A quick determination of root resistance to water transport in paddy rice

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**ABSTRACT**
Hydraulic resistance in plants is one of the most important factors responsible for changes in leaf water potential that is an indicator of plant water stress. Although the hydraulic resistance to passive water transport ($R_{pa}$) is a robust index in paddy rice (\textit{Oryza sativa}), measurement is both time-consuming and labour-intensive. Here, we describe a quick method to measure hydraulic resistance to osmotic water transport ($R_{os}$) by measuring the xylem sap exudation rate and osmotic water potential. In a greenhouse experiment, $R_{os}$ responded significantly to soil temperature, but under field conditions soil temperature varied considerably less than air temperature. In the field experiment, $R_{os}$ of six rice cultivars at two growth stages was strongly positively correlated with $R_{pa}$. We conclude that measuring $R_{os}$ could be used to evaluate root water transport capacity in paddy rice under conditions with adequate soil water.

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**INTRODUCTION**
Water stress is an important issue in crop production because it decreases yield dramatically. In rice (\textit{Oryza sativa} L.), even when soil water is adequate, water stress is observed as a mid-day and early afternoon depression of the rate of photosynthesis (Hirasawa & Hsiao, 1999; Ishihara & Saitoh, 1987). This phenomenon is caused by the closure of stomata in response to a reduction in the leaf water potential when transpiration of the leaf increases under a high vapour-pressure deficit (Hirasawa et al., 1989, 1992). To avoid this stomatal closure, plants must absorb enough water from their roots to meet the demand created by their leaves (Hirasawa et al., 1992); indeed, a rice cultivar with low hydraulic resistance tends to maintain higher stomatal conductance than a cultivar with high hydraulic resistance (Jiang et al., 1988).

In addition, Taylaron et al. (2011) showed that root water transport capacity affects both daytime and morning rates of photosynthesis under a low vapour-pressure deficit in paddy rice. A strong relationship between the rate of photosynthesis and hydraulic conductance, which is the inverse of hydraulic resistance, has been found in other plant species (Brodribb et al., 2007; Meinzer & Grantz, 1990). Hence, one important way to enhance photosynthesis would be to mitigate the mid-day depression by increasing the plant’s water transport capacity.

A water transport capacity in plants can be measured in terms of the resistance to water transport by analogy with Ohm’s Law (Steudle & Peterson, 1998). Hirasawa and Ishihara (1991) developed a procedure to calculate the hydraulic resistance to passive water transport from the roots to the leaves ($R_{pa}$) in paddy rice under conditions with sufficient soil moisture. This $R_{pa}$ is calculated from the leaf transpiration rate and the difference in water potential between the roots and the leaf. These authors also suggested that differences in $R_{pa}$ among plants could be used as an index of their root water transport capacity, since root hydraulic resistance often changes as plants age and in response to changes in growing conditions, whereas shoot hydraulic resistance remains unchanged (Hirasawa & Ishihara, 1991; Hirasawa et al., 1992). Although $R_{pa}$ has served as a robust index of root water transport capacity, measuring $R_{pa}$ remains time-consuming and labour-intensive, precluding widespread application of this method. In field studies, since $R_{pa}$ must be determined for many plants within a short time period. A quick determination of root hydraulic resistance is therefore desirable, as it could improve and promote studies of crop physiology.

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and support breeding to select plants with superior water transport. Such a method would be particularly suitable for making comparisons among different environments, analysing developmental profiles, evaluating natural genetic variation in water relations, screening of mutants, and analysing quantitative trait loci.

The hydraulic resistance to osmotic water transport ($R_{os}$) offers an alternative index for evaluating root water uptake capacity. It is well known that the xylem sap rises spontaneously from the cut surface of a plant stem (Schurr, 1998). This can be explained as follows: active xylem loading increases the concentration of ions inside the xylem relative to the surrounding medium (the apoplast of the stele), thereby generating an osmotic gradient that attracts water into the xylem vessels and creating a force that pushes the xylem sap towards the cut stem surface (Schurr, 1998). Therefore, by measuring the gradient of osmotic potential between the xylem sap and the solution around the roots, and combining this with measurements of the exudation rate, it becomes possible to calculate $R_{os}$ (by analogy with Ohm’s Law). In this way, several studies have evaluated the hydraulic conductance to osmotic water transport in maize (Zimmermann & Steudle, 1998) and rice (Miyamoto et al., 2001; Sakurai-Ishikawa et al., 2011). However, these studies were conducted under laboratory conditions, and this method has not yet been applied to rice grown in the fields. To determine the method would also be suitable under filed conditions, we examined whether $R_{os}$ could serve as an alternative to $R_{ps}$ to determine the water uptake capacity of paddy rice.

