Comparison of Nitrogen Uptake, Transpiration Rate and Exudation Rate between Upland NERICAs and Japanese Cultivars

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Abstract: Our previous study revealed that upland cultivars of New Rice for Africa (NERICAs) exhibited superior biomass production and N uptake compared with selected Japanese cultivars under upland conditions. The objective of this study was to examine whether the N uptake ability of upland NERICAs is attributable to their transpiration and exudation rates. Two NERICA cultivars (NERICA 1 and NERICA 5), two Japanese upland cultivars (Toyohatamochi and Yumenohatamochi), and a Japanese lowland cultivar Hitomebore were grown under rainfed upland conditions at two N levels. The NERICAs exceeded Japanese cultivars in the increment of aboveground dry weight and N content during the ripening stage. The transpiration rate and exudation rate of NERICAs tended to be higher than those of Japanese cultivars during the ripening stage. These results suggest that NERICAs are capable of maintaining higher water uptake ability during the ripening stage, leading to greater N uptake and biomass production at maturity.

Key words: Exudation rate, NERICA, Nitrogen uptake, Rainfed upland, Rice, Transpiration.

NERICA (New Rice for Africa) was developed by interspecific hybridization between the cultivated rice species Oryza sativa and O. glaberrima, as a new rice ecotype adapted to input-limited, weed- and drought-prone production ecosystems (Jones et al., 1997a, b). Previously, we found that two upland NERICAs (NERICA 1 and NERICA 5) exhibited superior biomass production and yield under rainfed upland conditions as compared with selected Japanese rice cultivars (Matsunami et al., 2009). Under upland conditions, these NERICAs were capable of absorbing greater amounts of N than the Japanese cultivars, a trait which may have contributed to the greater biomass production and sink formation, resulting in their higher grain yield.

Presumably, the high N absorption ability of NERICAs is associated with the physiological activity of their root system. The exudation rate of xylem sap pumped by root pressure can be used as an indicator of root activity (Hirasawa et al., 1983; Morita and Abe, 1999, 2002). In upland conditions, rice plants primarily absorb N in the form of nitrate (Arima, 1995). Mass flow, which is strongly regulated by transpiration, is the primary force in the uptake of most nutrients including nitrate (Gardner et al., 1985). In this regard, O’Toole and Baldia (1982) found a high correlation between the amount of N uptake and the level of cumulative transpiration in rice. Therefore, we evaluated the N uptake ability of NERICAs relative to the rates of transpiration and exudation, and examined whether these rates were responsible for their superior dry matter production and N uptake compared with selected Japanese cultivars.

Materials and Methods

Field experiments were conducted in the experimental field of the Graduate School of Agricultural Science, Tohoku University, located in Sendai, Japan (38°16’ N) in 2007. Two Japanese upland rice cultivars (Toyohatamochi and Yumenohatamochi), a Japanese lowland cultivar Hitomebore and two NERICAs (NERICA 1 and NERICA 5) were grown under rainfed upland conditions with high (HN plots) and low (LN plots) N application levels. In the HN plots, fertilizer mix (N: P₂O₅: K₂O = 12: 16: 18%) was applied at a rate of 5 g N m⁻² before transplanting and ammonium sulfate was additionally applied at a rate of 2 g N m⁻². In the LN plots, the fertilizer mix was applied at a rate of 2 g N m⁻² as a basal dressing and no additional N was applied. Plots were arranged using a split-plot design with N application level as the main plot and cultivar as the sub-plot.
sub-plot. Each cultivar was planted in five 6.0 m rows. The planting density was 22.2 hills m\(^{-2}\) (three plants per hill) with a 30 cm row spacing and 15 cm intra-row spacing. Details of cultural methods, climatic conditions and soil properties are provided in our previous paper (Matsunami et al., 2009).

At heading and maturity, five hills of average size were harvested from each plot, and dried at 80\(^\circ\)C in a ventilated oven for at least five days, then weighed. The dried samples were ground, and N concentration was analyzed with an automated Nitrogen Carbon analyzer (Sumigraph 80, SCAS, Osaka, Japan).

At heading, two weeks and four weeks after heading, the transpiration rate of the flag leaf from five hills of average size for each plot was measured with an LI-6400 portable photosynthesis system (LI-COR Inc., Lincoln, NE, USA). Measurements were conducted between 10:00 and 11:00 AM local time during fair weather. The plants were irrigated adequately three hours prior to taking measurements. The air flow rate, temperature, CO\(_2\) concentration and irradiance inside the leaf chamber were regulated at 500 \(\mu\)mol s\(^{-1}\), 25\(^\circ\)C, 350 \(\mu\)mol mol\(^{-1}\) and 1500 \(\mu\)mol m\(^{-2}\) s\(^{-1}\) PPFD, respectively. The relative humidity in the leaf chamber was regulated at 55%.

