Agronomic Traits for High Productivity of Rice Grown in Aerobic Culture in Progeny of a Japonica Cultivar and a High-Yielding Indica Cultivar

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Abstract: Aerobic rice culture is a promising way to save water and achieve a high yield. The present study was conducted to identify the agronomic traits required for high rice productivity in aerobic culture using chromosomal segment substitution lines (CSSLs) obtained as progeny from the cross between Sasanishiki (japonica), as the recurrent parent and Habataki, a high-yielding indica cultivar with high spikelet production ability, grown under flooded and aerobic conditions in 2009 and 2011. Grain yields of the CSSLs in aerobic culture were similar to or higher than those in flooded culture in 2009, but were similar to or lower than those in flooded culture in 2011. There were significant effects of genotype and water environment on grain yield in both years. Most of the CSSLs had a higher grain yield than Sasanishiki in aerobic culture, whereas their average was close to that of Sasanishiki in flooded culture. Rice plants grown in aerobic culture had larger biomass production, which enabled most of the CSSLs to produce more spikelets per unit area and maintain single-grain weight, thereby producing a higher grain yield than Sasanishiki. These results suggest that high spikelet producing ability would promote high grain yield in aerobic culture.

Key words: Aerobic rice, Chromosomal segment substitution line (CSSL), Rice, Yield.

Worldwide water shortage is threatening the sustainability of rice production because of the crop’s high water demand and sensitivity to water deficits (Bouman et al., 2007; Serraj et al., 2011). However, the demand for rice will continue to increase as the world’s population grows. Therefore, it will be necessary to increase the efficiency of water use in rice production systems. Aerobic rice culture, in which rice is grown in non-puddled soil under aerobic conditions, is a rice production system that requires less water than conventional flooded rice culture (Humphreys et al., 2010). In addition, aerobic rice culture is particularly productive when used with high-yielding cultivars and adequate crop management (George et al., 2002; Kato et al., 2009; Sudhir-Yadav et al., 2011). Thus, aerobic rice culture is a promising rice production system that can both save water and achieve high yields.

However, grain yield is less stable in aerobic culture than in conventional flooded culture, mainly owing to a smaller spikelet number per unit area and a smaller single-grain weight (Bouman et al., 2006; Kato et al., 2006; Peng et al., 2006; Matsuo and Mochizuki, 2009; Sudhir-Yadav et al., 2011). Kato and Katsura (2010) showed that the spikelet number per unit area in aerobic rice culture was determined by biomass production during the late reproductive period and by nitrogen uptake until 2 weeks before heading, as was shown by Yoshida et al. (2006) in rice plants grown in flooded culture. Katsura and Nakaide (2011) also found that water stress during the late reproductive period reduced the single-husk weight in rice, and that this reduced the single-grain weight. These results show that maintaining high biomass production and nitrogen uptake is essential for stable and high production of rice in aerobic culture.

Recently, the crop physiological traits important to achieve higher biomass production and nitrogen uptake in aerobic rice culture have been analyzed through varietal comparisons. The favorable traits include high root growth (Kato and Okami, 2010; Matsunami et al., 2012), high transpiration and root exudation rates (Matsunami et al., 2010), high stomatal conductance and leaf elongation rates (Nguyen et al., 2009), rapid leaf area growth (Okami et al., 2011), large individual shoot size (Okami et al., 2012), and high radiation-use efficiency (Bouman et al., 2006; Katsura et al., 2010). In these studies, many rice
cultivars with widely different genetic backgrounds were used. However, the diversity of the genetic backgrounds makes it difficult to accurately distinguish the effects of physiological parameters on biomass production, nitrogen accumulation, and grain yield from the genetic effects.

The agronomic traits responsible for high rice productivity under aerobic conditions were examined using chromosomal segment substitution lines (CSSLs) developed by Ando et al. (2008) from Sasanishiki (japonica), as the recurrent parent, and Habataki, a high-yielding indica cultivar (Kobayashi et al., 1990), grown in both flooded and aerobic culture. A previous study (Katsura and Nakaide, 2011) revealed that Sasanishiki and Habataki showed different grain yield responses in flooded and aerobic culture. Grain yield of Habataki was significantly higher in aerobic culture than in flooded culture, but that of Sasanishiki showed no significant difference. The yield performance of these CSSLs were examined under flooded and aerobic conditions to improve our understanding of crop physiology and reveal ways to save water while achieving a high and stable yield.

