Growth and Yield of Six Rice Cultivars under Three Water-saving Cultivations

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Abstract: We evaluated the genotypic differences in growth, grain yield, and water productivity of six rice (Oryza sativa L.) cultivars from different agricultural ecotypes under four cultivation conditions: continuously flooded paddy (CF), alternate wetting and drying system (AWD) in paddy field, and aerobic rice systems in which irrigation water was applied when soil moisture tension at 15 cm depth reached −15 kPa (A15) and −30 kPa (A30). In three of the six cultivars, we also measured bleeding rate and predawn leaf water potential (LWP) to determine root activity and plant water status. Soil water potential (SWP) in the root zone averaged −1.3 kPa at 15 cm in AWD, −5.5 and −6.6 kPa at 15 and 35 cm, respectively, in A15, and −9.1 and −7.6 kPa at 15 and 35 cm, respectively, in A30. The improved lowland cultivar, Nipponbare gave the highest yield in CF and AWD. The improved upland cultivar, UPLRi-7, and the traditional upland cultivar, Sensho gave the highest yield in A15 and A30, respectively. The yields of traditional upland cultivars, Sensho and Beodien in A30 were not lower than the yields in CF. However, the yields of the improved lowland cultivars, Koshihikari and Nipponbare, were markedly lower in A15 and A30. Total water input was 2145 mm in CF, 1706 mm in AWD, 804 mm in A15, and 627 mm in A30. The water productivity of upland rice cultivars in aerobic plots was 2.2 to 3.6 times higher than that in CF, while those of lowland cultivars in aerobic plots were lower than those in CF. The bleeding rate of Koshihikari was lower in A15 and A30 than in CF and AWD, and its LWP was significantly lower in A15 and A30 than in CF and AWD, but Sensho and Beodien showed no differences among the four cultivation conditions. We conclude that aerobic rice systems are promising technologies for farmers who lack access to enough water to grow flooded lowland rice. However, lowland cultivars showed severe growth and yield reductions under aerobic soil conditions. This might result from poor root systems and poor root function, which limits water absorption and thus decreases LWP. More research on the morphological and physiological traits under aerobic rice systems is needed.

Key words: Grain yield, Lowland rice, Upland rice, Water productivity, Water-saving cultivation.

Rice is the major staple food in Asia, where about 92% of the world’s rice is produced and consumed (IRRI, 2002). However, the quality of irrigation water is being reduced by chemical pollution and salinization, and the water resource itself is being depleted by falling groundwater tables, silting of reservoirs, and increased competition from urban and industrial uses (Guerra et al., 1998). We must grow more rice with less water to sustain the continuing population growth (Guerra et al., 1998; Tuong et al., 2005).

Field techniques to save irrigation water include direct (dry) sowing, keeping soils at saturation, and alternate wetting and drying systems (AWD). Researchers in China found that AWD significantly reduced water input and increased yields (Wu, 1999; Li, 2001). Bouman and Tuong (2001) reported that AWD in the tropics reduced water input, but yields usually declined when the soil water potential (SWP) during the non-submerged phase reached values between −10 and −40 kPa. However, it is unclear how much water input can be saved without plant growth and grain yield penalty in AWD.

A new development in water-saving technologies is “aerobic rice systems” (Bouman 2001; Bouman et al., 2005), in which fields remain unsaturated throughout the season. Many studies have focused on drought resistance in rice under temporal water stress (Turner, 1986; Ludlow and Muchow, 1990; Fukai and Cooper, 1995; Jackson et al., 1996; Cooper, 1999; Lafitte et al., 2003). However, it is unclear whether effective traits for drought resistance to temporal water stress are useful for aerobic rice systems or not.

The target environments of aerobic rice systems are irrigated lowlands where water is insufficient to keep fields flooded, and favorable uplands with access to supplementary irrigation in which plants are not imposed by severe water stress, and yields of 70%–80% of high-input flooded rice are achievable (Belder 2001).
et al., 2005a). Irrigation can be applied by flush or furrow irrigation or by sprinklers, and aims at keeping the soil wet but not flooded or saturated. In practice, irrigation is applied to bring the soil water content to field capacity after it has reached a certain lower threshold level, such as −30 kPa (Bouman et al., 2005; Peng et al., 2006). Therefore, soil moisture conditions in aerobic rice systems should be quite different from those of temporal water deficit under drought upland environments. The potential water savings when rice can be grown as an upland crop are large, especially on soils with high seepage and percolation rates (Bouman et al., 2001). In addition, evaporation decreases, since there is no water surface, and the large amount of water used for land preparation is eliminated.

