Yield response of high-yielding rice cultivar Oonari to different environmental conditions

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ABSTRACT
A new rice (*Oryza sativa* L.) cultivar, ‘Oonari’, was developed to reduce the shattering habit of the high-yielding cultivar ‘Takanari’. To evaluate the effects of environment on its yield and related traits, Oonari and Takanari were grown in multiple environmental conditions at three locations in Japan. The whole and filled brown rice yields of Oonari were around 1000 g m$^{-2}$, similar to those of Takanari. But the panicle number m$^{-2}$ of Oonari was slightly but significantly higher than that of Takanari and the spikelet number per panicle was slightly but significantly lower. With respect to the effect of environment on yield of Oonari, cumulative radiation during 40 days after heading was positively related to whole brown rice yield of Oonari. Yield tended to be higher under increased atmospheric CO$_2$ concentration than under ambient. Oonari was confirmed to exhibit high yield in various environmental conditions.

Introduction

Rice (*Oryza sativa* L.) is an important crop and a major source of food for more than a third of the world’s population (Khush, 1997). A continuous increase in rice production is required to meet the demands of increasing population (Tilman et al., 2011).

‘Takanari’ is one of the highest-yielding rice cultivars in Japan. The whole brown rice yield of Takanari is as high as about 1000 g m$^{-2}$ in Japan (Yoshinaga et al., 2013). However, Takanari, derived from a cross between indica- and japonica-type parents, is prone to seed shattering (Ando, 1990), which can lead to yield losses during harvesting. To reduce the shattering habit of Takanari, a new cultivar, ‘Oonari’ was developed by γ-irradiation of Takanari at the National Agriculture and Food Research Organization (NARO) of Japan and released in 2015 (Kobayashi et al., 2016). The whole brown rice yield of Oonari was higher than that of Takanari (Kobayashi et al., 2016), but the yield traits have not yet been clarified. It is important to reveal yield response of new high-yielding rice cultivars to various environmental conditions.

Crop growth and yield are affected by various environmental conditions (Horie et al., 1995; Peng...
et al., 2004; Porter et al., 2014; Yoshida & Parao, 1976). Among these, air temperature and solar radiation are the major environmental factors that determine crop yield. In addition, carbon dioxide concentration ([CO₂]) is a notable factor in light of the continuing global increase: atmospheric [CO₂] has risen from 280 μmol mol⁻¹ before the Industrial Revolution to 409 μmol mol⁻¹ in 2018 (Earth Systems Research Laboratory, 2018), and is projected to rise further during the next 50 years even if efforts are made to reduce emissions (Fisher et al., 2007). Yield responses to these conditions show varietal differences (Hasegawa et al., 2013; Nagata et al., 2016; Nakano et al., 2017; Shimono et al., 2009). However, the responsiveness of the yield-related traits of Oonari to environment has not yet been clarified.

Therefore, in this study, we compared brown rice yield and yield components between Oonari and Takanari at three distant locations in Japan: Tsukuba (eastern lowlands, 12 m above sea level) where these cultivars were developed, Fukuyama (western lowlands, 1 m above sea level) and Nagano (central highlands, 340 m above sea level) which is known to be high yielding region for rice in Japan. We investigated the effect of environmental conditions on the yield traits. We also investigated the responses of the yield traits of Oonari to increased atmospheric [CO₂] in a free-air CO₂ enrichment (FACE) facility.

**Materials and methods**

**Plant materials and cultivation**

Takanari and Oonari were grown in field experiments in all three locations. Cultivation methods in each location were shown in Table 1. Fertilizers were applied as following practice in each location.

In Tsukuba, we applied a basal dressing of manure at about 1 kg m⁻² and chemical fertilizers at rates of 16 and 12 g m⁻² (P₂O₅ and K₂O) in two cultivars and 12 g N m⁻² (as controlled-release fertilizer: equal parts LP40 and LP100; JCAM Agri, Tokyo, Japan). We applied a topdressing of LP40 at 4 g N m⁻² at the panicle formation stage. LP40 and LP100 fertilizers release 80% of their total N content at a uniform rate up to 40 and 100 days, respectively, after application, at soil temperature at 25°C.

