

Relationship between Resistance to Water Transport and Exudation Rate and the Effect of the Resistance on the Midday Depression of Stomatal Aperture in Rice Plants*

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Abstract : There was considerable difference in the degree of the midday depression in the stomatal conductance, and the photosynthetic rate among rice plants grown under different conditions, and the degree of the midday depression was supposed to depend on root-water uptake ability. The present study was conducted to investigate the difference in the exudation rate under practically zero transpiration, representing active water uptake capacity, and in the resistance to water transport under intense transpiration, representing passive water uptake capacity, among rice plants grown under different conditions. The relationship between passive and active water uptake capacities as well as between the passive water uptake capacity and the degree of midday stomatal closure was also investigated.

In the plants in which "root-rot" occurred as a result of the soluble starch added to the soil and in those which were grown under the conditions of low light intensity and high humidity and developed a smaller root system, the exudation rate was low and the resistance to water transport was high compared to the control plants. This means that active and passive water uptake capacities were lower in these plants than in the control plants. In the plants which were grown on the culture solution of low nitrogen level and developed larger root system, exudation rate was high and the resistance was low compared to the plants grown on the standard culture solution, that is, active and passive water uptake capacities were higher in the former than in the latter. The degree of the midday depression in the stomatal aperture was larger in the plants in which resistance to water transport was larger and there was a close correlation between the resistance, i.e. passive water uptake capacity, and the degree of the midday depression. On the other hand, in the plants whose leaf nitrogen content was increased by applying ammonium sulfate one week before measurement commenced, exudation rate increased markedly but the resistance to water transport did not change. The stomatal aperture was far larger in the plants supplied with additional ammonium sulfate than in the control plants in the morning, but the difference in the sizes of these respective stomatal apertures became smaller under intense midday transpiration because of the absence of any difference in their passive water uptake capacities. In view of the high correlation between gas exchange rate through stomata and photosynthetic rate, these results suggest that higher passive water uptake capacity is essential, in addition to the increase in leaf nitrogen content, in increasing the daily total photosynthesis.

Key words : Active water uptake, Exudation rate, Midday closure of stomata, Passive water uptake capacity, Resistance to water transport, Rice plants, Stomatal aperture, Transpiration.

水稻における水の通導抵抗と出液速度の関係及び水の通導抵抗が気孔開度の日中低下に及ぼす影響 : 平沢正・土田政憲・石原 邦 (東京農工大学農学部)

要 旨 : 水稻の気孔開度, 光合成速度の日中低下の程度は生育条件によって異なり, これには吸水能力が関係すると考えられている. 本報告では, 受動的吸水能力を表わす蒸散の盛んな時の水の通導抵抗と能動的吸水能力を表わす出液速度を生育条件の異なる水稻の間で比較し, さらに両吸水能力の関係, 受動的吸水能力と気孔開度の日中低下の程度の関係を検討した.

土壌に可溶性でんぷんを加え根ぐされをおこした水稻, 低照度, 高湿度条件に生育し, 根の発達程度の劣る水稻では対照の水稻に比較して出液速度が小さく, 水の通導抵抗が大きい, いいかえると能動的吸水能力と受動的吸水能力が低かった. また, 通常の水耕液に生育した水稻に比べて, 窒素濃度の低い水耕液に生育し根群のよく発達した水稻では出液速度が大きく, 水の通導抵抗が小さい, いいかえると能動的吸水能力と受動的吸水能力が高かった. 水の通導抵抗が大きい水稻ほど日中の気孔の閉鎖程度が大きく, 受動的吸水能力と日中の気孔閉鎖程度とは密接な関係があった. 一方, 測定の前1週間前に硫酸を追肥し, 葉身の窒素濃度を高めた水稻では出液速度は大きく, 能動的吸水能力は高かったが, 水の通導抵抗, いいかえると受動的吸水能力は対照区と変わらず, 対照区との気孔開度の差は早朝に比べて日中は小さかった. 気孔開度の日中低下には受動的吸水能力が関係するので, 日中の気孔開度が大きく, 高い光合成速度を維持するためには, 葉身の窒素濃度が高いことに加えて受動的吸水能力の高いことが必要であることがわかった.

キーワード : イネ, 気孔開度, 気孔の日中閉鎖, 出液速度, 受動的吸水能力, 蒸散, 水の通導抵抗, 能動的吸水能力.