**Materials and methods**

**Plant materials**

In our first experiment, we grew rice plants, (‘Sasanishiki’), in a greenhouse under natural sunlight. Seeds were sown on 14 April 2007. The seedlings were transplanted on 8 May 2007 into 1/5000a Wagner pots filled with a 1:1 (v/v) mixture of paddy soil (an alluvial clay loam) and upland soil (a diluvial volcanic ash), at 10 plants per pot. Within each pot, the plants were arranged in a circle around the periphery (Satake et al., 1969). A compound of NPK fertilizer (1.0 g each of N, P$_2$O$_5$, and K$_2$O per pot) was applied at planting; additional N fertilizer was applied as ammonium sulphate at 0.3 g per pot at the tillering stage and then again at 1.0 g per pot at the booting stage. The pots were watered daily to maintain the submerged growing conditions.

In our second experiment, we grew rice plants in a paddy field (an alluvial clay loam) at the University farm of Tokyo University of Agriculture and Technology (35°40’N, 139°28’E). We used six rice cultivars: ‘Sasanishiki,’ ‘Koshihikari,’ ‘Nipponbare,’ ‘Akenohoshi,’ ‘Takanari,’ and ‘Habataki.’ Seeds were sown on 26 April 2007 and the seedlings were transplanted on 17 May. The plant density was 22.2 hills m$^{-2}$ (at a spacing of 30 cm × 15 cm), with three plants per hill. As a basal dressing, manure was applied at 20 t per ha, and inorganic fertilizer was applied at 50 kg N ha$^{-1}$, 136 kg P$_2$O$_5$ ha$^{-1}$, and 72 kg K$_2$O ha$^{-1}$. One-third of the total N was applied as ammonium sulphate; another one-third was applied as elution-controlled urea (LP-50; Chisso Asahi Fertilizer, Tokyo, Japan), and the final one-third was applied as elution-controlled urea (LPS-100; Chisso Asahi Fertilizer). No top dressing was applied. The experimental plots (each 3 m$^2$) were arranged in a randomized complete block design with six replicates. The plants were measured at the full heading stage (1 to 2 weeks after flowering) and at late maturity (4 weeks after flowering).

**Hydraulic resistance to osmotic water transport ($R_{os}$)**

The $R_{os}$ ($\times 10^3$ MPa s g$^{-1}$ stem$^{-1}$) was calculated using the method of Miyamoto et al. (2001) as,

$$R_{os} = \sigma (\Psi_{soil\ os} - \Psi_{xylem\ sap}) / E$$

where $\sigma$ is the root-reflection coefficient for solutes in the xylem, $\Psi_{soil\ os}$ (MPa) is the osmotic potential of the soil solution immediately outside the roots, $\Psi_{xylem\ sap}$ (MPa) is the osmotic potential of the xylem sap, and $E$ (g s$^{-1}$) is the exudation rate per stem. The osmotic potentials of the paddy water (–0.012 MPa, on average) and of the surface water in the pots (–0.017 MPa, on average) were used as $\Psi_{soil\ os}$. For $\sigma$, we used a value of 0.4, following Miyamoto et al. (2001). Stems were cut at 15 cm above the ground, and their exudates were collected in pre-weighed absorbent cotton placed on each cut surface. To prevent loss of water by evaporation, the cotton was covered with a plastic bag and shaded with aluminium foil. The collection of stem exudates began at 08:30, when $E$ typically reaches its daily maximum (Hirasawa et al., 1983). $E$ shows a time-dependent decrease after cutting off the stems (Morita & Abe, 2002). Since $E$ didn’t change within 4 h after cutting and then decreased in our preliminary experiment, we collected the exudates for 3 h. To determine $E$, we used the increase in weight of the cotton divided by the collection time. After weighing, the collected exudates were quickly frozen at –80 °C and stored until the osmotic potential could be measured. After thawing the samples overnight at 4 °C, we measured the osmotic potentials of the stem exudates and those of the pot and paddy water with a freezing-point osmometer (OM802; Vogel, Giessen, Germany), and calculated $R_{ps}$ of the potted plants and the field plants. For the field-grown plants, we selected warm and sunny days for sampling. Six replicates were used and the values from two or three hills were averaged for each replicate.
To evaluate the temperature dependency of $E$, $\Psi_{\text{xylem sap}}$, and $R_{\text{os}}$, we manipulated the soil temperature by putting the pots in a water bath 12 h before the measurements. The water temperature was controlled within a range from 15 to 40 °C, with a heater and a cooler that were regulated and monitored by a thermocouple thermometer. The exudate was collected only from the main stems. During collection, we covered each plant with a polyethylene bag to limit the effects of transpiration from the remaining plant parts. Three plants grown in a single pot were measured at the full heading stage and an average value was calculated.