In Fukuyama, we applied a basal dressing of chemical fertilizers at 12 g N m⁻² (as controlled-release fertilizer: equal parts LP40 and LP100; JCAM Agri, Tokyo, Japan), rates of 10 g m⁻² each of P₂O₅ and K₂O. We applied a topdressing of LP40 at 6 g N m⁻² at the panicle formation stage. In 2014, we applied a basal dressing of 4.0 g m⁻² (N, P₂O₅ and K₂O each), and topdressings of 2 g m⁻² (N, P₂O₅ and K₂O each) at tillering, 3 g m⁻² (N, P₂O₅ and K₂O each) at panicle neck node differentiation and panicle formation, and 3 g N m⁻² at meiosis stage.

In Nagano, we applied a basal dressing of manure at about 2 kg m⁻² and a chemical fertilizer at the rate of 7.98 and 11.2 g m⁻² (N, P₂O₅ and K₂O). We applied topdressings of 3, 4.2 and 4.8 g m⁻² (N, P₂O₅ and K₂O) at tillering, 7.5 and 3.8 g m⁻² (N and K₂O) at panicle formation stage, and 4.5 and 2.5 g m⁻² (N and K₂O) 14 days later.

At maturity, when approximately 85% of grains became yellow, we sampled from each replicate to measure yield and its components in each site. Plants were harvested carefully by hand and packed immediately into nylon net bags to avoid loss by shattering during transport and drying.

**FACE experiment**

We transplanted Oonari on 24–25 May 2017 in the FACE experimental site as shown in Table 1. We applied a basal dressing of 19 g N m⁻² (as controlled-release fertilizer: equal parts LP40, LP500, and LP140; JCAM Agri, Tokyo, Japan as), and 10 g m⁻² each for P₂O₅ and K₂O. LP500 fertilizer releases 80% of its total N content

| Location | Site | Year | Plot area (m²) | Replication | Sampled hill no. per rep. |
|----------|------|------|---------------|-------------|--------------------------|
| Tsukuba  | Experimental paddy field at NARO Institute of Crop Science | 2013 | 5.4 | 6 | 48 |
| Fukuyama | Experimental paddy field at the NARO Western Region Agricultural Research Center | 2017 | 17.9 | 4 | 48 |
| Nagano  | Experimental paddy field at the Nagano Agricultural Experiment Station | 2014 | 11.5 | 3 | 60 |
| FACE    | Farmers’ fields | 2017 | 4.8 | 2 | 40 |

Table 1. Cultivation methods.

Planting density at 22.2 hills m⁻² (15 cm × 30 cm), with one plant per hill in Tsukuba and three plants per hill in the other sites.
Grain yield and yield components of Oonari and Takanari in experiments.

Detailed descriptions on the FACE experiment are presented by Nakamura et al. (2012). In brief, the elevated [CO$_2$] treatments were imposed on octagonal plots (‘FACE rings’) in the fields. Each ‘FACE ring’ which was 240 m$^2$ in area and 17 m in inside diameter, was prepared in combination with a corresponding ambient [CO$_2$] plot. We used four fields as replications, each with a pair of FACE and ambient control plots with their centers 75 m apart to minimize cross-contamination. From transplanting to harvest, the target [CO$_2$] was 200 µmol mol$^{-1}$ above ambient, and CO$_2$ was supplied during daylight hours. The season-long daytime average [CO$_2$] was 585 ± 1.6 µmol mol$^{-1}$ in the FACE plots and 391 µmol mol$^{-1}$ in the ambient plots.

**Weather conditions**

The weather conditions during the growing season at each site were shown in Supplementary Figure S1.

