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[Short Report]

Varietal Differences in Photosynthetic Rates in Rice Plants, with Special Reference to the Nitrogen Content of Leaves

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Abstract: The photosynthetic rate in the flag leaf of rice at the full heading stage was examined in three japonica varieties, Koshihikari, Aikoku and Asanohikari, and the indica high-yielding variety Takanari at the same level of leaf nitrogen. At an ambient CO₂ concentration of 350 μL L⁻¹, Takanari had a higher photosynthetic rate and stomatal conductance than the japonica varieties when plants were compared at a leaf nitrogen content of approximately 1.5 g m⁻². Stomatal conductance increased considerably with increases in leaf nitrogen content in the japonica varieties. As a result, at a leaf nitrogen content of approximately 2.0 g m⁻², differences in terms of the photosynthetic rate among varieties were small. By contrast, there were no clear varietal differences in Rubisco content at any identical nitrogen content of leaves. We conclude that stomatal conductance is responsible for the varietal differences in photosynthetic rate examined at the same leaf nitrogen content.

Key words: Nitrogen content, Photosynthetic rate, Rice variety, Rubisco content, Stomatal conductance.

The increase in leaf photosynthetic rate is important to increase the yield potential of rice (Long, 2006) because the photosynthetic rate of individual leaves, which form the canopy, affect dry matter production via photosynthesis within the canopy. There are several reports comparing photosynthetic rate among individual leaves (Ishii, 1995; Agarie, 2003), among japonica varieties (Murata, 1961; Osada, 1966; Hayami, 1982; Kuroda and Kumura 1990a; Sasaki and Ishii, 1992), and among indica and japonica varieties and other species of *Oryza* (Takano and Tsunoda, 1971; Cho and Murata, 1980; Cook and Evans, 1983; Xu et al., 1997; Masumoto et al., 2004), and some clear differences have been observed among varieties, among species and among progenies derived from crosses between species. However, the photosynthetic rate is strongly influenced by the leaf nitrogen level (Tsuno and Shimizu, 1965; Ishihara et al., 1979; Makino et al., 1988). It is significantly affected by stomatal conductance (Ishihara and Saito, 1987; Hirasawa et al., 1988), and Rubisco content of the leaf (Makino et al., 1987), which are greatly affected by leaf nitrogen content (Ishihara et al., 1979; Makino et al., 1988). The size of plants, the amount of nitrogen accumulated and the partitioning of nitrogen all affect the levels of leaf nitrogen. Although there are several reports showing the varietal difference in the photosynthetic rate at an ambient CO₂ concentration, little attention has been

paid to the effects of nitrogen on the varietal difference in the photosynthetic rate (Ishii, 1995), and the effects of stomatal and non-stomatal factors on the varietal difference in the photosynthetic rate. These nitrogen effects have made it difficult to clarify the actual status of the varietal difference in the photosynthetic rate, which is important for improving the photosynthetic rate in rice breeding.

The rate of photosynthetic evolution of oxygen has been reported to be higher in the certain japonica×indica varieties than in japonica varieties at the same level of leaf nitrogen (Cho and Murata, 1980). By contrast, Makino et al. (1987) observed that differences in K_m (CO₂) and V_{max} in the carboxylase reaction of Rubisco and its protein ratio to total soluble protein were very small among cultivars including japonica, indica, japonica × indica and javanica types. The varietal difference in the specific activity of Rubisco was estimated to be very small (Saka, 1985). To our knowledge, the varietal difference in the photosynthetic rate has not been clarified under identical levels of leaf nitrogen.