Hydraulic resistance to passive water transport ($R_{\text{pa}}$)

The $R_{\text{pa}} (\times 10^6 \text{ MPa s m}^{-1})$ was calculated using the method of Hirasawa and Ishihara (1991) as

$$R_{\text{pa}} = (\Psi_{\text{soil}} - \Psi_{\text{leaf}}) / T$$

where $\Psi_{\text{soil}}$ (MPa) is the water potential of the soil immediately outside the roots, $\Psi_{\text{leaf}}$ (MPa) is the water potential of a single leaf, and $T$ (mmol m$^{-2}$ s$^{-1}$) is the steady-state transpiration rate per unit leaf area. Since the plants were grown under submerged conditions, so $\Psi_{\text{soil}}$ was much higher than $\Psi_{\text{leaf}}$, and therefore $\Psi_{\text{soil}}$ could be regarded as negligible (assigned a value of zero). The $T$ of an intact leaf was measured in an air-sealed acrylic assimilation chamber (Tsunoda, 1974) under natural sunlight. Air, with a dew point controller at 10 (±0.1) °C, was pumped into the chamber at a rate of $6.67 \times 10^{-3}$ m$^{-3}$ s$^{-1}$. The humidity of the air pumped into and out of the chamber was measured with a dew point hygrometer (Model 660; EG & G Inc., Waltham, MA, USA). Once $T$ reached a constant value, the leaf water potential was measured in a pressure chamber (Model 3005; Soil Moisture Equipment Inc., Santa Barbara, CA, USA). Six replicates were used and the values of four to six leaves per replicate were averaged. The measurements were conducted from 09:00 to 15:00 during the period of 13 August to 20 September 2007.

Statistical analysis

Differences and interactions between the treatment effects on the $E$, $\Psi_{\text{xylem sap}}$, and $R_{\text{os}}$ response variables were tested separately using two-way analysis of variance (ANOVA) in each ANOVA, the two treatment factors were rice cultivar (six cultivars) and plant stage of development (full heading vs. late maturity). All tests were performed in JMP software v. 12 (SAS Institute, Cary, NC, USA).

Results and discussion

$E$ in rice is strongly affected by soil temperature (Yamaguchi et al., 1995). However, the responses of $\Psi_{\text{xylem sap}}$ and $R_{\text{os}}$ to soil temperature have not been determined before now. As we expected, the value of $E$ increased with increasing soil temperature (Figure 1(A)), but only in the range of 15–30 °C; $E$ peaked at about 30 °C and then decreased as temperature increased to 40 °C. In contrast, $\Psi_{\text{xylem sap}}$ varied little over the range of soil temperatures examined (Figure 1(B)). As a result, $R_{\text{os}}$ decreased from 20 to 33 °C and slightly increased in the range of 33 to 40 °C (Figure 1(C)). These results indicate that $R_{\text{os}}$ can respond to changes in soil temperature and that the response is likely driven by changes in $E$.