**Materials and Methods**

The field experiments were conducted at the Experimental Farm of Kyoto University in Osaka, Japan (34°51’N, 135°37’E), during the summers (May to September) of 2009 and 2011. The soil at the experimental site is a sandy loam (a Typic Fluvaquent) with pH 5.7, 16 to 19 g kg$^{-1}$ total C, and 1.5 to 1.9 g kg$^{-1}$ total N.

In flooded culture, the fields were puddled and kept flooded from transplanting until maturity. In aerobic culture, the fields were not puddled and there was no standing water. The fields were fully separated from each other. Sprinkler irrigation was used to supply 30 to 40 mm of water whenever the soil water potential fell below −20 kPa at a depth of 20 cm in the aerobic culture. However, sufficient water was not always available, especially during the late growth period, and the soil water potential sometimes decreased below −40 kPa. The soil water potential was measured using tensiometers (DIK-8333, Daiki Rika Kogyo Co., Saitama, Japan), with three replicates.

Sasanishiki (japonica) and 33 of the 39 CSSLs developed by Ando et al. (2008): SL401 – SL405, SL409 – SL416 and SL418 – SL437, were arranged in a randomized complete block design with three replicates. The sowing dates were 7 May 2009 and 24 May 2011. The transplanting dates were 3 June in 2009, and 15 and 16 June for aerobic and flooded culture, respectively, in 2011. Each line was planted in a single row of 10 hills at a spacing of 10 cm between hills and 30 cm between rows. An inorganic fertilizer (N : P$_2$O$_5$ : K$_2$O = 30 : 100 : 100 kg ha$^{-1}$) was applied before sowing, and ammonium sulfate (N = 20 kg ha$^{-1}$) was topdressed five times in 2009 and four times in 2011, at 2-week intervals, from transplanting until full heading in all trials in both years (total N = 130 kg ha$^{-1}$ in 2009 and 110 kg ha$^{-1}$ in 2011). Even though the N application rate in the two years was different, the N levels were high enough to achieve a high yield in both years based on previous experience (Katsura et al., 2007).

For the measurement of yield and yield components, six plants per line were harvested at ground level, avoiding the two plants at both ends of each line to avoid edge effects. All of the panicles from these plants (a bulk sample) were counted, and one plant from the bulk sample with an average number of panicles was selected as a subsample for

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**Table 1. Monthly means of daily air temperature, daily solar radiation, and total rainfall during the study period (May to September) in 2009 and 2011.**

| Month    | Mean temp. (°C) | Solar rad. (MJ m$^{-2}$ d$^{-1}$) | Rainfall (mm) |
|----------|-----------------|----------------------------------|---------------|
|          | 2009 | 2011 | 2009 | 2011 | 2009 | 2011 |
| May      | 19.1 | 19.6 | 18.8 | 17.3 | 76   | 308  |
| June     | 23.3 | 24.2 | 20.0 | 16.3 | 174  | 201  |
| July     | 26.6 | 27.8 | 17.0 | 17.5 | 306  | 145  |
| August   | 27.3 | 28.9 | 18.1 | 19.5 | 79   | 189  |
| September| 23.3 | 25.2 | 17.1 | 14.5 | 45   | 242  |
| Total (May – September) | 23.9 | 25.2 | 18.2 | 17.0 | 678  | 1084 |

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**Fig. 1. Seasonal changes in soil water potential at a depth of 20 cm. Arrows indicate the heading dates of Sasanishiki: solid arrow, 2009; dashed arrow, 2011.**
measuring the yield components. All of the panicles in the subsample were hand-threshed, and filled grains (which sank in tap water) were separated from unfilled grains. The filled and unfilled grains and the rachis branches were oven-dried at 80°C for 3 days, and their dry weights and the numbers of filled and unfilled grains were determined to calculate the single-grain weight and the ripening ratio. Grain yield was determined by multiplying the weight of the dried panicles in the bulk sample by the ratio of the weight of filled grains to the weight of the panicles in the subsample, and expressed at an assumed 0% moisture content. We calculated the spikelet number by dividing the grain yield by the single-grain weight and the ripening ratio. The aboveground dry weight (DW) at maturity was determined by summing the weights of the dried panicles and vegetative tissue from the bulk sample. The harvest index was calculated as the total grain weight divided by the total DW at maturity.

