Radiation-use efficiency, N accumulation and biomass production of high-yielding rice in aerobic culture

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Abstract

The concept of aerobic culture is to save water resource while maintaining high productivity in irrigated rice ecosystem. This study compared nitrogen (N) accumulation and radiation use efficiency (RUE) in the biomass production of rice crops in aerobic and flooded cultures. The total water input was 800–1300 mm and 1500–3500 mm in aerobic culture and flooded culture, respectively, and four high-yielding rice cultivars were grown with a high rate of N application (180 kg N ha^{-1}) at two sites (Tokyo and Osaka) in Japan in 2007 and 2008. The aboveground biomass and N accumulation at maturity were significantly higher in aerobic culture (17.2–18.5 t ha^{-1} and 194–233 kgN ha^{-1}, respectively) than in flooded culture (14.7–15.8 t ha^{-1} and 142–173 kgN ha^{-1}) except in Tokyo in 2007, where the surface soil moisture content frequently declined. The crop maintained higher N uptake in aerobic culture than in flooded culture, because in aerobic culture there was a higher N accumulation rate in the reproductive stage. RUE in aerobic culture was comparable to, or higher than, that in flooded culture (1.27–1.50 vs. 1.20–1.37 g MJ^{-1}), except in Tokyo in 2007 (1.30 vs. 1.37 g MJ^{-1}). These results suggest that higher biomass production in aerobic culture was attributable to greater N accumulation, leading to higher N concentration (N%) than in flooded culture. Cultivar differences in response to water

regimes were thought to reflect differences in mainly 1) early vigor and RUE under temporary declines in soil moisture in aerobic culture, and 2) the ability to maintain high N% in flooded culture.

Keywords; Rice (*Oryza sativa* L.); Biomass accumulation; Aerobic rice; Radiation use efficiency; Yield potential; Nitrogen.

Introduction

The demand for rice in Asia will continue to increase as populations in the region grow in line with economic development. On the other hand, a worldwide water shortage is threatening the sustainability of rice production because of the crop's high water demand and sensitivity to water deficiency. The demand for more efficient water use in rice production is therefore increasing rapidly. Various water-saving technologies have been developed (Tabbal et al., 2002; Belder et al., 2004; Humphreys et al., 2005; Bouman et al., 2006a). Among them, aerobic rice culture has become a particular focus of attention (Tuong et al., 2005; Haryanto et al., 2008). In aerobic rice culture, high-yielding cultivars are grown on non-puddled aerobic soil.

Recent studies of aerobic rice culture have focused mainly on water use efficiency (Bouman et al., 2006b; Matsunami et al., 2009; Matsuo and Mochizuki, 2009). Maximum yields of 5–6 t ha^{-1} with water inputs of only 500–900 mm have been achieved in aerobic rice culture in northern China (Yang et al., 2005; Bouman et al., 2006b; Xue et al., 2008). We attained a grain yield of over 10 t ha^{-1} in aerobic rice culture in a previous study in Japan (Kato et al., 2009). In this study (Kato et al., 2009), a grain yield of 11.4 t ha^{-1} was achieved in aerobic culture by Takanari, a lowland adapted high-yielding variety, and the average yield of four varieties under aerobic culture was similar to or even higher than that achieved with flooded culture. These results suggest that the productivity of aerobic rice culture is potentially comparable to, or even higher than, that of flooded rice culture. Unraveling the growth characteristics that resulted in the particularly high yield in aerobic culture in Japan might improve not only water use efficiency but also the yield potential of rice.

The concept of radiation use efficiency (RUE) has been widely used in crop growth analysis. Following the principles of Monteith (1977), aboveground total dry weight (TDW) is expressed as

$$TDW = RAD \cdot FRI \cdot RUE\ ,$$

where RAD is the incident radiation and FRI is the fraction of radiation intercepted by the crop. N is a key nutrient limiting crop growth (Sinclair and Horie, 1989). Hence, the objective of this study was to quantitatively characterize crop growth in aerobic rice culture in Japan with respect to N accumulation and radiation use efficiency by the rice canopy. This is the follow-up study of our previous reports (Kato et al., 2009).

