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On Resistance to Water Transport from Roots to the Leaves at the Different Positions on a Stem in Rice Plants*

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Abstract : The degree of the midday depression in the stomatal conductance and the photosynthetic rate is larger in the lower leaves than in the upper leaves on a stem. It was clarified in the previous report that resistance to water transport correlates closely with the degree of the midday depression in the stomatal conductance. The present study was to investigate the difference among the resistances to water transport from root surface to leaves (whole resistances to leaves) at different positions on the stem and also to investigate the factors related to the difference among the whole resistances to the leaves.

The whole resistance to the older leaves at the lower position on the stem was larger than that to the younger leaves at the upper position. There was no significant difference among the whole resistances to the leaves of the same age. The whole resistance to each leaf increased considerably after the leaf had fully expanded. It was concluded that the longer the time elapsed after the full leaf expansion, the higher the whole resistance to the leaf at the lower position of the stem. The increase in the resistance from the base of a stem to the leaf measured by using the excised stem was far smaller than that in the whole resistance. Since older leaves and younger leaves were closely connected with older crown roots and younger crown roots, respectively, it was suggested that an increase in the whole resistance to the leaf with time after full leaf expansion might result from the increase in the resistance of the roots connected with the leaf, i. e. the reduction in passive water uptake capacity of the roots due to age of the roots. Also, the larger midday depression in the stomatal conductance of the lower leaves was supposed to be due to the larger whole resistance to them. Moreover, it was also found out that resistance to water transport in the stem and the leaf is the dominant resistance in the whole plant resistance when the leaf had just expanded fully. The ratio of the root resistance to the whole resistance, however, increased considerably with age of the leaf.
Key words : Ageing, Lower leaf, Midday stomatal closure, Resistance to water transport, Rice plants, Root resistance to water transport, Stem and leaf resistance to water transport, Upper leaf.

水稲における根から葉身までの水の通導抵抗の葉位による相違：平沢　正・後藤敏之・石原　邦（東京農工大学農学部）

要　旨：水稲における気孔開度，光合成速度の日中低下の程度は，同一茎に着生する葉身でも下位の葉が上位の葉に比較して大きい．本報告では，日中の気孔の閉鎖程度と密接に関係する水の通導抵抗を葉位別に測定し，さらに葉位によって水の通導抵抗の異なる要因を検討した．

根から葉身までの水の通導抵抗（全抵抗）は上位の若い葉で小さく，下位の古い葉で大きかった．展開完了後の日数の等しい葉身では葉位が異なっても全抵抗には相違がなく，展開完了後の日数の経過に伴ってすべての葉位で全抵抗が大きくなった．このことから，下位の葉で全抵抗が大きいのは，下位の葉ほど展開完了後の日数が経過しているためであることがわかった．下位の葉は古い根と，上位の葉は新しい根と密接な関係があること，切断茎を用いて求めた茎基部から葉身までの水の通導抵抗は展開完了後の日数が経過しても大きく変化しないことから，葉身展開完了後の日数の経過に伴って全抵抗が増加するのは，それぞれの葉身と関係している根が老化し，根の水の通導抵抗が増加する，いいかえると吸水能力が低下するためであると推察された．このことから，気孔の日中の閉鎖程度が下位の葉ほど大きいのは，下位の葉と関係している根ほど水の通導抵抗が大きいことによると考えられた．さらに，葉が若い時には全抵抗に対する茎葉部の抵抗の割合が大きいが，葉の age が進むとともに全抵抗に占める根の抵抗の割合が大きくなることがわかった．
キーワード：イネ，エイジング，下位葉，気孔の日中閉鎖，茎葉の水の通導抵抗，上位葉，根の水の通導抵抗，水の通導抵抗．

In rice plants, the stomatal conductance and the photosynthetic rate decrease under intense transpiration in the afternoon on a clear day due to water deficits even though they are growing under submerged soil conditions[7,8,9]. The degree of the midday

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depression in the stomatal conductance and the photosynthetic rate is larger in the lower leaves than in the upper leaves in a stem[8]. In a previous report[6], it was found out that there was a close correlation between the resistance to water transport and the degree of midday depression in the stomatal conductance in rice plants grown under different conditions.

The present study was conducted to investigate the factors responsible for the differences in the degrees of the midday depression in the stomatal conductances among the leaves at the different positions on a stem. It was observed that the resistance to water transport from the root surface to older leaves at lower positions on a stem was higher than that from roots to younger leaves at the upper positions of a stem[#] and that the whole resistance increased as time proceeded after the leaf had expanded fully. Also, it was observed that there were only small differences in the resistances from the base of the stem to the leaves at the different positions on a stem measured by using the excised stem, and that the increase in the resistance with time after full expansion of the leaf was far smaller than that in the whole resistance to the leaf.

