RESEARCH PAPER

Genotypic variation in rice yield enhancement by elevated CO2 relates to growth before heading, and not to maturity group

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Abstract

Maturity group (based on the number of days to maturity) is an important growth trait for determining crop productivity, but there has been no attempt to examine the effects of elevated [CO2] on yield enhancement of rice cultivars with different maturity groups. Since early-maturing cultivars generally show higher plant N concentration than late-maturing cultivars, it is hypothesized that [CO2]-induced yield enhancement might be larger for early-maturing cultivars than late-maturing cultivars. To test this hypothesis, the effects of elevated [CO2] on yield components, biomass, N uptake, and leaf photosynthesis of cultivars with different maturity groups were examined for 2 years using a free-air CO2 enrichment (FACE). Elevated [CO2] significantly increased grain yield and the magnitude significantly differed among the cultivars as detected by a significant [CO2]×cultivar interaction. Two cultivars (one with early and one with late maturity) responded more strongly to elevated [CO2] than those with intermediate maturity, resulting mainly from increases in spikelet density. Biomass and N uptake at the heading stage were closely correlated with grain yield and spikelet density over [CO2] and cultivars. Our 2 year field trial rejected the hypothesis that earlier cultivars would respond more to elevated [CO2] than later cultivars, but it is revealed that the magnitude of the growth enhancement before heading is a useful criterion for selecting rice cultivars capable of adapting to elevated [CO2].

Key words: Biomass, breeding, carbon dioxide, climate change, grain yield, photosynthesis, radiation-use efficiency, rice.

Introduction

The atmospheric CO2 concentration ([CO2]) has been rising due to human activities since the Industrial Revolution, and is projected to double before the end of this century (IPCC, 2007). This [CO2] increase is expected to enhance the growth and yield of C3 crops, including rice. Rice, with an annual harvest of 0.6 billion metric tonnes, is and will continue to be the most important cereal crop for feeding the world’s population (IRRI, 2002). More than half of the world’s population, particularly in Asia, depends on rice as their staple food. Compared with other major cereals such as maize and wheat, rice is more often consumed near where it is produced. The proportion of rice used for world trade in 2005 was only 3.8% of total rice production, versus 12.7% of maize and 19.1% of wheat (FAO, 2005. FAOSTAT. http://faostat.fao.org/site/291/default.aspx). A slight gap between rice demand and supply could thus potentially

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lead to critical food insecurity. The world population is projected to increase from 6 billion to 9 billion by 2050 (United Nations, 2005. The 2004 world population prospects. Revision population database. http://esa.un.org/unpp/), thereby enlarging the demand for rice. However, areas used for rice production will be under increasing pressure because of ongoing economic development and the expanding use of land for biofuel production and the planting of cash crops. To meet the future rice demand, it is therefore essential to produce rice more efficiently under elevated [CO2].

Breeding is an important way to improve crop yield under elevated [CO2]. Several studies have tested genotypic variations in the responses of crops to elevated [CO2] in terms of hypotheses based on year of cultivar released (Manderscheid and Weigel, 1997; Ziska et al., 2004; Ziska and Blumenthal, 2007), ecosystems and origins (Ziska et al., 1996), growth habits (Moya et al., 1998; Ziska and Bunce, 2000; Ziska et al., 2001, 2004; Baker, 2004), and source–sink balances (Ainsworth et al., 2004). However, no reliable criterion has been identified for breeding rice cultivars that will be better adapted to elevated [CO2] (Ziska et al., 1996; Moya et al., 1998; Baker, 2004), and this is also true for wheat (Manderscheid and Weigel, 1997; Ziska et al., 2004), soybeans (Ziska and Bunce, 2000; Ziska et al., 2001; Ainsworth et al., 2004), and oats (Ziska and Blumenthal, 2007). Recently, Ziska and Blumenthal (2007) argued that empirical selection did not work for [CO2]-responsive cultivars based on examinations of the growth of old and new oat cultivars. It is essential to find criteria for breeding new cultivars for adapting future [CO2].

Maturity group is one of the important growth traits for determining crop productivity under a local climate condition. It has generally been observed that the biomass production of early-maturing cultivars during a full growing season is smaller than that of late-maturing cultivars resulting from a lower use of energy and resources (e.g. solar radiation, temperature, and [CO2]). However, early-maturing cultivars have a higher plant N concentration, which strongly relates to leaf photosynthetic capacities, than the late-maturing cultivars when compared at the same growth stage. Increased N availability has generally been seen to have positive effects on the yield enhancement induced by elevated [CO2] in rice and other crops, and increased N fertilization can ensure higher yield increases under elevated [CO2] (Kimball et al., 2002). This increase has been attributed to the increased plant N concentration, which allows the plant to maintain a higher photosynthetic rate under elevated [CO2], in addition to the increased N supply to meet the demand by elevated [CO2] associated with growth enhancement. Weerakoon et al. (2000) showed a relationship between radiation-use efficiency (RUE) and leaf N concentration in rice plants grown under different N fertilization and [CO2] regimes, and demonstrated that the enhancement of RUE by elevated [CO2] was smaller at lower N concentrations. Similar responses have also been reported by Sakai et al. (2006), suggesting a benefit for early-maturing cultivars under elevated [CO2]. In addition, it is commonly reported that the [CO2]-induced photosynthetic enhancement declines with the later growth stages, known as ‘photosynthetic acclimation’ (Moore et al., 1999). Early-maturing cultivars might escape photosynthetic acclimation under elevated [CO2]. We, therefore, hypothesized that a [CO2]-induced yield enhancement is larger for early-maturing cultivars than late-maturing cultivars. To test this hypothesis, four rice cultivars with different maturity groups were used, which are all current dominant cultivars in the northern part of Japan.

