cultivars was increased by E-[CO_2] by 12.8% at heading and 15.9% at maturity ($P < 0.001$, Table 3). Total dry weight of each cultivar was generally lower in 2010 than in 2011 at both stages owing to shortened growth duration at the higher temperature, though that of Akihikari was higher in 2010 at heading, resulting in a significant cultivar × year interaction ($P < 0.01$). It also differed significantly among cultivars at both stages ($P < 0.001$). Norin 8 had the largest total dry weight, followed by Akidawara and Koshihikari, and Akihikari had the smallest in both years. Although there was no significant cultivar × CO_2 interaction, Aikoku had the highest response to E-[CO_2] at maturity in both years.

E-[CO_2] increased shoot (living and dead leaf blade, leaf sheath and stem) and root dry weights at the maturity ($P < 0.01$, Table 3). Both differed significantly among cultivars at both stages ($P < 0.001$). Means across years were highest in Norin 8 at both stages and lowest in Koshihikari at heading and in Akihikari at maturity. The responses of shoot and root dry weights at maturity to E-[CO_2] differed significantly among cultivars (cultivar × CO_2: $P < 0.01$). The oldest cultivar, Aikoku, had the highest response of shoot dry weight over years, as in total dry weight. However, Norin 8 had the highest response of root dry weight, as well as the largest root mass among cultivars.

Total N uptake was stimulated by E-[CO_2] by 4.6% at heading ($P > 0.05$) and 9.2% at maturity over years and cultivars ($P < 0.01$, Table 3). Year had a significant effect: total N uptake over cultivars was larger in 2011 than in 2010, by 13.6% at heading and by 8.7% at maturity ($P < 0.01$). Total N uptake over years differed

significantly among cultivars at heading ($P < 0.001$) but not at maturity. There was no significant cultivar × CO_2 interaction at either stage, though two old cultivars (Aikoku, Norin 8) tended to respond better to E-[CO_2] at maturity than the others.

Single leaf photosynthesis rates

E-[CO_2] stimulated A_{sat} by 27.9% across the years and cultivars ($P < 0.001$, Figure 1). A_{sat} over [CO_2] and cultivars was 8.4% higher in 2010 than in 2011 ($P < 0.05$), but no year × CO_2 interaction was found. A_{sat} averaged over years and [CO_2] differed significantly among cultivars ($P < 0.001$): newer cultivars (Akihikari, Akidawara) had higher A_{sat} under both A-[CO_2] and E-[CO_2] than older ones (Aikoku, Norin 8). Akidawara and Norin 8 responded most to E-[CO_2] (>40%) over years, resulting in a significant cultivar × CO_2 interaction ($P < 0.05$).

Yield and yield components

E-[CO_2] increased brown rice yield by 16.7% across the years and cultivars ($P < 0.001$, Table 4). Yield over [CO_2] and cultivars was 6.7% higher in 2010 than in 2011 ($P < 0.001$). The response to E-[CO_2] was also higher in 2010 (21.3%) than in 2011 (12.6%), resulting in a moderate year × CO_2 effect ($P = 0.059$). Yield over years and [CO_2] differed significantly among cultivars ($P < 0.001$): Koshihikari had the highest yield, followed by Akidawara and Akihikari, while the older cultivars had low yields. This difference was more apparent under A-[CO_2]. However, Norin 8 had a strong yield response to E-[CO_2] (2-year mean; 30.3%, Figure 2), followed by Aikoku (19.3%) and Akidawara (19.0%). In contrast, yields of Koshihikari and Akihikari increased by 15.9% and 3.4%, respectively, resulting in a significant cultivar × CO_2 interaction ($P < 0.01$, Table 4). Norin 8 had the highest response to E-[CO_2], 36.2%, in 2010. It is worth noting that older cultivars (Aikoku, Norin 8) responded better to E-[CO_2] than modern ones (Koshihikari, Akihikari) ($P = 0.053$, Figure 2). The net increase in yield was also largest in Norin 8, averaged over the years.

E-[CO_2] significantly increased all of the yield components except single-grain weight across the years and cultivars ($P < 0.05$, Table 4). The overall effect of E-[CO_2] was most apparent in spikelet density (10.6%). All yield components differed significantly among cultivars across the years and [CO_2] ($P < 0.001$). E-[CO_2] effects differed between yield components: In panicle number, Koshihikari had the largest response over years (12.9%), resulting in a significant cultivar × CO_2 interaction ($P < 0.05$). In spikelets per panicle, Akidawara had

Table 3. Effects of elevated [CO₂] on total dry weight, shoot and root dry weight, and total N uptake at heading and maturity of five cultivars tested under FACE conditions in 2 years.