Table 2. Yield and its component parameters of Sasanishiki and the average, maximum, and minimum values in the CSSLs in flooded and aerobic culture in 2009 and 2011.

|               | Grain yield (t ha⁻¹) | Panicle number (m⁻²) | Spikelet number per unit land area (× 10⁴ m⁻²) | Spikelet number per panicle | Grain weight (mg) | Ripening ratio | Aboveground dry weight at maturity (t ha⁻¹) | Harvest index |
|---------------|----------------------|----------------------|------------------------------------------------|-----------------------------|------------------|--------------|-------------------------------------------|---------------|
|               |                      |                      |                                                |                             |                  |              |                                           |               |
| 2009          |                      |                      |                                                |                             |                  |              |                                           |               |
| Flooded       |                      |                      |                                                |                             |                  |              |                                           |               |
| Sasanishiki   | 6.9                  | 417                  | 3.6                                            | 88                          | 22.5             | 0.85         | 13.6                                      | 0.51          |
| Ave. of CSSLs | 6.7                  | 433                  | 3.6                                            | 85                          | 22.1             | 0.84         | 14.1                                      | 0.48          |
| Max. of CSSLs | 8.1                  | 485                  | 4.5                                            | 113                         | 23.9             | 0.92         | 16.7                                      | 0.52          |
| Min. of CSSLs | 5.0                  | 365                  | 3.0                                            | 65                          | 19.9             | 0.64         | 11.1                                      | 0.41          |
| Aerobic       |                      |                      |                                                |                             |                  |              |                                           |               |
| Sasanishiki   | 6.7                  | 394                  | 3.0                                            | 77                          | 24.0             | 0.91         | 15.8                                      | 0.42          |
| Ave. of CSSLs | 7.2                  | 445                  | 3.5                                            | 80                          | 22.9             | 0.90         | 16.8                                      | 0.43          |
| Max. of CSSLs | 8.6                  | 527                  | 4.3                                            | 111                         | 25.4             | 0.95         | 20.3                                      | 0.48          |
| Min. of CSSLs | 6.0                  | 353                  | 2.8                                            | 62                          | 20.0             | 0.82         | 13.1                                      | 0.38          |
| 2011          |                      |                      |                                                |                             |                  |              |                                           |               |
| Flooded       |                      |                      |                                                |                             |                  |              |                                           |               |
| Sasanishiki   | 6.2                  | 330                  | 3.2                                            | 97                          | 23.3             | 0.83         | 11.4                                      | 0.54          |
| Ave. of CSSLs | 6.1                  | 327                  | 3.3                                            | 101                         | 23.1             | 0.80         | 11.8                                      | 0.52          |
| Max. of CSSLs | 7.2                  | 383                  | 4.1                                            | 138                         | 25.0             | 0.92         | 13.9                                      | 0.55          |
| Min. of CSSLs | 4.6                  | 278                  | 2.6                                            | 74                          | 20.5             | 0.60         | 9.6                                       | 0.45          |
| Aerobic       |                      |                      |                                                |                             |                  |              |                                           |               |
| Sasanishiki   | 5.0                  | 417                  | 2.9                                            | 70                          | 21.3             | 0.81         | 11.2                                      | 0.45          |
| Ave. of CSSLs | 5.5                  | 430                  | 3.2                                            | 76                          | 20.9             | 0.81         | 12.2                                      | 0.45          |
| Max. of CSSLs | 6.8                  | 533                  | 4.1                                            | 102                         | 22.9             | 0.90         | 14.7                                      | 0.50          |
| Min. of CSSLs | 4.1                  | 363                  | 2.6                                            | 59                          | 19.1             | 0.69         | 10.9                                      | 0.37          |
| Significance  |                      |                      |                                                |                             |                  |              |                                           |               |
| Genotype      | ***                  | ***                  | ***                                            | ***                         | ***              | ***          | ***                                       | ***           |
| Environment   | NS                   | ***                  | **                                             | ***                         | ***              | ***          | ***                                       | ***           |
| Year          | ***                  | ***                  | ***                                            | ***                         | ***              | ***          | ***                                       | ***           |
| G × E         | **                   | NS                   | NS                                             | **                          | ***              | ***          | *                                         | ***           |
| G × Y         | NS                   | NS                   | NS                                             | NS                          | ***              | ***          | *                                         | ***           |
| E × Y         | ***                  | ***                  | NS                                             | ***                         | ***              | ***          | ***                                       | ***           |
| G × E × Y     | NS                   | NS                   | NS                                             | ***                         | ***              | ***          | NS                                        | *             |

