Rice Adaptation to Aerobic Soils: Physiological Considerations and Implications for Agronomy

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Abstract: Aerobic culture is a water-saving technique for direct-seeded rice cultivation. Growing rice under continuously unsaturated soil conditions can maximize water-use efficiency and minimize both labor requirements and greenhouse-gas emissions. Under a temperate climate, aerobic culture can produce a rice yield greater than 9 t ha\textsuperscript{3} especially in central Japan (11.4 t ha\textsuperscript{3}). Aerobic culture using large-scale center-pivot sprinklers is being established in the central United States, where yields can surpass 10 t ha\textsuperscript{3}. However, yields remain at less than 8 t ha\textsuperscript{3} in the tropics. The high yield of Japanese aerobic culture is mainly attributed to vigorous nitrogen uptake during the reproductive stage, which allows rice plants to produce more spikelets and biomass. Fertilizer management for aerobic culture must satisfy both the nitrogen demand and control spikelet density to achieve an appropriate sink–source balance. Unfortunately, the poor development of the root system in rice limits its water uptake from unsaturated soil. Adaptive responses such as adventitious root emergence, lateral root branching, and deep root penetration would protect the plants against dehydration stress in aerobic culture. Intermediate plant height with a few large tillers rather than semi-dwarf stature with profuse tillering should be a suitable plant type for aerobic culture, and plants should show leaf expansion despite fluctuations of soil moisture. The development and identification of suitable genotypes and crop management options are underway worldwide for more resource-use efficient and productive aerobic rice culture.

Key words: Aerobic rice, Dry-seeded rice, Rainfed lowland rice, Upland rice, Water-saving irrigation.

Rice (\textit{Oryza sativa} L.) is the staple food for more than half of the world’s population, and more than 90% of the world’s rice is produced in Asia. However, rice-growing areas are usually overpopulated and have some of the world’s most impoverished communities. Thus, improving rice productivity is becoming essential, particularly because of the recent shortage of rice in international markets. Continuing efforts to improve rice cultivation systems to increase their productivity and sustainability will enhance food security and alleviate poverty in rice-producing areas (FAO, 2009).

The rice production areas can be classified into irrigated, which accounts for about 55% of the total rice cultivation area, and rainfed, which consists of upland rice (about 14 Mha, about 11% of the total rice cultivation area), rainfed lowland rice (about 46 Mha in Asia, consisting of 30% of the total rice cultivation area), and deepwater rice and floating rice (about 4 Mha in Asia). Global statistics (IRRI, 2002) show that the yield of rainfed rice (1.0 to 2.5 t ha\textsuperscript{1}) is considerably lower than that of irrigated rice (4.5 to 6.5 t ha\textsuperscript{1}).

Since the Green Revolution in Asia, rice culture has been intensified mainly in irrigated areas. In irrigated rice, the field is maintained under shallow water to maximize its grain yield and quality, except for temporary mid-season drainage. However, increasing water scarcity around the world means that rice farmers in an increasing area of the world will not be able to obtain enough water to keep their fields flooded (Humphreys et al., 2010). Aerobic rice culture, which consists of dry-seeded rice cultivation under non-flooded conditions with irrigated upland rice cultivation, is being developed to enhance water-use efficiency. In this system, the plants are grown in non-irrigated, unsaturated and well-drained soils, although the fields may have embankments if necessary. Access to irrigation is assured, and the soil is fully moistened as needed by the crop. Unlike traditional upland rice cultivation in which rainfall and any capillary rise are the only source of water, the plants in aerobic rice culture do not encounter drought or infertile soil conditions because of deliberate water and nutrient management. This approach uses less than 50% of the irrigation water...
required by conventional flooded rice (Bouman et al., 2007). In addition to coping with water scarcity, this form of cultivation also reduces labor requirements (Kumar and Ladha, 2011) and decreases greenhouse-gas emissions (Alberto et al., 2009). Efforts to breed superior accessions suitable for aerobic rice culture are underway in China, India, and Brazil, as well as at the International Rice Research Institute (Wang et al., 2002; Zhao et al., 2010; Breseghello et al., 2011). In Japan, an aerobic rice breeding program was conducted in Ibaraki Prefecture, Kanto region, from 1929 to 2005, to increase rice yield in uplands with irrigation provided by sprinklers. A popular glutinous variety, ‘Yumeno-Hatamochi’ (its meaning is “miracle” aerobic rice in Japanese) (Hirasawa et al., 1998), which has a yield potential of 6 to 7 t ha\(^{-1}\), in addition to good eating quality and high drought resistance, was released.

### 1. Rationale for focusing on rice adaptation to aerobic soils

Various aspects of aerobic rice culture have already been reviewed: weed management (Chauhan et al., 2012), irrigation schemes (Humphreys et al., 2010), yield decline as a result of monocropping of aerobic rice (Nie et al., 2012), soil-borne pests such as nematodes (Prasad, 2011), and the decline in soil fertility and decomposition of soil organic matter (Kumar and Ladha, 2011). We will not recapitulate these issues here. Although agriculturalists are paying more attention to the looming water crisis confronting rice production in this century, we found that the physiological aspects of aerobic rice culture have not been comprehensively reviewed despite the importance of rice physiology for water use. In addition, few researchers have studied rice physiological responses to aerobic soil conditions (Clerget and Bueno, 2012).

By examining the response to aerobic conditions separately from the response to drought, we will gain new insight into better crop management in irrigated rice. Although rainfed rice has a lower yield than irrigated rice, this does not necessarily mean that rice cannot adapt well to aerobic soil. For example, George et al. (2002) reported a rice yield of 7.8 t ha\(^{-1}\) with ample irrigation and fertilizer application on aerobic soils in the Philippines. A similar yield can also be expected in Indonesia (Suwarno et al., 2009). Skilled farmers in the Kanto region of Japan can achieve rice yields greater than 6 t ha\(^{-1}\) on aerobic soils (approx. 1000 mm of water supply during the crop growth