Year	Cultivar	Total dry weight (g m⁻²)[1] Heading A-[CO₂][2]	Heading E-[CO₂]	Maturity A-[CO₂]	Maturity E-[CO₂]	Shoot dry weight (g m⁻²) Heading A-[CO₂]	Heading E-[CO₂]	Maturity A-[CO₂]	Maturity E-[CO₂]	Root dry weight (g m⁻²) Heading A-[CO₂]	Heading E-[CO₂]	Maturity A-[CO₂]	Maturity E-[CO₂]	Total N uptake (g m⁻²) Heading A-[CO₂]	Heading E-[CO₂]	Maturity A-[CO₂]	Maturity E-[CO₂]
2010	Aikoku	984	1154	1308	1664	740	866	662	810	98	107	92	102	8.8	9.2	10.3	12.7
	Norin 8	1313	1483	1739	1990	1043	1169	1087	1149	131	139	104	135	10.0	10.2	11.1	12.5
	Koshihikari	1105	1144	1632	1764	882	891	818	907	89	98	121	91	9.2	8.6	12.6	12.0
	Akihikari	957	1041	1279	1472	714	769	603	709	102	96	82	91	8.7	8.6	10.7	10.6
	Akidawara	1173	1351	1667	1963	943	1080	977	1069	116	127	107	110	10.1	10.2	11.6	12.6
	Mean	1107	1235	1525	1770	864	955	829	929	107	113	101	106	9.4	9.4	11.3	12.1
2011	Aikoku	1026	1099	1383	1730	812	860	657	821	99	99	98	112	10.0	10.1	11.8	14.2
	Norin 8	1388	1610	1721	2007	1066	1262	1004	1080	156	140	101	139	12.0	12.1	11.7	13.0
	Koshihikari	1244	1410	1686	1844	986	1115	878	968	91	93	96	94	9.9	11.7	12.6	12.9
	Akihikari	906	1019	1335	1572	706	781	613	714	81	100	70	94	8.8	9.8	11.8	13.0
	Akidawara	1222	1460	1786	2007	984	1162	914	1023	108	135	116	128	10.2	11.7	12.2	13.6
	Mean	1157	1319	1582	1832	911	1036	813	921	107	114	96	113	10.2	11.1	12.0	13.3
2y-mean	Aikoku	1005	1126	1345	1697	776	863	659	816	98	103	95	107	9.4	9.7	11.1	13.5
	Norin 8	1351	1546	1730	1998	1055	1215	1046	1114	144	139	102	137	11.0	11.2	11.4	12.8
	Koshihikari	1175	1277	1659	1804	934	1003	848	938	90	96	109	92	9.6	10.2	12.6	12.5
	Akihikari	931	1030	1307	1522	710	775	608	712	92	98	76	92	8.8	9.2	11.3	11.8
	Akidawara	1198	1405	1727	1985	963	1121	945	1046	112	131	112	119	10.2	11.0	11.9	13.1
	Mean	1132	1277	1554	1801	888	995	821	925	107	113	99	110	9.8	10.2	11.6	12.7
ANOVA results[3]																	
	Year	**		0.099		ns		ns		ns		ns		***		**	
	CO₂	***		***		0.070		**		ns		**		ns		**	
	Year×CO₂	ns		ns		ns		ns		ns		0.085		0.099		ns	
	Cultivar	***		***		**		***		***		***		***		ns	
	Cultivar×Year	**		ns		ns		***		ns		ns		ns		ns	
	Cultivar×CO₂	ns		ns		ns		**		ns		***		ns		ns	
	Cultivar×Year×CO₂	ns		ns		ns		ns		ns		ns		ns		ns	