Materials and Methods

Experimental design

The field experiments were conducted at the Field Production Science Center of The University of Tokyo (Tokyo), Japan (lat. 35°43′N, long. 139°32′E) and at the Experimental Farm, Kyoto University (Osaka), Japan (lat. 34°51′N, long. 135°37′E) during summer (May to October) in 2007 and 2008. The soils at the experimental sites are clay loam (Typic Melanudand) in Tokyo and sandy loam (Typic Fluvaquent) in

Osaka. Hourly global solar radiation (incident radiation) was recorded by pyranometers at both experimental sites. The average incident radiation during the summer season was 14.9 and 13.8 MJ m^{-2} in 2007 and 2008, respectively, in Tokyo, and 17.7 and 16.9 MJ m^{-2} in 2007 and 2008, respectively, in Osaka. The average air temperature during the summer season was 23.6 and 23.1 °C in 2007 and 2008, respectively, in Tokyo, and 23.4 and 22.8 °C in 2007 and 2008, respectively, in Osaka. The total amount of water supplied (sprinkler irrigation plus rainfall) in the aerobic culture was 800–1300 mm, which was 21–74% less than the flood-irrigation plus rainfall in the flooded culture. In 2007, an especially limited irrigation supply resulted in chronically dry soil conditions during the vegetative stage in Tokyo and during later growth stages in Osaka.

Aerobic and flooded culture (one of each) were set up at each of the two sites. In the aerobic culture, fields were non-puddled and the rice seeds were directly sown into the soil. In the other trial, the fields were puddled and kept flooded after transplanting. In each trial, four high-yielding rice (*Oryza sativa* L.) cultivars were grown: Takanari (lowland-adapted indica, one of the highest yielding cultivars in Japan; Katsura et al., 2007, 2008), Akihikari (lowland-adapted japonica), Lemont (lowland-adapted japonica), and IRAT109 (upland-adapted japonica). The four cultivars were arranged in a randomized complete-block design with three replications. The area of each replicate was 50–70 m^2. Further details of the climate data, crop management are reported in Kato et al. (2009).

At both sites in both years, the sowing dates were early May. In aerobic culture, 4 or 5 seeds were sown into each hill at a density of 22.2 hills m^{-2} (30×15 cm), and plants were thinned to one plant per hill after seedling establishment. In flooded culture, one 25-day-old seedling was transplanted into each hill at the same density as in aerobic culture. A chemical fertilizer (N, P, K = 60, 39, 67 kg ha^{-1}, respectively) was applied before sowing, and ammonium sulfate (N = 30 kg ha^{-1}) was top-dressed at 6, 10, 13, and 16 weeks after sowing in all trials (total N = 180 kg ha^{-1}).

Measurements

For each cultivar, 30 plants from flooded culture and 50 plants from aerobic culture were harvested at 25–28 days after sowing (at transplanting for flooded culture) in both years. Eight plants were sampled from each plot periodically during the growth stage, and 24 plants were sampled at maturity from each plot. The total number of harvests during crop growth was 6 or 7 for each cultivar at both sites in both years. Plant samples were oven-dried at 80 °C for at least 72 h to determine aboveground biomass. For the determination of aboveground N content (total N), dried samples were ground, and the N concentration was analyzed with an NC analyzer (Sumigraph NC-90A, SCAS, Tokyo, Japan) at Tokyo and by the Kjeldahl method at Osaka. To ensure that the measurements from the different analytical methods were comparable between the two experimental sites, ten of validation samples were run with both methods (Y=0.99X, R^2=0.975).