In Asia, upland rice is already grown aerobically with minimal input in upland fields, but mostly as a low-yielding subsistence crop to give a stable yield under the adverse environmental conditions (Laffite et al., 2002). Upland rice cultivars have drought-resistant characteristics (e.g., deep root and high root-shoot ratio) to avoid plant water shortage by extracting water with deep or extensive root systems, but have a low yield potential and tend to lodge under high levels of fertilizer and irrigation. High-yielding lowland rice cultivars grown in aerobic soil with supplemental irrigation have been shown to save water, but at a severe yield penalty (Blackwell et al., 1985; Wescott and Vines, 1986; McCauley, 1990). To achieve high yield under irrigated aerobic conditions, we need new cultivars that have the drought-resistant characteristics of lowland cultivars (Laffite et al., 2002). In China, breeders have produced aerobic rice cultivars with an estimated yield potential of 6–7 t ha⁻¹, and research is under way to study the water-use and yield potential of these cultivars under well-defined hydrological conditions (Yang et al., 2005). In the Philippines, De Datta et al. (1973) grew the lowland cultivar, IR20, in aerobic soil with furrow irrigation. Aerobic culture saved 45% of water input compared with flooded conditions, but yield fell from about 8 t ha⁻¹ under flooded conditions to 3.4 t ha⁻¹ under aerobic conditions. In Japan, Kato et al. (2006) reported genotypic differences under aerobic conditions. However, there is little information on the difference in crop performance between aerobic and flooded conditions and on the optimum threshold for re-irrigation when cultivars that are adapted to aerobic conditions are grown. Furthermore, the physiological basis of the yield gap between aerobic and flooded rice has not been studied extensively. Such information is crucial to identify the morphological and physiological traits for the selection and breeding of high-yielding aerobic rice cultivars.

In the present study, we evaluated the growth and yield response of six cultivars from different agricultural ecotypes (two japonica upland, two indica upland, and two japonica lowland) to different water-saving cultivations. The objectives were to determine how much water could be saved and to analyze the genotypic differences in plant growth, grain yield and water productivity. We also determined the bleeding rate and predawn leaf water potential (LWP) of three of these six cultivars to determine the root activity and plant water status.

### Materials and Methods

#### 1. Experimental design

All experiments were conducted at the Experimental Farm of Kyushu University, Fukuoka, Japan (33° 37’ N, 130° 27’ E) in 2006. The soil contained 20.7% clay, 23.2% silt, and 56.1% sand (clay-loam) in the lowland fields and 21.7% clay, 12.8% silt and 68.6% sand (sandy clay-loam) in the upland fields. Four water treatments were imposed: continuously flooded paddy (CF); alternate wetting and drying systems (AWD) in the lowland field; and aerobic rice systems where irrigation water was applied when SWP at 15 cm depth reached −15 kPa (A15) and −30 kPa (A30). The decision of irrigation was made based on the average readings of four tensiometers (see below). A randomized complete design with three replications was conducted within a treatment. Each treatment covered 58.2 m². Six rice cultivars (i.e. *japonica* traditional upland cultivar, Senso; *japonica* improved upland cultivar, Hataminorimochi; *indica* traditional upland cultivar, Beodien; *indica* improved upland cultivar, UPLRi-7, *japonica* improved upland cultivar, Koshikihari and Nipponbare; Table 1) were selected based on our previous study (Matsuo et al., 2007), which assessed

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### Table 1. Background of plant materials used in this study.

| Name       | Group | Origin       | Ecosystem | History            |
|------------|-------|--------------|-----------|--------------------|
| Senso      | japonica | Japan       | Upland    | Traditional        |
| Hataminorimochi | japonica | Japan       | Upland    | Improved           |
| Beodien    | indica | Vietnam      | Upland    | Traditional        |
| UPLRi-7    | indica | Philippines  | Upland    | Improved           |
| Koshikihari | japonica | Japan       | Lowland   | Improved           |
| Nipponbare | japonica | Japan       |           | Improved           |
grain yields of 12 rice cultivars under a temporal water deficit condition around flowering stage.

In CF and AWD, seeds were sown in seed beds on June 10 and 21 d-old seedlings were transplanted at one seedling per hill at a spacing of 30 cm × 15 cm on 1 July. Plots were puddled 2 d before transplanting. In both plots, the water depth above soil surface was initially 20 mm. A flash irrigation of about 50 mm depth was applied whenever the surface water disappeared in CF and SWP at 15 cm depth reached -5 kPa in AWD. SWP was maintained above -5 kPa in AWD, except for 1 wk during the mid-vegetative stage, for mid-season drainage (Mao, 1995). We installed plastic sheets down to 60 cm between CF and AWD to prevent seepage and water flow between the plots. Nitrogen fertilizer was applied three times: 4 g m\(^{-2}\) as basal fertilizer 2 d before transplanting, 4 g m\(^{-2}\) as topdressing at 25 d after transplanting (DAT), and 2 g m\(^{-2}\) at 56 DAT. Phosphorus (12 g m\(^{-2}\)) and potassium (12 g m\(^{-2}\)) were also applied 2 d before transplanting.