1) Shoot, root and panicle dry weight. 2) A-[CO₂], ambient CO₂ concentration; E-[CO₂], elevated CO₂ concentration (ambient + 200 μmol mol⁻¹). 3) ***, P < 0.001; **, P < 0.01; *, P < 0.05; ns, not significant.
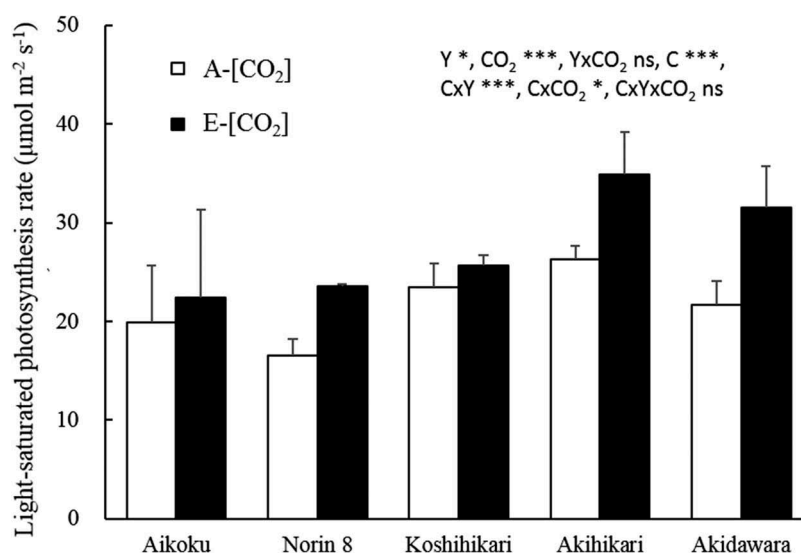
Figure 1. Light-saturated photosynthesis rates of uppermost fully expanded leaves measured at heading stage and the respective growth $[CO_2]$ in ambient (A) and elevated (E) $[CO_2]$. Data are 2-year averages with SD ($n = 4$). ANOVA results are shown in inset. Y, year; C, cultivar; ***, $P < 0.001$; *, $P < 0.05$; ns, not significant.

the largest response (8.4%), but there was no significant cultivar × CO_2 interaction. It is worth noting that the three older cultivars (Aikoku, Norin 8, Koshihikari) responded to E-$[CO_2]$ more strongly in panicle number than in spikelets per panicle, while the newest one (Akidawara) responded conversely. As a result, cultivar × CO_2 interaction was not significant in spikelet density (panicle number × spikelets per panicle; Figure 3(a)). The effect of E-$[CO_2]$ on the percentage of ripened grain was highest in Norin 8, followed by Akidawara and Aikoku (Figure 3(b)).

Harvest index was increased by E-$[CO_2]$ over the years and cultivars ($P < 0.001$, Table 3). Harvest index over years and $[CO_2]$ was highest in Akihikari and lowest in Norin 8 ($P < 0.001$). E-$[CO_2]$ increased that of Norin 8 by 9.3% over years. On the other hand, Koshihikari and Akihikari showed negligible effects, resulting in a significant cultivar × CO_2 interaction ($P < 0.01$).

E-$[CO_2]$, overall, increased brown rice yield mainly through spikelet density, followed by percentage of ripened grain, but not through single-grain weight (Table 5).

Relationships between yield components and N uptake

There was a linear and positive relationship between root mass and N uptake at both heading and maturity (Figure 4). Spikelet density was linearly and positively correlated with total N uptake at heading irrespective of year, CO_2

treatment or cultivar when Norin 8 was excluded (Figure 5). Norin 8 had a lower spikelet density than the other cultivars at the same N uptake. Overall, the percentage of ripened grain was positively correlated with N uptake from heading to maturity (Figure 6).

Discussion

We grew five rice cultivars released since 1882 under ambient and elevated $[CO_2]$ to examine the effects of past breeding on rice $[CO_2]$ sensitivity and associated traits.

Difference in $[CO_2]$ sensitivity between old and new cultivars

Our results showed improvements in rice productivity with breeding era. Under A-$[CO_2]$, the brown rice yield of newer cultivars (Koshihikari, Akihikari, Akidawara) was on average 19% higher than that of older ones (Aikoku, Norin 8; Table 4). Single leaf photosynthesis rates were also higher in newer cultivars (Figure 1). This result is consistent with the study of Taylaran et al. (2009), who grew six cultivars – 'Sekitori' (released in 1848), 'Aikoku' (1882), 'Koshihikari' (1956), 'Nipponbare' (1963), 'Asanohikari' (1987) and 'Takanari' (1990) – and reported that the newest cultivar, Takanari, had the highest yield, followed by the next newest cultivars, Asanohikari and Nipponbare. Although rapid yield increases in the second half of the twentieth century are often attributed to improvements in harvest index

Table 4. Effects of elevated [CO_2] on yield, yield components and harvest index of five cultivars tested under FACE conditions in 2 years.

