



Role of early vigor in adaptation of rice to water-saving aerobic culture: Effects of nitrogen utilization and leaf growth

Midori Okami, Yoichiro Kato, Junko Yamagishi*

Institute for Sustainable Agro-ecosystem Services, The University of Tokyo, 1-1-1 Midori-cho, Nishitokyo, Tokyo 188-0002, Japan

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ABSTRACT

Early vigor and rapid canopy development are important characteristics in aerobic rice culture, where they are highly susceptible to soil water deficits. To elucidate the response of rice's vegetative growth to water management regimes, we evaluated the leaf growth and the concomitant nitrogen (N) utilization of nine cultivars grown in flooded and aerobic culture in 2 years. In aerobic culture, the soil water potential at a depth of 20 cm frequently reached -60 kPa in 2007, but remained above -30 kPa in 2008. The average leaf area index (LAI) in the middle of the vegetative growth stage, N uptake and leaf N content per unit leaf area (specific leaf N; SLN) in aerobic culture were comparable to those in flooded culture. However, there was a significant cultivar \times water regime interaction in LAI: cultivars with higher LAI during the vegetative growth stage achieved higher yield in aerobic rice culture. IR72 and Takanari (high-yielding cultivars of flood-irrigated rice) showed poor leaf growth as well as lower N uptake and higher SLN in aerobic culture compared with flooded culture. Our results show that early vigor is closely associated with yield stability to the soil moisture fluctuations in aerobic rice culture, even if weeds are properly controlled. Greater N uptake from aerobic soil and better balancing between the N demand for leaf growth and the N supply to the leaves under fluctuating soil moisture would be, at least in part, relevant to a rice cultivar's adaptation to aerobic conditions.

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1. Introduction

Rice (*Oryza sativa* L.) culture consumes 30% of the world's developed freshwater resources (Bouman et al., 2007). However, increasing water scarcity in agriculture, caused by competition for water from urbanization and industrialization, threatens the sustainability of irrigated rice culture (Peng et al., 2009; Humphreys et al., 2010). To alleviate the problem of water shortages, several alternatives to conventional irrigation have been proposed. Among them, aerobic rice culture is one of the most promising alternative managements, since rice plants are grown in non-puddled and non-saturated soils, thereby reducing irrigation requirements (Tuong et al., 2005). Aerobic culture can reduce water requirements by 50–70% compared with conventional flooded culture (Bouman et al., 2007) and is highly productive when used with high-yielding cultivars (George et al., 2002; Kato et al., 2009; Sudhir-Yadav et al., 2011). However, previous studies often reported a significant reduction in rice yield in aerobic culture compared with flooded culture even when soil was maintained near field capacity (Belder et al., 2005; Peng et al., 2006). Therefore, successful establishment of aerobic rice culture as a water-saving technology will require the

development of new cultivars that are adapted to aerobic soils and occasional soil water deficits (Atlin et al., 2006).

Grain yield is determined by a combination of radiation capture, radiation-use efficiency, and harvest index. For radiation capture, early vigor (early leaf growth during tillering stage; Laza et al., 2001) is the most important growth characteristic in annual crops when water is not limiting (Passioura, 2006). This is because crop biomass accumulation during the vegetative stage is proportional to the cumulative radiation that is intercepted (Monteith, 1977; Horie and Sakuratani, 1985). The importance of early vigor in aerobic rice culture has also been emphasized in terms of the crop's ability to outcompete weeds (Dingkuhn et al., 1999; Zhao et al., 2006a,b, 2007). In rice, early vigor is attributable mostly to a high leaf area index (LAI) during vegetative stage, which has a significant cultivar \times water regime interaction (Dingkuhn et al., 1999; Kato et al., 2006; Zhao et al., 2007; Matsuo and Mochizuki, 2009). Cultivars that are suitable for use in aerobic rice culture would therefore exhibit superior early leaf growth so that they could capture incident radiation efficiently under aerobic conditions (Kato et al., 2006; Katsura et al., 2010).

Leaf expansion is closely linked to nitrogen (N) uptake and plant N status during the vegetative growth stage (Sinclair and Muchow, 1995). In the absence of N stress, 60–80% of the aboveground N is partitioned to the leaf blades during vegetative stage in grain crops (Lemaire et al., 2007; Hammer et al., 2010; van Oosterom et al.,

* Corresponding author. Tel.: +81 42 463 1611; fax: +81 42 464 4391.
E-mail address: ajunya@mail.ecc.u-tokyo.ac.jp (J. Yamagishi).

2010). However, the ratio of leaf N content to total N content and leaf N content per unit leaf area (specific leaf N; SLN) depend on the rice cultivars that are used and on crop management characteristics (Dingkuhn et al., 1990; Schnier et al., 1990; Borrell et al., 1998; Johnson et al., 1998). LAI is more likely to be restricted in aerobic culture than in flooded culture as a result of frequent soil drying (Belder et al., 2005; Matsuo and Mochizuki, 2009; Sudhir-Yadav et al., 2011). The response of rice LAI to hydrological conditions would also be accompanied with the changes in plant N uptake, the proportion of N partitioned to the leaves and SLN.

Comparative studies of vegetative growth under the two water management regimes will improve our understanding of how rice adapts to aerobic soil conditions. Hence, the objective of the present study was to test whether early vigor can improve grain yield of rice in water-saving aerobic culture, and whether there is any relationship between early vigor and SLN.