Along with air temperature, we monitored the rice paddy field’s actual soil temperature at a depth of 15 cm from 19 August to 28 September in 2007 (Figure 2). The average air temperature during the period when most of the sampling occurred (i.e. from 09:00 to 12:00) varied greatly (by 13 °C), from 17 to 30 °C, whereas soil temperature varied less (by 4.9 °C, from 20.5 to 25.4 °C). The specific

![Figure 1](attachment:image-url)
he heat of water is 4.18 J g⁻¹ K⁻¹, which is four times that of air, so the soil (which is in contact with the water) will change temperature more slowly. Furthermore, canopy vegetation cover can slow the transfer of heat between the soil and the air (Takami et al., 1989). Both factors might explain the smaller changes in soil temperatures. Moreover, we selected warm and sunny days for sampling in the paddy field; excluding the data for one cool day, soil temperature ranged from 24.6 to 26.6 °C. The effect of this variation on os can be ignored, since the changes in os over this range were much smaller than the between-plant variation at a given soil temperature (Figure 1(C)).

We compared E, Ψxylem sap, and Rps of the six cultivars at full heading and late maturity (Table 1). There were significant between-cultivar differences in E at both stages. ‘Akenohoshi’ had the highest E at both stages. E was always higher at full heading than at late maturity; significant differences were detected between stages, and there was a significant cultivar × stage interaction. There were also significant differences in Ψxylem sap among the cultivars at both stages, although the range of values was smaller than that for E. Ψxylem sap was always higher (less negative) at full heading than at late maturity, and significant differences were detected at both stages; the cultivar × stage interaction was also significant. There were significant differences in Rps among the cultivars at both stages. ‘Akenohoshi’ had the lowest Rps among the cultivars at both stages owing to its higher E at full heading and its higher E and higher (less negative) Ψxylem sap at late maturity than the other cultivars. Rps was always lower at full heading than at late maturity, and the difference between stages and the cultivar × stage interaction were also significant. These results are consistent with those of Jiang et al. (1988), who showed that ‘Akenohoshi’ maintained a lower Rps than ‘Nipponbare’ throughout the ripening stage, and that Rps of both cultivars gradually declined as the plants aged, suggesting that Rps may reliably reflect variable differences in root water transport capacity among rice cultivars and between growth stages.

We also measured the Rps of these rice plants to examine the relationship between Rps and Rpa across the six cultivars and two growth stages (Figure 3). We found that Rps provides a good estimate of Rpa (R² = 0.91, n = 11). Taken together, our results suggest that Rps can be as reliable as Rpa as an index of water uptake capacity in paddy rice.

Table 1. The exudation rate from the cut stem surface (E), water potential of the xylem sap (Ψxylem sap), and the hydraulic resistance to osmotic water transport (Rps) in six rice cultivars grown in a paddy field.

| Cultivar       | Type       | Stage  | E (10⁻¹ g s⁻¹ stem⁻¹) | Ψxylem sap (MPa) | Rps (10³ MPa s g⁻¹ stem⁻¹) |
|----------------|------------|--------|------------------------|------------------|---------------------------|
| Sasanishiki    | Japonica   | Full heading | 0.077 ± 0.004          | −0.044 ± 0.005   | 0.17 ± 0.02               |
|                |            | Late maturity | 0.039 ± 0.004          | −0.077 ± 0.017   | 0.74 ± 0.15               |
| Koshihikari    | Japonica   | Full heading | 0.079 ± 0.002          | −0.045 ± 0.005   | 0.17 ± 0.01               |
|                |            | Late maturity | 0.031 ± 0.003          | −0.076 ± 0.009   | 0.88 ± 0.13               |
| Nipponbare     | Japonica   | Full heading | 0.076 ± 0.001          | −0.051 ± 0.004   | 0.20 ± 0.01               |
|                |            | Late maturity | 0.037 ± 0.001          | −0.063 ± 0.007   | 0.59 ± 0.05               |
| Akenohoshi     | Indica/Japonica | Full heading | 0.131 ± 0.004          | −0.050 ± 0.004   | 0.11 ± 0.01               |
| Habataki       | Indica     | Full heading | 0.067 ± 0.005          | −0.057 ± 0.009   | 0.27 ± 0.02               |
|                |            | Late maturity | 0.103 ± 0.006          | −0.059 ± 0.005   | 0.18 ± 0.02               |
| Takanari       | Indica     | Full heading | 0.058 ± 0.005          | −0.070 ± 0.009   | 0.52 ± 0.07               |
|                |            | Late maturity | 0.099 ± 0.003          | −0.061 ± 0.006   | 0.20 ± 0.02               |
| ANOVA          | Cultivar   | Full heading | ND                     | ND               | ND                        |
|                |            | Late maturity | ND                     | ND               | ND                        |
|                | Stage      | ***        | ***                    | ***              | ***                       |
|                | Cultivar × Stage | ***        | ***                    | ***              | ***                       |