### Table 1. High yield records of rice (greater than 8 t ha\(^{-1}\)) grown under aerobic culture in the world.

| Variety     | Country | State/province | Year | Water supply (mm) | Grain yield (t ha\(^{-1}\)) | Irrigation method | Soil moisture | Soil type | Citation                  |
|-------------|---------|----------------|------|-------------------|----------------------------|-------------------|---------------|-----------|----------------------------|
| Takanari    | Japan   | Osaka          | 2007 | 911               | 11.4                       | Sprinkler         | > – 80 kPa    | Clay loam | Kato et al., 2009b         |
| Takanari    | Japan   | Osaka          | 2008 | 1313              | 11.3                       | Sprinkler         | > – 80 kPa    | Clay loam | Kato et al., 2009b         |
| Takanari    | Japan   | Tokyo          | 2008 | 1301              | 10.6                       | Sprinkler         | > – 80 kPa    | Clay loam | Kato et al., 2009b         |
| RT CLXL729  | USA     | Missouri       | 2009 | 750               | 10.3                       | Center pivot      | > – 70 kPa    | Silt loam | Stevens et al., 2012       |
| Takanari    | Japan   | Osaka          | 2009 | 797               | 9.9                        | Sprinkler         | > – 60 kPa    | Clay loam | Katsura and Nakaide, 2011  |
| Takanari    | Japan   | Tokyo          | 2009 | 868               | 9.6                        | Sprinkler         | > – 30 kPa    | Clay loam | Okami et al., 2013         |
| Takanari    | Japan   | Osaka          | 2010 | 802               | 9.2                        | Sprinkler         | > – 60 kPa    | Clay loam | Katsura and Nakaide, 2011  |
| Suweon290   | Japan   | Tochigi        | 1994 | 822               | 8.8\(^{a}\)                | Rainfed           | –             | Clay loam | Yun et al., 1997           |
| Lemont      | Australia| Queensland     | 1989 | 930 – 960         | 8.6                        | Sprinkler         | Near field capacity | Heavy clay | Boonjung and Fukai, 1996 |
| 9516        | China   | Jiangsu        | 1999 | 1414              | 8.4                        | Flush irrigation  | > – 20 kPa    | Sandy loam | Shi et al., 2001           |
| PAU-201     | India   | Ludhiana       | 2009 | 3860\(^{b}\)      | 8.3                        | Piped irrigation  | Near field capacity | Clay loam | Sudhir-Yadav et al., 2011 |
| Lemont      | Japan   | Tokyo          | 2007 | 891               | 8.1                        | Sprinkler         | > – 80 kPa    | Clay loam | Kato et al., 2009b         |
| NERICA5     | Japan   | Miyagi         | 2007 | 1143              | 8.1                        | Rainfed           | –             | Light clay | Matsunami et al., 2009     |

\(^{a}\) irrigation + rainfall, \(^{b}\) estimated amount, \(^{c}\) estimated as brown rice yield is 80% of grain yield.
period). These facts raise many questions about the best crop management in irrigated rice. For instance, are flooded soils the ideal habitat for rice? What aspects of aerobic rice cultivation should be considered separately from drought studies? These unique perspectives would be useful for both varietal improvement and better water management in dry-seeded rice cultivation.

Rice adaptation to aerobic soil conditions has long been discussed in the context of drought resistance. Accordingly, we still have no conclusive answer to the fundamental question about whether aerobic conditions would be negative or harmful for rice growth in the absence of drought. In this review, we summarize recent research on intensive rice cultivation in aerobic soils, with a focus on the potential yield, yield stability, and related physiological and morphological characteristics of rice.

2. What is the potential yield in aerobic rice culture?

Drought stress has been assumed to limit the attainable yield of rice plants grown under unsaturated soil conditions in aerobic culture. However, high productivity of aerobic rice culture was documented in Japan as long as 50 to 60 years ago (Hasegawa and Nakayama, 1959). Grain yield exceeding 5 t ha\(^{-1}\) was achieved in aerobic culture with sprinkler irrigation, which was comparable to the productivity in flooded culture at that time. However, research on aerobic rice culture became less popular, thereafter, and the reported maximum yield therefore did not increase. In the 1990s, research efforts were focused on flooded culture, and the potential rice yield in flooded culture increased steadily to and surpassed 10 t ha\(^{-1}\) (Fischer and Edmeades, 2010; Hayashi et al., 2012, Yoshinaga et al., 2013). In contrast, few studies reported grain yield exceeding 8 t ha\(^{-1}\) under aerobic culture was not reported during the entire 20th century (Table 1). In the 21st century, research efforts were again being focused on aerobic culture to cope with the increasing worldwide water shortage. In Osaka Prefecture Japan, aerobic culture was found to give a high yield (11.4 t ha\(^{-1}\)) (Fig. 1). This yield is equivalent to the current potential yield of flooded rice (11 to 12 t ha\(^{-1}\)). In Wuhan, central China, in 2012 aerobic culture yielded 10 t ha\(^{-1}\) of rice (Dr. Lixiao Nie, Huazhong Agricultural University, China, unpublished data). Thus, the attainable yield of aerobic rice appears to
be comparable to that of flooded rice in a temperate environment. In other words, there would be little yield penalty for rice grown in unsaturated soils if the adverse effects of aerobic culture could be properly overcome.

All the records of aerobic rice yield greater than 8 t ha\(^{-1}\) were achieved under subtropical or temperate conditions (Table 1); none in the tropics. This may be due to the shorter growth duration (110 to 120 days in the tropics, vs. 140 to 170 days in subtropical and temperate environments), which results from the rapid growth at a high temperature (Ying et al., 1998). Another reason may be the soil drying during the dry season in the tropics, since grain yield was higher in flooded culture (Bouman et al., 2007). However, there may be other reasons for the low rice yield under aerobic conditions in the tropics. In order to elucidate the causes, systematic multi-location field trials that cover a range of climatic regions will be necessary.

Aerobic culture has been reported to produce high yields in the central watershed of the Mississippi River, the largest rice-production region in the United States (Table 1). For example, in Missouri and Arkansas, farmers have large farms (1000 to 3000 ha) and grow rice, soybean, wheat, maize, and cotton in rotation. In this region, the energy costs associated with pumping groundwater make up a substantial portion of the rice production budget, and water scarcity is becoming more serious. Accordingly, more attention is being paid to the use of water-saving rice cultivation. The center-pivot irrigation system is being developed (Fig. 1); irrigation, fertigation, and herbicide application are automatically controlled by the software simulating the water balance and predicting soil water deficits (Stevens et al., 2012). In addition, an alert system notifies farmers by e-mail or via their mobile phone when the average soil water potential drops below a critical value. Vories et al. (2013) reported that the water-use efficiency (the ratio of the yield increase above that in rainfed production to the amount of irrigation) of the center-pivot system ranged from 1.4 to 2.0 kg m\(^{-2}\), higher than the values reported by Vories et al. (2005) under conventional irrigation systems (0.9 kg m\(^{-2}\)). This means that it is possible to achieve both high productivity and efficient use of water in aerobic rice culture.

The high rice yields in aerobic culture that are summarized in Table 1 were achieved by lowland-adapted varieties that have high yields under flooded conditions. The highest yield was achieved by ‘Takanari’ (11.4 t ha\(^{-1}\), Table 1), a high-yielding variety developed for flooded culture and released in 1990 in Japan. On the other hand, ‘IRRI132’, an aerobic rice variety recently released by the International Rice Research Institute under the names ‘Apo’ and ‘NSIC Rc9’, produced a 25% lower yield than ‘Takanari’ in aerobic culture in Japan (Kato et al., 2009b). Although ‘IRRI132’ is adapted to unfavorable environments (Saito et al., 2007), excessively high plant height under very productive environments as listed in Table 1 (150 to 170 cm) appears to be a disadvantage. Stevens et al. (2012) also suggested that hybrid rice varieties used in flooded culture were more suitable for a center-pivot irrigation system. Taken together, these studies in temperate regions and the study of George et al. (2002) in the tropics suggest that high-yielding lowland-adapted varieties can also achieve high yield in aerobic culture. However, the traits that rice plants require to achieve high yield stably in aerobic culture may differ from those in flooded culture (see the discussion below).