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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^{5,7,8,9}). It has been found that there are large differences in the degree of the midday depression in the stomatal conductance and the photosynthetic rate among rice plants under different growth conditions^{5,7,8}) or among cultivars¹⁰). It was supposed that the degree of the midday depression in the stomatal conductance and the photosynthetic rate should depend on water uptake ability of roots relating to the development of the root system and/or the physiological activity of roots^{5,7,8,10}). There are two water uptake mechanisms, namely, passive and active (osmotic) water uptake. In a previous report⁴), it was clarified that resistance to water transport calculated from the measurements of transpiration rate and leaf water potential according to Ohm's law could be adopted in estimating passive water uptake ability. This is because resistance to water transport changed considerably when the root system was partly excised or when the conditions affecting water uptake were changed. On the other hand, the differences in active water uptake capacity among plants could be compared by measuring the exudation rate in the plants with practically zero transpiration.

The present study was conducted to investigate (i) differences in the exudation rate (active water uptake capacity); (ii) differences in the resistance to water transport (passive water uptake capacity) among rice plants under different growth conditions where the physiological activity of roots, the extent of root-system development and nitrogen content of leaves are affected; (iii) relationship between passive and active water uptake capacities in the plants; and (iv) relationship between the passive water uptake capacity and the degree of midday stomatal closure.

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 6th

leaf stage were transplanted at the rate of 3 hills per pot (3 plants per hill) after fertilizer was applied at rates of 1.0, 1.0, 1.0 g/pot of N, P₂O₅, K₂O, respectively. Additional fertilizer applications were carried out according to circumstances in order to prevent nutrient deficiencies in the plants.

Four plots were prepared in soil-cultured rice plants, as mentioned in a previous report⁷). One was a control and the others were as follows: (i) a plot with soluble starch and additional ammonium sulfate where 3 l of 1% soluble starch solution and 5 g of ammonium sulfate were applied to soil in a pot several days before measurements to make the soil reductive and to decrease the physiological activity of roots without decreasing the nitrogen content of the leaves (SA plants); (ii) a shaded plot where rice plants were grown in a greenhouse with low light intensity and high humidity (light intensity was lower by 40%, relative air humidity was higher by 15–20% and air temperature was lower by 2–3°C compared to outdoors) for about 6 weeks before measurements to decrease the root-top ratio and root-leaf area ratio (SP plants); (iii) a plot with additional ammonium sulfate where 5 g ammonium sulfate was applied to soil in a pot several days before measurements to increase the nitrogen content of the leaves (AS plants). Soil-cultured rice plants were growing under submerged soil conditions at the time when the exudation rate, transpiration rate and leaf xylem water potential were measured.

Solution-cultured rice plants were also used for measurements. They were grown in 1/2,000 a Wagner pots at the rate of 3 hills per pot (5 plants per hill). There were two plots prepared as follows: (i) a plot where rice plants were grown on a standard culture solution (Kimura B) (SN plants); (ii) a plot where rice plants were grown about 2 months before measurements on a culture solution of which the nitrogen concentration was reduced to about 41% of the standard culture solution by partially substituting CaCl₂ for Ca(NO₃)₂ and also reducing (NH₄)₂SO₄ concentration to increase the top-root ratio and root-leaf area ratio (LN plants). To increase the leaf nitrogen content of the LN plants relative to that of the SN plants, the former plants were grown on the standard culture solution for about 1

week before measurements were made and, if necessary, $(\text{NH}_4)_2\text{SO}_4$ was added to the culture solution. The standard culture solutions were used in both plots during measurements.

Measurements of exudation rate from the leaf blade were taken at 3 cm distance from the base of the leaf blade. The exudated sap was collected by attaching sanitary cotton to the cut surface of the leaf blade for 2 hours in the dark room where air temperature and relative humidity were 25°C and almost 100%, respectively. The increase in the cotton weight was measured as mentioned in a previous report²⁾.

Transpiration measurements were taken by weighing methods⁷⁾. The stems of rice plants in a pot were kept apart by a cotton thread spreading them outward in order to minimize mutual shading. All the leaves on each stem were thus exposed to the same solar radiation and wind speed at the time of transpiration rate measurements. Leaf xylem water potentials of three or five leaves from fully expanded uppermost leaves attached to a main stem or on primary tillers coming from lower nodes were measured with the pressure chamber (PMS, Inc.). The mean of the 3 (at the panicle formation stage) or 5 (at the ripening stage) leaf xylem water potentials was taken as the leaf xylem water potential of the plant.