The fraction of radiation intercepted (FRI) was measured about once a week during crop growth for each replication by linear photosynthetic active radiation ceptometer (AccuPAR, Decagon Devices Inc., Washington, USA). The number of times FRI was measured ranged from 12 to 17 for each cultivar at both sites in both years. The daily FRI values between two measurement dates were estimated by linear interpolation. The amount of radiation interception was calculated by multiplying daily FRI value and incident radiation. The cumulative total dry weight was plotted against cumulative intercepted radiation from the first harvesting time to a given harvesting time, and values of RUE were obtained from the slopes of the regression lines forced through the origin for each replication.

Greenwood et al. (1990) suggested that the critical N% in plants, which is defined as the minimum needed for maximum growth rate (Ulrich, 1952), can be expressed as a function of aboveground total dry weight (TDW):

$$critical\ N\% = a \cdot TDW^{-b} \quad (TDW \geq 1 t\, ha^{-1}) \quad \text{(Eq. 1)},$$

where a and b are parameters. The Eq. (1) could be expressed as follows:

$$\log critical\ N\% = -b \cdot \log TDW + \log a \quad (TDW \geq 1 t\, ha^{-1}).$$

In the present study, we estimated the parameters log a and b from intercept and slope of regression line between logarithm of N% in plants and that of TDW for each watering regime and experimental site (TDW $\geq$ 1 t ha^{-1}) so as to minimize the sum of square errors between the measured and estimated logarithm of N% in plants.

Data were analyzed by using the generalized linear model (GLM) procedure. Individual analyses of variance were conducted separately for each trial for each year according to a randomized-block design to assess cultivar differences. The effect of water regimes (aerobic culture vs. flooded culture) and the cultivar × water interaction were assessed by combined analysis of variance over trials. Differences were compared by least significant difference (LSD) tests at the 5% level.

Results

Aboveground biomass at maturity was greater in aerobic culture than in flooded culture for all cultivars and experimental sites and in both years, with the exceptions of Akihikari and Takanari at Tokyo in 2007, where the soil water potential fell to a particularly low level (sometimes below –60kPa at 20cm soil depth, Kato et al., 2009) during the early growth stage (Fig. 1). Takanari achieved aboveground biomass at maturity of over 20 t ha^{-1} in three out of the four experiments in aerobic culture. The highest aboveground biomass at maturity of all replicates, 23.6 t ha^{-1}, was recorded for Takanari in aerobic culture at Tokyo in 2008.

Total N at maturity in the rice plants was also greater in aerobic culture than in flooded culture in all cultivars, experimental sites and years, with the exception of Takanari at Tokyo in 2007 (Fig. 2). The highest total N of 315 kg ha^{-1} was recorded for Takanari grown in aerobic culture at Tokyo in 2008. In general, total N steadily increased during the early growth stage, but the N accumulation rate decreased in the ripening stage in both water regimes (Table 1). The N accumulation rate in the reproductive stage (from 9 weeks after sowing to heading) was generally larger in aerobic culture than in flooded culture, whereas in the ripening stage there was no significant difference in the N accumulation rate between the two water regimes in three out of four experiments (Table 1). Hence, the larger total N at maturity in aerobic culture relative to that in flooded culture was caused by the difference in accumulated N that had occurred by the heading stage. The N accumulation rate in the ripening stage for IRAT109 and Lemont was significantly larger in aerobic culture relative to that in flooded culture, except at Tokyo in 2007, when there was no significant difference between the two. On the other hand, N accumulation by Akihikari in aerobic culture was significantly lower at Tokyo in 2007 and at Osaka in 2008, and that by Takanari was significantly lower at Tokyo in 2007.

There were no notable differences in intercepted radiation between the two watering regimes, except at Osaka in 2007. Neither were there any consistent trends in the averaged FRI during crop growth between the two watering regimes, and the values of FRI were relatively stable, mostly ranging between 0.65 and 0.70 (Table 2 and Table 3). The FRI values of the lowland-adapted cultivars Akihikari and Takanari were, however, lower in aerobic culture relative to those in flooded culture in the early growth stage, and the FRI values of IRAT109 and Lemont in aerobic culture were higher than those in flooded culture in the early growth stage (data not shown). The cultivar differences in FRI in the early growth stage were relatively large at Tokyo in 2007 and at Osaka in 2008. The values of FRI exceeded 0.90 in the later growth stage in all cultivars and years and at all experimental sites.