| Year	Cultivar	Brown rice yield[1] (g m^{-2})		Panicle number (m^{-2})		Spikelets per panicle		Spikelet density (10^3 m^{-2})		% of ripened spikelets (%)		Single-grain weight (mg)		Harvest index[3]	
		A-[CO_2][2]	E-[CO_2]	A-[CO_2]	E-[CO_2]	A-[CO_2]	E-[CO_2]	A-[CO_2]	E-[CO_2]	A-[CO_2]	E-[CO_2]	A-[CO_2]	E-[CO_2]	A-[CO_2]	E-[CO_2]
2010	Aikoku	479	606	292	324	101.5	101.2	29.6	32.7	66.2	76.6	23.4	23.1	44.0	46.5
	Norin8	430	586	304	335	86.6	87.9	26.3	29.4	60.3	77.2	25.0	24.8	33.1	36.4
	Koshihikari	552	642	321	351	89.7	92.1	28.8	32.4	85.7	88.6	21.4	21.4	46.1	46.7
	Akihikari	545	559	290	294	90.5	91.1	26.3	26.8	85.3	86.6	23.4	23.7	51.3	50.0
	Akidawara	499	647	280	291	105.3	113.2	29.4	32.9	75.0	88.3	21.9	21.9	37.3	40.9
	Mean	501	608	298	319	94.7	97.1	28.1	30.9	74.5	83.5	23.0	23.0	42.3	44.1
2011	Aikoku	511	573	276	298	94.8	98.2	26.2	29.3	77.0	79.6	22.9	22.9	47.3	47.6
	Norin8	478	596	292	326	93.2	95.4	27.2	31.1	64.9	71.4	24.9	25.3	38.1	41.3
	Koshihikari	604	698	347	403	92.2	94.2	32.0	38.0	82.9	82.4	21.4	20.8	45.7	45.5
	Akihikari	577	601	288	296	95.4	97.8	27.5	28.9	88.4	87.3	23.5	23.8	51.5	51.1
	Akidawara	612	664	299	290	114.1	124.6	33.9	36.0	75.7	77.6	22.4	22.4	44.6	45.2
	Mean	556	626	300	323	98.0	102.1	29.4	32.7	77.8	79.7	23.0	23.0	45.5	46.1
2y-mean	Aikoku	495	589	284	311	98.1	99.7	27.9	31.0	71.6	78.1	23.1	23.0	45.7	47.0
	Norin8	454	591	298	331	89.9	91.7	26.7	30.3	62.6	74.3	25.0	25.1	35.6	38.9
	Koshihikari	578	670	334	377	91.0	93.2	30.4	35.2	84.3	85.5	21.4	21.1	45.9	46.1
	Akihikari	561	580	289	295	93.0	94.4	26.9	27.9	86.8	87.0	23.5	23.7	51.4	50.6
	Akidawara	556	655	289	290	109.7	118.9	31.7	34.5	75.4	82.9	22.1	22.2	40.9	43.1
	mean	529	617	299	321	96.3	99.6	28.7	31.8	76.1	81.6	23.0	23.0	43.9	45.1
ANOVA results[4]															
Year		***		ns		*		*		ns		ns		***	
CO_2		***		***		*		***		***		ns		***	
Year×CO_2		0.059		ns		ns		ns		**		ns		ns	
Cultivar		***		***		***		***		***		***		***	
Cultivar×Year		ns		**		*		***		*		**		***	
Cultivar×CO_2		**		*		ns		ns		*		ns		**	
Cultivar×Year×CO_2		ns		ns		ns		ns		ns		ns		ns	

1) At a 15% moisture content. 2) A-[CO_2], ambient CO_2 concentration; E-[CO_2], elevated CO_2 concentration (ambient + 200 µmol mol^{-1}). 3) Brown rice yield divided by aboveground biomass at a 0% moisture content. 4) ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; ns, not significant.

(Evans, 1999; Takeda, Oka & Agata, 1984), we did not find significant trends in harvest index (Table 4), nor did Taylaran et al. (2009). Since many complex processes contribute to yield formation, other traits may have contributed to past yield improvements.

In contrast, E-[CO_2] sensitivity was not responsible. Old cultivars (Aikoku, Norin 8) responded better to E-[CO_2] than modern ones (Koshihikari, Akihikari), except the most recent, Akidawara (Figure 2, Table 4). Similar results were found in wheat (Manderscheid & Weigel, 1997; Ziska, 2008; Ziska et al., 2004) and oats (Ziska & Blumenthal, 2007), in which higher responsivity of older cultivars to E-[CO_2] was associated with increased tiller and thus panicle numbers. Here, older cultivars also tended to respond better in panicle number (Table 4). On the other hand, newer cultivars responded relatively well in spikelets per panicle (Table 4), canceling out any significant differences between old and new cultivars (Figure 3(a)). In addition to responses in panicle number, old cultivars also responded better in percentage of ripened grain (Figure 3(b)). The percentage of ripened grain was the second major contributor to E-[CO_2] sensitivity (Table 5). These results suggest that simultaneous responses of panicle number (spikelet density) and percentage of ripened grain (Table 4) led to the higher yield responses of older cultivars to E-[CO_2].