Materials and Methods

Rice plants (*Oryza sativa* L. cv. Manryo) were grown in 1/2,000 a Wagner pots filled with mixed soil of the Tama river alluvial and the Kanto diluvial soils (1 : 1, v/v) under submerged soil conditions. Seedlings at the 6 th leaf stage were transplanted at the rate of 3 hills (3 plants per hill) per pot after fertilizer was applied at the rate of 1.0, 1.0, 1.0 g/pot of N, P_2O_5, K_2O, respectively. Additional fertilizer was applied when necessary in order not to expose the plants to nutrient deficiency.

Transpiration rate of a single intact leaf on the main stem was measured outdoors and under artificial light in the laboratory with an acrylic assimilation chamber[5]. Leaf xylem water potential was measured with a pressure chamber (PMS, Inc). Since rice plants were grown under submerged soil conditions, the resistance to water transport from the roots to the leaf (R) was calculated as follows:

$$R = -\Psi x / T \quad (1)$$

where Ψx is leaf xylem water potential and T is transpiration rate on a leaf area basis.

According to a previous report[5], the resistance to water transport from the base of a stem to the leaf was measured as follows: The plants were left in the dark room for a few hours and, after guttation emerged from the leaf tips, the main stem was excised under water at its base just above the ground, 0.5—1 hour before taking measurements. With the cut end of the stem under water, the transpiration rate and the leaf xylem water potential were measured. The resistance to water transport from the base of the stem to the leaf was calculated using equation (1).

Results

The whole resistance to the older leaves at the lower positions on a stem was larger than to the younger leaves at the upper positions on a stem both at the maximum tillering stage and at the panicle formation stage (Figs. 1 A and B). Although whole resistances to the 16 th (flag), 15 th and 14 th leaves did not differ significantly from each other at the ripening stage, the whole resistances to these upper three leaves were smaller than to the 13 th and 12 th leaves. Also the whole resistance to the 12 th leaf was significantly larger than to the 13 th leaf (Fig. 1 C).

Whole resistances to the leaves at the different positions on a stem were compared with reference to the time after the leaves had fully expanded (Table 1). There was no significant difference among the whole resistances to the leaves of the same age. For example, there were no significant differences between whole resistances to the 12 th and 14 th leaves at about 1 week after full leaf expansion, among the resistances to the 11 th, 12 th, 13 th and 16 th (flag) leaves at 2—3 weeks after full leaf expansion, among the resistances to the 11 th, 14 th and 15 th leaves at 4—5 weeks after full leaf expansion, and between the resistances to the 12 th and 13 th leaves at 6—7 weeks after full leaf expansion. However, the whole resistance to each leaf increased with time after full expansion. That is, the whole resistances were

#) In this manuscript, resistance to water transport from the root surface to a leaf is described simply as a whole resistance, and the resistance to water transport from the root surface to a leaf at some position on a stem (for example, Nth leaf) is described as "the whole resistance to the Nth leaf". In other cases, the particular resistances to water transport in the plants are identified.

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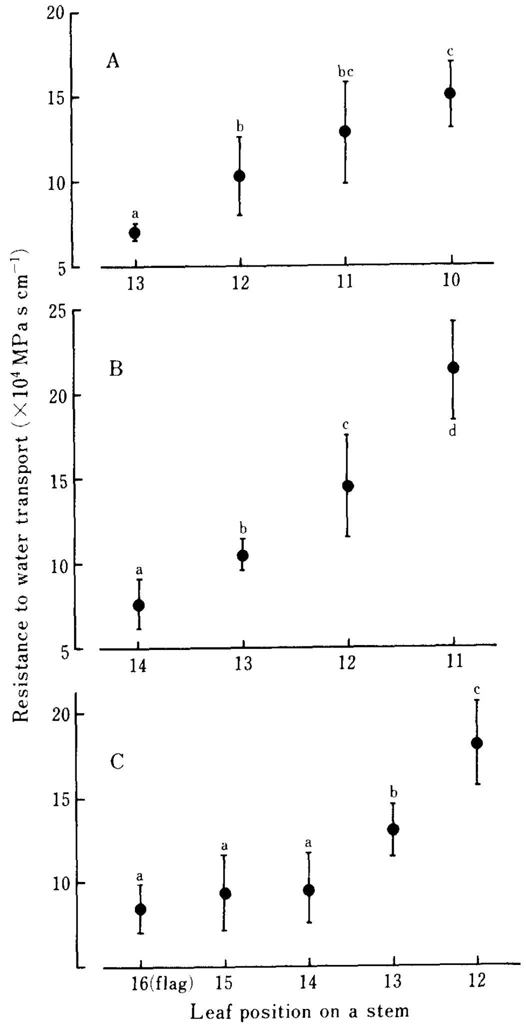

Fig. 1. Resistance* to water transport from roots to the leaves at the different positions on a stem at the maximum tillering stage (A), at the panicle formation stage (B) and at the ripening stage (C). The means followed by the different letters are significantly different at 5% level.
* Resistance at above 1.1 $gH_2O\ dm^{-2}\ h^{-1}$ transpiration rate, which applies correspondingly to Table 1, 2 and 3.