33 CSSLs were tested (for details, see the text).

*, ** and *** indicate significant at 0.05, 0.01 and 0.001 probability levels, respectively.
NS means non-significant at P = 0.05 level.
Daily mean temperature, solar radiation, and rainfall were recorded at meteorological stations beside the fields. Data for all treatments in a given year were analyzed by analysis of variance (ANOVA) in SigmaPlot v. 12.0 software (http://www.sigmaplot.com/). The effect of genotype, water environment, year, and their interactions were assessed by ANOVA using the combined data from all trials. Dunnett’s pairwise multiple-comparison test, using Sasanishiki as the control, was used to detect differences between the values of each trait in Sasanishiki and the corresponding values in each CSSL.

Results

The daily average air temperature was higher in 2011 than in 2009 in all months (Table 1). On the other hand, solar radiation in 2011 was lower than that in 2009, except in July and August, and rainfall in 2009 was more than 400 mm lower than in 2011. Soil water potential at a depth of 20 cm was higher during the early growth period in both years, but it frequently approached or dropped below −40 kPa during the ripening period in 2009 and dropped below −20 kPa around the heading stage in 2011 (Fig. 1). There was a period with especially severe water stress during the week preceding heading in 2011.

Overall, grain yield in 2009 was significantly higher than that in 2011 (Table 2, Fig. 2). There was a significant year × water environment interaction in grain yield, which means that the relationship between grain yields in the two water regimes showed different trends in the two years, and a significant genotype × water environment interaction, which means that the response of grain yield to the two water regimes differed between the genotypes. In 2009, the grain yield of the CSSLs in aerobic culture ranged from 6.0 to 8.6 t ha\(^{-1}\), similar to or higher than in flooded culture (5.0 to 8.1 t ha\(^{-1}\)), but there was no significant difference in grain yield in Sasanishiki between the two water regimes (Table 2, Fig. 2). In 2011, the grain yield of the CSSLs in aerobic culture ranged from 4.1 to 6.8 t ha\(^{-1}\) (Table 2, Fig. 2), similar to or lower than in flooded culture (4.6 to 7.2 t ha\(^{-1}\)), and the grain yield of Sasanishiki in aerobic culture (5.0 t ha\(^{-1}\)) was significantly lower than that in flooded culture (6.2 t ha\(^{-1}\)).

In addition, no significant genotype × year interaction in grain yield was found. In both years, most of the CSSLs
respectively, in 2011 (Table 2, Fig. 2). Sasanishiki had a lower DW at maturity than the average of the CSSLs under both water regimes and in both years (Table 2). Line SL420 had a significantly higher DW at maturity than Sasanishiki under both water regimes and in both years. In addition, lines SL429 and SL430 had a significantly higher DW at maturity than Sasanishiki in aerobic culture: SL429 in both years and SL430 in 2009 (Dunnett’s multiple-comparison test, data not shown).