RUE ranged from 1.05 to 1.72 g MJ^{-1} and was greater in aerobic culture than in flooded culture when averaged across all cultivars at both sites in 2008. The RUEs of IRAT109 and Lemont were significantly greater in aerobic culture than in flooded culture, except at Osaka in 2007, when there was no significant difference (Table 2 and Table 3). RUE in aerobic culture was sometimes lower relative to that in flooded culture in Akihikari (at Tokyo in 2007) and Takanari (at Tokyo in 2007 and at Osaka in 2008). The highest RUE value of 1.72 g MJ^{-1} was recorded by Takanari in aerobic culture at Tokyo in 2008.

The relationships between aboveground biomass and crop N% are shown in Fig. 3. Crop N% decreased as aboveground biomass increased, but was appeared greater in aerobic culture than in flooded culture at the same levels of aboveground biomass. Estimated parameter b in Eq. (1) was significantly larger in aerobic culture that in flooded culture in Osaka (Table 4). The N% in flooded culture at Osaka tended to be lower than that at Tokyo at the same levels of aboveground biomass.

Discussion

1. N accumulation in aerobic culture

Total N at maturity was significantly larger in aerobic culture (194–233 kg ha^{-1}) than in flooded culture (142–173 kg ha^{-1}), except with Takanari at Tokyo in 2007. The highest value of total N at maturity—315 kg ha^{-1} by Takanari at Tokyo in 2007—comparable to, or rather higher than, that of rice grown in flooded culture with exceptionally high grain yields of over 15 t ha^{-1} (Ying et al., 1998; Katsura et al., 2008; Li et al., 2009). The difference in total N at maturity between aerobic and flooded cultures was produced by differences in the N accumulation rate in the reproductive stage (Table 1; Fig. 2). Our results are in agreement with Wada et al. (2002). The N accumulation rate in aerobic culture in the reproductive stage (2.26–4.08 kg ha^{-1} d^{-1}) was higher than that in aerobic culture in northern China, which is in the range 1.13–2.28 kg ha^{-1} d^{-1} (averaged value from panicle initiation to heading, Zhang L et al., 2009). Besides, it also higher than in flooded culture with high-yielding rice in Yunnan, China, which is in the range 1.53–2.59 kg ha^{-1} d^{-1} (averaged value from panicle initiation to heading, Ying et al., 1998), even though the maximum instantaneous N uptake rates can reach 9 to 12 kg ha^{-1} d^{-1} for a period of 4 days after heavy N application at panicle initiation in rice (Peng and Cassman, 1998). It is noteworthy that the N accumulation rates in the reproductive stage of IRAT109 and Lemont did not significantly differ between the aerobic and flooded cultures, while that of Takanari in aerobic culture were significantly lower than that in flooded culture, at Tokyo in 2007, which was when the soil water potential was particularly low. Rice varieties often experience N deficiencies when grown in dry soils, and there is considerable genetic variation for tolerance to this (Fukai et al., 1999; Wade et al., 1998).

Sheehy et al. (1998) suggested that the function shown in Eq. (1) defines a critical N dilution curve for high-yielding rice and was the same independent of climatic zone and cultivar. N% in plants in the present study changed lower compared with that by Sheehy et al. (1998) when aboveground biomass was low (Fig. 3) as represented by significantly lower value of parameter *a* (Table 4). On the other hand, the reduction of N% as the increase of aboveground biomass was slower than that by Sheehy et al. (1998) as represented by significantly lower value of parameter *b* (Fig. 3, Table 4). Consequently, our relationships between N% and aboveground biomass under aerobic culture closely fit the N dilution curve for high yielding rice estimated by Sheehy et al. (1998), the exception being when aboveground biomass was low (Fig. 3). We suggest that the C/N ratio that maximizes biomass productivity in aerobic culture is approximately the same as that in flooded culture.