$(7.5-7.7)\times10^4$, $(8.9-9.3)\times10^4$, $(9.9-10.9)\times10^4$, and $(11.1-12.0)\times10^4$ MPa s cm^{-1} at about 1 week, 2—3 weeks, 4—5 weeks and 6—7 weeks, respectively, after full leaf expansion. From these results, it is clear that the longer the time elapsed after full leaf expansion the higher the whole resistance to the leaf.

There were no significant differences among the resistances from the base of a stem to the leaves of the same age (Table 2). The resistance from the base of a stem to a leaf seemed to have increased with time after the leaf had expanded fully (Table 2). The degree of the increase in the resistance was very small when compared to the increase in the whole resistance from roots to the leaves. For example, during the period from 1 week to 7 weeks after the 12 th leaf had expanded fully, the whole resistance to the leaf increased by 48% but the resistance from the base of the stem to the leaf increased by only 12%. During the period from 1 week to 5 weeks after the 14 th leaf had expanded fully, the whole resistance to the leaf increased by 42% but the resistance from the base of the stem to the leaf increased by only 17%. These results indicate that the ratio of the resistance from the base of the stem to a particular leaf to the whole resistance to the leaf changes with time after the leaf had fully expanded.

Discussion

In a previous report[5], it was concluded that since the whole resistance changed considerably depending on the conditions affecting root water uptake capacity, the change of whole resistance to water transport could represent the change of root resistance to water transport and the whole resistance to water

Table 1. Changes in resistance to water transport from roots to leaves at different positions on a stem ($\times10^4$ MPa s cm^{-1}) with time after full leaf expansion.

Leaf position of a stem	Weeks after full expansion			
	1	2—3	4—5	6—7
11th	—	9.2±0.8	10.7±1.2	—
12th	7.5±1.5	8.9±0.8	—	11.1±2.2
13th	—	9.0±1.0	—	12.0±2.4
14th	7.7±1.6	—	10.9±2.1	—
15th	—	—	9.9±2.4	—
16th (flag)	—	9.3±0.9	—	—

*There were not significant differences among the whole resistances to leaves at each week after full expansion.

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transport could be adopted in estimating passive water uptake ability in crop plants transpiring intensively. In this report, it was clarified that the whole resistances to leaves at different positions on the stem differ considerably from each other, that is, the whole resistance to older leaves at lower positions on a stem was larger than that to younger leaves at upper positions on the stem (Fig. 1). But only small differences were found in the resistances from the base of a stem to the leaves at the different positions on the stem because the degree of the increase in the resistance with time after full leaf expansion was far smaller than that in the whole resistance (Table 2). Based on the facts that the difference in the whole resistance resulted from that in the resistance from roots to the base of a stem, and that the resistance in the portion of the base consisting of the resistance of vascular tissue was not large compared to the resistances in other parts of a plant[2,3], the difference in the whole resistance should result from the difference in the root resistance consisting of the radial and axial hydraulic resistances in roots. The ratio of the root resistance to the whole resistance was to be larger for the older leaves than for the younger leaves. For example, for the 14 th leaf, which was the youngest fully expanded leaf at the panicle formation stage, the ratio of the resistance from the roots to the base of the stem, i.e. the root resistance, to the whole resistance was 18.2% (Table 3). On the other hand, for the 11 th and 10 th leaves, which were older than the 14 th and 13 th leaves, the ratio of the root resistances to the whole resistances were 42.1% and 45.2%, respectively (Table 3).

The whole resistance to the older leaves at the lower positions on the stem was larger than for the younger leaves at the upper positions on the stem. Based on the "leaf-internode unit"[12] or the "shoot units"[10] theories the older leaves and the younger leaves were closely connected with the older crown roots and the younger crown roots, respectively. It was suggested that the larger resistance to the older leaves at the lower positions on the stem resulted from the connection of the leaves with the older roots whose resistance to water transport is larger, that is, passive water uptake capacity is low. A similar root-leaf relationship was observed in the exudation measurements[4]. Exudation rates of younger leaves were larger than those of older leaves. The older crown roots emerging from the

Table 2. Changes in resistance to water transport from the base of a stem to the leaf ($\times 10^4$ MPa s cm^{-1}) with time after full leaf expansion in an excised stem*.