In order to test the yield responses of rice to elevated [CO2], it is essential for the experiments to be conducted with a full crop canopy in the field. To meet this need, researchers developed the free-air CO2 enrichment (FACE) technology in the late 1980s, and this approach has been widely used for several crop species, including rice (Long et al., 2004). The FACE apparatus raises [CO2] by releasing CO2 directly into the atmosphere and diluting it with natural winds. FACE currently appears to be the best method to quantify a crop’s yield response to elevated [CO2] with minimal interference from experimental artefacts. Our hypothesis was tested under enhanced [CO2] in a 2-year FACE study conducted in years with contrasting weather conditions: an anomalously cool summer in 2003, and a warmer-than-usual summer in 2004. This is the first FACE study we are aware of that investigated genotypic variations in the responses of rice yield to elevated [CO2].

**Materials and methods**

**Growth conditions**

Four rice cultivars from different maturity groups were grown: Kirara397, Kakehashi, Akitakomachi, and Hitomebore. These cultivars are currently dominant cultivars used in the northern part of Japan. Kirara397 is the leading variety in the Hokkaido region of the northern-most island of Japan (44.8% of a total cultivated area of 0.12 million ha in the Hokkaido region in 2005). Akitakomachi and Hitomebore are the leading two varieties for the Tohoku region in the northern part of Honshu island (25.8% and 32.1%, respectively, of a total cultivated area of 0.40 million ha in the Tohoku region in 2005) while Kakehashi is the variety ranked 11th in the Tohoku region. The growth duration of cultivars at the locations where these cultivars were grown ranged from 118 d to 141 d in 2003 and from 110 to 128 d in 2004 (Table 1). The earliest-maturing cultivar is Kirara397, followed by Kakehashi and Akitakomachi, and the latest-maturing cultivar is Hitomebore. The crops were grown under two levels of atmospheric [CO2]: ambient [CO2] and elevated [CO2] created using FACE with a target [CO2] level of ambient+200 µmol mol$^{-1}$. Both treatments continued throughout the crop season from germination to maturity for 24 h d$^{-1}$. Germinated seeds of four cultivars were sown on 26 April in 2003 and in 2004 in a sun-lit growth chamber controlled at ambient and elevated [CO2]. The seedlings were transplanted into eight paddy fields at Shizukuishi, Iwate, Japan (39°38’ N, 140°57’ E) on 21 May in 2003 and 20 May in 2004.
Table 1. Growth durations of four rice cultivars in 2003 and 2004 at the locations where the cultivars were released

Numbers in parenthesis after the name of cultivars indicated the year released. Kirara397, Kakehashi, Akitakomachi and Hitomebose were released at Hokkaido Agricultural Research Station (43°52’ N, 142°30’ E), Iwate Agricultural Research Station (39°20’ N, 141°07’ E), Akita Agricultural Research Station (39°34’ N, 140°11’ E) and Miyagi Agricultural Research Station (38°35’59” N, 140°54’28” E), respectively. Data were derived from the rice database (Ohta et al., 2006).

| Traits                      | Year  | Kirara397 (1988) | Kakehashi (1994) | Akitakomachi (1984) | Hitomebose (1991) |
|-----------------------------|-------|------------------|------------------|---------------------|-------------------|
| Days to heading from transplanting | 2003  | 73               | 80               | 83                  | 97                |
|                             | 2004  | 66               | 70               | 80                  | 85                |
| Days to maturity from transplanting | 2003  | 118              | 130              | 131                 | 140               |
|                             | 2004  | 110              | 113              | 127                 | 128               |

Seedlings of all cultivars at transplanting were at the 4th leaf stage (2003) and the 5th leaf stage (2004) on the main stem, and the dry weight at transplanting ranged from 1.4 g m⁻² to 1.5 g m⁻² in 2003 and from 9.7 g m⁻² to 11.2 g m⁻² in 2004 with a slight positive effect of elevated [CO₂], measured for 20 plants (2003) and 60 plants (2004) per cultivar at each [CO₂]. Hills and rows were 17.5 cm and 30 cm apart, respectively (19.05 hills m⁻²) (three plants per hill). Four paddy fields were assigned to the elevated [CO₂] treatment in both years. In each of the elevated [CO₂] plots, an octagonal FACE ring 12 m in diameter was installed. [CO₂] at the centre of the ring was monitored at 5 s intervals, and pure CO₂ was released from the peripheral emission tubes at a height of 0.5 m above the canopy, with the emission source chosen based on the current wind direction so as to maintain [CO₂] within the ring at a level 2 to 11.2 g m⁻² above that in the ambient [CO₂] plots. The daytime [CO₂] averaged over the season was 570±35 µmol mol⁻¹ (2003) and 548±27 µmol mol⁻¹ (2004) in the elevated [CO₂] plots and 366±12 µmol mol⁻¹ (2003) and 365±127 µmol mol⁻¹ (2004) in the ambient [CO₂] plots. The 24 h mean [CO₂] was 600±40 µmol mol⁻¹ (2003) and 576±33 µmol mol⁻¹ (2004) in the elevated [CO₂] plots and 383±15 µmol mol⁻¹ (2003) and 385±14 µmol mol⁻¹ (2004) in the ambient [CO₂] plots. All fertilizer was applied before transplanting: 8 g N m⁻² was supplied as 6 g N in controlled-release urea fertilizer (Kumiai-42-Hifuku-Nyouso-LP70, Zen-Noh, Tokyo, Japan) and 2 g in ammonium sulphate, plus 13 g P m⁻² and 12.5 g K m⁻². The rate of N release was a function of the soil temperature: according to the manufacturer, 80% of the total applied N is released within 1750 °C of accumulated soil temperature. Although all cultivars were grown under the same amount of N fertilization (8 g m⁻²), the mineralized N supply from the soil during a season was estimated to be ca. 8 g m⁻² (S Miura et al., unpublished data). This suggested that the total N supply, up to 16 g m⁻² during a season, would be sufficient even for the latest-maturing cultivar of Hitomebose. The experimental design was a blocked split-split-plot design with four replicates (main plot=year; split-plot= [CO₂]; split-split plot= cultivar). There were four blocks, each having an elevated and an ambient [CO₂] plot located in separate paddies having similar soils and agronomic history.