**Statistical analysis**

All statistical analyses were conducted in statistical analysis software R (Core Team, 2017). Yield and components in Tsukuba and Fukuyama were tested by analysis of variance (ANOVA). Pearson’s correlation analysis and a test for no correlation in Oonari were conducted using five sets of data obtained from Tsukuba, Fukuyama and Nagano. FACE experiment data were analyzed by paired t-test ($p < 0.05$).

### Results

#### 1. Yield and its components between Oonari and Takanari at three sites

The whole and filled brown rice yields of Oonari were ranged from 983 to 1053, and from 908 to 1016 g m$^{-2}$, respectively, in Tsukuba and Fukuyama (Table 2). These brown rice yields of Takanari were ranged from 905 to 1068, and from 884 to 1042 g m$^{-2}$, respectively. There were no significant differences in whole and filled brown rice yields between Oonari and Takanari in Tsukuba and Fukuyama in each year (Table 2; Supplementary Tables S1 and S2). Among yield components, Oonari had a significantly higher panicle number m$^{-2}$ and a significantly lower spikelet number per panicle than Takanari in Tsukuba and Fukuyama. The grain yield and its components in Nagano showed a similar tendency as in Tsukuba and Fukuyama (Table 2). In Tsukuba, Oonari had more total spikelets m$^{-2}$ than Takanari. Furthermore, Oonari had a significantly lower percentage of filled spikelets, but a significantly higher 1000-grain weight than

| Year | Cultivar | Whole brown rice yield (g m$^{-2}$) | Filled brown rice yield (g m$^{-2}$) | Panicle no. (m$^{-2}$) | Spikelet no. (panicle$^{-1}$) | Total spikelets (>103 m$^{-2}$) | Filled spikelets (%) | 1000-grain wt. (g) |
|------|----------|----------------------------------|----------------------------------|------------------------|-------------------------------|-------------------------|---------------------|------------------|
| Tsukuba 2013 | Oonari | 1053 | 1016 | 321 | 208 | 66.6 | 72.2 | 21.1 |
| 2017 | Oonari | 1068 | 1042 | 289 | 220 | 63.3 | 79.0 | 20.8 |
| | Takanari | 983 | 951 | 315 | 177 | 55.8 | 78.4 | 21.8 |
| | 2017 | 905 | 884 | 283 | 190 | 53.7 | 76.6 | 21.5 |
| Fukuyama 2013 | Oonari | 1044 | 962 | 394 | 142 | 55.9 | 80.5 | 21.4 |
| | Takanari | 1049 | 990 | 371 | 148 | 54.8 | 84.6 | 21.4 |
| 2014 | Oonari | 1003 | 908 | 368 | 170 | 62.6 | 66.1 | 22.0 |
| | Takanari | 1009 | 922 | 326 | 190 | 61.7 | 68.3 | 21.9 |
| Nagano 2017 | Oonari | 1013 | 996 | 288 | 183 | 52.6 | 86.6 | 19.9 |
| | Takanari | 984 | 961 | 278 | 201 | 55.8 | 81.3 | 21.3 |

Grains thicker than 1.6 mm in Tsukuba and Nagano and 1.8 mm in Fukuyama were considered as filled brown rice and were counted to calculate 1000-grain weight. Yield and 1000-grain weight are presented at a water content of 15%. The percentage of filled spikelets was calculated as the number of filled spikelets divided by the total number of spikelets.