We reported previously that the photosynthetic rate in an indica high-yielding variety, Takanari, was significantly higher at the heading stage through ripening than that in older and newer japonica varieties (Ozawa et al., 2004; Taylaran et al., 2007), as reported by Xu et al. (1997) and

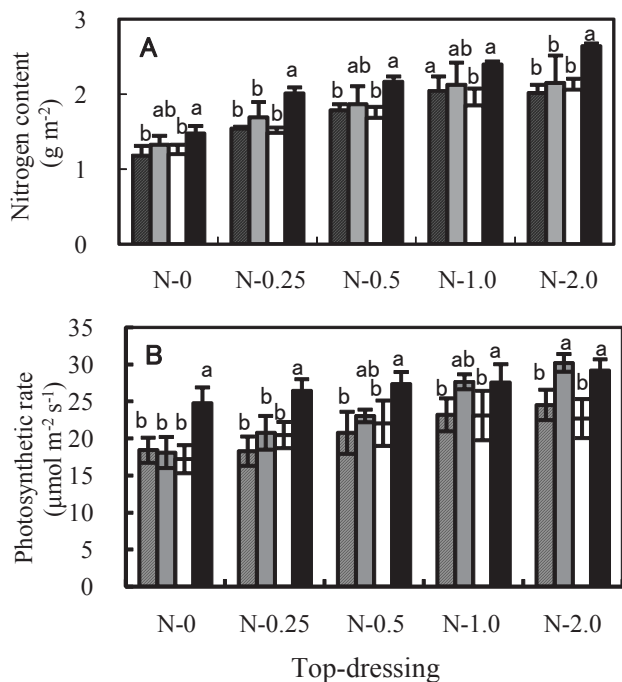


Fig. 1. The leaf nitrogen content (A) and photosynthetic rate at an ambient CO₂ concentration of 350 μL L⁻¹ (B) for flag leaves of rice plants that were top-dressed at rates of 0 (N-0), 0.25 (N-0.25), 0.5 (N-0.5), 1.0 (N-1.0) and 2.0 (N-2.0) g of nitrogen at the booting stage as described in the text. Hatched, grey, white and black bars represent Koshihikari, Aikoku, Asanohikari and Takanari, respectively. Measurements were made at the full heading stage. Vertical bars represent standard deviations (n=4). Identical letters indicate the absence of a significant difference at the 5% level (Tukey-Kramer's test).

Ohsumi et al. (2007). In the present study, we examined the differences in the photosynthetic rate in flag leaves among the selected varieties of rice examined previously (Ozawa et al., 2004; Taylaran et al., 2007) at the full heading stage at identical levels of leaf nitrogen by changing the rate of nitrogen top-dressing, and we investigated the reasons for these differences.

Materials and Methods

We grew one indica variety, Takanari, and three japonica varieties, Asanohikari, Koshihikari and Aikoku, of rice (*Oryza sativa* L.) in 1/2000 a pots that had been filled with a mixture (1:1, v/v) of alluvial soil from the Tama River and Kanto diluvial soil. We transplanted seedlings at the sixth-leaf expanding stage at a rate of four plants per hill and three hills per pot and applied fertilizer at a rate of 0.5, 1.0 and 1.0 g per pot for N, P₂O₅ and K₂O, respectively, as a basal dressing. Nitrogen was top-dressed at a rate of 0, 0.25, 0.5, 1.0 and 2.0 g as ammonium sulfate, in order to be varied levels of leaf nitrogen, at the booting stage (approximately 10 d prior to measurements). Each nitrogen top-dressing treatment included four pots (one pot per replicate) for all varieties. After transplanting, plants were

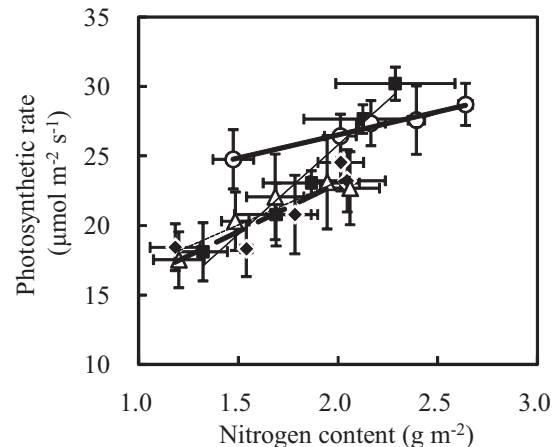


Fig. 2. Relationships between leaf nitrogen content and the photosynthetic rate at an ambient CO₂ concentration of 350 μL L⁻¹ in flag leaves of rice plants. Diamonds, squares, triangles and circles represent Koshihikari, Aikoku, Asanohikari and Takanari, respectively, in this figure and Figs. 3, 4. Regressions represented by thick broken, thin solid, thin broken and thick solid lines are for Koshihikari, Aikoku, Asanohikari and Takanari, respectively, in this Figure and Figure 3. Vertical and horizontal bars represent standard deviations (n=4), in this figure and Figs. 3, 4.

grown outdoors until the measurements were made.