Since the rice plants were grown under submerged soil conditions and the water potential of the culture solution was above -0.03 MPa, the water potential of the soil or the culture solution could be regarded as 0 MPa. Consequently, according to a previous report⁴⁾, the resistance to water transport through the roots to the leaves (R) was calculated as follows:

$$R = -\Psi_x/T$$

where Ψ_x is the leaf xylem water potential and T the transpiration rate on the basis of leaf

area. Comparisons of the resistance to water transport were made at a transpiration rate of above $1.5 \text{ gH}_2\text{O dm}^{-2} \text{ h}^{-1}$, where the resistance remained constant.

After taking measurements of the transpiration rate, roots and leaf blades were detached from the rice plants. Leaf area was measured with automatic area meter (Hayashi-Denko, AAM-5). All the organs of some of the plants were dried at 90°C in a ventilated oven, whereas the roots and stems of others were fixed with formalin-acetic-alcohol (FAA) for measurements of root length with the root length scanner (Commonwealth Aircraft).

Leaf nitrogen content on a dry weight basis was determined by titration following semi-micro Kjeldahl digestion.

Results and Discussion

1. Growth

Shoot and root growths of the rice plants grown under the different conditions were compared (Table 1). The shoot weight of the SP plants was smaller than that in the SA plants and that in the control plants but there was no significant difference in leaf area among the plants in the three plots. Root weight was considerably smaller in the SP plants. Also, both the root weight per shoot weight and root weight per leaf area were far lower in the SP plants than those in the SA plants as well as in the control plants. These results indicate that the SP plants grown under the conditions of low light intensity and high humidity develop smaller root systems compared to the plants of the other plots, which agrees with the results of the previous report⁷⁾. The roots were colored black in the SA plants, that is, they developed a sign of the so-called "root-rot" disease. On the other hand, shoot weight and leaf area were smaller, but root length per stem was larger, in the LN

Table 1. Shoot weight, leaf area and root weight of rice plants grown in (i) a plot supplied with soluble starch and ammonium sulfate (SA), (ii) a shaded plot (SP), (iii) a plot with ammonium sulfate (AS), and (iv) a control at the panicle formation stage.

Plot	Shoot	Leaf	Root	Root wt.	Root wt.	Root wt.
	wt. (g)	area (dm ²)	wt. (g)	per stem (g)	Shoot wt. (g/g)	Leaf area (g/dm ²)
Control	17.2	17.14	3.06	0.18	0.18	0.19
SA	17.5	15.20	2.88	0.16	0.16	0.19
SP	11.4	15.96	1.41	0.09	0.12	0.09
AS	16.8	17.44	2.85	0.16	0.17	0.16

Table 2. Shoot weight, leaf area, root weight and root length of rice plants grown on a culture solution of low nitrogen level(LN) and grown on a standard culture solution(SN) at the booting stage.

Plot	Shoot	Leaf	Root	Root	Root length per stem (m)	Root wt.	Root length
	wt. (g)	area (dm ²)	wt. (g)	length (m)		Shoot wt. (g/g)	Leaf area (m/dm ²)
SN	31.1	21.15	4.54	342.6	15.5	0.15	16.2
LN	27.2	18.06	4.72	345.0	18.1	0.18	19.1

Table 3. Exudation rate (mg/h)* and leaf nitrogen content (% of dry weight) of rice plants grown in (i) a plot supplied with soluble starch and additional ammonium sulfate (SA), (ii) a shaded plot(SP), (iii) a plot with additional ammonium sulfate (AS), and (vi) a control plot.

Growth stage	Plot	Exudation rate	Nitrogen content
Panicle formation	Control	424.0 ± 40.0a**	2.57
	SA	228.1 ± 30.8b	3.18
	AS	675.9 ± 42.3c	4.17
Booting	Control	228.3 ± 45.9a	2.13
	SP	144.4 ± 20.2b	2.69
	AS	343.9 ± 60.0c	3.15

*Total amount of exudation rate of upper three expanded leaves attaching on a main stem.