After measurement of the transpiration rate, the exudation rate of the same plants was measured between 11:00 and 12:00 AM. For this measurement, the plants were topped approximately 5 cm above the ground and the exudate from the cut surface was collected for an hour using cotton wool which was covered with aluminum foil to prevent evaporation. The exudation rate was determined as the increase in the weight of the cotton wool.

ANOVA was applied to determine the significance of differences in the measured data among N levels and cultivars. Where there were significant differences, means were compared using Tukey’s means comparison test. Standard errors (SE) of the means are presented in the figures.

### Results and Discussion

Table 1 shows aboveground dry weight (DW), N concentration and N content at heading and maturity in five rice cultivars grown under upland conditions at two N levels (HN and LN).

| Nitrogen | Cultivar         | Heading DW (g m\(^{-2}\)) | N concentration (g m\(^{-2}\)) | N content (g m\(^{-2}\)) | Maturity DW (g m\(^{-2}\)) | N concentration (g m\(^{-2}\)) | N content (g m\(^{-2}\)) |
|----------|-----------------|----------------------------|-------------------------------|--------------------------|-----------------------------|-------------------------------|--------------------------|
| HN       | Toyohatamochi   | 503 ab                     | 1.78 a                        | 9.0 a                    | 836 c                       | 1.28 a                        | 10.7 c                   |
|          | Yumenohatamochi | 515 ab                     | 1.61 a                        | 8.3 ab                   | 1189 ab                     | 1.15 a                        | 13.7 bc                  |
|          | Hitomebore      | 365 b                      | 1.35 b                        | 4.1 b                    | 980 bc                       | 1.21 a                        | 11.9 c                   |
|          | NERICA 1        | 470 ab                     | 1.22 b                        | 5.7 ab                   | 1436 ab                     | 1.21 a                        | 17.4 ab                  |
|          | NERICA 5        | 692 a                      | 1.25 b                        | 7.6 ab                   | 1446 a                      | 1.25 a                        | 18.1 a                   |
| LN       | Toyohatamochi   | 281 b                      | 1.18 a                        | 3.3 b                    | 707 b                       | 1.08 a                        | 7.7 b                    |
|          | Yumenohatamochi | 338 ab                     | 1.10 ab                       | 3.7 ab                   | 743 b                       | 0.91 b                        | 6.7 b                    |
|          | Hitomebore      | 338 ab                     | 1.14 a                        | 3.8 ab                   | 953 b                       | 0.93 b                        | 8.9 b                    |
|          | NERICA 1        | 539 a                      | 1.05 bc                       | 5.7 a                    | 1437 a                      | 0.92 b                        | 13.2 a                   |
|          | NERICA 5        | 448 ab                     | 0.98 c                        | 4.4 ab                   | 1442 a                      | 0.91 b                        | 13.1 a                   |

Significance of differences between N levels and cultivars:
- \(N \times C\) ns.
- \(N\) * *** *** ***
- \(C\) * *** n.s. ***
- \(N \times C\) n.s. n.s. n.s. n.s.

Table 1: Aboveground dry weight (DW), N concentration and N content at heading and maturity in five rice cultivars grown under upland conditions at two N levels (HN and LN).

| Nitrogen | Cultivar         | Heading DW (g m\(^{-2}\)) | N concentration (g m\(^{-2}\)) | N content (g m\(^{-2}\)) | Maturity DW (g m\(^{-2}\)) | N concentration (g m\(^{-2}\)) | N content (g m\(^{-2}\)) |
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HN: 7 g N m\(^{-2}\); LN: 2 g N m\(^{-2}\).

Values followed by the same letter in a column within each N level are not significantly different at P < 0.05. Levels of significance: *significant at P < 0.05, **significant at P < 0.01, ***significant at P < 0.001, ns = not significant at P < 0.05.
tended to be higher in Japanese upland cultivars in the HN plot, whereas it was higher in NERICAs in the LN plot. At maturity, NERICAs showed markedly higher N content as compared with the Japanese cultivars.

Plotting an increment of DW (ΔDW) against that of N (ΔN) during the ripening stage clearly indicated that ΔDW was significantly correlated with ΔN, and that both values were substantially higher in NERICAs than in Japanese cultivars (Fig. 1). In this regard, Wada et al. (2002) studied N absorption characteristics of japonica-indica hybrids previously found to produce higher yields under upland conditions (Yun et al., 1997), and ascribed their high yield to their high N absorption ability and superior N use efficiency.