Photosynthetic rate and stomatal conductance were measured with a portable gas-exchange system (LI-6400; LI-COR, Lincoln, NE) on flag leaves on the main stem, in the morning from 0800 to 1100 at the full heading stage. Stomatal conductance was calculated by the method described by von Caemmerer and Farquhar (1981). The quantum flux density at the leaf surface, the leaf temperature and the difference in vapor pressure between the leaf and the air in the assimilation chamber were 2,000 μmol m⁻² s⁻¹, 30°C and approximately 1.5 kPa, respectively. After the CO₂ assimilation rate had been measured at an ambient CO₂ concentration of 350 μL L⁻¹, the rate was measured at an intercellular CO₂ concentration of 260 μL L⁻¹ by changing the ambient CO₂ concentration.

Levels of Rubisco and nitrogen in individual leaves were determined as follows. Flag leaves were collected immediately after completion of measurements of CO₂ assimilation rates and stomatal conductance, and stored at -80°C prior to analysis. The area and fresh weight of each leaf were determined, and each leaf was separated into two equal parts for separate quantification of Rubisco and nitrogen. The halves of leaves were homogenized separately with a mortar and pestle in a solution that contained 50 mM Tris-HCl (pH 7.5), 1 mM EDTA, 10 mM MgCl₂, 10 mM 2-mercaptoethanol, and 5% (w/w) insoluble polyvinylpyrrolidone (Polyclar VT; Wako Chem., Tokyo). Each homogenate was centrifuged at 10,000×g for 10 min at 4°C. The supernatant was used for quantitation of Rubisco by the single radial immunodiffusion method

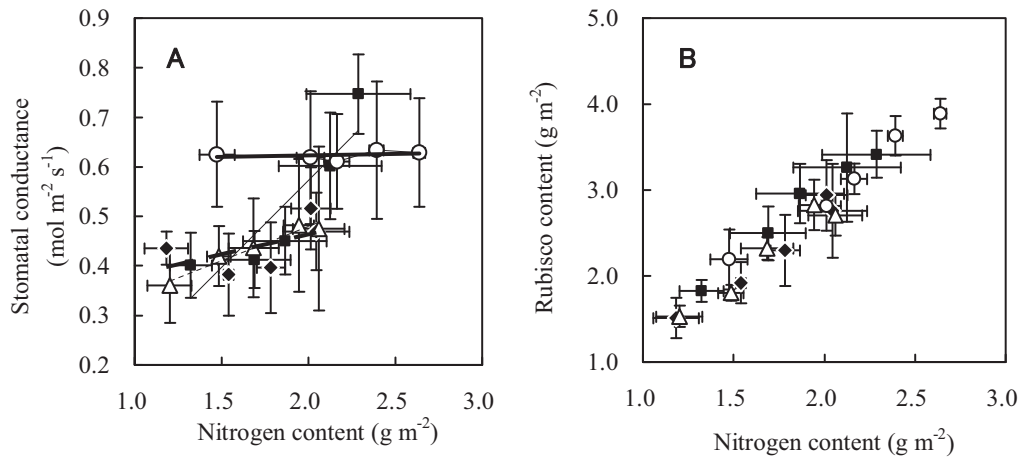


Fig. 3. Relationships between leaf nitrogen content and stomatal conductance (A) and between leaf nitrogen content and leaf Rubisco content (B) in flag leaves of rice plants. See legend to Fig. 2 for explanation of symbols.

(Sugiyama and Hirayama, 1983) with rabbit polyclonal antibodies raised against purified Rubisco from rice. Nitrogen was quantified with a CN analyzer (MT600; Yanako, Kyoto).