In aerobic rice systems (A15 and A30), plants were grown under a rainout shelter from sowing to 17 September, when a typhoon hit the experimental site. Because there is much precipitation in the summer season in Japan, we used the rainout shelter to control the amount of irrigation water and to reproduce the environments of aerobic rice systems. The experiment was carried out without the rainout shelter after 17 September. Three to four pre-germinated seeds were sown at a spacing of 30 cm × 15 cm on 19 June. The aerobic plots were dry-ploughed and harrowed 2 d before sowing. The soil was irrigated 1 d before sowing (20 mm), and irrigation water of 10 mm was applied everyday for the first 2 wk to keep SWP at 15 cm depth above -10 kPa for promoting crop establishment. Afterward, about 20 mm of water was applied whenever SWP at 15 cm depth reached -15 kPa in A15 and -30 kPa in A30. Irrigation water was applied by line source sprinklers that were placed between every two rows. Seedlings were thinned to one per hill at 21 d after sowing (DAS). Nutrients were applied in the same way as in CF and AWD. A combination of insecticide, herbicide and manual weed control was used to maximize yields in the experiment.

2. Measurements and calculation

A weather station set up near the field recorded daily mean temperature, radiation, and rainfall. The amount of irrigation water applied was measured with flow meters (RK500S, KOFLOC Co., Ltd, Tokyo, Japan) connected to the irrigation hoses. Four gauged tensiometers (DIK-3126, Daiki Rika Kogyo Co., Ltd, Saitama, Japan) were installed at 15 cm depth in AWD and at 15 and 35 cm depth in A15 and A30 for daily measurement of SWP. The places where tensiometers were installed were selected randomly. The depth of ponded water in CF and AWD was measured daily by using perforated PVC pipes (inner diameter, 30 cm; height, 60 cm) installed down to 40 cm from the soil surface.

Crop samples were taken five times in CF and AWD (at 21, 53, 65, 84, 107 DAS) and four times in A15 and A30 (at 45, 57, 76, and 99 DAS) to determine total dry biomass and leaf area index (LAI). Plants of four hills per replication were collected at each sampling. LAI was determined with a leaf area meter (AAM-9, Hayashi Denko Co. Ltd., Tokyo, Japan). Then, dry biomass was determined after oven-drying at 70°C for at least 3 d. At maturity, plants of eight hills per replication were sampled to determine aboveground biomass, yield, and yield components. The number of panicles per hill was counted to determine the panicle number per m\(^{2}\). Panicles were hand-threshed, and filled spikelets were separated from unfilled spikelets by submerging them in tap water. Spikelets per panicle, grain-filling percentage (100 × filled spikelet number per total spikelet number), and water productivity (g grain per kg input water) were calculated. The grain moisture content within each plot was determined with a grain moisture tester (Riceter m, Kett Electric laboratory Co. Ltd., Tokyo, Japan) to convert the samples to 14% moisture content.

We measured the bleeding rate in Sensho, Beodien, and Koshihikari from 0700 to 1100 on 14 August in all plots, because bleeding rate has been used as an index of root activity in many studies (e.g., Yamaguchi et al., 1995). One day before bleeding rate measurements, irrigation water, imposed by the design of irrigation treatment, was applied in each treatment. Shoots were cut with a sharp razor at a height of approximately 10 cm from the soil surface, and preweighed cotton pads were attached to the cut surface and cotton pads were covered with plastic film sealed with rubber bands to protect against water loss. Each sap sample was collected for 120 min and then cotton pads were weighed to determine bleeding rate. Then, we calculated bleeding rate on a leaf area basis to analyze the relation with the recovery of plant water status during night.

We measured LWP (0300-0530) in Sensho, Beodien, and Koshihikari with a dewpoint psychrometer (WP4, Decagon Devices Inc., Pullman, WA, USA) on 24 August in all plots. Two fully expanded youngest leaves on the main stems were sampled randomly from each replication for measurement of LWP. One day before LWP measurements, irrigation water, imposed by the design of irrigation treatment, was applied in each treatment.

Results

1. Weather

Table 2 shows the mean monthly weather data in 2006 and during 1996 to 2005. The mean monthly temperature was lower in 2006 than the 10yr average
throughout the experiment. Solar radiation was lower in June and July and higher in August, October, and November in 2006 than the 10-yr average. Sufficient rain fell in June to September in 2006.