Nitrogen absorption capacity can be assessed from the transpiration rate and exudation rate (O’Toole and Baldia, 1982; Hirasawa et al., 1983; Morita and Abe, 1999). Therefore, we measured the rate of transpiration from the flag leaf and the rate of exudation from the cut stem using the same individual plants. Figure 2 shows the changes in these two parameters during the ripening stage. Generally, the transpiration rate was higher in Toyohatamochi and NERICAs regardless of N level (Fig. 2A). The transpiration rate peaked at two weeks after heading in the NERICAs in both HN and LN plots, but it was fairly constant in Yumenohatamochi in the HN plot and in Yumenohatamochi and Hitomebore in the LN plot. The cultivar difference in the transpiration rate was relatively small at heading, but it was larger at two weeks after heading when the transpiration rate of the NERICAs peaked.

Regardless of N level, the exudation rate was higher in the NERICAs than in the Japanese cultivars, particularly at
two weeks after heading (Fig. 2B). Hitomebore, which was the only cultivar adaptable to lowland conditions in the present study, exhibited the lowest exudation rate among the five cultivars throughout the ripening stage. The exudation rate in Yumenohatamochi was comparable to that in the NERICAs at heading and four weeks after heading and was lower than those in NERICAs at two weeks after heading.

Figure 3A shows the relationship between the transpiration rate of the flag leaf and N increment (ΔN) during the ripening period in five rice cultivars grown under upland conditions at two N levels (HN and LN). Values of transpiration rate and exudation rate are the average values of three time measurements. Vertical bars and horizontal bars indicate standard errors for measurements on plants sampled from five hills. Closed and open symbols indicate HN and LN plots, respectively.

Two weeks after heading (Fig. 2B), Hitomebore, which was the only cultivar adaptable to lowland conditions in the present study, exhibited the lowest exudation rate among the five cultivars throughout the ripening stage. The exudation rate in Yumenohatamochi was comparable to that in the NERICAs at heading and four weeks after heading and was lower than those in NERICAs at two weeks after heading.

Figure 3A shows the relationship between the transpiration rate of the flag leaf and N increment (ΔN) during the ripening period. The transpiration rate tended to correlation (r=0.818, P<0.01) was obtained. It is not clear why Toyohatamochi showed an exceptional response, but a possible explanation is that Toyohatamochi, which is the earliest maturing cultivar in this study, absorbs a large amount of N before heading (Table 1), resulting in a lower ability to absorb more N during the ripening stage.

The exudation rate averaged over the three measurements during the ripening stage was significantly correlated with ΔN (Fig. 3B). Jing et al. (2006) also observed a close correlation between the exudation rate and N uptake in both a Japanese cultivar (Hinohikari) and a Chinese high-yielding cultivar (Yangdao 4) grown under lowland conditions, and found that the correlation was significant during the period before heading. Yamaguchi et al. (1995) found a highly positive correlation between exudation rate and root respiration during the ripening stage. Furthermore, Tsuno and Yamaguchi (1989) reported that the amount of N absorption correlated with root respiration and dry matter production.

This study revealed that upland NERICAs had a transpiration rate and exudation rate exceeding those of elite Japanese upland cultivars, suggesting that their superior capacity for N uptake and dry matter production could be ascribed to their greater water uptake ability. Given that N uptake is regulated by multiple morphological and physiological traits, further studies are needed to identify which traits are responsible for this advantage.

References

Arima, Y. 1995. In T. Matsuo et al. eds., Science of the Rice Plant, vol. two. Food and Agr. Policy Res. Cen. Tokyo. 327-339.

Gardner F.P. et al. 1985. Physiology of Crop Plant. Iowa State Univ. Press. Ames. 98-131.

Hirasawa, T. et al. 1983. Jpn. J. Crop Sci. 52: 574-818*.

Jing, J. et al. 2006. Jpn. J. Crop Sci. 75: 249-256*.

Jones, M.P. et al. 1997a. Euphytica 92: 237-246.

Jones, M.P. et al. 1997b. Breed. Sci. 47: 395-398.

Matsunami, M. et al. 2009. Plant Prod. Sci. 12: 381-388.

Morita, S. and Abe, J. 1999. Root Research 8: 117-119**.

Morita, S. and Abe, J. 2002. Jpn. J. Crop Sci. 71: 383-388*.

O’Toole, J.C. and Baldia, E. P. 1982. Crop Sci. 22: 1144-1150.

Tsuno, Y. and Yamaguchi, T.1989. Jpn. J. Crop Sci. 58: 74-83*.

Wada, Y. et al. 2002. Jpn. J. Crop Sci. 71: 28-30*

Yamaguchi, T. et al. 1995. Jpn. J. Crop Sci. 64: 703-708*.

Yun, S. et al. 1997. Jpn. J. Crop Sci. 66: 386-393*.

* In Japanese with English abstract.

** In Japanese without English abstract.