The statistical significance of difference among means was determined by Tukey-Kramer's test.

Results and Discussion

1. Varietal differences in photosynthetic rate at identical levels of leaf nitrogen

The level of leaf nitrogen increased with increases in the rate of nitrogen top-dressing in all varieties (Fig. 1A). However, at each rate of nitrogen application, the level of leaf nitrogen tended to be highest in Takanari, followed by Aikoku, and it tended to be lowest in Koshihikari and Asanohikari at all rates of nitrogen top-dressing. Photosynthetic rate at an ambient CO_2 concentration of $350 \mu\text{L L}^{-1}$ increased with increases in the rate of nitrogen top-dressing in all cultivars (Fig. 1B). The photosynthetic rate was highest significantly in Takanari at nitrogen top-dressing rates of 0 and 0.25 g, and it tended to be higher not only in Takanari but also in Aikoku than in Koshihikari and Asanohikari at nitrogen top-dressing rates of 0.5, 1.0 and 2.0 g.

Photosynthetic rate at an ambient CO_2 concentration of $350 \mu\text{L L}^{-1}$ increased with increases in leaf nitrogen content in all varieties examined (Fig. 2). There was a close linear correlation between leaf nitrogen content and the photosynthetic rate for each individual cultivar. However, the specific relationships differed among cultivars. The photosynthetic rate was higher in Takanari than in the other three cultivars at a leaf nitrogen content of approximately 1.5 g m^{-2} . This level of leaf nitrogen is commonly found in rice plants that are growing in paddy fields (Ookawa et al., 2003; Taylaran et al., 2007). Increases in photosynthetic rate with increases in leaf nitrogen

content tended to be smaller in Takanari and larger in Aikoku. The photosynthetic rate tended to be even higher in Takanari than in Koshihikari and Asanohikari at a leaf nitrogen content of approximately 2.0 g m^{-2} . However, it was somewhat higher in Aikoku than in Takanari when the leaf nitrogen content exceeded 2.0 g m^{-2} .

The photosynthetic rate is influenced by stomatal and non-stomatal factors (Hirasawa et al., 1989; Kramer and Boyer, 1995). We shall focus here on the influence of these two factors on the varietal differences in photosynthetic rate at the same leaf nitrogen content.

2. Varietal differences in stomatal conductance and Rubisco content at identical levels of leaf nitrogen

The stomatal conductance of leaves was far greater in Takanari than in the other three cultivars at leaf nitrogen content of approximately 1.5 g m^{-2} . The stomatal conductance increased with increases in leaf nitrogen content in all varieties with the exception of Takanari (Fig. 3A). In Takanari, stomatal conductance of leaves remained constant irrespective of the leaf nitrogen content. Stomatal conductance was higher in Takanari than in Koshihikari and Asanohikari at a leaf nitrogen content of approximately 2.0 g m^{-2} even though stomatal conductance increased with increases in leaf nitrogen content in the latter varieties. The increase in stomatal conductance was marked in Aikoku, which tended to be greater than that in Takanari at a leaf nitrogen content above 2.0 g m^{-2} . By contrast, no differences in Rubisco content of leaves were observed among varieties at any level of leaf nitrogen content and there was a close correlation between nitrogen and Rubisco contents of leaves in all varieties (Fig. 3B).

The intercellular CO_2 concentration in a leaf at an ambient CO_2 concentration of $350 \mu\text{L L}^{-1}$ was in the range from 260 to $280 \mu\text{L L}^{-1}$. We can estimate the leaf photosynthetic activity without considering the effect of

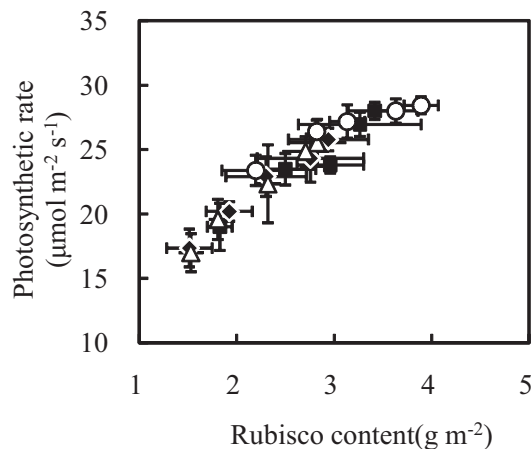


Fig. 4. Relationships between leaf Rubisco content and the photosynthetic rate at an intercellular CO₂ concentration of 260 μL L⁻¹ in flag leaves of rice plants. See legend to Fig. 2 for explanation of symbols.