Measurements

Air temperature was recorded at a height of 1.5 m in each plot (eight plots in total) using a Pt-100 thermometer with an aspirated double-tube radiation shield. Air temperature signals were taken every 10 s and their 10 min averages were recorded by a datalogger (CR10X for the ambient ring, CR23X for the FACE ring, Campbell Sci. Inc., Logan, Utah, USA). Every Pt-100 probe was calibrated with an error below 0.1 °C for a range of 0–40 °C by comparing with a JIS-standard double-glass-tube thermometer. Soil temperature at 10 cm below ground level was measured in each plot using a Pt-100 thermometer. Air temperature and soil temperature averaged for eight plots was used for analysis. Solar radiation was measured with a pyranometer (LI-200X, Li-Cor, Lincoln, Nebraska, USA) at the experimental site. The signals were taken every second and their 10 min averages were recorded by a datalogger (CR10X). The light sensors, including the line quantum sensor, were calibrated by comparing with their respective reliable sensors before and after the season every year. Relative atmospheric humidity was not measured in the present experiment and was derived from the database in the National Agricultural Research Station in Tohoku Region measured at Morioka (39°44’ N, 141°08’ E), Japan about 30 km east from the FACE site.

At the heading and maturity stages, rice plants from eight hills per plot were sampled to determine their dry weight. Plants were separated into leaf laminae, leaf sheaths and culms, and panicles, if present, and dry weights were determined after drying at 80 °C for 72 h. After grinding the samples, the N concentrations were determined by Kjeldahl analysis. Photosynthetically active radiation (PAR) was measured above and below the canopy using a line quantum sensor (LI-191SB, Li-Cor, Lincoln, Nebraska, USA) under diffuse radiation conditions at 2 week intervals. From the fraction of radiation intercepted by the plant canopy, the intercepted PAR (IPAR) was calculated and integrated across the season. Radiation-use efficiency (RUE) was calculated as the total dry weight increase (above-ground) divided by IPAR.

Panicle initiation was defined as the time when the young panicle of the main stem reached 1 mm in length, and the date of panicle initiation was estimated from the length of
young panicles measured under a stereoscopic microscope for samples of eight (2003) or four (2004) plants per plot. Heading date, defined as the date when 50% of the heads had fully emerged, was determined by monitoring five hills per plot at 2 d intervals.

Photosynthesis of the uppermost leaves was measured for all cultivars except Kakehashi in 2004 using a LI-6400 portable photosynthesis system (Li-Cor Lincoln, NE, USA). Two to three plants were measured per replicate (one leaf per plant) for each cultivar. Measurements were made using the uppermost leaf during the period of vegetative growth (26–28 d after transplanting (DAT) for all cultivars) and during reproductive growth (82 DAT for Kirara397, and 97 DAT for Akitakomachi and Hitomebore). The photosynthetic photon flux density (PPFD) during these measurements was maintained at 2000 μmol m⁻² s⁻¹, the leaf temperature was 25 °C, and [CO₂] was controlled at 350 μmol mol⁻¹ for the ambient [CO₂] plots and at 550 μmol mol⁻¹ for the elevated [CO₂] plots.

Yield and yield components were measured for plants from 24 hills in each plot of cultivar–treatment combination. Spikelets were separated from all plants and were categorized into three groups: ripened spikelets (which sank in salt water with a specific gravity of 1.06), incompletely ripened spikelets (which floated in the salt water but were fertile), and sterile spikelets (which floated in the salt water but were sterile). Sterile spikelets were carefully identified by backlighting the heads with fluorescent lightbulbs; spikelets that showed no shadowy area (i.e. no developing embryo or grain) were considered to be sterile. The plant samples used for all measurements were taken from a predetermined location in each treatment plot.

**Statistic analysis**

To test for significant differences in the effects of [CO₂] in the two years, analysis of variance (ANOVA) with year as the main plot, [CO₂] as the subplot, and genotype as the split-split plot was used. Leaf photosynthesis was measured only in 2004 with three replicates, and ANOVA for these data was conducted for split-plot ([CO₂] as the main plot and genotypes as the split-plot). Statistical calculations used the SPSS statistical software (SPSS Inc., Chicago, IL, USA).