The tendency towards lower N% in plants in flooded culture than in aerobic culture especially in Osaka (Fig. 3) indicates that lower N absorption limits biomass production in flooded culture, even though very high aboveground biomass was achieved. There are two possible explanations for the lower N absorption in flooded culture: either a limitation in soil N supply or a limitation in plant N uptake. The dynamics of N mineralization would of course be different between aerobic and flooded cultures (Birch, 1960; Tsujimoto et al., 2009). But it is unlikely that soil N supply would have differed appreciably between the two water regimes, because the N application rate was extremely high in our study (180 kg ha^{-1}) compared with those in previous studies in Japan (San-oh et al., 2004; Takai et al., 2006). Further, Katsura et al. (2007) demonstrated that there was no difference in biomass accumulation between N levels of

140 kg ha^{-1} and 280 kg ha^{-1} under flooded culture in Japan. We also saw that the N accumulation rate decreased in the later growth stage under both watering regimes, and was not different between the two regimes, even though we periodically top-dressed N (Table 1). Hence, the difference in N accumulation in our study would most likely have been caused not by a difference in environmental N supply but by a difference in the N uptake capacity of the rice plants during the reproductive stage.

2. Radiation use in aerobic culture

Only a few studies have analyzed radiation interception and RUE of rice plants in aerobic culture. Here, the intercepted radiation, ranging from around 1000 MJ m^{-2} to 1700 MJ m^{-2}, was comparable to that in studies of aerobic rice culture in northern China (Bouman et al., 2006b) and flooded rice culture in central Japan and southern China (Katsura et al., 2008; Zhang Y et al., 2009). Bouman et al (2006b) reported that rice plants sometimes intercepted more radiation in aerobic culture than in flooded culture owing to a greater FRI and longer growth period. Our results agreed with their findings, although the factors affecting radiation interception in aerobic culture differed among the four cultivars (Table 2 and Table 3).

The high levels of radiation interception by IRAT109 and Lemont in aerobic culture were brought about by high FRI in the early growth stage relative to those in flooded culture, whereas the high levels by Takanari and Akihikari were caused by their longer growth periods, which compensated for relatively low FRI in the early growth stage. The FRI of Takanari at Tokyo in 2007, where soil water potential was frequently low, declined and resulted in a more than 30% reduction in aboveground biomass at maturity. Cultivar differences in FRI in the early growth stage were also reported by

Kato et al. (2006). Hence the improvement of FRI in lowland-adapted high-yielding cultivars in the vegetative stage—namely, early vigor—would be one way of achieving stable, high rice yield in aerobic culture.

Bouman et al (2006b) showed that, in northern China, RUE in aerobic culture (0.65–1.05 g MJ^{-1}) was lower than that in flooded culture (1.05–1.27 g MJ^{-1}) and was the major factor limiting rice yield, even though rice varieties adapted to aerobic culture was used. In our study, however, the RUE of aerobic culture was comparable to, or higher than, that of flooded culture (1.27–1.50 vs. 1.20–1.37 g MJ^{-1}), except in Tokyo in 2007 (1.30 vs. 1.37 g MJ^{-1}) (Table 2 and Table 3). Both studies strongly suggest the importance of high RUE for biomass production in aerobic rice culture. The inconsistency in the trends in RUE between the different studies may be attributable to the dynamics of surface soil moisture arising from the difference in water inputs and soil type. The water input to the aerobic rice in northern China was 500–900 mm and the soil was sandy (Bouman et al., 2006b), while the water input was 800–1300 mm and the soil was clay loam (Tokyo) and sandy loam (Osaka) in the present study (Kato et al., 2009). More frequent declines in surface soil moisture in northern China would cause the reduction in RUE in aerobic culture. RUE in aerobic culture in our study was comparable to that in flooded culture (1.0–1.7 g MJ^{-1}) in other studies in Asia (Hayashi, 1972; Sinclair and Horie, 1989; Horie et al., 1997; Sheehy et al., 1999; Sinclair and Muchow, 1999) and the United States (Kiniry et al., 2001). Moreover, the RUE of 1.72 g MJ^{-1} for Takanari in aerobic culture was similar to other values (1.31–1.72 g MJ^{-1}) reported for the same cultivar (Katsura et al., 2008).