3. Physiological attributes that increase rice yield under aerobic soil conditions

(1) Biomass production and nitrogen (N) uptake

As discussed in the previous section, a potentially high yield can be obtained in aerobic culture in temperate regions. Various researchers have dissected the underlying mechanisms. The high yield under aerobic culture in Japan results mainly from vigorous biomass production (Matsumani et al., 2009; Katsura et al., 2010), with a harvest index that ranges from 0.40 to 0.48 (Kato et al., 2009b). For instance, the aboveground biomass at maturity was higher in aerobic culture than in flooded culture in one study (on average across varieties, 17.2 to 18.5 t ha\(^{-1}\) vs. 14.7 to 15.8 t ha\(^{-1}\)), with the highest value reaching 23.6 t ha\(^{-1}\) for ‘Takanari’ in aerobic culture (Katsura et al., 2010). Some of this difference can be explained by differences in radiation use by rice plants. Total dry weight (TDW) can be expressed using the following equation:

\[
TDW = RAD \times FRI \times RUE
\]

where RAD is the total incident solar radiation, FRI is the fraction of the radiation intercepted by the plants, and RUE is radiation-use efficiency. The rice plants in aerobic culture intercepted more than 1500 MJ m\(^{-2}\) of solar radiation (Bouman et al., 2006; Katsura et al., 2010), which was comparable to the interception in flooded culture (Katsura et al., 2008). The large radiation interception in aerobic culture resulted from a longer growth duration and greater FRI during later growth stages. On the other hand, Katsura et al. (2010) also showed that the RUE in aerobic culture was comparable to, or higher than, that in flooded culture (1.13 to 1.72 g MJ\(^{-1}\) vs. 1.05 to 1.68 g MJ\(^{-1}\)). The highest value of RUE (1.72 g MJ\(^{-1}\)), achieved by ‘Takanari’ in aerobic culture in Tokyo, represents one of the highest values reported for rice (Sinclair and Muchow, 1999).

The high RUE in aerobic culture in Japan is partly supported by vigorous N uptake. The N accumulation at maturity was higher in aerobic culture (194 to 233 kg N ha\(^{-1}\)) than in flooded culture (142 to 173 kg N ha\(^{-1}\)), mainly due to a higher N uptake rate during the reproductive growth stage in aerobic culture (Katsura et al., 2010). Consequently, the rice plants under aerobic conditions had an N
The critical N concentration is defined as the minimum N concentration higher than under flooded conditions. The critical N concentration required to achieve the maximum growth rate by Sheehy et al. (1998). Theoretically, it declines as the crop biomass increases; for example, the value is 13 mg N g$^{-1}$ when the crop biomass is 15 t ha$^{-1}$ (Sheehy et al., 1998). After the reproductive stage, the rice plants in aerobic culture had an N concentration equivalent to or higher than the above critical N concentration (Katsura et al., 2010). On the other hand, the N uptake rate after the reproductive stage declined sharply in aerobic culture compared with flooded culture in the Philippines (Belder et al., 2005), and this may cause poor growth of aerobic rice after flowering in the tropics (Peng et al., 2006).

Root function plays a key role in achieving high N uptake in aerobic culture. Katsura and Nakaide (2011) showed that the ability of rice roots to oxidize substances in the rhizosphere in aerobic culture was higher than in flooded culture. High root physiological activity is essential for N uptake (Samejima et al., 2004; Matsunami et al., 2012, 2013). Many researchers have suggested that aeration of the soil is important in conventional flooded culture because it allows the plants to maintain high root activity (Ramasamy et al., 1997; Yang et al., 2004). In addition to differences in root function, the dynamics of N mineralization in aerobic culture differs from that in flooded culture because of the different chemical and biological conditions (Ramasamy et al., 1997; Ladha et al., 2005). Achieving appropriate proportions of nitrate and ammonium in the soil promotes N uptake by rice plants (Toriyama and Ando, 2011). Hence, the effect of nitrate uptake and assimilation in aerobic culture on dry matter production should be studied comprehensively to explore the possibility of raising the yield potential in aerobic culture.

(2) Yield components

Important findings have been obtained on the yield components. For example, the panicle number in aerobic culture was comparable to, or higher than, that in flooded culture in Japan (Kato et al., 2009b; Matsumani et al., 2009) and in the Philippines (Peng et al., 2006). Standing water sometimes restricts tiller emergence (Ohe et al., 2010), which would reduce panicle number in flooded culture, especially when the rice is transplanted rather than directly seeded (Sudhir-Yadav et al., 2011). Okami et al. (2012) showed that high-yielding indica varieties produce more tillers in aerobic culture than in flooded culture. For example, ‘IR72’ produced more than 1000 tillers m$^{-2}$ in aerobic culture versus fewer than 700 tillers m$^{-2}$ in flooded culture.

Although young panicle formation is very sensitive to drought stress during the early reproductive growth stage (Kato et al., 2008), Kato et al. (2009a) found that when the soil was mostly near field capacity, the number of spikelets per unit area was also larger in aerobic culture than in flooded culture ($40 \times 10^3$ to $44 \times 10^3$ m$^{-2}$ vs. $32 \times 10^3$ to $38 \times 10^3$ m$^{-2}$). In conventional flooded culture, the number of differentiated spikelets is proportional to the N level between 4 and 2 weeks before anthesis (Horie et al., 1997). This was also true for rice plants in aerobic culture: vigorous N uptake during the reproductive period in aerobic culture enables rice plants to produce a large number of spikelets (Kato and Katsura, 2010). Katsura (2013) found genotypic differences in spikelet production efficiency (the ratio of the number of spikelets to N uptake) among chromosome segment substitution lines in the ‘Sasanishiki’ (a lowland-adapted japonica variety) background with ‘Habatat’ (a high-yielding indica variety) as the donor (Ando et al., 2008). ‘Habatat’ and most of the lines had more spikelets and higher yield in aerobic culture than in flooded culture. However, there were no significant differences in spikelet number and yield for ‘Sasanishiki’ between the two water regimes. Because vigorous N uptake during the reproductive period can be expected in aerobic culture, the varieties with high spikelet production efficiency should also have high yield.

Soil drying at the flowering stage increases spikelet sterility in aerobic rice culture (Boonjung and Fukai, 1996). In field experiments at the International Rice Research Institute, for example, spikelet sterility was 20% and 73% when the fraction of transpirable soil water at flowering was 95% and 29%, respectively (Cruz and O’Toole, 1984). In addition, spikelet sterility will be increased if water limitation occurs under high midday temperature conditions because of less self-cooling effect by plant transpiration (Fukuoka et al., 2012; Ishimaru et al., 2012). However, previous research has demonstrated that providing irrigation at least before the soil water potential decreased below $–30$ kPa could eliminate the risk of spikelet sterility in aerobic rice culture not only in Japan (Kato et al., 2009b) and China (Bouman et al., 2006) but also in the tropics; for example, in the Philippines (Peng et al., 2006) and India (Sudhir-Yadav et al., 2011). In these reports, spikelet sterility was mostly less than 30% in aerobic culture and equivalent to that in flooded culture.