| Site | Year | Transplanting date | Heading date | Harvest date | Mean air temperature Before heading | 40 days after heading | Cumulative solar radiation Before heading | 40 days after heading |
|------|------|-------------------|-------------|-------------|-------------------------------|---------------------|-------------------------------|---------------------|
| Tsukuba | 2013 | May 10 | Aug 1 | Sep 10 | 22.5 | 26.8 | 1488 | 719 |
| | 2017 | May 18 | Aug 4 | Sep 27 | 23.6 | 24.6 | 1476 | 530 |
| Fukuyama | 2013 | May 13 | Jul 30 | Sep 13 | 24.8 | 27.8 | 1535 | 723 |
| | 2014 | May 13 | Jul 31 | Sep 13 | 23.6 | 26.1 | 1471 | 544 |
| Nagano | 2017 | May 11 | Aug 15 | Sep 30 | 21.9 | 21.6 | 2027 | 663 |
Takanari. On the other hand, in Fukuyama, there was no significant difference in total spikelet number between cultivars. In addition, Oonari had significantly lower percentage of filled spikelets than Takanari, but there was no significant difference in 1000-grain weight between cultivars.

2. Effects of weather on yield and its components among sites of Oonari

The mean air temperature during the growing periods of Oonari was lower in Nagano than in Tsukuba and Fukuyama (Table 3; Supplementary Figure S1). The solar radiation in June was higher in Nagano than in Tsukuba and Fukuyama, whereas that in August was higher in Tsukuba and Fukuyama in 2013 than in other sites and years (Supplementary Figure S1). The cumulative solar radiation before heading was higher in Nagano than in Tsukuba and Fukuyama, whereas that during the 40 days after heading was highest in Tsukuba and Fukuyama in 2013. There was a significant correlation of whole brown rice yield with cumulative radiation during 40 days after heading, but not with cumulative radiation before heading or with mean air temperature either before heading or during 40 days after heading (Figure 1; Supplementary Table S3). Takanari had also the same tendency as Oonari (data not shown).

There was a significant correlation of panicle number with mean air temperature before heading, but not with mean air temperature during 40 days after heading or with cumulative radiation either before heading or during 40 days after heading (Figure 2; Supplementary Table S3). There were no significant correlations with spikelet number either. Takanari also had the same tendency as Oonari (data not shown).

3. Effects of increased atmospheric [CO₂] on yield and its components of Oonari

Under increased [CO₂] in FACE, the whole and filled brown rice yields of Oonari were 937 and 900 g m⁻², respectively. There were no significant differences in yields or yield components of Oonari (Table 4). However, whole and filled brown rice yields tended to be higher (FACE/ambient = 1.17 and 1.16, respectively) and total spikelet number m⁻² tended to be larger (FACE/ambient = 1.15) in Oonari under increased [CO₂].

Discussion

We investigated the yield traits of Oonari at three locations in Japan and to clarify the effects of environment on the yield traits of this high-yielding cultivar. We also investigated the responses of the yield traits to increased [CO₂].

Table 4. Grain yield and yield components of Oonari affected by CO₂ concentration in Tsukubamirai in 2017.

| CO₂ concentration | Whole brown rice yield (g m⁻²) | Filled brown rice yield (g m⁻²) | Panicle no. (m⁻²) | Spikelet no. (panicle⁻¹) | Total spikelets ×10⁶ m⁻² | Filled spikelets (%) | 1000-grain wt. (g) |
|-------------------|---------------------------------|---------------------------------|-------------------|-------------------------|--------------------------|---------------------|---------------------|
| Ambient (A)       | 803                             | 776                             | 325               | 158                     | 51.2                     | 67.9                | 22.3                |
| FACE (F)          | 937                             | 900                             | 358               | 164                     | 59.0                     | 69.0                | 22.1                |
| F/A               | 1.17                            | 1.16                            | 1.10              | 1.04                    | 1.15                     | 1.02                | 0.99                |
| t-test results    | n.s.                            | n.s.                            | n.s.              | n.s.                    | n.s.                     | n.s.                | n.s.                |

n.s., not significant.
The yield of Oonari was as high as that of the high-yielding Takanari at all three locations. In a previous report, the whole brown rice yield was higher in Oonari than in Takanari (Kobayashi et al., 2016). Unlike the previous study, we harvested plants using nylon net bags to avoid loss by shattering. We found no significant difference in the whole and filled brown rice yields between Oonari and Takanari (Table 2; Supplementary Tables S1 and S2). We attribute the equally high yield of Oonari to its improved shattering habit. Therefore, we would expect practical yields of Oonari to be higher than those of Takanari when rice is harvested by machine.