The most recent cultivar, Akidawara, responded as well to E-[CO_2] as Norin 8 and Aikoku (Figure 2). Among our cultivars, only Akidawara has *indica* ancestors (Fig. S1). It has an allele of the high-yielding Akenohoshi (*indica/japonica*) at the Gn1 locus (Ando et al., 2011), which increases spikelet number per panicle (Ashikari et al., 2005). Akidawara responded better in spikelets per panicle to E-[CO_2] than the other cultivars (Table 4). A larger spikelet density often leads to poor grain filling and thus lower yield (Nakano et al., 2017). However, Akidawara had high dry weight at maturity under both ambient and elevated [CO_2] (Table 3), consistent with a previous study (Yoshinaga et al., 2018). High dry matter production after heading could support a high grain filling ability. (The responsivity of grain filling
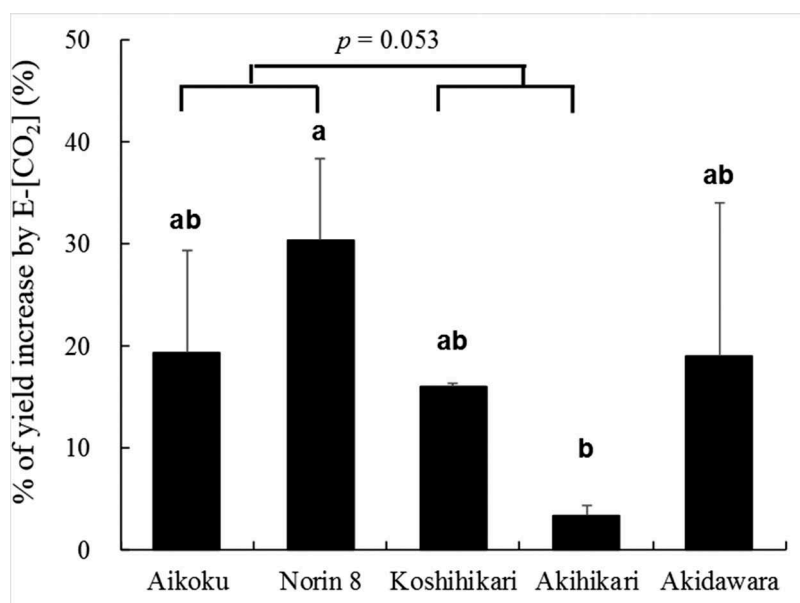
Figure 2. Percentage yield increase by E-[CO_2] of five cultivars tested under FACE conditions in 2 years. Data are from Table 4 and are 2-year averages with SD ($n = 4$). Bars with different letters are significantly different at 5% level by Tukey's multiple comparison test. *P* value indicates the statistical significance between old (Aikoku, Norin 8) and modern (Koshihikari, Akihikari) cultivars.
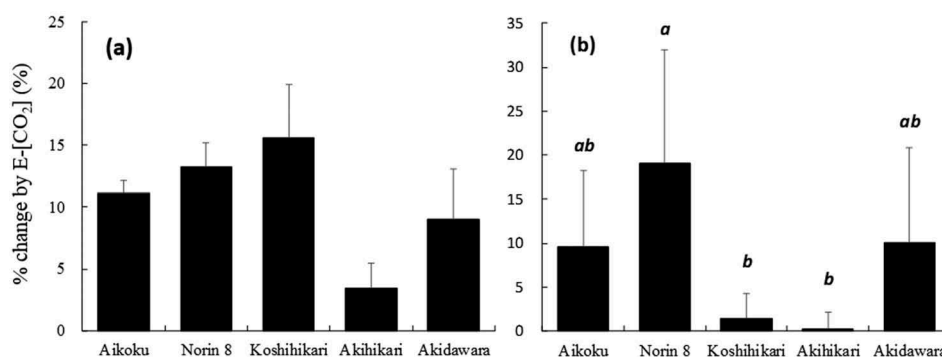
Figure 3. Percentage increase in (a) spikelet density and (b) percentage of ripened grain under E-[CO_2] of five cultivars tested under FACE conditions in 2 years. Data are from Table 4 and are 2-year averages with SD ($n = 4$). Bars with different italic letters are significantly different at 10% level by Tukey's multiple comparison test.