**Means followed by different letters are significantly different at 1% level.

plants than those in the SN plants (Table 2). Since a smaller number of tillers emerged in the LN plants than in the SN plants, there was very small difference in the root weight and root length per plant between the plants of both plots (Table 2). However, root weight per shoot weight and root length per leaf area were larger in the former than in the latter (Table 2). Therefore it could be concluded that the LN plants developed larger root system compared to the SN plants.

2. Exudation rate

The exudation rate of the SA plants whose roots developed the sign of "root-rot" decreased markedly, indicating that such plants were inferior to the control plants in active water uptake capacity. The exudation rate of the SP plants which developed smaller root systems was lower than that in the control plants (Table 3). On the other hand, the exudation rate of AS plants which had in-

Table 4. Exudation rate* (mg/h) and leaf nitrogen content (%) on a dry weight basis in rice plants grown on a culture solution of low nitrogen level (LN) and on a standard culture solution (SN) at the booting stage.

Plot	Exudation rate	Nitrogen content
SN	228.9 ± 77.2 a**	2.73
LN	282.7 ± 42.4 b	2.84

*Total amount of exudation rate of upper three fully expanded leaves attaching on a main stem. The culture solutions of both plots were the standard during measurements, which applies correspondingly to Table 6 and 7 and Fig. 2.

**The means followed by different letters are significantly different at 1% level.

creased leaf nitrogen content as a result of the application of additional ammonium sulfate increased markedly (Table 3). This indicates that the plants supplied with additional ammonium sulfate were superior to the control plants in active water uptake capacity. The LN plants which developed larger root system had a higher exudation rate than the SN plants (Table 4).

3. Resistance to water transport

Resistance to water transport was compared among rice plants whose active water uptake capacities were different from each other. The resistance to water transport in the SA plants was larger than that in the control plants both at the panicle formation stage and at the ripening stage (Table 5). Also, the resistance in the SP plants was larger than that in the control plants both at the panicle formation stage and at the ripening stage (Table 5). The resistance in the LN plants was smaller than that of the SN plants (Table 6). These results indicate that there was considerable difference in passive water uptake capacity among the

Table 5. Resistance to water transport in rice plants grown in (i) a plot supplied with soluble starch and additional ammonium sulfate (SA), (ii) a shaded plot (SP), (iii) a plot with additional ammonium sulfate (AS) and (iv) a control plot.

Growth stage	Plot	Range of measurement		Resistance to water transport ($\times 10^4$ MPa s cm $^{-1}$)
		Transpiration rate (gH $_2$ O dm $^{-2}$ h $^{-1}$)	Leaf xylem water potential (MPa)	
Panicle formation	Control	1.6~2.7	-0.34~-0.68	7.8 \pm 1.2 a*
	SA	1.5~2.2	-0.50~-0.82	11.6 \pm 1.6 b
	SP	2.1~2.8	-0.54~-0.80	9.4 \pm 0.9 c
	AS	1.6~3.3	-0.20~-0.82	8.1 \pm 0.9 a
Ripening	Control	1.8~2.3	-0.31~-0.46	6.3 \pm 0.7 a
	SA	1.5~1.8	-0.46~-0.74	13.1 \pm 1.5 b
	SP	1.5~2.2	-0.36~-0.57	8.8 \pm 0.8 c
	AS	1.5~2.8	-0.31~-0.56	7.0 \pm 1.1 a

*Means followed by different letters are significantly different at 5% level at each growth stage.

Table 6. Resistance to water transport in rice plants grown on a culture solution of low nitrogen level (LN) and on a standard culture solution (SN).

Growth stage	Plot	Range of measurement		Resistance to water transport ($\times 10^4$ MPa s cm $^{-1}$)
		Transpiration rate (gH $_2$ O dm $^{-2}$ h $^{-1}$)	Leaf xylem water potential (MPa)	
Panicle formation	SN	2.1~4.2	-0.19~-0.59	4.3 \pm 0.6 a*
	LN	2.8~4.7	-0.30~-0.52	3.5 \pm 0.5 b
Booting	SN	2.1~4.2	-0.19~-0.42	3.6 \pm 0.3 a
	LN	2.0~4.9	-0.18~-0.42	3.2 \pm 0.2 b

*Means followed by different letters are significantly different at 5% level at each growth stage.

plants grown in the three different plots, and also between the LN plants and the SN plants. This means that passive water uptake capacity was lower in rice plants in which "root-rot" occurred as well as in those which developed a small root system but was superior in rice plants which developed large root system. On the other hand, there was no difference in the resistance to water transport between the plants whose leaf nitrogen content was increased by the application of ammonium sulfate and the control plants (Table 5) although the former was superior to the latter in active water uptake capacity.