Leaf position of a stem	Weeks after full expansion 1	2—3	4—5	6—7
11th	—	7.1±1.0	6.2±1.6	—
12th	6.7±0.6	6.9±1.7	—	7.5±1.1
13th	—	7.1±1.2	—	8.4±1.2
14th	6.3±0.5	—	7.4±1.1	—
15th	—	—	8.0±1.1	—
16th (flag)	—	8.3±2.2	—	—

*There were no significant differences among the resistances at each week after full expansion.

Table 3. Resistance to water transport from roots to leaves on intact plants (A) and resistance from the base of a stem to leaves on an the excised stem (B) at the panicle formation stage.

	Leaf position on a stem 14th	13th	12th	11th	10th
A*	7.7±1.6	9.0±1.0	8.9±0.8	10.7±1.2	12.4±1.6
B**	6.3±0.5	7.1±1.2	6.1±0.6	6.2±1.6	6.8±1.1
(1−B/A)×100 (%)	18.2	21.1	31.5	42.1	45.2

*Figures come from Table 1.
**Figures come from Table 2.

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lower nodes were inferior to the younger crown roots emerging from the upper nodes in active water uptake capacities. The younger crown roots emerging from the upper nodes and the older crown roots emerging from the lower nodes were supposed to be continuous with the upper leaves and the lower leaves, respectively. The exudation rate of the flag leaf was smaller than in each of the second and third leaves from the flag leaf—probably because the crown roots did not emerge from the node above the elongated internode with which the flag leaf was connected[4]. However, the whole resistance to the flag leaf was not higher than that to the second and third leaves from the flag leaf and the difference among the whole resistances to the three leaves was very small (Fig. 1). Hence, the relationship among the whole resistances to the leaves at the different positions on the stem was somewhat different from the relationship among the exudation rates of such leaves.

The degree of midday depression in the stomatal conductance on a clear day is larger in the lower leaves than in the upper leaves on a stem[8]. Since there is a close correlation between whole resistance to water transport and the degree of midday depression in the stomatal conductance[6], the difference in the degree of the midday depression in the stomatal conductance among the leaves at different positions is supposed to result from the difference in the resistance to water transport in roots connected with each leaf. The whole resistances to water transport in rice plants in the plot treated with soluble starch and additional ammonium sulfate (SA plants) and in the shaded plot (SP plants) were larger than in the control plants as shown in the previous report[6]. The degree of midday depression in the stomatal conductance was larger in the SA plants and the SP plants than in control plants[6]. However, no difference was found in the resistance from the base of the stem to the leaf between each of the above treatments and the control plants. From these results, it was confirmed that the differences in the degree of midday depression in the stomatal conductance among these plants should result from the differences in their root resistance.

The resistance from the base of the stem to the younger fully expanded leaves was dominant in the whole resistance from roots to the leaves, and the resistance from roots to the base of a stem occupied a small part of the whole resistance (Table 3). Therefore, root resistance is not always said to be the dominant resistance in rice as well as other plants[1]. However, the whole resistance to the old leaves at the lower positions on the stem increased probably due to the increase in the resistance in roots connected with these leaves (Fig. 1). The ratio of the root resistance to the whole resistance to the leaves was supposed to have increased considerably with time after full leaf expansion (Table 3). Therefore, the root resistance was to account for a major portion of the whole resistance for the older leaves. Whole resistance to water transport increased markedly in the SA plants in which root-rot occured and in the SP plants which developed smaller root systems[6]. This was not due to the increase in the resistance from the base of the stem to the leaf but was rather due to the increase in root resistance, as mentioned above. From these facts, it was concluded that (i) root resistance to water transport changes markedly with age of roots, or depends on the prevailing growth conditions (ii) increase in root resistance causes the ratio of root resistance to whole resistance to increase.

The increase in resistance from the base of a stem to the leaf with time after its full expansion was far smaller than that in the whole resistance to the leaf. There was also no difference in the resistance from the base of a stem to the leaf among the rice plants grown under the different conditions. It was supposed then that the changes in the stem and leaf resistances might be very small except in special circumstances such as the occurrence of a xylem embolism due to severe water stress[11,14]. The observations that the degree of midday depression in the stomatal aperture was large at the panicle formation stage[7] when the portion of the stem at the internode was elongating rapidly, and that the degree of injury to the panicle due to water stress under strong dry wind was smaller in the cultivars in which the diameter of xylem vessels in the stem was larger[13] would suggest that water transport in the stem could limit water supply to the leaves and ear considerably. We therefore suggest that the characteristics relating to water transport in a stem should be investigat-

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ed in detail.

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