### 2. Hydrological conditions

Fig. 1 shows the actual irrigation and rain inputs in all plots. Irrigation water was applied 25 times in CF, 15 times in AWD, 36 times in A15, and 25 times in A30. The amount applied each time was smaller in A15 and A30 than in CF and AWD and average total amount of irrigated water was 1119, 679, 663, and 486 mm in CF, AWD, A15 and A30, respectively (Table 3). The total amount of input water was calculated by including total amount of irrigated water and rainfall and it was on average 2146, 1706, 804 and 627 mm, in CF, AWD, A15 and A30, respectively. Total amount of input water was 20.5% less in AWD than in CF, 62.5% less in A15,

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**Table 2.** Average monthly temperature, solar radiation, and accumulated total rainfall from June to November in 2006 and during 1996–2005 at the Experimental Farm of Kyushu University.

| Month  | Mean temperature (°C) | Solar radiation (MJ m⁻² d⁻¹) | Rainfall (mm) |
|--------|------------------------|-------------------------------|---------------|
| | 2006 | Average | 2006 | Average | 2006 | Average |
| June | 23.2 | 27.5 | 12.1 | 17.1 | 320 | 266 |
| July | 27.3 | 30.9 | 13.5 | 16.9 | 373 | 271 |
| August | 29.0 | 32.2 | 18.4 | 17.7 | 347 | 169 |
| September | 23.3 | 28.6 | 14.9 | 14.9 | 234 | 181 |
| October | 20.8 | 23.8 | 14.2 | 12.8 | 25 | 89 |
| November | 15.0 | 18.3 | 9.7 | 9.4 | 87 | 105 |

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Fig. 1. Amount and timing of irrigation application in CF (a), AWD (b), A15 (c) and A30 (d), and rainfall (e).
and 70.8% less in A30. The rainout shelter over the aerobic plots from sowing to 17 September kept the rain water inputs small.

The dynamics of the water table in CF and AWD are given in Fig. 2. The water table was nearly always at or above the soil surface in CF. AWD had periods of 3-10 d without surface-ponded water.

Fig. 3 shows SWP at 15 cm in AWD and that at 15 and 35 cm in A15 and A30. In AWD, SWP at 15 cm stayed mostly within -5 kPa, but dropped to -30 kPa once, when mid-season drainage was imposed. In A15, SWP at 15 cm stayed mostly within -15 kPa, as intended, and dropped below -15 kPa six times. At 35 cm, SWP was smaller than that at 15 cm and fluctuated mostly between 0 and -10 kPa. The maximum value recorded was -33 kPa at 15 cm and -20 kPa at 35 cm. In A30, SWP at 15 cm stayed mostly within -30 kPa and dropped below -30 kPa six times. At 35 cm, the tension was smaller than that at 15 cm and fluctuated mostly between 0 and -15 kPa. The minimum value recorded was -36 kPa at 15 cm and -19 kPa at 35 cm. The average SWP was -1.3 kPa at 15 cm in AWD; -5.5 kPa at 15 cm and -6.6 kPa at 35 cm in A15; and -9.1 kPa at 15 cm and -7.6 kPa at 35 cm in A30.

The average SWP was -1.3 kPa at 15 cm in AWD; -5.5 kPa at 15 cm and -6.6 kPa at 35 cm in A15; and -9.1 kPa at 15 cm and -7.6 kPa at 35 cm in A30.

Table 4 shows the phenology of the crops. The japonica cultivars had similar flowering dates and growth durations in all treatments, differing by 4 to 7 d. However, the flowering date was later and growth duration was longer in indica upland cultivars than in the japonica cultivars. Flowering date in CF and AWD was earliest in Koshihikari (23 August), and it was 2 d later in Sensho and Nipponbare, 4 d later in Hataminorimochi, 16 d later in UPLRi-7, and 19 d later in Beodien. In A15, Sensho and Hataminorimochi had the earliest flowering date (3 September), and it was 3 d later in Nipponbare, 6 d later in Koshihikari, 13 d later in UPLRi-7, and 26 d later in Beodien. In A30, Sensho had the earliest flowering date (1 September).
Table 4. Flowering and physiological maturity dates of the six rice cultivars in CF, AWD, A15, and A30.