**Results**

**Climate conditions**

Air temperature averaged 18.4 °C during the 2003 growing season, which was 1.5 °C lower than in 2004 (Fig. 1); the difference was most notable from c. 30 d to 75 d after transplanting in 2003. Soil temperature, which was higher than air temperature, showed a similar pattern. Solar radiation was lower in 2003 than in 2004 (by a mean of 2.6 MJ m⁻² d⁻¹) throughout most of the growing season. Relative humidity was higher in 2003 than in 2004.

**Growth stages**

Panicle initiation date ranged from 29 d to 58 d after transplanting (DAT), and heading date ranged from 59 to 79 DAT (Table 2). Both panicle initiation date and heading date were earliest for Kirara397, followed by Kakehashi, Akitakomachi, and Hitomebore. This order
Table 2. Days to panicle initiation and heading, tiller number at heading stage, total biomass, N concentration, and N uptake at the heading and mature stages, canopy PAR interception (IPAR), and radiation-use efficiency (RUE) before and after the heading stages for four rice cultivars grown under two [CO2] levels in 2003 and 2004.

| Year | Cultivar          | [CO2] | Days to panicle initiation | N density at heading (g m⁻²) | N concentration (mg g⁻¹) | Total biomass (g m⁻²) | N uptake (g m⁻²) | IPAR (mol m⁻² d⁻¹) | RUE (g mol⁻¹) |
|------|-------------------|-------|-----------------------------|-----------------------------|--------------------------|----------------------|------------------|-------------------|-----------------|
| 2003 | Kirara397         | AMB   | 31±0.4                      | 68±0.6                      | 512±31                   | 15.5±0.7             | 10.2±0.3         | 407±8             | 6.3±0.3         |
|      | ELV               | 29±0.3| 67±0.0                      | 635±11                      | 13.4±0.3                 | 9.5±0.2              | 571±20           | 1089±26          | 7.7±0.3         |
|      | Ratio             | (–2)  | (–1)                        | (1.24)                      | (0.86)                   | (0.93)               | (1.40)           | (1.14)           | (1.21)          |
|      | Kakehashi         | AMB   | 38±0.6                      | 74±0.3                      | 477±29                   | 12.8±0.4             | 9.4±0.3           | 615±26           | 7.9±0.1         |
|      | ELV               | 39±0.6| 74±0.4                      | 515±33                      | 11.4±0.3                 | 8.1±0.1              | 692±22           | 1244±36          | 7.9±0.5         |
|      | Ratio             | (–2)  | (0)                         | (1.08)                      | (0.89)                   | (0.86)               | (1.13)           | (1.07)           | (1.00)          |
|      | Akitakomachi      | AMB   | 56±0.4                      | 84±0.3                      | 485±30                   | 12.3±0.3             | 8.0±0.1           | 653±33           | 8.0±0.3         |
|      | ELV               | 53±0.9| 84±0.4                      | 502±17                      | 11.1±0.3                 | 7.4±0.1              | 684±32           | 1407±47          | 7.6±0.4         |
|      | Ratio             | (–2)  | (0)                         | (1.03)                      | (0.91)                   | (0.92)               | (1.05)           | (1.17)           | (1.05)          |
|      | Hitomebore        | AMB   | 58±0.6                      | 92±1.3                      | 548±26                   | 11.3±0.4             | 7.8±0.1           | 755±48           | 8.5±0.4         |
|      | ELV               | 57±0.8| 89±1.0                      | 698±16                      | 9.6±0.1                  | 7.1±0.0              | 988±41           | 1468±16          | 9.5±0.4         |
|      | Ratio             | (–2)  | (–3)                        | (1.27)                      | (0.85)                   | (0.91)               | (1.31)           | (1.17)           | (1.12)          |
| 2004 | Kirara397         | AMB   | 34±0.7                      | 60±0.5                      | 464±27                   | 11.5±0.1             | 8.7±0.1           | 576±25           | 6.6±0.3         |
|      | ELV               | 31±0.2| 59±0.5                      | 555±31                      | 10.9±0.2                 | 8.1±0.1              | 716±33           | 1278±32          | 7.8±0.4         |
|      | Ratio             | (–2)  | (–3)                        | (1.20)                      | (0.95)                   | (0.92)               | (1.24)           | (1.18)           | (1.18)          |
|      | Kakehashi         | AMB   | 66±0.3                      | 66±0.3                      | 464±41                   | 11.2±0.2             | 9.0±0.4           | 741±57           | 8.9±0.5         |
|      | ELV               | 65±0.0| 65±0.0                      | 467±16                      | 10.1±0.4                 | 8.5±0.1              | 815±13           | 1425±85          | 8.2±0.4         |
|      | Ratio             | (–2)  | (–3)                        | (1.01)                      | (0.90)                   | (0.95)               | (1.10)           | (1.19)           | (1.00)          |
|      | Akitakomachi      | AMB   | 49±0.8                      | 76±0.3                      | 410±21                   | 10.3±0.3             | 8.2±0.2           | 818±22           | 8.4±0.4         |
|      | ELV               | 46±0.3| 70±0.3                      | 477±19                      | 9.3±0.2                  | 7.4±0.2              | 1008±22          | 1522±53          | 9.1±0.4         |
|      | Ratio             | (–2)  | (–3)                        | (1.10)                      | (0.88)                   | (0.91)               | (1.22)           | (1.19)           | (1.08)          |
|      | Hitomebore        | AMB   | 52±0.3                      | 79±0.3                      | 477±10                   | 9.4±0.1              | 7.7±0.4           | 972±21           | 9.2±0.3         |
|      | ELV               | 50±0.5| 77±0.3                      | 514±10                      | 8.6±0.2                  | 7.0±0.1              | 1102±13          | 1563±44          | 9.4±0.3         |
|      | Ratio             | (–2)  | (–3)                        | (1.06)                      | (0.91)                   | (0.91)               | (1.13)           | (1.09)           | (1.03)          |

| Interaction | p-value |
|-------------|---------|
| AMB×[CO2] | 0.01    |
| ELV×[CO2] | 0.01    |
| AMB×cultivar | ***    |
| ELV×cultivar | ***    |
| AMB×year | ns      |
| ELV×year | ns      |
| AMB×cultivar×year | ns      |
| ELV×cultivar×year | ns      |