Rice plants have a potential to produce heavier single-grain weight under aerobic conditions than under flooded conditions in Japan (Katsura and Nakaide, 2011; Katsura, 2013), while it decreases in the tropics even if the soil water potential is maintained above $–30$ kPa (Peng et al., 2006; Sudhir-Yadav et al., 2011). Rice grain weight is determined by individual husk size, by sink activity (often measured using the activity of enzymes involved in the conversion of sucrose to starch), and by source capacity (the capacity to supply carbohydrates to the grains). A positive relationship between root activity and sink activity has been suggested in flooded rice (Ramasamy et al., 1997). In aerobic culture, husk size and sink activity are better than in flooded
culture, but vigorous N uptake is more likely to lead to excessive spikelet production, thereby reducing the single-grain weight in rice varieties with a high spikelet production efficiency in Japan (Katsura and Nakaide, 2011). This would be attributable to the limited source ability for the growth of a large number of grains during the grain-filling period. Furthermore, increasing plant N status beyond the optimal level might interfere with grain filling by accelerating the translocation of N from the vegetative organs to the grain in the early ripening stage, thereby slowing the transport of photoassimilate out of the leaves (Tsuno et al., 1990; Yamaguchi et al., 1995). These researchers showed that excess capacity of N supply to the grain causes a delay in grain growth. Therefore, a key issue for achieving a high and stable yield in aerobic culture is how to control N uptake by rice plants to maintain an appropriate sink–source balance. In highly productive environments, the recommended N fertilizer management for aerobic culture should match the crop N demand with the soil N supply, but should also control N uptake during the reproductive stage to avoid excessive spikelet production.

4. Rice adaptation to aerobic soil conditions

(1) General problems

Problems similar to those in traditional upland rice cultivation also occur in aerobic culture. Since rice is directly sown on an unsaturated soil and grows aerobically, it is difficult to fully protect rice plants against pest damage and weed infestations. Early research with aerobic rice in the United States showed more blast disease (caused by Pyricularia grisea [Cooke] Sacc.) in center-pivot irrigated fields than in flooded fields (Westcott and Vines, 1986; McCauley, 1990). Fortunately, blast-resistant rice cultivars and strobilurin fungicides are now available to control the disease. Other diseases such as seedling blight (caused by Pseudomonas plantarrii) and foot rot (caused by Erwinia chrysanthemi pv. zeae) are also observed at higher levels on rice seedlings grown under aerobic conditions than under flooded conditions.

If we sow rice seeds at a shallow depth to promote germination and tillering, the risk of damage by rodents and birds increases sharply. Where these pests are a problem, the seeds should be treated with repellents. Damage by invertebrates such as armyworm larvae (Mythimna separata), root aphids (Tetranoea nigradomalialis), and mole crickets (Gryllotalpa orientalis Burmeister) is a major problem for crop establishment, as they attack the stem base and roots (Saito et al., 2006). During the vegetative stage, stem borers (Scirtophaga incertulas) become a more serious problem for rice plants under aerobic conditions than under flooded conditions, and varieties with thick stems (traditional upland rice varieties) seem to be more susceptible to these pests.

Nutrient availability is also a critical issue for growing rice under aerobic conditions. Problems include the immobilization of P in acidic soils (Kirk et al., 1998) and increased N leaching and volatilization (Ladha et al., 2005). In addition, rice plants are more likely to suffer deficiencies of micronutrients such as Fe (Fan et al., 2012), Mn (Kreye et al., 2009), and Zn (Gao et al., 2012) under aerobic conditions when the soil pH is higher than 6.0.

(2) Root growth response to aerobic soil conditions

In addition to the abovementioned problems, rice must take up sufficient amounts of water from the aerobic soil to sustain its transpirational demand. In developing an irrigation schedule suitable for aerobic rice culture, care must be taken to manage soil moisture so that rice plants do not suffer from internal water deficits. Judging from its stomatal response to internal water deficits, a range of soil water potential from −15 kPa to −25 kPa at a depth of 20 cm is the threshold for maintaining transpiration (Kato and Okami, 2010, 2011). The quite high threshold of soil water potential suggests that root water uptake is a limited ability to take up soil water under aerobic conditions. Accordingly, the ability of roots to function efficiently under aerobic conditions is important for the rice plant to survive under aerobic conditions, and is an important target in the development of varieties that are adapted to aerobic rice culture.

Water absorption by the root system can be divided into two main components: root hydraulic conductivity and uptake of water by the root, which is proportional to total root length or root surface area. These correspond approximately to two different aspects of the response to hydrological conditions: fine-tuning and coarse-tuning. Fine-tuning of root traits includes regulation of the hydraulic conductivity of cell membranes and anatomical changes in the root tissue, and these changes are, at least in part, reversible (Steudle and Peterson, 1998). Hydraulic conductivity of exodermal and endodermal cell membranes in the root tissue may also adjust to changes in the soil water regime (Maurel et al., 2010). Under soil water deficits, down-regulation of root hydraulic conductivity can be brought about by root anatomical changes, such as the development of Casparian bands and suberin lamellae that reduce the backflow of water from the plant to the soil (Aroca et al., 2012). Other changes in root anatomy, such as thickening of the cell walls and accelerated lignification of the endodermis, exodermis, and sclerenchyma, are also observed in rice plants grown in well-watered aerobic fields (Mostajeran and Rahimi-Eichi, 2008). The cell walls of rice roots might therefore be sensitive to even a slight reduction in soil moisture. Alternatively, rice may be quite sensitive to the higher mechanical impedance to root growth of aerobic soil compared with flooded soil, in which the friction between root and soil is very small.
Changes in assimilate partitioning under water limitation tend to favor the development of deep roots in rice (Gowda et al., 2011). In our previous research, the relationship between near-surface soil moisture, transpiration, and yield components was mediated by rooting depth in aerobic culture (Kato et al., 2009b; Kato and Okami, 2010), suggesting that genetic improvement aimed at deeper rooting would be an effective goal. This suggestion has recently been supported by performance evaluations of backcross-derived lines of ‘IR64’, a popular lowland-adapted tropical indica variety, which showed increased rooting depth in aerobic culture at lower irrigation intensities (Fujita et al., 2009; Kato et al., 2011).

(3) Response of leaf growth to aerobic soil conditions

Since good agricultural practices such as precise puddling, effective herbicide application, appropriate nursery management techniques, and appropriate fertilizer application have been developed for flooded rice, leaf expansion and the amount of radiation intercepted are no longer the primary yield constraints in conventional flooded rice culture (Ohsumi et al., 2012). However, in water-saving aerobic culture, it is still necessary to learn how to achieve stable and rapid leaf expansion and thereby provide high yield (Katsura et al., 2010; Okami et al., 2011; Okami et al., 2013). First, good crop establishment is necessary when farmers sow dry seeds. The cloddy soil should be fully broken by means of a few passes with rotary tillers and the field should be leveled using a cultipacker to facilitate seedling emergence from the dry soil. Crop establishment is often poor when the surface soil is too crusted or too loose. Breaking of hardpans by plows or subsoilers and appropriate compaction using equipment such as Cambridge rollers can promote upward migration of soil moisture and thereby accelerate germination and root anchorage, especially in loamy soils (e.g., Andosols). Needless to say, these soil conditions are favorable for weeds as well, so it is necessary to apply pre-emergence herbicides.

Leaf area index in the vegetative stage is more likely to be restricted in aerobic culture than in flooded culture as a result of frequent soil drying and the resulting dehydration stress (Sudhir-Yadav et al., 2011). Japonica and indica rice groups respond differently to soil moisture: tropical japonica cultivars are better adapted to aerobic culture than indica and temperate japonica cultivars (Okami et al., 2012). Selection for maximum yield potential during the breeding of irrigated rice, most of which is indica or temperate japonica, has promoted high photosynthetic capacity at the cost of the development of internal water deficits (Tomar and O’Toole, 1982). In contrast, traditional upland-adapted cultivars, most of which are tropical japonica types, tend to have sensitive stomatal responses to dehydration, which results in more effective prevention of water loss (O’Toole and Cruz, 1980). In addition, most

(Enstone et al., 2003). The rice root develops aerenchyma (air spaces formed by programmed cell death in the cortex layer to improve oxygen transport) to a lesser extent under aerobic conditions (Ghildyal and Tomar, 1982; Henry et al., 2012). However, the role of root porosity in root hydraulic conductivity under aerobic conditions remains to be examined (Yang et al., 2012).