Different cultivar responses to water management in RUE were observed in aerobic culture. At Tokyo in 2007, when soil water potential fell to low levels (sometimes below –60 kPa at 20cm soil depth, Kato et al., 2009), RUE in aerobic culture was less than in flooded culture. Takanari, in particular, recorded a 23% lower RUE in aerobic culture relative to that of flooded culture. Other studies have suggested that stomatal conductance is decreased in aerobic culture (Nguyen et al., 2009; Kato and Okami, 2009). Cultivar differences in RUE in aerobic culture could partly relate to cultivar differences in stomatal response to water deficiency. Our study was aimed at achieving high rice yield in aerobic culture, so we attempted to avoid any signs of plant water deficits (leaf rolling and drying). Plants of IRAT109 were found by Kato and Okami (2009) to keep their stomata open to a greater extent than Takanari when the soil water potential was temporarily less than –50 kPa; this was related to IRAT109 having a deeper root morphology. However, the RUEs of IRAT109 and Lemont were lower in flooded culture than in aerobic culture in three of the four growth trials—a trend similar to that of N accumulation. Root oxidation activity of rice declines in the later growth stage in flooded culture (Samejima et al., 2004; Zhang H et al., 2009), reducing the N accumulation rate (Samejima et al., 2004) and RUE (Horie et al., 1997). Previous studies have shown that aeration of the soil by intermittent drainage can minimize the decline in root oxidation activity during the reproductive stage in flooded culture (Ramasamy et al., 1997; Yang et al., 2004; Zhang et al., 2008). The habitat of wild rice ranges from deep-water swamps to mountainous uplands, and there is an array of genetic variation in adaptation to wetland and dryland conditions. The cultivar differences in RUE in flooded culture may arise from differences in tolerance to hypoxia, although semi-aquatic rice plants can survive in anaerobic soils. The N uptake ability and RUE of IRAT109 and Lemont may be more susceptible to decline under continuously flooded conditions than those of Akihikari and Takanari.

In conclusion, we demonstrated that biomass production of over 20 t ha^{-1} is attainable in aerobic culture in Japan, and that this production is supported by the accumulation of large amounts of N, especially in the reproductive stage. The maximum RUE we achieved in aerobic culture was comparable to values previously reported from extremely high-yielding rice in flooded culture in Asia. Further studies of the influence of genotype × water management interactions on RUE and related traits are needed to enhance the water use efficiency and yield potential of irrigated rice.

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Figure captions

Figure 1. Seasonal changes in aboveground biomass of four high-yielding rice cultivars grown at two experimental sites under aerobic or flooded culture in two consecutive years. Each data value is the average of three replicates.

Figure 2. Seasonal changes in aboveground nitrogen accumulation of four high-yielding rice cultivars grown at two experimental sites under aerobic or flooded culture in two consecutive years. Each data value is the average of three replicates.

Figure 3. Relationships between aboveground total dry weight and N concentration as a percentage of dry weight in aboveground dry matter of four high-yielding rice cultivars at (a) Tokyo and (b) Osaka. Solid and open symbols indicate flooded and aerobic culture, respectively. The lines show regression curve for each water regimes and estimated curve by Sheehy et al (1998). The values of estimated parameters were shown in Table 4. Each data value is the average of three replicates.