|        | CF       | AWD     | A15     | A30     |
|--------|----------|---------|---------|---------|
| **Flowering** |          |         |         |         |
| Sensho | 25 August| 25 August| 3 September | 1 September |
| Hataminorimochi | 27 August| 27 August| 3 September | 2 September |
| Beodien | 11 September| 11 September| 29 September | 18 September |
| UPLR-7 | 8 September| 8 September| 16 September | 16 September |
| Koshihikari | 23 August| 23 August| 9 September | 6 September |
| Nipponbare | 25 August| 25 August| 6 September | 5 September |
| Maturity |          |         |         |         |
| Sensho | 13 October | 13 October | 25 October | 19 October |
| Hataminorimochi | 13 October | 13 October | 22 October | 21 October |
| Beodien | 29 October | 29 October | 5 November | 5 November |
| UPLR-7 | 26 October | 26 October | 5 November | 5 November |
| Koshihikari | 6 October | 6 October | 24 October | 26 October |
| Nipponbare | 6 October | 8 October | 24 October | 25 October |
| **Growth duration (days)** |          |         |         |         |
| Sensho | 126 | 126 | 126 | 122 |
| Hataminorimochi | 126 | 126 | 125 | 124 |
| Beodien | 142 | 142 | 139 | 139 |
| UPLR-7 | 139 | 139 | 139 | 139 |
| Koshihikari | 119 | 119 | 127 | 129 |
| Nipponbare | 119 | 121 | 127 | 126 |

Fig. 4. Leaf area index (LAI) of six rice cultivars in CF (a), AWD (b), A15 (c) and A30 (d). Bars indicate the standard error (n = 3).
and it was 1 d later in Hataminorimochi, 4 d later in Nipponbare, 5 d later in Koshihikari, 15 d later in UPLRi-7, and 17 d later in Beodien.

4. Crop growth

Fig. 4 shows the LAI values. In CF, LAI reached a maximum of 4 to 5, except for that of UPLRi-7, which exceeded 6. LAI in indica upland cultivars Beodien and UPLRi-7 peaked later than those in japonica cultivars due to the longer growth duration. The same tendency was seen in AWD. LAIs of the upland cultivars in the aerobic plots were the same as or slightly lower than those in CF and AWD, but those of lowland cultivars were markedly lower. The biomass accumulation shows the same trend as in LAI (Fig. 5). The lowland cultivars, Koshihikari and Nipponbare, showed significantly lower biomass than upland cultivars in A15 and A30. The difference in shoot growth between lowland and upland cultivars were observed after 57 DAS in aerobic plots (at second sampling).

5. Yield components

Table 5 shows the yield components. Lowland cultivars, Koshihikari and Nipponbare, had more panicles per m² than upland cultivars in CF and AWD. Panicle numbers were almost identical in CF and AWD. However, they decreased in aerobic plots in all cultivars, especially in the lowland cultivars. UPLRi-7 had the largest number of spikelets per panicle in all treatments. The spikelet number in Koshihikari was markedly decreased in aerobic plots relative to that in CF and AWD, whereas that of upland cultivars tended to increase in aerobic plots. In CF and AWD, Nipponbare had the highest percentage of filled grain. In aerobic plots, the percentage of filled grain was maintained in Sensho and Hataminorimochi, increased in Beodien and UPLRi-7, and decreased in Koshihikari and Nipponbare relative to those in CF and AWD. Genotypic differences in grain weight were apparent: Sensho had the heaviest grain weight followed by Beodien in all treatments. Grain weights of Beodien, UPLRi-7, Koshihikari, and Nipponbare tended to decrease in aerobic plots.

6. Yield and water productivity

Grain yield and water productivity are shown in Table 6. Although Nipponbare had the highest grain yield in CF and AWD, no statistically significant differences were detected among cultivars. Grain yield in AWD was higher (on average 15%) than in CF in all cultivars except Sensho. The yields of Koshihikari and Nipponbare were considerably reduced in aerobic plots. Grain yields of Sensho, Beodien, and UPLRi-7 were higher in A15 than in CF. Yields of Hataminorimochi and UPLRi-7 were approximately 25% lower in A30 than in CF, whereas those of Sensho and Beodien were the same as in CF. Nipponbare had the highest water productivity in CF and AWD. Average water productivity in AWD (0.30) was higher than that in CF (0.21), probably owing to lower water input and higher yield in AWD than in CF. In aerobic plots, however, the lowland cultivars, Koshihikari and Nipponbare, had significantly lower water productivity than upland cultivars owing to the considerable yield
5. Yield components of six rice cultivars in CF, AWD, A15, and A30.