Among yield components, the number of panicles m$^{-2}$ was 2–9% larger and the number of spikelets per panicle was 6–9% smaller in Oonari than in Takanari at all three locations (Table 2; Supplementary Tables S1 and S2). Therefore, Oonari differs from Takanari not only in shattering habit but also slightly in these yield-related traits.

Grain yield is determined by the complex sink (total number of spikelets per unit area × filled grain weight)–source (carbohydrate supply to panicle) balance. The improvement of sink production efficiency would result in the increase in the yield potential in the indica-dominant varieties (Yoshinaga et al., 2013). However, in this study, under heavy N fertilization (15–19 kg N m$^{-2}$), total spikelets number was high (>52.6 × 10$^3$ m$^{-2}$) at all three locations (Table 2; Supplementary Tables S1 and S2). There was no correlation between the number of total spikelets and whole brown rice yield ($r = 0.41$, Table 2; Supplementary Tables S1 and S2), irrespective of year or location. In addition, cumulative radiation during the 40 days after heading was related to whole brown rice yield of Oonari (Figure 1; Supplementary Table S3). Kobayashi and Nagata (2018) also reported that solar radiation during 20 days after heading had a significant positive correlation with yield of a japonica-dominant high-yielding cultivar, Yamadawara. These results may imply that carbohydrate supply to grains after heading, not spikelet productivity before heading, is the major factor determining brown rice yield of Oonari, which is indica-dominant cultivars, under heavy N fertilization.

We presume that yield can be increased further if the ability to supply carbohydrates to grain after heading could be increased, such as through genetic improvement by breeding or the development of field management methods more suitable for Oonari.

Nagano Prefecture is ranked the highest in rice yield per unit area almost every year in Japan (Ministry of Agriculture, Forestry and Fisheries, 2019). Therefore, we expected that the whole brown rice yield of Oonari would be highest in Nagano. Instead, yields were similar at all three locations (Table 2; Supplementary Tables S1 and S2). Among yield components, the number of panicles was smaller, and therefore the number of total spikelets tended to be smaller, in Nagano than in the other regions. There was significant correlation between panicle number and mean air temperature before heading (Figure 2). This may imply that the tiller number was reduced by the low mean air temperature before heading in Nagano, and so the number of panicles at heading was low.

We also investigated the effects of increased [CO$_2$] on yield traits of Oonari to assess the effects on a high-yielding cultivar, as yield responses to increased [CO$_2$] have shown varietal differences (Hasegawa et al., 2013; Nakano et al., 2017; Shimono et al., 2009). The grain yield of Takanari, with a large sink capacity, increased more in response to increased [CO$_2$] than that of Koshihikari, with a smaller sink capacity (Hasegawa et al., 2013). Our results suggest that the yield of Oonari, with an equally large sink capacity, also increased under increased [CO$_2$] (Table 4). Among yield components, the number of total spikelets m$^{-2}$ tended to be larger, while the percentage of filled spikelets was similar under increased [CO$_2$]. Thus, the larger sink capacity of Oonari and the improvement of source ability by increased [CO$_2$] increased the whole brown rice yield, as in Takanari.

The results of our field experiments to clarify the effects of environment on the yield response of Oonari in different locations lead to the conclusion that the grain yield of Oonari can reach around 1000 g m$^{-2}$ in various environments, including under higher [CO$_2$], similar to that of the high-yielding Takanari, which is already in production. Our results also suggest that carbohydrate supply to grains after heading is an important factor in achieving the higher yield of Oonari. To attain higher and stable grain yields, further study is needed to clarify the physiological mechanisms underlying the source abilities of Oonari.

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**Disclosure statement**

No potential conflict of interest was reported by the authors.
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