Table 5. Coefficients of multiple regression of yield enhancement by elevated [CO_2] on those of yield components.

Explanatory variable	Standardized multiple regression coefficient
Response ratio (E/A) of	
Spikelet density	1.031***
Percentage of ripened grain	0.841***
Single grain mass	−0.009 ns

Coefficients significantly different from 0 are indicated: ***, $P < 0.001$; ns, not significant. E, Elevated CO_2 concentration; A, Ambient CO_2 concentration.

ability under E-[CO_2] is discussed in the next section.) As a result, larger sink formation ability and higher source function of Akidawara might be the main factors in its E-[CO_2] sensitivity. In addition to Akidawara, recent high-yielding *indica* or *indica*-derived cultivars showed higher E-[CO_2] sensitivity, for example, 'Takanari' (Hasegawa et al., 2013). Since continuous inbreeding has reduced genetic diversity (Yamamoto et al., 2010; Yonemaru et al., 2012), the introduction of *indica* cultivars or *indica* traits may improve E-[CO_2] sensitivity.
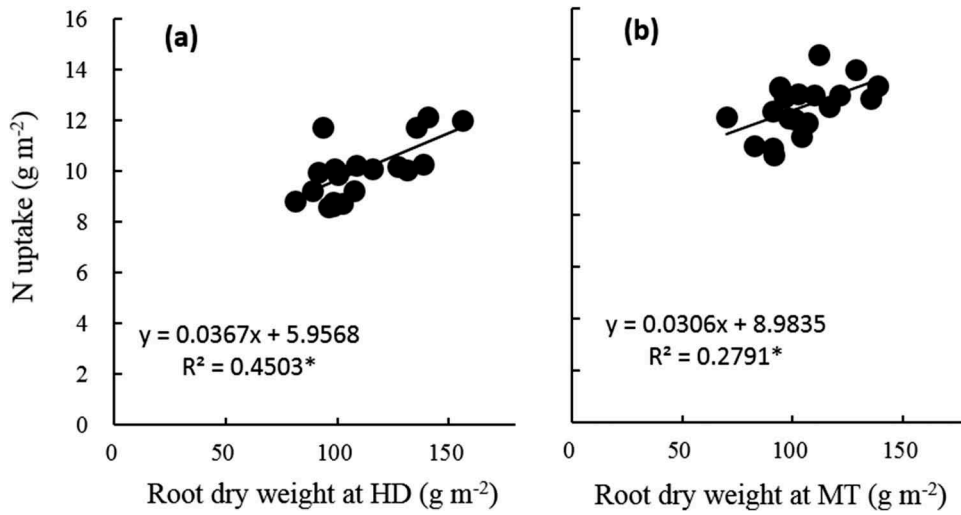
Figure 4. Relationship between root dry weight and N uptake at (a) heading and (b) maturity. HD, heading; MT, maturity; *, $P < 0.05$.
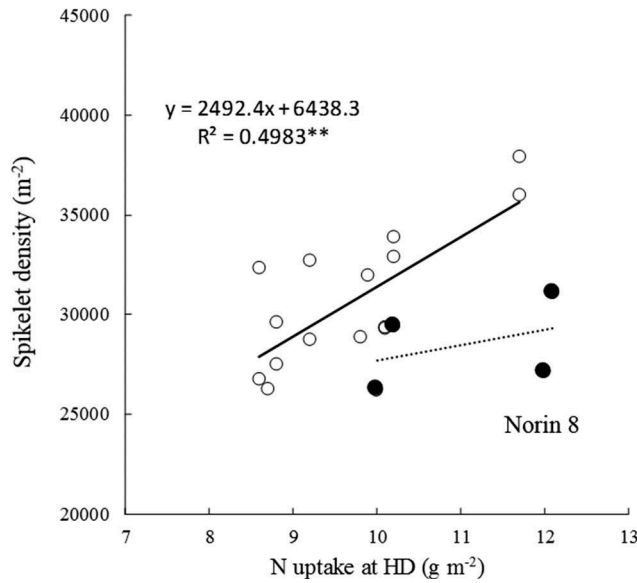