| Panicle number (m²⁻¹) | CF     | AWD    | A15    | A30    | Mean |
|----------------------|--------|--------|--------|--------|------|
| Sensho               | 258 bc | 233 b  | 218 a  | 180 a  | 222  |
| Hataminorimochi      | 269 b  | 268 b  | 194 a  | 179 a  | 227  |
| Beodien              | 214 bc | 220 b  | 187 a  | 147 a  | 192  |
| UPLRi-7              | 197 c  | 199 b  | 177 a  | 138 ab | 178  |
| Koshihikari          | 364 a  | 369 a  | 117 b  | 90 b   | 235  |
| Nipponbare           | 382 a  | 381 a  | 132 b  | 125 ab | 255  |
| Mean                 | 281    | 278    | 171    | 143    |      |

| Spikellet number per panicle | CF     | AWD    | A15    | A30    | Mean |
|-----------------------------|--------|--------|--------|--------|------|
| Sensho                      | 96 b   | 102 b  | 121 b  | 127 ab | 112  |
| Hataminorimochi             | 96 b   | 96 bc  | 121 b  | 114 b  | 107  |
| Beodien                     | 81 bc  | 88 bcd | 123 b  | 106 b  | 100  |
| UPLRi-7                     | 169 a  | 158 a  | 182 a  | 160 a  | 107  |
| Koshihikari                 | 81 bc  | 85 cd  | 59 c   | 46 c   | 68   |
| Nipponbare                  | 71 c   | 73 d   | 56 c   | 62 c   | 65   |
| Mean                        | 99     | 100    | 110    | 103    |      |

| Percentage of filled grain (%) | CF     | AWD    | A15    | A30    | Mean |
|--------------------------------|--------|--------|--------|--------|------|
| Sensho                        | 53.9 c | 55.8 d | 63.4 ab| 56.8 bc| 57.5 |
| Hataminorimochi               | 62.2 bc| 64.8 c | 57.2 ab| 59.1 bc| 60.8 |
| Beodien                       | 75.5 ab| 75.7 ab| 81.0 a | 85.0 a | 79.3 |
| UPLRi-7                       | 57.9 c | 62.4 cd| 71.4 ab| 70.8 ab| 65.6 |
| Koshihikari                   | 58.7 c | 68.9 bc| 46.4 b | 42.5 c | 54.1 |
| Nipponbare                    | 78.6 a | 80.2 a | 55.0 ab| 42.3 c | 64.0 |
| Mean                          | 64.5   | 68.0   | 62.4   | 59.4   |      |

| 1000 grains weight (g)        | CF     | AWD    | A15    | A30    | Mean |
|--------------------------------|--------|--------|--------|--------|------|
| Sensho                        | 31.2 a | 31.6 a | 30.9 a | 32.1 a | 31.5 |
| Hataminorimochi               | 24.9 cd| 25.4 b | 25.1 bc| 25.8 bc| 25.3 |
| Beodien                       | 28.2 b | 28.2 ab| 26.9 b | 27.7 b | 27.8 |
| UPLRi-7                       | 26.0 c | 26.8 b | 24.6 cd| 23.8 cd| 25.3 |
| Koshihikari                   | 24.2 d | 24.7 b | 22.3 e | 21.5 e | 23.2 |
| Nipponbare                    | 24.1 d | 24.4 b | 23.0 de| 23.2 de| 23.7 |
| Mean                          | 26.4   | 26.9   | 25.5   | 25.7   |      |

*Within a column for each parameter, means followed by different letters are significantly different at P = 0.05 according to Tukey’s test.

7. Bleeding rate and LWP

No significant differences in bleeding rate per leaf area were observed among water regimes in traditional upland cultivars, Sensho and Beodien, but significant differences were observed in Koshihikari (Fig. 6); bleeding rates of Koshihikari in aerobic plots were significantly lower than those in CF and AWD. LWP investigated 10 d after the measurements of bleeding rate showed the similar trend (Fig. 7). Sensho and Beodien showed identical values in all water regimes (on average −0.34 and −0.37 Mpa, respectively). In Koshihikari, however, LWP was significantly lower in
Table 6. Grain yield and water productivity of six rice cultivars in CF, AWD, A15, and A30.

|                  | CF    | AWD   | A15   | A30   | Mean |
|------------------|-------|-------|-------|-------|------|
| Grain yield (g m\(^{-2}\)) |       |       |       |       |      |
| Sensho           | 421 a | 419 a | 519 ab| 418 a | 444  |
| Hataminorimochi  | 403 a | 458 a | 339 b | 310 a | 377  |
| Beodien          | 371 a | 410 a | 499 ab| 376 a | 414  |
| UPLRi-7          | 499 a | 527 a | 570 a | 375 a | 493  |
| Koshihikari      | 415 a | 536 a | 80 c  | 38 b  | 267  |
| Nipponbare       | 512 a | 545 a | 95 c  | 82 b  | 308  |
| Mean             | 437   | 482   | 350   | 266   |      |

| Water productivity (g grain kg\(^{-1}\) water) |       |       |       |      |
| Sensho           | 0.20 ab| 0.26 ab| 0.66 ab| 0.71 a| 0.46 |
| Hataminorimochi  | 0.19 ab| 0.28 ab| 0.44 b | 0.52 a| 0.36 |
| Beodien          | 0.17 b | 0.24 b | 0.62 ab| 0.60 a| 0.41 |
| UPLRi-7          | 0.25 ab| 0.31 ab| 0.71 a | 0.60 a| 0.46 |
| Koshihikari      | 0.21 ab| 0.34 a | 0.10 c | 0.06 b| 0.18 |
| Nipponbare       | 0.26 a | 0.34 a | 0.12 c | 0.14 b| 0.22 |
| Mean             | 0.21   | 0.30   | 0.44   | 0.44   |      |