4. Active and passive water uptake relations

From the results mentioned above, it is clear that active water uptake capacity and passive water uptake capacity change together in many cases but in some case they do not change simultaneously. It could therefore be concluded that there is no direct relationship between active water uptake capacity and passive water uptake capacity. A gradient

between osmotic potential in root xylem affected by ion absorption capacity and soil water potential, and root resistance to water transport (or root hydraulic conductance) in osmotic water uptake are important internal factors that influence the exudation rate¹⁴). On the other hand, a gradient between hydrostatic pressure in root xylem caused by intense transpiration and soil water potential is a major driving force in passive water uptake. The only internal factor for passive water uptake is root resistance to water transport. Root resistance to water transport consists of radial hydraulic resistance (resistance from the root surface to the xylem of the root) and axial hydraulic resistance. The former is far larger than the latter¹). Root resistance in active water uptake and in passive water uptake might change simultaneously because water must pass through root cell membranes even though the radial water pathway in active water uptake was reported to be different from that in passive water uptake¹⁹). Ion uptake is much affected by the physiological

Table 7. Resistance to water transport per root length ($\times 10^5$ MPa s cm^{-2}) in rice plants grown on a culture solution of low nitrogen level (LN) and on a standard culture solution (SN).

Growth stage	Plot	Resistance
Panicle formation	SN	6.8 ± 1.0 a*
	LN	7.8 ± 1.1 b
Booting	SN	5.7 ± 0.4 a
	LN	6.1 ± 0.2 a

*The means followed by different letters are significantly different at 5% level at each growth stage.

activity of roots^{15,16)} and the nitrogen condition^{17,18)}. So the simultaneous changes of active and passive water uptake capacities in the SA plants, the SP plants and the LN plants were supposed to result from (1) the changes in active ion uptake and in the radial hydraulic resistance of roots, or (2) only the change in radial hydraulic resistance of roots. On the other hand, the higher active water uptake capacity without the change of passive water uptake capacity in the AS plants was supposed to result from the increase of active ion uptake, not from the decrease of radial hydraulic resistance.

In order to investigate the factors relating to the occurrence of the difference in passive water uptake capacity between the LN plants and the SN plants, the resistance to water transport per unit root length was calculated from transpiration rate per hill, leaf xylem water potential and root length per hill (Table 7). The resistance in the LN plants was higher than that in the SN plants at the panicle formation stage but there was no significant difference in the two respective resistances at the booting stage. It was therefore concluded that the higher passive water uptake capacity in the LN plants might have been realized through the development of longer roots even though they were inferior to the SN plants in passive water uptake capacity per root length. It should therefore be noted that root passive water uptake capacity is able to increase only by increasing the amount of roots. On the other hand, the exudation rate and the resistance to water transport decreased markedly in the SA plants even though their root weight did not decrease considerably, which indicates

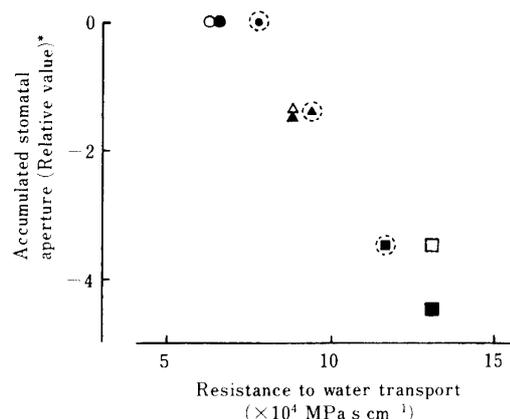


Fig. 1. Relationship between resistance to water transport and midday stomatal aperture. Squares, triangles and circles represent the plants in the plot with soluble starch and additional ammonium sulfate (SA), the plants in the shaded plot (SP), and the control plants, respectively. Closed and circled symbols, closed symbols and open symbols represent the measurements on Jul. 29, Aug. 29, Aug. 31, respectively.