Figure 5. Relationship between total N uptake at heading and spikelet density of five cultivars grown under ambient or elevated $[CO_2]$ in 2 years. Open circle and solid line, all cultivars except Norin 8. Closed circle and dashed line, Norin 8. HD, heading; **, $P < 0.01$.
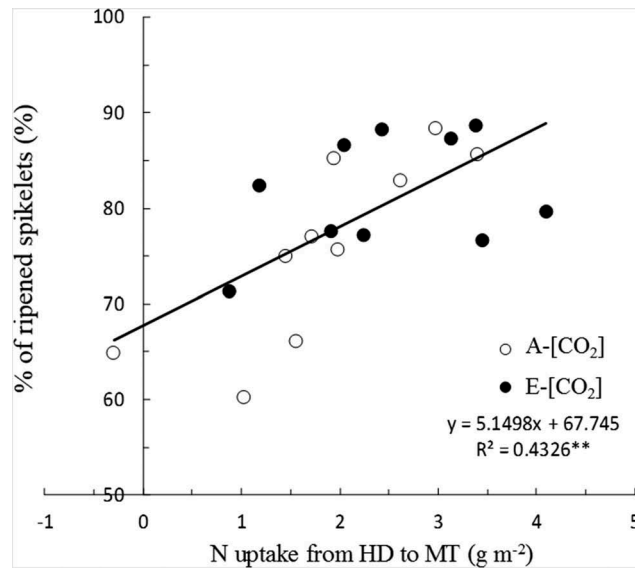

Figure 6. Relationship between N uptake from heading to maturity (grain filling period) and percentage of ripened grain of five cultivars grown under ambient or elevated $[CO_2]$ in 2 years. A-$[CO_2]$, ambient CO_2; E-$[CO_2]$, elevated CO_2; HD, heading; MT, maturity; **, $P < 0.01$.

In this study, we applied N fertilizers at the current standard level. Since N application level was low in the era when old cultivars had been bred, old cultivars were expected to show higher yields than modern cultivars did. However, previous studies reported that modern and new high-yielding cultivars had higher yields than old ones did even under low or no N application conditions (Hasegawa, 2003; Taylaran et al., 2009; Zhang & Kokubun, 2004). As for [CO$_2$] responsivity, high-yielding cultivar Takanari showed larger yield responses than modern cultivar Koshihikari did under no N application condition, resulting in a significant cultivar × CO$_2$ × N interaction (Hasegawa et al., 2019). However, it remains still unclear that old cultivars show a CO$_2$ × N interaction. Therefore, the order in the [CO$_2$] responsivity among the five cultivars tested in this study may change depending on N application levels.

A 2-year field trial with limited cultivars cannot, of course, clarify all of the past breeding improvements associated with [CO$_2$] sensitivity of rice. However, our results suggest that past breeding had not necessarily been selecting E-[CO$_2$]-responsive cultivars.

Traits associated with [CO$_2$] sensitivity

E-[CO$_2$] increased the yield of the old Japanese cultivar Norin 8 by 30.3% on average under open-field conditions. This response is comparable to those of Chinese hybrid and *indica* inbred cultivars: increases of 34.1% in the hybrid cultivar 'Shanyou 63' and 30.1% in 'Liangyoupeijiu' (Liu et al., 2008; Yang et al., 2009), and of 32.9% in the *indica* inbred cultivar 'Yangdao 6 Hao' by FACE (Zhu et al., 2015). Ours is the first report of a yield increase of >30% in a *japonica* inbred cultivar in a multi-year FACE experiment.

Among the yield components, spikelet density contributed most strongly to the yield increase by E-[CO$_2$] (Table 5). Similar results were reported in previous FACE studies using different rice cultivars under different N regimes and environments (Hasegawa et al., 2013; Kim et al., 2003; Liu et al., 2008; Shimono et al., 2009; Yang et al., 2006, 2009; Zhu et al., 2015). Therefore, the responsivity of spikelet density is the most important factor in [CO$_2$] sensitivity in rice. It is well known that spikelet density is closely and positively correlated with N uptake by rice before heading, irrespective of [CO$_2$] (Hasegawa et al., 2019; Kim et al., 2001; Shimono et al., 2009). We found a similar relationship (Figure 5). These results suggest that the responsivity of spikelet density under E-[CO$_2$] was closely related to the increased N acquisition before heading. Interestingly, the [CO$_2$]-responsive Norin 8 had a much lower spikelet production efficiency than the other cultivars (Figure 5),

somewhat mitigated by its large N uptake by heading stage (Table 3).