AMB, ambient [CO2]; ELV, elevated [CO2]. Average ± standard error (n=4). Ratio: values in parentheses represent the difference between ELV and AMB for the other parameters. ***, P < 0.001; **, P < 0.01; *, P < 0.05; +, P < 0.10; ns, not significant.
corresponded to maturity group over years and over [CO₂]. Reflecting the temperature difference between the two years, both the panicle initiation and heading dates were generally later in 2003 than in 2004, except for the panicle initiation stage in Kirara397. Elevated [CO₂] accelerated heading date of all cultivars in 2004, but elevated [CO₂] in 2003 had smaller effects on heading date of earlier three cultivars (Kirara397, Kakehashi, and Akitakomachi) than that in 2004. The low temperature in 2003 coincided with the reproductive growth stage of the cultivars with earlier maturity (Kirara397, Kakehashi, and Akitakomachi), whereas the late-maturing cultivar Hitomebore did not experience these low temperatures during its reproductive growth stage.

**Tiller number**

The number of tillers per square meter (tiller density) at heading stage, which was significantly greater in 2003 than in 2004, was increased by elevated [CO₂] for all cultivars by 1–24% (Table 2). The magnitude was not affected by years, but the magnitude differed between cultivars. Kirara397 and Hitomebore showed the highest increase by elevated [CO₂] by 22% and 18%, respectively (averaged over two years), followed by the intermediate maturity cultivars Akitakomachi (10%) and Kakehashi (4%).

**Plant N concentration, biomass, and N uptake**

Plant N concentrations of the whole plant at both heading and maturity were higher in 2003 than in 2004, and differed significantly between cultivars. The earlier-maturing cultivars generally had higher N concentrations (Table 2), as hypothesized. Elevated [CO₂] significantly decreased plant N concentration, without a significant [CO₂]×cultivar interaction.

Biomass at the heading stage was smaller in 2003 than in 2004 by an average of 21% across cultivars and [CO₂] levels, and was generally larger in the later-maturing cultivars compared with the early-maturing cultivars (Table 2). Elevated [CO₂] significantly increased biomass, and there was a significant [CO₂]×cultivar interaction; the magnitude of the biomass difference caused by elevated [CO₂] was greater for the early cultivar Kirara397 (a mean of 32% for the two years) and the late cultivar Hitomebore (22%) than for the intermediate cultivars Akitakomachi (14%) and Kakehashi (12%). In addition, this order did not correspond to the order of maturity groups or plant N concentrations which decreased consistently from the earliest to the latest cultivars in both years. At maturity, elevated [CO₂] significantly increased biomass (by 5–18%), but there was no significant [CO₂]×cultivar interaction. The two factors that determined biomass accumulation (canopy radiation capture, IPAR; radiation-use efficiency, RUE) were both significantly increased by elevated [CO₂] before heading, with a marginally significant [CO₂]×cultivar interaction (P <0.1). The contribution of RUE was significant for both [CO₂] and cultivar, and generally increased biomass under elevated [CO₂]. After heading, however, there was no significant effect of elevated [CO₂] on RUE or IPAR.

N uptake was less affected by elevated [CO₂], in which the plants had a lower N concentration (Table 2). Elevated [CO₂] had a marginal significant effect on N uptake at the heading stage, and there was a significant [CO₂]×cultivar interaction as well as biomass at this stage.

**Light-saturated leaf photosynthesis**

Light-saturated leaf photosynthesis was higher under elevated [CO₂], especially during the vegetative growth stage, but the magnitude of the difference decreased at the reproductive growth stage (Fig. 2). There was no significant [CO₂]×cultivar interaction at either growth stage.

**Yield and yield components**

Grain yield in 2003 was significantly lower than in 2004 by around 25% averaged across all cultivars and [CO₂] levels (Table 3). Elevated [CO₂] significantly increased grain yield.
Table 3. Grain yield and yield components for the four rice cultivars grown under ambient (AMB) and elevated (ELV) CO₂ in 2003 and 2004.