Coarse-tuning of root traits results from changes in the root system architecture, including the emergence and elongation of adventitious roots, and lateral root branching. These changes are not reversible in the short term but have a larger impact on water uptake in the longer term. Water regime as well as soil type affect root growth under aerobic conditions: Ghildyal and Tomar (1982) reported that total root length was longer in rice plants grown in silty clay loams than in other soils. In field studies, we confirmed that the emergence of adventitious roots and branching of lateral roots are down-regulated under aerobic conditions (Kato and Okami, 2011). In aerobic culture, where the soil water potential at 20-cm depth averaged between –15 and –30 kPa, total root biomass was significantly lower than in flooded culture, due to a reduction in root biomass in the surface layer (Kato and Okami, 2010). The emergence of adventitious roots is up-regulated when rice plants are subjected to hypoxia, facilitated by the death of epidermal cells at the stem nodes that lie between root primordia and the surrounding soil (Mergemann and Sauter, 2000). On the other hand, lateral roots that are differentiated from the pericycle of adventitious roots must penetrate the outer cell layers, including the endodermis, exodermis, and sclerenchyma. Accordingly, the fine-tuning of root anatomy in response to aerobic or drought conditions described earlier in this section may impede the coarse-tuning of root traits, that is, the branching of lateral roots. Another possibility is that programmed cell death in outer root layers might facilitate lateral root emergence under hypoxia (e.g., flooded conditions).

A recent field experiment showed that the ability of rice to take up water in aerobic culture is lower than in flooded culture, and this is mostly attributable to significantly reduced total root length despite the effect of fine-tuning of root traits (Kato and Okami, 2011). Wide genetic diversity exists in the response of lateral root branching to soil moisture regimes (Kano-Nakata et al., 2011), which should provide a basis for genetic improvement of the water uptake ability of rice in aerobic culture.

Rice shows a shallower rooting pattern than most dryland crops. As an adaptation to the dry spells that occur between irrigation events in aerobic culture, rice plants must have vigorous deep root development. In fact, more of the assimilate allocated to the roots is allocated to deep roots (i.e., there is a higher deep-root ratio) in aerobic culture than in flooded culture (Kato and Okami, 2010).
tropical japonica cultivars adopt a dehydration avoidance strategy through the development of a vigorous root system (Lafitte et al., 2001). The ability of tropical japonica cultivars to maintain leaf expansion despite fluctuations in soil moisture can be partly attributed to their dehydration avoidance characteristics. Rice breeders have noticed these advantages of tropical japonica cultivars: the breeding strategies for aerobic rice in Brazil and at the International Rice Research Institute are based on intercrosses between high-yielding lowland indica and tropical japonica cultivars (Atlin et al., 2006; Pinheiro et al., 2006).

Apart from their different transpiration characteristics, tropical japonica cultivars have different development patterns from those of semi-dwarf, lowland-adapted indica cultivars (Okami et al., 2012). In general, tropical japonica cultivars have a larger tiller size and fewer tillers than indica cultivars (Peng et al., 2008). The “New Plant Type” lines (tropical japonica) and the indica variety ‘IR64’ differ in the plasticity of their shoot responses to aerobic conditions: leaves and tillers tend to become larger in New Plant Type lines, whereas they tend to be smaller and more numerous in ‘IR64’. In flooded culture, early vigor is highly correlated with tiller number (Yoshida and Parao, 1972). In contrast, the leaf area index during the vegetative stage was closely associated with plant height and tiller size in aerobic culture. In aerobic culture, leaf expansion was inhibited more in semi-dwarf types that produce a large number of tillers than in intermediate types that produce a small number of tillers (Okami et al., 2012). These results suggest that the ideotype for aerobic culture would differ from that for conventional flooded culture: the development of larger tillers and large, thick leaves rather than a larger tiller number would promote leaf expansion (Table 2).

5. Benefiting from aerobic adaptations in rainfed lowland rice

Our knowledge of aerobic rice culture also helps us to understand the yield constraints faced by rainfed lowland rice. In rainfed lowlands, rice plants experience water regime fluctuations during their life cycle, ranging from flash flooding and stagnation of semi-deep water to moderate drought. Especially on sandy soils in drought-prone areas such as northeastern Thailand and southern Laos, the standing water quickly disappears during dry spells; consequently, paddy fields turn from waterlogged to dry conditions or vice versa, depending on the rainfall patterns and topographic position (Fukai and Ouk, 2012). Aerobic conditions occur during the initial stage, when soil moisture is near field capacity but below the saturation level.

To explore these conditions, the research team of The University of Tokyo, Kyoto University and Tohoku University, Japan, and Ubon Ratchathani Rice Research Center, Thailand, began an aerobic cultivation trial in northeastern Thailand (Kato et al., 2013). In this study, rice seedlings were transplanted into puddled and flooded soils, but the field was drained soon after the seedlings had recovered from the transplanting shock and irrigated the soil whenever it dried. The yield decreased by 34% under aerobic conditions compared with that under flooded conditions during the first year. This was attributed mostly to reduced P uptake and lower biomass accumulation under aerobic conditions, as there was little difference in the harvest index, crop N concentration, and mid-day leaf water potential between the two trials. Crop N concentration increased sharply when we applied an adequate amount of N fertilizer under aerobic conditions. However, the crop P concentration (approx. 1.4 mg g⁻¹) did not change even when P fertilizer was applied under aerobic conditions. The N availability in the soil is often very low in the rainfed lowlands of northeastern Thailand, but rice plants can take up topdressed N even after the disappearance of standing water. These results suggest that the available P in the soil, which can quickly be mobilized under flooded conditions, might be less mobile in unsaturated sandy soil in northeastern Thailand, even though it is still extractable to some degree.

As found in aerobic rice studies in Japan, fine-root development in the topsoil layer was also inhibited under

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### Table 2. Characteristics of ideotype adapted to aerobic rice culture.

|                  | Brazil (1990 onward) | China (1984 onward) | IRRI, Philippines (early 2000s) | IRRI, Philippines (late 2000s) |
|------------------|----------------------|---------------------|-------------------------------|-------------------------------|
| Yield potential  | 6                    | 6 – 7               | 4 – 6                         | –                             |
| Plant posture    | 90 – 100 cm, 200 – 250 tillers m⁻², erect leaves | Less height than upland rice, erect leaves | Intermediate height, intermediate tiller number | Intermediate height (< 150 cm) |
| Other characters | Lodging resistance, moderate drought tolerance | Lodging resistance, drought tolerance | Early vigor, lodging resistance, moderate drought tolerance | Early vigor, lodging resistance, drought tolerance |
| Parental cross   | indica × japonica     | upland cv. × lowland cv. | indica × japonica              | aerobic cv. × indica, aerobic cv. × aerobic cv. |
| Citation         | Pinheiro et al. (2006) | Wang et al. (2002) | Atlin et al. (2006)            | Zhao et al. (2010)            |
aerobic conditions in the rainfed lowlands of northeastern Thailand (Kato et al., 2013). Reduced fine-root length is detrimental to P uptake in rainfed lowlands, where the available P for plants is less mobile in the soil (Kirk et al., 1998). Immobilization of soil P and inhibited branching of lateral roots due to the frequent disappearance of standing water in sandy soils may explain, at least in part, why rice yield did not respond to P application and why the N-use efficiency of fertilizer (the yield increase per unit applied N) is quite low in this region (Homma et al., 2007; Haeffle and Konboon, 2009). Unless we can find soil and crop management options that will counteract the negative effects of aerobic conditions on P uptake or can develop new varieties that can tolerate P deficiency, farmers will remain reluctant to increase fertilizer application rates because this will not guarantee improved yield. Even if aerobic culture itself is not a realistic solution for these farmers, repeated aerobic trials at local agricultural institutes may be able to reveal the main problems in these drought-prone rainfed lowlands.