*Within a column for each parameter, means followed by different letters are significantly different at P = 0.05 according to Tukey’s test.

Discussion

In AWD, reduction in soil water potential was very small (Fig. 3), thus LAI and biomass accumulation differed little from those in CF (Figs. 4, 5). Grain yield in AWD tended to be higher (13% on average) than in CF (Table 6). Moreover, AWD saved 20% of total water input in comparison with CF (Table 3), resulting in higher water productivity than in CF (39% on average, Table 6). Intermittent irrigation is believed to improve aerobic plots (−0.69 MPa in A15 and −0.80 MPa in A30) than in CF and AWD (on average −0.43 MPa).

Fig. 6. Bleeding rate of Sensho, Beodien, and Koshihikari in CF, AWD, A15, and A30 on 14 August. Means followed by different letters are significantly different at P=0.05 among water regimes in each cultivar by Tukey’s test. Bars indicate the standard error (n=3).

Fig. 7. Predawn leaf water potential of Sensho, Beodien, and Koshihikari in CF, AWD, A15, and A30 on 24 August. Means followed by different letters are significantly different at P=0.05 among water regimes in each cultivar by Tukey’s test. Bars indicate the standard error (n=3). Bleeding rate is expressed on leaf area basis.

oxygen supply to rice roots, with potential advantages for nutrient uptake (Stoop et al., 2002), and to avoid accumulation of toxic substances such as ferrous iron and hydrogen sulfide, which are potentially toxic to root growth. Yang et al. (2004) reported that, in rice plants, active absorption area of root and root activity parameters (root g-naphthylamine oxidation and root surface phosphatase) in AWD tended to be higher than those in CF (though insignificant) at the late growth stage (90 and 120 DAT). High root activity secures a high photosynthetic rate by
supplying a sufficient amount of nutrients to shoot, thus ensure high productivity (Osaki et al., 1997). We measured bleeding rate only once in this experiment and statistical significance was not observed between CF and AWD in three cultivars (Fig. 6). It may be worthwhile to further investigate bleeding rate and nutrients in root sap at the later growth stage. The absence of yield reduction in AWD in comparison with CF was consistent with the results obtained in China and the Philippines (Belder et al., 2005b). However, the threshold at which plant growth and yield began to decrease was unclear in this experiment. Therefore, further investigations are needed to clarify the threshold of re-irrigation to save much water without a reduction in plant growth and grain yield in AWD.

Although aerobic rice systems could save more than 60% of input water (Table 3), there were large genotypic differences in plant growth and grain yield. Grain yields of Sensho, Beodien, and UPLRi-7 increased in A15, where the soil was wet throughout the growth phase, relative to those in CF. Furthermore, yields of Sensho and Beodien (traditional upland cultivars) in A30 were the same as in CF, indicating the existence of promising traditional upland cultivars for aerobic rice systems. Many studies on aerobic rice systems have used improved upland cultivars (Belder et al., 2005a; Bouman et al., 2005; Peng et al., 2006). In A30, the spikelet number per panicle of Sensho and Beodien increased by up to 30%, although panicle number per m² decreased by 30%, relative to that in CF. Thus, decreased sink size caused by reduction of panicle number might be compensated by increase of spikelet number per panicle. Peng et al. (2006) pointed out that among yield components, sink size contributed more to the yield gap between aerobic and flooded rice than the percentage of filled grain and the 1000-grain weight. Therefore, sink size may be important to achieve high yield under aerobic rice systems. Even in relatively wet aerobic soil, yields of Hataminorimochi and UPLRi-7 were 25% lower in A30 than in CF. In this respect, these two cultivars behaved similarly to the tropical cultivars used in Philippine by Bouman et al. (2005) and to the temperate cultivars used in the USA by Wescott and Vines (1986) and McCauley (1990) and in Australia by Blackwell et al. (1985). Traditional upland cultivars may have more stable yield than improved upland cultivars under aerobic rice systems where the threshold for re-irrigation is lower. The lowland cultivars, Koshihikari and Nipponbare, had markedly lower yields in aerobic soil conditions, resulting in reduced water productivity. Bouman et al. (2005) reported that total water input in aerobic rice systems was from 696 to 1341 mm and could be saved 11.5 to 50.7% in comparison with aerobic rice systems. This information will help breed new rice cultivars for aerobic rice systems.