Values in parentheses represent the ratio of ELV to AMB. ***, P < 0.001; **, P < 0.01; *, P < 0.05; +, P < 0.10; ns, not significant. Average yield ± standard error (n=4).

| Year | Cultivar | [CO₂] | Grain yield (g m⁻²) | Panicles (m⁻²) | Spikelets per panicle | Spikelets per spikelet | Ripened grains (%) | Unripe grains (%) | Sterile grains (%) | Individual grain weight (mg) |
|------|----------|-------|---------------------|----------------|-----------------------|-----------------------|--------------------|-------------------|------------------------|-----------------------------|
| 2003 | Kirara397| AMB   | 396±13              | 496±19         | 52±0.4               | 25620±960           | 67.8±2.4           | 8.6±0.3          | 23.6±2.4             | 22.5±0.2                   |
|      |          | ELV   | 442±12              | 612±23         | 53±0.2               | 32421±1175          | (1.13)             | (1.23)            | (1.03)                | (0.92)                      |
|      |          |       |                     |                |                       |                       | (1.27)             | (1.27)            | (0.92)                | (0.92)                      |
|      |          |       |                     |                |                       |                       | (0.92)             | (1.25)            | (0.97)                |                             |
|      | Kakehashi| AMB   | 468±7               | 429±25         | 67±2.5               | 28462±1453          | 77.4±2.2           | 8.0±0.4           | 14.6±2.2             | 21.3±0.2                   |
|      |          | ELV   | 482±20              | 469±14         | 65±1.3               | 30666±1233          | 75.0±2.1           | 8.8±0.4           | 16.2±1.8             | 21.0±0.1                   |
|      |          |       |                     |                |                       |                       | (1.03)             | (1.09)            | (0.98)                | (1.06)                      |
|      |          |       |                     |                |                       |                       | (1.06)             | (1.06)            | (0.97)                | (1.10)                      |
|      | Akitakomachi| AMB | 452±10              | 401±25         | 74±1.4               | 29860±1402          | 79.6±2.5           | 7.7±1.0           | 12.7±1.7             | 19.1±0.1                   |
|      |          | ELV   | 448±11              | 442±27         | 72±4.1               | 31483±895           | 75.7±1.8           | 9.6±1.0           | 14.7±0.8             | 18.8±0.0                   |
|      |          |       |                     |                |                       |                       | (0.99)             | (1.10)            | (0.97)                | (1.06)                      |
|      |          |       |                     |                |                       |                       | (1.06)             | (0.95)            | (1.24)                | (1.16)                      |
|      |          |       |                     |                |                       |                       | (1.24)             | (1.16)            | (0.98)                |                             |
| 2004 | Kirara397| AMB   | 458±32              | 456±14         | 69±1.9               | 31304±516           | 72.5±4.4           | 19.9±3.6          | 7.7±0.8              | 20.2±0.2                   |
|      |          | ELV   | 535±13              | 532±27         | 69±2.1               | 35691±988           | 74.8±2.8           | 18.1±2.4          | 7.1±0.4              | 19.7±0.2                   |
|      |          |       |                     |                |                       |                       | (1.17)             | (1.17)            | (1.00)                | (1.16)                      |
|      |          |       |                     |                |                       |                       | (1.16)             | (1.03)            | (0.91)                | (0.93)                      |
|      |          |       |                     |                |                       |                       | (0.93)             | (0.98)            |                       |                             |
|      | Kakehashi| AMB   | 575±15              | 419±16         | 53±1.5               | 22962±686           | 89.1±0.5           | 3.0±0.4           | 7.9±0.6              | 24.0±0.1                   |
|      |          | ELV   | 603±6               | 530±13         | 53±1.1               | 28145±464           | 89.9±1.0           | 3.2±0.6           | 6.9±0.4              | 23.8±0.2                   |
|      |          |       |                     |                |                       |                       | (1.23)             | (1.22)            | (1.00)                | (1.23)                      |
|      |          |       |                     |                |                       |                       | (1.23)             | (1.01)            | (1.08)                | (0.87)                      |
|      |          |       |                     |                |                       |                       | (0.87)             | (0.99)            |                       |                             |
|      | Akitakomachi| AMB | 618±14              | 391±11         | 76±3.2               | 29790±843           | 92.7±0.3           | 4.6±0.2           | 2.7±0.1              | 22.4±0.1                   |
|      |          | ELV   | 699±25              | 438±19         | 77±1.6               | 33770±1564          | 93.1±0.5           | 3.6±0.5           | 3.3±0.1              | 22.2±0.2                   |
|      |          |       |                     |                |                       |                       | (1.13)             | (1.12)            | (1.01)                | (1.01)                      |
|      |          |       |                     |                |                       |                       | (1.01)             | (0.78)            | (1.20)                | (0.99)                      |
|      | Hitomebore| AMB  | 612±20              | 438±8          | 70±3.3               | 30709±1034          | 88.6±0.7           | 7.9±0.4           | 3.5±0.3              | 22.5±0.1                   |
|      |          | ELV   | 701±8               | 480±14         | 71±2.0               | 33893±600           | 90.9±1.0           | 6.0±0.7           | 3.1±0.4              | 22.8±0.1                   |
|      |          |       |                     |                |                       |                       | (1.15)             | (1.10)            | (1.01)                | (1.10)                      |
|      |          |       |                     |                |                       |                       | (1.10)             | (1.03)            | (0.76)                | (0.88)                      |
|      |          |       |                     |                |                       |                       | (0.88)             | (1.01)            |                       |                             |

(by up to 23% compared with yield under the ambient [CO₂] level), and there was a significant [CO₂]×cultivar interaction. The yield increase was larger for Kirara397 (18% averaged across the two years) and Hitomebore (16%) than for Akitakomachi (6%) and Kakehashi (3%), the cultivars with intermediate maturity dates. A [CO₂]×year interaction was also significant because of the smaller yield increase in 2003 (a mean of 8% across cultivars) than in 2004 (13%). The number of spikelets per square metre (spikelet density) was significantly greater under elevated [CO₂], and was the major contributor to the increased grain yield and the significant [CO₂]×cultivar interaction. This is shown by the high and significant correlation between the increased grain yield and increased spikelet density across cultivars and years (r=0.70, P < 0.001; Table 4).