stomatal conductance by measuring the photosynthetic rate at an identical intercellular CO₂ concentration. No differences were found in the photosynthetic rate at an intercellular CO₂ concentration of 260 μL L⁻¹ among varieties at any Rubisco content of a leaf (Fig. 4). From the results shown in Figs. 2, 3 and 4, we can conclude that stomatal conductance rather than non-stomatal factor, is responsible for the varietal differences in the photosynthetic rate when leaf nitrogen content is identical.

Stomatal conductance has a significant effect on the photosynthetic rate (Ishihara et al., 1979; Hirasawa et al., 1988). Significant differences among rice varieties in stomatal conductance have been reported (Maruyama and Tajima, 1990; Xu et al., 1997; Ohsumi et al., 2007, 2008; Asanuma et al., 2008b). In those studies, stomatal conductance was found to be higher in indica varieties than in japonica varieties. Stomatal conductance is affected by leaf nitrogen content (Ishihara et al., 1979). However, the indica variety Takanari was able to maintain a higher stomatal conductance at a given leaf nitrogen content (Fig. 3A). Takanari has a larger stomatal apparatus than other varieties and this feature is responsible for the elevated stomatal conductance of leaves (Ohsumi et al., 2007). On the other hand, the ability to open stomata widely has been proposed to explain the higher stomatal conductance of indica varieties (Maruyama and Tajima, 1990; Asanuma et al., 2008b). Stomatal conductance is very sensitive to reductions in leaf water potential in rice (Hirasawa et al., 1988), and hydraulic conductance affects leaf stomatal conductance in rice under conditions of intense transpiration (Hirasawa et al., 1992). Takanari has a better developed root system and higher hydraulic conductance (Asanuma et al., 2008a; Taylaran et al., 2007). This might be a cause of the larger stomatal conductance in Takanari even under the mild water stress conditions at the relatively

small vapor pressure deficit in this research (Brodrribb et al., 2007; Asanuma et al., 2008b).

Kuroda and Kumura (1990b) found varietal differences in stomatal conductance even when leaf nitrogen contents were identical and they reported that newer japonica varieties had higher stomatal conductance than older japonica varieties at the ripening stage. In our study, stomatal conductance was higher in the older variety, Aikoku (released in 1882) than in the newer variety, Asanohikari (released in 1987) as well as in Koshihikari (released in 1956) at a leaf nitrogen content of approximately 2.0 g m⁻² (Fig. 3A). Enrichment of soil with nitrogen around roots increases the hydraulic conductivity of roots (Radin and Matthews, 1988; Gorska et al., 2008). An elevated nitrogen application rate might increase hydraulic conductance, which might increase leaf stomatal conductance in japonica varieties with a smaller hydraulic conductance, particularly, in Aikoku (Brodrribb et al., 2007; Asanuma et al., 2008b). The mechanisms responsible for the varietal differences in stomatal conductance at an identical level of leaf nitrogen and in the response of stomatal conductance to the application rate of nitrogen remain to be determined.

In conclusion, the indica high yielding variety, Takanari, had a high photosynthetic rate even at the same nitrogen application rate compared with the japonica varieties not only due to the high capacity of accumulating a larger amount of nitrogen in leaves but also due to the capacity of increasing stomatal conductance at the same level of leaf nitrogen at the relatively low nitrogen application rate. When the nitrogen application rate increased, the photosynthetic rate of Aikoku, a japonica variety, increased due to the larger amount of nitrogen accumulation in leaves and stomatal conductance increased like Takanari, compared with other japonica varieties.

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** In Japanese with English summary.