Spikelet number per unit area in Sasanishiki and the CSSLs was significantly smaller in aerobic culture than in flooded culture in both years, but the difference between the two water regimes was small (Table 2). The average numbers of spikelets per unit area in the CSSLs were $3.6 \times 10^4 \text{ m}^{-2}$ in flooded culture and $3.5 \times 10^4 \text{ m}^{-2}$ in aerobic culture in 2009, and $3.3 \times 10^4 \text{ m}^{-2}$ and $3.2 \times 10^4 \text{ m}^{-2}$, respectively, in 2011 (Table 2, Fig. 2). Sasanishiki had a lower DW at maturity than the average of the CSSLs under both water regimes and in both years (Table 2). Line SL420 had a significantly higher DW at maturity than Sasanishiki under both water regimes and in both years. In addition, lines SL429 and SL430 had a significantly higher DW at maturity than Sasanishiki in aerobic culture: SL429 in both years and SL430 in 2009 (Dunnett’s multiple-comparison test, data not shown).

Spikelet number per unit area in Sasanishiki and the CSSLs was significantly smaller in aerobic culture than in flooded culture in both years, but the difference between the two water regimes was small (Table 2). The average numbers of spikelets per unit area in the CSSLs were $3.6 \times 10^4 \text{ m}^{-2}$ in flooded culture and $3.5 \times 10^4 \text{ m}^{-2}$ in aerobic culture in 2009, and $3.3 \times 10^4 \text{ m}^{-2}$ and $3.2 \times 10^4 \text{ m}^{-2}$, respectively, in 2011. Most of the CSSLs had a higher spikelet number per unit area than Sasanishiki in aerobic culture, but that of Sasanishiki was close to the average of the CSSLs in flooded culture (Table 2, Fig. 3). On the other hand, the relationship between the single-grain weights under the two water regimes showed different
trends between the two years. The single-grain weight was significantly larger in aerobic culture than in flooded culture in 2009, but was significantly lower in 2011 (Table 2, Fig. 3). The single-grain weight of Sasanishiki was significantly larger than the average of the CSSLs in both flooded and aerobic culture in both years. According to Dunnett’s multiple-comparison test, 10 CSSLs in 2009 and 4 in 2011 produced significantly lower single-grain weight in aerobic culture than in flooded culture, whereas no CSSL produced a significantly lower single-grain weight than Sasanishiki in flooded culture.

Sasanishiki had 17% fewer spikelets in aerobic culture than in flooded culture in 2009, and 9% fewer in 2011 (Fig. 4). Most of the CSSLs had a higher ratio of spikelet number in aerobic culture to that in flooded culture, whereas no CSSL produced a significantly lower single-grain weight than Sasanishiki in flooded culture.

Fig. 4. Relationships between the ratio of spikelet number in aerobic culture to that in flooded culture and the ratio of single-grain weight in aerobic culture to that in flooded culture in (a) 2009 and (b) 2011.

Fig. 5. Relationships between the ripening ratios in aerobic and flooded culture in (a) 2009 and (b) 2011. The solid line represents \( y = x \), and the dotted lines represent the regression lines. ** indicates significant at 0.001 probability level.

Even though the difference in the mean ripening ratio between the two water regimes was small (Table 2), the ripening ratio was significantly higher in aerobic culture than in flooded culture in 2009, and a significant genotype × water environment interaction was observed in both years (Table 2). Regressions for the relationship between the ripening ratios in aerobic and flooded culture showed that the ripening ratio was higher in aerobic culture than in flooded culture in CSSLs with a low ripening ratio in flooded culture (Fig. 5), and this would cause a genotype × environment interactions in the single-grain weight.
Discussion

The responses of grain yield to the two water regimens in 2009 differed from those in 2011: grain yields were generally higher in aerobic culture than in flooded culture in 2009, but lower in 2011 (Fig. 2). This difference was caused mainly by the different water environments during the late reproductive period (Fig. 1). Katsura and Nakaide (2011) showed that water stress during this period can decrease the single-husk size, thereby reducing the single-grain weight. In fact, single-grain weight was significantly lower in aerobic culture than in flooded culture in 2011, but was significantly lower in flooded culture in 2009. These results confirm the dangers of water deficits, especially during the late reproductive period, in aerobic rice culture. Some CSSLs achieved high yields (e.g., 8.6 t ha$^{-1}$ by line SL420) in aerobic culture in 2009, but all the genotypes were grown in a single row with only three replicates. Hence, the absolute values of these results should be discussed with caution for specific CSSLs, and further study will be required in the canopy level.