The percentage of ripened grain was substantially lower in 2003 than in 2004, by 17 points (averaged over cultivars and [CO₂]), and this can be attributed to the higher percentage sterile grains in 2003 (Table 3). There was a marginally significant [CO₂]×cultivar interaction (P < 0.1) for the sterility percentage, but the cultivar×year and [CO₂]×cultivar×year interactions were highly significant (P < 0.001 and P < 0.01, respectively). In the cool summer of 2003, the change in the sterility percentage between elevated and ambient [CO₂] was higher in the three earlier-maturing cultivars (Kirara397, +25%; Kakehashi, +11%; and Akitakomachi, +16%) than in the late-maturing cultivar (Hitomebore, –7%). By contrast, the percentage of unripe grains was higher in the late cultivar Hitomebore than in the other cultivars in 2003. The percentage of unripe grains was not significantly affected by elevated [CO₂]. Individual grain weight was significantly lower in 2003 than in 2004, and was significantly affected by elevated [CO₂] with a [CO₂]×year interaction (P < 0.05); elevated [CO₂] slightly decreased individual grain weight by 1–3% in 2003, not in 2004.

Table 4 presents the correlations between growth traits and grain yield and spikelet density. The increase in grain
yield was more closely correlated with the increase in biomass and N uptake at heading than at maturity. This correlation before the heading stage was associated with higher correlations for RUE before heading.

Discussion

The 2-year FACE study showed that elevated [CO₂] significantly increased rice yield, as has been reported previously (Kim et al., 2003; Yang et al., 2006; Shimono et al., 2008). The magnitude of the observed increase was within the range (0–23%) reported in previous rice FACE studies (Kim et al., 2003; Yang et al., 2006; Shimono et al., 2008). It was found that the magnitude of the yield enhancement by elevated [CO₂] differed significantly among cultivars, ranging from 0–23% (Table 3). The present study is the first to detect significant genotypic variations in the yield response of grain yield to elevated [CO₂] under FACE conditions. However, these results did not find any relationship between the cultivar’s maturity group and the responsiveness to elevated [CO₂]. The yield enhancement for the early-maturing cultivar Kirara397 (18% averaged over the 2 years) and for the late-maturing cultivar Hitomebore (16%) were both higher than the corresponding increases for the cultivars with intermediate maturation times (6% and 3%).

Table 4. Correlations between the relative increase in grain yield or spikelet density with elevated [CO₂] and the relative change in other characteristics of rice cultivars

| Parameters                     | Correlation coefficient (r)  |
|--------------------------------|------------------------------|
|                                | Grain yield                  | Spikelet density |
| Yield components               |                              |
| Number of panicles m⁻²         | 0.40 *                       | 0.81 ***         |
| Number of spikelets per panicle| 0.46 **                      | 0.27 ns          |
| Spikelet density (number m⁻²)  | 0.70 ***                     | –                |
| Ripened grains (%)             | 0.48 **                      | –0.27 ns         |
| Unripened grains (%)           | –0.25 ns                     | 0.12 ns          |
| Sterile grains (%)             | –0.46 **                     | 0.06 ns          |
| Individual grain weight (mg)   | –0.12 ns                     | –0.47 **         |
| Growth characteristics         |                              |
| Heading date of ambient [CO₂]  | –0.18 ns                     | –0.34 ns         |
| Tiller density at heading (m⁻²)| 0.28 ns                      | 0.38 *           |
| Biomass at heading (g m⁻²)     | 0.53 **                      | 0.48 **          |
| Biomass at maturity (g m⁻²)    | 0.31 ns                      | 0.40 *           |
| N concentration at heading (mg g⁻¹)| 0.07 ns                   | 0.19 ns          |
| N concentration at maturity (mg g⁻¹)| 0.26 ns                  | 0.41 *           |
| N uptake at heading (g m⁻³)    | 0.54 **                      | 0.57 ***         |
| N uptake at maturity (g m⁻³)   | 0.33 ns                      | 0.46 **          |
| RUE preheading (g mol⁻¹)       | 0.39 *                       | 0.21 ns          |
| RUE postheading (g mol⁻¹)      | –0.15 ns                     | –0.04 ns         |
| IPAR preheading (mol m⁻² d⁻¹)  | 0.35 ns                      | 0.58 ***         |
| IPAR postheading (mol m⁻² d⁻¹) | 0.43 *                       | 0.65 ***         |

* n=32 (2 years×4 cultivars×4 replicates), *** P <0.001; **, P <0.01; *, P <0.05; ns, not significant.

Among the yield components, spikelet density was the major contributors to the response of grain yield to elevated [CO₂] between cultivars over years (Table 4) (r=0.70, P <0.001). A similar contribution of spikelet density on yield enhancement under elevated [CO₂] has been reported in previous studies using a single cultivar under different N inputs (Kim et al., 2003; Yang et al., 2006) and under different temperature conditions (Shimono et al., 2008). The present study revealed that yield enhancement by elevated [CO₂] even for genotypic variation could be explained by the response of spikelet density which was mostly determined before heading (Yoshida, 1981). Spikelet density is a result of panicle number per square metre (panicle density) and spikelet number per panicle (individual panicle size). The present study showed that spikelet density was more related to panicle density at maturity (Table 4) (r=0.81, P <0.001) and tiller density at heading (r=0.38, P <0.05) rather than to individual panicle size (r=0.27, ns).