In addition to spikelet density, the percentage of ripened spikelets contributed to yield responses to E-[CO$_2$] (Table 5). As discussed above, all cultivars with high [CO$_2$] sensitivity in this study, especially Norin 8, responded to E-[CO$_2$] in both spikelet density and percentage of ripened grain (Figure 3, Table 4). On the other hand, Koshihikari had the highest response in spikelet density with a lower response in percentage of ripened grain, resulting in a moderate increase in grain yield (Figure 3, Table 4). These results are consistent with those of highly responsive Chinese hybrid and inbred cultivars – Shanyou 63 (Liu et al., 2008), Liangyoupeijiu (Yang et al., 2009) and Yangdao 6 Hao (Zhu et al., 2015) – in which yield increases of >30% were not only attributed to stronger sink generation but also enhanced grain filling capacity. It may be possible to achieve a >30% yield increase by increasing spikelet density by >30% at the same grain filling percentage, although previous studies did not (Liu et al., 2008; Yang et al., 2009; Zhu et al., 2015). Therefore, for large yield responsivity (say, >30%) to E-[CO$_2$], enhanced grain filling ability can be effective in addition to increased spikelet production by E-[CO$_2$].

What traits are associated with the responsivity in percentage of ripened spikelets to E-[CO$_2$]? We found a close relationship across the cultivars between percentage of ripened spikelets and N uptake during grain filling (Figure 6). All cultivars with a high response in percentage of ripened spikelets increased N uptake under E-[CO$_2$] during grain filling (Table 3). Increased N uptake during grain filling will maintain leaf N concentration and hence source ability by avoiding N translocation from leaf to grain and leaf senescence. Although we did not measure A$_{sat}$ during grain filling, Chen et al. (2014) reported that the [CO$_2$]-sensitive Takanari could retain a higher leaf N concentration until late grain filling, resulting in a high grain filling ability. Thus, we suggest that enhanced N uptake during grain filling could allow a response in percentage of ripened spikelets under E-[CO$_2$] mainly through enhanced or maintained source ability.

Meteorological conditions during panicle formation and grain filling periods differed between the cultivars because of the maturity differences (Table 1, 2). Since the clear relationship was found between spikelet density and N uptake before heading in this and previous studies under different meteorological regimes (Hasegawa et al., 2019; Kim et al., 2001; Shimono et al., 2009), the differences of mean air temperature and solar radiation seemed not to have strong effects on the extent of [CO$_2$] responsivity of the cultivars. In

contrast, grain filling has been known to be affected by air temperature and solar radiation (Yoshida, 1981). In this study, the differences of both air temperature and solar radiation between the cultivars during the grain filling periods were relatively small in 2010 (up to 0.3°C, 1.1 MJ m^{-2} day^{-1}, Table 1). In 2011, however, the mean air temperature and solar radiation ranged 25.2°C to 26.1°C and 15.5 MJ m^{-2} day^{-1} to 17.8 MJ m^{-2} day^{-1}, respectively, among the cultivars. Though the mean air temperatures were slightly higher than the optimum range for grain filling (20–25°C: Matsushima & Manaka, 1957; Morita, 2000a; Yoshida & Hara, 1977), the negative effect of higher temperature on grain weight was counteracted by solar radiation (Morita, 2000b), mainly because of the positive relationships between both under normal weather conditions. Therefore, the differences of meteorological conditions in this study might have limited effects on the differences of [CO_2] responsivity between the five cultivars.

Under A-[CO_2], percentage of ripened spikelets was relatively lower in the old and newest cultivars than the modern ones (Table 4). The similar result was found in the previous studies (Zhang & Kokubun, 2004). These results may suggest that the old cultivars are source-limited and there is a room to be improved by enhanced N uptake and source ability by E-[CO_2]. The cultivars with a high percentage of ripened spikelets will hardly respond to E-[CO_2] without increase in spikelet density. In other words, such cultivars may be already well adapted to current [CO_2].

Our results show that both spikelet density and percentage of ripened spikelets were associated with high [CO_2] sensitivity and were closely related to the response in N uptake. We found a positive relationship between root mass and N uptake at heading and maturity (Figure 4), as did Kim et al. (2001). As detailed study of the response of root mass and its functions to E-[CO_2] are limited, especially under open-field conditions (Yang et al., 2008), further studies to reveal their genotypic variation in E-[CO_2] response are needed for the improvement of E-[CO_2] sensitivity.

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Disclosure statement

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ORCID

Takeshi Tokida http://orcid.org/0000-0001-7245-2952
Toshihiro Hasegawa http://orcid.org/0000-0001-8501-5612

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