6. Conclusions
Aerobic rice cultivation represents an attractive solution to water scarcities on agricultural land around the world. However, the physiological responses of rice to aerobic soil conditions remain poorly understood compared with the responses in flooded cultivation, and fewer rice varieties are suited to aerobic cultivation. Particular challenges involve the identification of the most suitable cultivars and most appropriate nutrient management options that can improve early vigor (leaf growth at the early stage) and sink–source balance for better grain growth. Unraveling the mechanisms that cause a different performance of rice on aerobic soils among various climatic conditions is also an important topic. Since the physical water scarcity will become more severe and ubiquitous under global climate change, more research is required for new water-saving technologies such as drip irrigation in order to curtail the irrigation cost in aerobic rice culture. High-yielding aerobic culture in the United States gives us some clues to the future direction in irrigated rice. Smart agriculture, such as automatic and centralized control of field management, would allow more labor-saving and resource-use efficient rice-based cropping systems on a large scale.

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References
Alberto, M.C.R., Wassmann, R., Hirano, T., Miyata, A., Kumar, A., Padre, A. and Amante, M. 2009. CO₂/heat fluxes in rice fields: comparative assessment of flooded and non-flooded fields in the Philippines. Agric. For. Meteorol. 149: 1737-1750.
Ando, T., Yamamoto, T., Shimizu, T., Ma, X., Shomura, A., Takeuchi, Y., Lin, S. and Yano, M. 2008. Genetic dissection and pyramiding of quantitative traits for panicle architecture by using chromosomal segment substitution lines in rice. Theor. Appl. Genet. 116: 881-890.
Aroca, R., Porcel, R. and Ruiz-Lozano, J.M. 2012. Regulation of root water uptake under abiotic stress conditions. J. Exp. Bot. 63: 43-57.
Atlin, G.N., Lafitte, H.R., Tao, D., Laza, M., Amante, M. and Courtois, B. 2006. Developing rice cultivars for high-fertility upland systems in the Asian tropics. Field Crops Res. 97: 43-52.
Beld, P., Bouman, B.A.M., Spieritz, J.H.J., Peng, S., Castañeda, A.R. and Visperas, R.M. 2005. Crop performance, nitrogen and water use in flooded and aerobic rice. Plant Soil 273: 167-182.
Boonjung, H. and Fukai, S. 1996. Effects of soil water deficit at different growth stages on rice growth and yield under upland conditions. 2. Phenology, biomass production and yield. Field Crops Res. 48: 47-55.
Bouman, B.A.M., Yang, X., Wang, H., Wang, Z., Zhao, J. and Chen, B. 2006. Performance of aerobic rice varieties under irrigated conditions in North China. Field Crops Res. 97: 53-65.
Bouman, B.A.M., Humphreys, E., Tsong, T.P. and Barker, R. 2007. Rice and water. Adv. Agron. 92: 187-237.
Breseghelli, F., Peixoto de Morais, O., Pinheiro, P.V., Silva, A.C.S., da Maia de Castro, E., Guimarães, E.P., Pereira de Castro, A., Pereira, J.A., de Matos Lopes, A., Utumi, M.M. and Pereira de Oliveira, J. 2011. Results of 25 years of upland rice breeding in Brazil. Crop Sci. 51: 914-923.
Chauhan, B.S., Mahajany, G., Sardanay, V., Timsina, J. and Jat, M.L. 2012. Productivity and sustainability of the rice-wheat cropping system in the Indo-Gangetic plains of the Indian subcontinent: problems, opportunities, and strategies. Adv. Agron. 117: 315-369.
Clerget, B. and Bueno, C. 2012. The effect of aerobic soil conditions, soil volume and sowing date on the development of four tropical rice varieties grown in the greenhouse. Funct. Plant Biol. 40: 79-88.
Cruz, R.T. and O’Toole, J.C. 1984. Dryland rice response to an irrigation gradient at flowering stage. Agron. J. 76: 178-183.
Enstone, D.E., Peterson, C.A. and Ma, F. 2003. Root endodermis and exodermis structure, function, and responses to the environment. J. Plant Growth Regul. 21: 335-351.
Fan, X., Karim, M.R., Chen, X., Zhang, Y., Gao, X., Zhang, F. and Zou, C. 2012. Growth and iron uptake of lowland and aerobic rice genotypes under flooded and aerobic cultivation. Commun. Soil Sci. Plant Anal. 43: 1811-1822.
FAO. 2009. How to feed the world in 2050. www.fao.org/fileadmin/templates/wsfs/docs/expert_paper/How_to_Feed_the_World_in_2050.pdf
Fischer, R.A. and Edmeades, G.O. 2010. Breeding and cereal yield progress. Crop Sci. 50: S85-S98.
Fujita, D., Santos, R.E., Ebron, L.A., Yanoria, M.J., Kato, H., Kobayashi, S., Uga, Y., Araki, E., Takai, T., Tsumatsuru, H., Imbe, T., Khush, G.S., Brat, D.S., Fukuta, Y. and Kobayashi, N. 2009. Development of introgression lines of an indica–type rice variety, IR64, for unique agronomic traits and detection of the responsible chromosomal regions. Field Crops Res. 114: 244-254.

Fukai, S. and Ouk, M. 2012. Increased productivity of rainfed lowland rice cropping systems of the Mekong region. Crop Pasture Sci. 63: 944-973.

Fukuoka, M., Yoshimoto, M. and Hasegawa, T. 2012. Varietal range in transpiration conductance of flowering rice panicle and its impact on panicle temperature. Plant Prod. Sci. 15: 258-264.

Gao, X., Hoffland, E., Stomph, T.J., Grant, C.A., Zou, C. and Zhang, F. 2012. Improving zinc bioavailability in transition from flooded to aerobic rice. A review. Agron. Sustain. Dev. 32: 460-478.

George, T., Magbanua, R., Garrity, D.P., Tuba, Angkana, S., and Quiton, J., 2002. Rapid yield loss of rice cropped successively in aerobic soil. Agron. J. 94: 981-989.

Ghildyal, B.P. and Tomar, V.S. 1982. Soil physical properties that affect rice root systems under drought. In O’Toule, J.C. ed., Drought Resistance in Crops with Emphasis on Rice. International Rice Research Institute, Los Baños, Philippines. 83-96.

Gowda, V.R.P., Henry, A., Yamauchi, A., Shashidhar, H.E. and Serraj, R. 2011. Root biology and genetic improvement for drought avoidance in rice. Field Crops Res. 122: 1-13.