Grain yield was also significantly correlated with biomass and N uptake at the heading stage (r=0.53 and r=0.54, respectively, both at P <0.01; Table 4). It has generally been reported that N uptake before heading is a critical factor in spikelet production (Hasegawa et al., 1994; Kim et al., 2001). Figure 3 reveals that a close relationship between N uptake at heading and spikelet density at maturity existed across years, cultivars, and [CO₂]. The present study showed that enhanced N uptake and increased biomass in response to elevated [CO₂], rather than maturity group, are the critical factors responsible for the increased spikelet density and grain yield under elevated [CO₂]. Similar relationships have previously been reported in FACE experiments that used a single cultivar (Kim et al., 2001). Enhancement of growth at the heading stage would thus appear to be a good
criterion for the selection of cultivars with a high potential response to increased [CO2].

It is unclear what physiological traits are related to the observed genotypic variations in the responses of biomass and N uptake to elevated [CO2]. The results showed that RUE, which is an integral characteristic of photosynthesis of individual leaves and of plant respiration throughout a season (Sinclair and Muchow, 1999), was closely related to the biomass and N uptake responses at the heading stage (Tables 2, 4). However, there was no significant [CO2]×cultivar interaction for photosynthesis of the uppermost leaves at either growth stage (Fig. 2). Osborne et al. (1998) examined the photosynthetic acclimation to elevated [CO2] for leaves at different positions, and showed that the acclimation differed between leaf positions. Photosynthesis was promoted in lower, shaded leaves in the canopy. Thus, the RUE response that was observed might have resulted from differences among cultivars in the photosynthetic responses of their lower leaves to elevated [CO2]. RUE is also affected by respiration. Because of the difficulty of measuring respiration under high [CO2], the direct effects of elevated [CO2] on respiration per unit dry weight are still debated (Baker et al., 2000; Jahnke and Krewitt, 2002), but it is widely accepted that enhanced growth in response to elevated [CO2] can also increase the canopy respiration per unit of land area (Baker et al., 2000; Sakai et al., 2006). The proportion of gross photosynthesis consumed by respiration at night was reported to be more than 20% in rice (Sakai et al., 2006). Thus, differences among cultivars in respiration rates may also be a possible candidate for explaining the genotypic variations in the responses of RUE to elevated [CO2]. In addition, it is noteworthy that there was no significant [CO2]×cultivar interaction for plant N concentrations, and that the N concentration decreased by 11% at the heading stage across the cultivars and by 9% at maturity with elevated [CO2] (Table 2). This indicates that cultivars with a stronger response to elevated [CO2] have a higher ability to take up N so that N concentrations are not decreased excessively (‘diluted’) by the biomass enhancement that occurs under these conditions. A cultivar’s N uptake ability might thus partially explain the genotypic variations in RUE.

The significant [CO2]×year interaction for grain yield (Table 3) was also reported in a previous study that examined two levels of N fertilization using Akitakomachi (Shimono et al., 2008). The present study confirmed this finding; elevated [CO2] increased the percentage of sterile grains in Kirara397 and Kakehashi in addition to Akitakomachi in 2003. In our field trials, the duration and magnitude of cold temperatures during the sensitive stage of panicle development differed between years, so it is difficult to identify genotypic variation in cold tolerance under elevated [CO2]. However, there may be a highly tolerant cultivar that is not affected by elevated [CO2]. At present, researchers are optimistic about future rice production in cool areas, which is expected to compensate for the predicted yield decline in tropical areas (IPCC, 2007). However, Shimono (2008) has analysed yield fluctuation in rice over the past 26 years in the northern part of Japan (using 275 data sets obtained from agricultural experimental stations) and showed that yield fluctuation by low temperature did not decrease during this period even though annual temperature had been increasing. Air temperature in summer, which is a sensitive period for low temperature-induced sterility in rice, did not increase during this period. Considering the negative interaction of elevated [CO2] on cold damage reported in the present study and the previous study (Shimono et al., 2008), the risk of cold damage could not be overlooked under future climates with elevated [CO2].

Sensitivity to coldness during reproductive growth is known to be particularly high for a few days at the young microspore stage (10-12 d before heading) and the sensitivity sharply decreases before and after this stage. An estimate of how elevated [CO2] affects developmental stage is important for accurately predicting how a cold spell would impact future rice production. Elevated [CO2] generally accelerates heading date by 1–3 d (Kim et al., 2003; Shimono et al., 2008). In the present study, in 2004 a warmer than average year, heading date of all cultivars was enhanced by elevated [CO2], but in 2003, a cold and cloudy year, heading date of the earlier three cultivars was less affected by elevated [CO2] than in 2004 (Table 2). Since elevated [CO2] can increase canopy temperature through stomatal closure with decreasing transpiration rate (Yoshimoto et al., 2005), this positive effect might be smaller in 2003 than in 2004 in these cultivars. Further studies focusing on genotypic variation of developmental stage in response to elevated [CO2] might be expected.

Conclusion

We hypothesized that early-maturing cultivars might have a higher [CO2]-induced yield enhancement than late-maturing cultivars, but our 2-year field trials rejected this hypothesis. The magnitude of [CO2]-induced yield enhancement corresponded to the magnitude of growth enhancement at the heading stage over cultivars and over years. The criteria would be good indicators for efficiently selecting and breeding new cultivars, and offers the advantage of a shorter experimental period, i.e. the results will become evident by the heading stage.

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