* The difference in the accumulated stomatal aperture between the treated plants and the control plants under intense transpiration and sufficient solar radiation during the period when the difference in the stomatal aperture between the plots existed. Negative values mean the accumulated stomatal aperture in the treated plants was smaller than that in the control plants, that is, stomata in the former was closed more than those in the latter. Stomatal aperture was measured by the improved infiltration method⁶⁾.

that active and passive water uptake capacities per unit root length in such plants are lower than control plants because root weight correlates with root length in rice plants. This means that both total root length and water uptake capacity per unit root length might contribute to water uptake capacity.

5. Relationship between resistance to water transport and the midday stomatal closure

Since the depression in the stomatal conductance and the photosynthetic rate were remarkable in rice plants with lower leaf water potential under intense transpiration⁷⁾, the relationship between resistance to water trans-

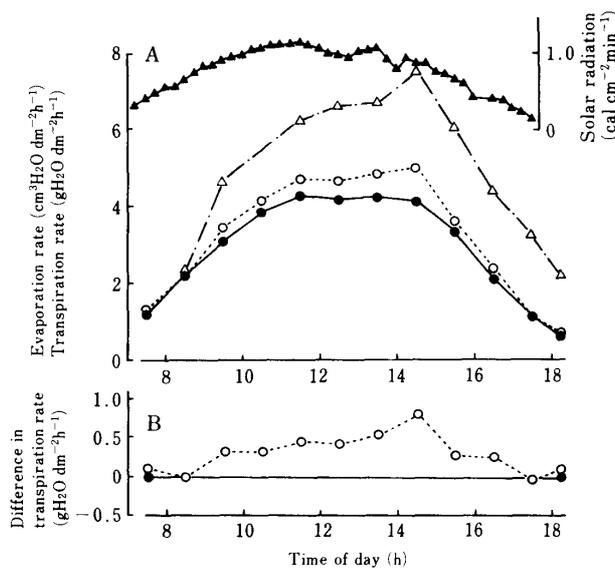


Fig. 2. Diurnal course of solar radiation (solid triangles), evaporation rate* (open triangles) and transpiration rate in rice plants grown on the culture solution of low nitrogen level (LN, open circles) and the standard culture solution (SN, closed circles) (A) and the difference in transpiration rate between the plants** (B) (Booting stage).

* Evaporation from a wet filter paper (5.5 cm diameter) indicating potential transpiration rate.

** (Transpiration rate in the LN plants) — (Transpiration rate in the SN plants).

port and the degree of the depression was investigated. Fig. 1 shows that the midday stomatal aperture became smaller in the plants whose resistance to water transport was higher. It was confirmed that passive water uptake capacity affects the degree of the midday depression in the stomatal conductance and the photosynthetic rate. On the other hand, even though the stomatal aperture in the AS plants was far larger than that in the control plants in the morning, the difference between them became small during the intense midday transpiration^{7,8)} because there was no difference in passive water uptake capacity between them.

The midday stomatal aperture of the LN plants which developed larger root systems as well as showing greater passive water uptake capacity was compared with that of the SN plants by measuring the diurnal changes of

transpiration rates on a clear day (Fig. 2). The nitrogen contents in leaves of these plants were not different from each other (Table 4) and the difference in transpiration rate between them was very small in the early morning. However, at higher transpiration rates, the transpiration rate in the LN plants became higher than that in the SN plants (Fig. 2 A) with the difference in transpiration rates reaching maximum at the maximum transpiration rate (Fig. 2 B). These results indicate that there was no difference in the stomatal conductances of the LN plants and the SN plants in the early morning. A difference, however, appeared and even increased as the transpiration rate increased in the daytime. In the view of the high correlation between gas exchange rate through stomata and photosynthetic rate, these results also confirmed the suggestion in previous reports^{7,8)} that higher passive water uptake capacity is essential, in addition to the increase in leaf nitrogen content, in increasing the total daily photosynthesis.

Morphological and physiological characteristics of roots relating to water uptake and the development of the root system are affected by soil conditions and cultivation practices, but many cultivars are known to respond differently to such factors. It was found out that the differences in the root characteristics and the development of a particular root system are closely related to the differences in dry matter production and yield^{3,11,12,13)}. However, root water uptake capacity, especially passive water uptake capacity, had not been investigated quantitatively. It will be necessary therefore to analyze how the differences in root water uptake capacity occur with reference to the physiological and ecological characteristics of the shoot.

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* In Japanese with English summary.

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