Hacefele, S.M. and Konboon, Y. 2009. Nutrient management for rainfed lowland rice in northeast Thailand. Field Crops Res. 114: 374-385.

Hasegawa, S. and Nakayama, K. 1959. Comparison of the growth and yield of paddy and upland rice grown under paddy and upland field conditions. Jpn. J. Crop Sci. 27: 354-365.

Hayashi, S., Ohshita, Y., Kimiwada, K., Tsuji, H., Ushiki, J., Miyaura, S. and Shibuya, Y. 2012. Yielding performance of “Kitaoaoha”, high-yielding rice variety for Hokkaido region, northern Japan. Plant Prod. Sci. 15: 209-215.

Henry, A., Cal, A.J., Batoto, T.C., Torres, R.O. and Serraj, R. 2012. Root attributes affecting water uptake of rice (Oryza sativa) under drought. J. Exp. Bot. 63: 4751-4763.

Hirasawa, H., Nemoto, K., Sugahara, R., Ishihara, M., Hirayama, M., Okamoto, K. and Miyamoto, M. 1998. Breeding of a new upland rice variety “Yaménohatamochi” with high drought resistance and good eating quality. Breed. Sci. 48: 415-419**.

Homma, K., Horie, T., Shiraiba, T. and Supapoj, N. 2007. Evaluation of transplanting date and nitrogen fertilizer rate adapted by farmers to toposequential variation of environmental resources in a mini-watershed (Nong) in northeast Thailand. Plant Prod. Sci. 10: 488-496.

Horie, T., Ohnishi, M., Angus, J.F., Lewin, L.G., Tsukaguchi, T. and Matano, T. 1997. Physiological characteristics of high-yielding rice inferred from cross-location experiments. Field Crops Res. 52: 55-67.

Humphreys, E., Kulak, S.S., Christen, E.W., Hira, G.S., Balwinder-Singh, Sudhir-Yadav and Sharma, R.K. 2010. Halting the groundwater decline in west–north India–Which crop technologies will be winners? Adv. Agron. 109: 155-217.

IRRI. 2002. Rice Almanac. 3rd edition. International Rice Research Institute, Los Baños, Philippines. 181.

Ishimaru, T., Hirabayashi, H., Kuwagata, T., Ogawa, T. and Kondo, M. 2012. The early-morning flowering trait of rice reduces spikelet sterility under windy and elevated temperature conditions at anthesis. Plant Prod. Sci. 15: 19-22.

Kano-Nakata, M., Inukai, Y., Wade, L.J., Siopongo, J.D.L.C. and Yamauchi, A. 2011. Root development, water uptake, and shoot dry matter production under water deficit conditions in two CSSL of rice: Functional roles of root plasticity. Plant Prod. Sci. 14: 307-317.

Kato, Y., Kamoshita, A. and Yamagishi, J. 2008. Preflowering abortion reduces spikelet number in upland rice (Oryza sativa L.) under water stress. Crop Sci. 48: 2389-2395.

Kato, Y., Nemoto, K. and Yamagishi, J. 2009a. QTL analysis of panicle morphology response to irrigation regime in aerobic rice culture. Field Crops Res. 114: 295-303.

Kato, Y., Okami, M. and Katsura, K. 2009b. Yield potential and water use efficiency of aerobic rice (Oryza sativa L.) in Japan. Field Crops Res. 113: 328-334.

Kato, Y. and Katsura, K. 2010. Panicle architecture and grain number in irrigated rice, grown under different water management regimes. Field Crops Res. 117: 297-304.

Kato, Y. and Okami, M. 2010. Root growth dynamics and stomatal behaviour of rice (Oryza sativa L.) grown under aerobic and flooded conditions. Field Crops Res. 117: 917.

Kato, Y., Henry, A., Fujita, D., Katsura, K., Kobayashi, N. and Serraj, R. 2011. Physiological characterization of introgression lines derived from an indica rice cultivar, IR64, adapted to drought and water-saving irrigation. Field Crops Res. 123: 130-138.

Kato, Y. and Okami, M. 2011. Root morphology, hydraulic conductivity and plant water relations of high-yielding rice grown under aerobic conditions. Ann. Bot. 108: 575-583.

Kato, Y., Tajima, R., Homma, K., Toriumi, A., Yamagishi, J., Shiraiba, T., Mewatanakam, P. and Jongdee, B. 2013. Root growth response of rainfed lowland rice to aerobic conditions in northeastern Thailand. Plant Soil 368: 557-567.

Katsura, K., Maeda, S., Lubis, I., Horie, T., Gao, W. and Shiraiba, T. 2008. The high yield of irrigated rice in Yunnan, China: ‘a cross-location analysis’. Field Crops Res. 107: 1-11.

Katsura, K., Okami, M., Mizumura, H. and Kato, Y. 2010. Radiation-use efficiency, N accumulation and biomass production of high-yielding rice in aerobic culture. Field Crops Res. 117: 81-89.

Katsura, K. and Nakaide, Y. 2011. Factors that determine grain weight in rice under high-yielding aerobic culture: the importance of husk size. Field Crops Res. 123: 266-272.

Katsura, K. 2013. Agronomic traits for high productivity of rice grown in aerobic culture in progeny of a japonica cultivar and a high-yielding indica cultivar. Plant Prod. Sci. 16: 317-324.

Kirk, G.J.D., George, T., Courtot, B. and Senadhira, D. 1998. Opportunities to improve phosphorus efficiency and soil fertility in rainfed lowland and upland rice ecosystems. Field Crops Res. 56: 73-92.

Kreye, C., Bouman, B.A.M., Castañeda, A., Lampayan, R.M., Faronilo, J.E., Lactaoen, A.T. and Fernandez, L. 2009. Possible causes of yield failure in tropical aerobic rice. Field Crops Res. 114: 73-92.

Kumar, V. and Ladha, J.K. 2011. Direct seeding of rice: recent developments and future research needs. Adv. Agron. 111: 297-413.

Ladha, J.K., Pathak, H., Krupnik, T.J., Six, J. and van Kessel, C. 2005.
Efficiency of fertilizer nitrogen in cereal production: retrospects and prospects. *Adv. Agron.* 87: 85-156.

Lafitte, H.R., Champoux, M.C., McLaren, G. and O’Toole, J.C. 2001. Rice root morphological traits are related to isozyme group and adaptation. *Field Crops Res.* 71: 57-70.

Matsunami, M., Matsunami, T. and Kokubun, M. 2009. Growth and yield of new rice for Africa (NERICAs) under different ecosystems and nitrogen levels. *Plant Prod. Sci.* 12: 381-389.

Matsunami, M., Matsunami, T., Ogawa, A., Toyofuku, K., Kodama, I. and Kokubun, M. 2012. Genotypic variation in biomass production at the early vegetative stage among rice cultivars subjected to deficient soil moisture regimes and its association with water uptake capacity. *Plant Prod. Sci.* 15: 82-91.

Mostajeran, A. and Rahimi–Eichi, V. 2008. Drought stress effects on root anatomical characteristics of rice cultivars. *Pakistan J. Biol. Sci.* 11: 2173-2183.

Nie, L., Peng, S., Chen, M., Shah, F., Huang, J., Cui, K. and Xiang, J. 2012. Aerobic rice for water-saving agriculture: a review. *Agron. Sustain. Dev.* 32: 411-418.