2. Materials and methods

2.1. Experimental design

Details of the soil properties, crop management and climatic data are reported in Kato et al. (2009). Briefly, the field experiments were conducted at the Institute for Sustainable Agro-ecosystem Services of the University of Tokyo, Japan (35°43'N, 139°32'E), during the summers (May–October) of 2007 and 2008. The soil at the experimental site is a clay loam (Typic Melanudand). The mean maximum and minimum temperatures from sowing to anthesis were 30.0 °C and 20.3 °C in 2007, respectively, and were 29.2 °C and 20.1 °C in 2008, respectively. In aerobic culture, the field was not puddled, and the rice seeds were sown directly in the soil. The total amount of water supplied (sprinkler irrigation plus rainfall) in the aerobic culture was 749–912 mm in 2007 and 1206–1347 mm in 2008, depending on growth duration of rice cultivars. The soil water potential at a depth of 20 cm frequently reached –60 kPa during the vegetative growth stage in 2007, but remained near field capacity (above –30 kPa) during the vegetative growth stage in 2008 (see Fig. 1 in Kato et al., 2009). In flooded culture, the field was puddled and kept flooded after transplanting.

We grew nine improved cultivars, including upland- and lowland-adapted types, in 2007, and six in 2008 (Table 1). The cultivars were arranged in a randomized complete-block design with three replicates in each trial. Each plot consisted of four to ten 5.4-m rows (row spacing of 30 cm). The sowing date in 2007 was 9 May

sowing in both trials (total N = 180 kg ha⁻¹). Weeds were controlled by means of hand weeding and herbicide application.

2.2. Measurements

After counting the number of stems, we harvested eight plants from each plot in the middle of the vegetative growth stage (60 days after sowing in 2007 and 66–67 days after sowing in 2008) and at anthesis, and selected two to four plants as a sub-sample; the others were used as a bulk sample. Sub-samples were separated into green leaf blades, dead leaf blades, leaf sheaths + culms (if any), and panicles (if any). Green leaf area in the sub-samples was determined using a leaf area meter (LI-3100, LI-COR, Lincoln, NE, USA). Samples were oven-dried at 80 °C for at least 72 h to determine dry weights. The dried sub-samples were ground with an automated mill (Heiko Sample Mill TI-300, Heiko Seisakusyo Ltd., Tokyo, Japan), and the N concentration was analyzed with an NC analyzer (Sumigraph NC-90A, Sumika Chemical Analysis Service, Tokyo, Japan). The LAI and the N content of each organ were then calculated. The N content of dead leaf blades was added as part of aboveground N content, and no material loss was considered. The proportion of the N partitioned to the leaves (g g⁻¹) and SLN (g m⁻²) were calculated as follows:

Proportion of N partitioned to leaves

$$= \frac{\text{green leaf blades N content}}{\text{total aboveground N content}} \quad (1)$$

$$\text{SLN} = \frac{\text{green leaf blades N content}}{\text{LAI}} \quad (2)$$

The N content of individual shoots (mg shoot⁻¹) was calculated from the aboveground N content and the number of stems. Because of the difference in days to anthesis among cultivars and water regimes (Table 1), we calculated the growth rate from the middle of the vegetative stage (first sampling date) to anthesis instead of comparing leaf area and N content at anthesis. A previous study demonstrated that crops grow at an almost constant rate from mid-vegetative stage to reproductive stage and the growth rate rather than the relative growth rate better fits the case of linear growth phase (Goudriaan and Monteith, 1990). We calculated the leaf growth rate (m² m⁻² day⁻¹), aboveground N uptake rate (g m⁻² day⁻¹), proportion of N partitioned to the leaves (g g⁻¹), and increase in N per unit leaf area (g m⁻²) as follows:

$$\text{Leaf growth rate} = \frac{(\text{LAI at } t_2) - (\text{LAI at } t_1)}{t_2 - t_1} \quad (3)$$

$$\text{Aboveground N uptake rate} = \frac{(\text{total aboveground N content at } t_2) - (\text{total aboveground N content at } t_1)}{t_2 - t_1} \quad (4)$$

$$\text{Proportion of N partitioned to leaves} = \frac{(\text{green leaf blades N content at } t_2) - (\text{green leaf blades N content at } t_1)}{(\text{total aboveground N content at } t_2) - (\text{total aboveground N content at } t_1)} \quad (5)$$

$$\text{Increase in N per unit leaf area} = \frac{(\text{green leaf blades N content at } t_2) - (\text{green leaf blades N content at } t_1)}{(\text{LAI at } t_2) - (\text{LAI at } t_1)} \quad (6)$$

for aerobic culture and 10 May for flooded culture; in 2008, the corresponding dates were 7 and 8 May. In aerobic culture, four to five seeds were sown in each hill at a density of 22.2 hills m⁻², and plants were thinned to one plant per hill immediately after emergence. In flooded culture, seeds were sown in nursery trays, and one 25-day-old seedling was transplanted into each hill, at the same density as in aerobic culture. We applied an inorganic fertilizer (N, P, K = 60, 39, 67 kg ha⁻¹, respectively) before sowing, and top-dressed ammonium sulfate (N = 30 kg ha⁻¹) at 6, 10, 13, and 16 weeks after

where t_1 was the date in the middle of the vegetative stage (first sampling date) and t_2 was the date at anthesis. At maturity, we harvested 24 plants from each plot, and determined the grain yield (standardized for a 0% grain moisture content) and aboveground biomass (oven-dry weight).

2.3. Data analysis

Data were analyzed using the generalized linear model (GLM) procedure (SAS Institute, 2003). Analysis of variance (ANOVA) was performed separately for each trial in each year according to the

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