The bleeding rate of Koshihikari was lower than those of Sensho and Beodien in aerobic plots, and those of Koshihikari in aerobic plots were significantly lower than that in CF and AWD (Fig. 6). Moreover, bleeding rate of Koshihikari decreased as water input decreased. These results suggest that the root activity of Koshihikari decreased in water-saving cultivations, especially in aerobic rice systems. Therefore, it might be difficult for the root systems of Koshihikari to extract enough soil water, explaining the significantly lower LWP measured about 10 h after irrigation application (Fig. 7). Matsuo et al. (2008), who measured root systems of three cultivars with minirhizotron, reported that the root systems of Sensho and Beodien reached a depth of 80 cm and that of Koshihikari reached a depth of 60 cm. In an unpublished experiment under aerobic rice systems, we found that root length density (RLD) and root weight density (RWD) concentrated in the top 0-20
cm depth in three cultivars and RLD and RWD at 0-20 cm depth were the largest in Beodien, followed by Sensho, and Koshihikari in this order. Therefore, these quantitative differences of root systems among cultivars might result in the genotypic difference of bleeding rate and LWP. On the other hand, in China, Bouman et al. (2006) investigated root systems of two aerobic rice cultivars and one lowland rice cultivar under aerobic rice systems and reported that there were no significant differences in rooting depth, distributions, RLD and RWD among the cultivars, although yield of the lowland cultivar was lower than those of the aerobic rice cultivars. Matsuo et al. (2009) measured the root hydraulic conductance, which is often regarded as water uptake ability of root systems (e.g. Clarkson et al., 2000), for these three cultivars grown aerobically under two water regimes (well-irrigated and repetitive cycles of wet and dry conditions) in a pot experiment. They reported that (1) root hydraulic conductance of Koshihikari was the lowest among three cultivars under both water regimes, (2) the reduction rate of the conductance in Koshihikari (the ratio of the value in the repetitive water stress condition to that in the well-irrigated condition) was the highest among three cultivars, and (3) root hydraulic conductance was significantly and positively correlated with shoot dry weight only in repetitive water stress condition. Trillo and Fernández (2005) also reported that root hydraulic conductivity of wheat plants subjected to repetitive cycles of wet and dry condition was significantly lower than that of well-irrigated plants. These results suggested that repetitive water stress had negative effects on root activity or function and its effects varied with the cultivar, resulting in genotypic differences in the bleeding rate and LWP. Araki and Iijima (2005), who investigated a water extraction pattern of root systems of an upland rice cultivar in pot experiments, reported that when water content of the shallow layer (0-25 cm depth) was ample, more than 90% of water was extracted from shallower layer, and water extraction area sited to deeper layer as surface soil dried out. Integrating these reports on root function, besides the quantitative difference in root systems among cultivars (described above), qualitative difference in root function among cultivars may be one of the important traits under aerobic rice systems. Since studies on root morphological or physiological traits under aerobic rice systems are still limited, further studies are needed to clarify the suitable traits for good crop performance under aerobic rice systems.

**Conclusion**

AWD could save more than 20% of total input water and aerobic rice systems could save 60%, relative to CF. Although yields tended to increase in AWD in comparison with CF, genotypic differences in yield was large under aerobic rice systems. In A15, where the soil was kept wet throughout the growth period, yields of the upland cultivars Sensho, Beodien, and UPLRi-7 increased in comparison with CF, but those of the lowland cultivars, Koshihikari and Nipponbare, decreased markedly. Moreover, yields of Sensho and Beodien in A30 were the same as in CF, suggesting that promising cultivars exist among traditional upland cultivars. The yield reduction in the lowland cultivars in aerobic rice systems might be due to changes in root activity or function as well as root morphology.

AWD is easier for farmers to use than aerobic rice systems, which need extra irrigation equipments. The selection of technique largely depends on the situation of the farmers. Further study should examine the optimization of irrigation water input (amount and timing of irrigation to maximize yield) in AWD. Aerobic rice systems can save more water than AWD and promise water savings for farmers in environments where water availability is low or water is too expensive to grow flooded lowland rice. Further breeding is required to develop cultivars that can achieve high yield under aerobic rice systems. Understanding how to maintain high yields under aerobic rice systems will be crucial. However, the concept of aerobic rice is new, and there is yet little information to support the breeding of new cultivars. Future studies should address morphological and physiological traits under aerobic rice systems.

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