Ohse, M., Okita, N. and Daimon, H. 2010. Effects of deep-flooding irrigation on growth, canopy structure and panicle yield under different planting patterns in rice. *Plant Prod. Sci.* 13: 193-198.

Ohsumi, A., Furuhata, M. and Matsumura, O. 2012. Varietal differences in biomass production of rice early after transplanting at low temperatures. *Plant Prod. Sci.* 15: 32-39.

Okami, M., Kato, Y. and Yamagishi, J. 2011. Role of early vigor in adaptation of rice to water–saving aerobic culture: effects of nitrogen utilization and leaf growth. *Field Crops Res.* 124: 124-131.

Okami, M., Kato, Y. and Yamagishi, J. 2012. Allometric relationship between the size and number of shoots as a determinant of adaptations in rice to water-saving aerobic culture. *Field Crops Res.* 131: 17-25.

Okami, M., Kato, Y. and Yamagishi, J. 2013. Grain yield and leaf area growth of direct-seeded rice on flooded and aerobic soils in Japan. *Plant Prod. Sci.* 16: 276-279.

O’Toole, J.C. and Cruz, R.T. 1980. Response of leaf water potential, stomatal resistance, and leaf rolling to water stress. *Plant Physiol.* 65: 428-432.

Peng, S., Bouman, B.A.M., Visperas, R.M., Castañeda, A., Nie, L. and Park, H. 2006. Comparison between aerobic and flooded rice in the tropics: agronomic performance in an eight-season experiment. *Field Crops Res.* 96: 252-259.

Peng, S., Khush, G.S., Virk, P., Tang, Q. and Zou, Y. 2008. Progress in ideotype breeding to increase rice yield potential. *Field Crops Res.* 108: 32-38.

Pinheiro, B., Castro, E. and Guimarães, C.M. 2006. Sustainability and profitability of aerobic rice production in Brazil. *Field Crops Res.* 97: 34-42.

Prasad, R. 2011. Aerobic rice systems. *Adv. Agron.* 111: 207-247.

Ramasamy, S., ten Berge, H.F.M. and Purushothaman, S. 1997. Yield formation in rice in response to drainage and nitrogen application. *Field Crops Res.* 51: 65-82.

Saito, K., Linquist, B., Keobualapha, B., Phanthaboon, K., Shi, Y., Shen, Q., Mao, Z. and Li, W. 2001. Biological response of rice cultivated on upland soil condition and the effect of mulching on it. *Plant Nutr. Fert. Sci.* 7: 271-277.

Sinclair, T.R. and Muchow, R.C. 1999. Radiation use efficiency. *Adv. Agron.* 65: 215-265.

Steudle, E. and Peterson, C.A. 1998. How does water get through roots? *J. Exp. Bot.* 49: 775-788.

Stevens, G., Vories, E., Heiser, J. and Rhine, M. 2012. Experimentation on cultivation of rice irrigated with a center pivot system. *In T.S. Lee ed., Irrigation systems and practices in challenging environments.* InTech. 233-254. Available at www.intechopen.com/books/irrigation-systems-and-practices-in-challenging-environments/experimentation-on-cultivation-of-rice-irrigated-with-a-center-pivot-system

Sudhir-Yadav, Gill, G., Humphreys, E., Kukal, S.S. and Waila, U.S., 2011. Effect of water management on dry seeded and puddled transplanted rice. Part I: Crop performance. *Field Crops Res.* 120: 112-122.

Swarno, Lubis, E. and Kustiano, B. 2009. Progress of upland rice breeding in Indonesia since 1991. In M. Hossain, J. Bennett, D. Mackill, B. Hardy, eds., Progress in Crop Improvement Research. Limited Proceedings No. 14. International Rice Research Institute, Los Baños, Philippines. 98-105.

Tomar, V.S. and O’Toole, J.C. 1982. A field study on leaf water potential, transpiration and plant resistance to water flow in rice. *Crop Sci.* 22: 5-10.

Toriyama, K. and Ando, H. 2011. Towards an understanding of the high productivity of rice with System of Rice Intensification (SRI) management from the perspectives of soil and plant physiological processes. *Soil Sci. Plant Nutr.* 57: 636-649.

Tsuno, Y., Yamaguchi, T. and Ushimi, T. 1990. Relationship between the grain weight and ammonium concentration in the rice grain of restrained ripening. *Jpn. J Crop Sci.* 59: 481-485.
Agric. 29: 51-60.
Vories, E.D., Tacker, P.L. and Hogan, R. 2005. Multiple inlet approach to reduce water requirements for rice production. *Appl. Eng. Agric.* 21: 611-616.

Wang, H., Bouman, B.A.M., Zhao, D., Wang, C.G. and Moya, P.F. 2002. Aerobic rice in northern China: opportunities and challenges. *In B.A.M. Bouman, H. Hengsdijk, B. Hardy, P.S. Bindraban, T.P. Tuong, J.K. Ladha eds., Water–wise rice production.* International Rice Research Institute, Los Baños, Philippines. 143-154.

Westcott, M.P. and Vines, K.W. 1986. A comparison of sprinkler and flood irrigation for rice. *Agron. J.* 78: 637-640.

Yamaguchi, T., Tsuno, Y., Nakano, J. and Miki, K. 1995. Influence of leaf nitrogen content on grain weight at early ripening period and relationship between root respiration and leaf area per spikelet of rice plant. *Jpn. J. Crop Sci.* 64: 251-258*.

Yang, C., Yang, L., Yang, Y. and Ouyang, Z. 2004. Rice root growth and nutrient uptake as influenced by organic manure in continuously and alternately flooded paddy soils. *Agric. Water Manage.* 70: 67-81.

Yang, X., Li, Y., Ren, B., Ding, L., Gao, C., Shen, Q. and Guo, S. 2012. Drought-induced root aerenchyma formation restricts water uptake in rice seedlings supplied with nitrate. *Plant Cell Physiol.* 53: 495-504.

Ying, J., Peng, S., He, Q., Yang, H., Yang, C., Visperas, R.M. and Cassman, K.G. 1998. Comparison of high-yield rice in tropical and subtropical environments: I. Determinants of grain and dry matter yields. *Field Crops Res.* 57: 71-84.

Yoshida, S. and Parao, F.T. 1972. Performance of improved rice varieties in the tropics with special reference to tillering capacity. *Exp. Agric.* 8: 203-212.

Yoshinaga, S., Takai, T., Arai-Sanoh, Y., Ishimaru, T. and Kondo, M. 2013. Varietal differences in sink production and grain-filling ability in recently developed high-yielding rice (*Oryza sativa* L.) varieties in Japan. *Field Crops Res.* 150: 74-82.

Yun, S.I., Wada, Y., Maeda, T., Miura, K., Watanabe, K. 1997. Growth and yield of japonica × indica hybrid cultivars under direct seeding and upland cultivation conditions. *Jpn. J. Crop Sci.* 66: 386-393*.

Zhao, D.L., Atlin, G.N., Amante, M., Cruz, M.T.S. and Kumar, A. 2010. Developing aerobic rice cultivars for water–short irrigated and drought–prone rainfed areas in the tropics. *Crop Sci.* 50: 2268-2276.

* In Japanese with English abstract.
** In Japanese.
*** In Chinese.