Although, there was a significant year × water environment interaction in grain yield, we detected no significant genotype × year interaction in grain yield. Habataki has a higher photosynthetic rate than Sasanishiki (Adachi et al., 2011; Ohsumi et al., 2011) and a larger spikelet number per panicle (Ando et al., 2008; Ohsumi et al., 2011), which led to higher grain yield in Habataki (Katsura and Nakaide, 2011). Therefore, most of the CSSLs would be expected to show a higher grain yield than Sasanishiki, because the CSSLs have chromosome regions containing one or more QTLs for grain yield from Habataki. Indeed, the results showed that most of the CSSLs had a higher grain yield than Sasanishiki in aerobic culture. However, the grain yield of Sasanishiki was close to the average grain yield of the CSSLs in flooded culture, and there was a significant genotype × water environment interaction in grain yield (Table 2, Fig. 2). These results suggest that it is not always effective to utilize rice genes or genetic regions related to high yield to achieve high yield, because it may be equally important to understand the effects of genotype × environment interactions on yield formation.

High grain yield in aerobic culture resulted in part from a higher DW at maturity, even though the harvest index was lower in aerobic culture than in flooded culture in both years and in both genotypes. DW at maturity was significantly larger in aerobic culture even though grain yield was significantly lower in aerobic culture in 2011. With appropriate crop management, high biomass productivity could be achieved in aerobic culture, due to the higher nitrogen uptake, especially during the reproductive period, and higher radiation-use efficiency reported previously (Katsura et al., 2010). Root function would also play a key role in the larger biomass productivity in aerobic culture. Rice plants grown in aerobic culture showed higher root function (root oxidation activity) than in flooded culture (Katsura and Nakaide, 2011), and root function is essential for nitrogen uptake (Samejima et al., 2004; Yang et al., 2004; Matsumani et al., 2010).

The average grain yield across all of the CSSLs in aerobic culture was higher than that of Sasanishiki in both years, but lower in flooded culture (Table 2, Fig. 2). This means that most of the CSSLs had a higher grain yield in aerobic culture than in flooded culture compared to Sasanishiki. Spikelet number per unit area showed a similar trend; the average spikelet number was 3% larger in the CSSLs than in Sasanishiki in aerobic culture in 2009 and 9% larger in 2011, and the ratios of the average spikelet number in the CSSLs to that in Sasanishiki in flooded culture were lower than those in aerobic culture. Kato and Katsura (2010) showed that the spikelet number per unit area was determined by the nitrogen uptake until 2 weeks before heading and the biomass production during the 2 weeks before heading, and that rice cultivars with a large number of spikelets per primary rachis branch had efficient spikelet production per unit nitrogen uptake. Habataki has a large number of spikelets per primary rachis branch, and many CSSLs used here had QTLs related to large panicle size that were inherited from Habataki (Ando et al., 2008). This means that Habataki and many CSSLs had efficient spikelet production per unit nitrogen uptake. In a previous study, the spikelet number in Habataki and some of its CSSLs responded more strongly to nitrogen application than that in Sasanishiki (Ohsumi et al., 2011). These results suggest that vigorous nitrogen uptake by rice plants in aerobic culture (Katsura et al., 2010) would enable most of the CSSLs to produce more spikelets per unit area than Sasanishiki.

On the other hand, some CSSLs had a lower single-grain weight than Sasanishiki in aerobic culture. However, this low weight was compensated for by a large spikelet number in many CSSLs (Fig. 4). Ohsumi et al. (2011) demonstrated that increased spikelet number resulted in a decrease in single-grain weight because of source limitations, using near-isogenic lines with increased spikelet number. In the present study, the large source of photosynthate produced by the large biomass in aerobic culture would alleviate the decrease in single-grain weight in most of the CSSLs relative to that in Sasanishiki. In addition, the ripening ratio in aerobic culture was higher than that in flooded culture (Fig. 5), which supports the hypothesis of increased source capacity in aerobic culture. These results suggest that high spikelet production ability would improve grain yield in aerobic culture.

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