Values are means ± SE (n = 6). ND, not determined. Significance: *p < 0.05; **p < 0.01; ***p < 0.001. Data were not obtained for ‘Takanari’ at late maturity. The ANOVA for cultivar at the full heading stage was performed for six cultivars, whereas the ANOVA for cultivar at late maturity, stage, and cultivar × stage was performed with only five cultivars, excluding ‘Takanari’.
transport (pa) for rice plants of six cultivars grown in a paddy. Radial passage of water, potential barriers include several transport is thought to occur via an apoplastic bypass,ated by transpiration (Zimmermann et al., 1995). Water that the apoplastic pathway in passive water transport is differed significantly in maize (R). However, the root structures: the exodermis, sclerenchyma, aerenchyma, and endodermis. Miyamoto et al. (2001) suggested that the root endodermis is the main barrier to water transport in rice. Furthermore, they found that the values of L_pr measured osmotically and hydrostatically were similar in rice, but differed significantly in maize (Zea mays). This suggests that the apoplastic pathway in passive water transport is highly impeded in rice and that a large portion of the water moves via the cell-to-cell pathway. If so, this might explain the close relationship we observed between R_pa and R_os. Although we were unable to directly compare R_pa and R_os in the same units (because R_pa should be expressed per unit leaf area), we can still use R_os to compare root water uptake capacity among cultivars and growth stages. The measurement of R_pa is time-consuming and labour-intensive. For example, it typically takes 5–10 min per leaf to obtain a stable transpiration rate after inserting a leaf into the chamber. The measurement of Ψ_leaf then takes an additional 5 min. To do this work, it requires two persons: one to measure the transpiration rate and another to measure Ψ_leaf. This method also requires a humidity control system, a plastic chamber, a dew-point hygrometer for measuring T, and a pressure chamber to measure Ψ_leaf (Hirasawa & Ishihara, 1991). In contrast, measuring R_os takes a single person only 2 min, to set the absorbent cotton upon the cut stem surface. After the exudate has been collected, the cotton can be stored in a freezer before measurements of its weight increase (i.e. the amount of exudate absorbed) and Ψ xylem sap. The osmotic method demonstrated in this paper therefore offers the large advantages of simplicity and ease of measurement, thus enabling plant researchers to process more samples per unit of sampling time than they could with the passive method. In this paper, we have shown how a quick method to measure the hydraulic resistance to root water transport (an index of root water uptake capacity), could be used under conditions with adequate soil water by simply evaluating the exudation rate and the difference in osmotic potential between the soil and the exudates. The proposed method offers a promising approach for evaluating the root water uptake capacity of different rice cultivars, investigating lines grown in several areas under a wide range of environmental conditions, and supporting genetic studies designed to identifying quantitative trait loci and genes associated with differences among rice cultivars in their root water transport capacity. Disclosure statement No potential conflict of interest was reported by the authors. Funding This work was supported in part by the Japan Science and Technology Agency, Precursory Research for Embryonic Science and Technology (to S. A.), by the Ministry of Agriculture, Forestry and Fisheries of Japan (Genomics-based Technology for Agricultural Innovation, RBS-2006, to T. H.), and by the Global Innovation Research Organization in Tokyo University of Agriculture and Technology (to S. A. and T. H.).

Figure 3. The relationship between hydraulic resistance to osmotic water transport (R_os) and hydraulic resistance to passive water transport (R_pa) for rice plants of six cultivars grown in a paddy field. The filled and open symbols indicate the measurements at full heading and late maturity, respectively. The dashed curves represent the 95% confidence interval. Values are means ± SE for n = 6 replicates per symbol.
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