Japan. Jour. Crop Sci. 59(4) : 801—808 (1990)

Leaf Conductance in Japonica and Indica Rice Varieties

I. Size, frequency, and aperture of stomata*

Sachio MARUYAMA and Koichi TAJIMA**
(*National Institute of Agrobiological Resources, Tsukuba, Ibaraki 305, Japan*)
Received April 23, 1990

Abstract : Varietal differences in leaf conductance were studied in field conditions using 51 rice varieties, including japonica, indica, and japonica-indica hybrid. Leaf conductance of indica and japonica-indica hybrid was clearly larger than that of japonica at panicle formation stage. Cuticular conductance was much lower as compared to leaf conductance, indicating the stomata is the major path of water loss. Thus, we measured size, frequency, and aperture of stomata, and evaluated the relative importance of these factors to leaf conductance.

Only slight differences were observed in length of the pore and the guard cells of stoma among rice varieties. By contrast, stomatal frequency of japonica-indica hybrid and semidwarf indica was clearly higher than that of japonica and tall indica. In addition, stomatal aperture of indica and japonica-indica hybrid was remarkably larger than that of japonica. Analysis of relative importance of frequency and aperture of stomata to leaf conductance showed that the leaf conductance was strongly affected by stomatal aperture, whereas it was slightly influenced by stomatal frequency in rice. It is concluded that the stomatal sperture is the major factor which causes the difference of leaf conductance between japonica and indica or japonica-indica hybrid.
Key words : Indica rice, Japonica rice, Leaf conductance, Stomatal aperture, Stomatal frequency.

日本稲とインド稲の葉の拡散伝導度の差異について　第1報　気孔の大きさ，密度，および気孔開度：丸山幸夫・田嶋公一（農林水産省農業生物資源研究所）

要　旨：日本稲，インド稲，および日印交雑種，合わせて51品種を用い，葉の拡散伝導度の品種間差異を圃場条件下で検討した．幼穂形成期に測定した，インド稲と日印交雑種の葉の拡散伝導度は，日本稲より明らかに大きかった．クチクラ拡散伝導度が葉の拡散伝導度より著しく小さいことから，この葉の拡散伝導度の品種群間の差異は，気孔に関連した特性に起因するものと判断された．そこで，これらについて調べたところ，気孔開口長や孔辺細胞の大きさの品種群間の差異は小さいが，気孔密度と気孔開度には明らかな差異があり，インド稲半矮性種および日印交雑種の気孔密度と気孔開度は，日本稲より大きい傾向が認められた．さらに，この両者と葉の拡散伝導度との関係を詳しく検討したところ，気孔密度より気孔開度の方がより強く葉の拡散伝導度を支配していることが明らかとなった．したがって，日本稲とインド稲または日印交雑種の葉の拡散伝導度の差異をもたらす主要な要因は気孔開度と結論される．
キーワード：インド稲，気孔開度，気孔密度，日本稲，葉の拡散伝導度．

Crop plants uptake CO_2 for assimilation from the atmosphere, which requires an intensive gas exchange, accompanied by water loss to their environment. However, excessive water loss reduces their photosynthetic activities, and crop plants cannot maintain growth in extreme cases. In order to resolve this dilemma, land plants developed an epidermis covered with cuticle and stomata which control the diffusion resistance through their openings. Thus, it is highly important to understand what mechanism(s) regulates the gas exchange, for improvement of productivity and water use efficiency in crop plants[11].

Although rice is generally characterized as a semiaquatic species well adapted to submerged soil, rice varieties have adapted to a wide range of habitats, from flooded lowland to dry upland culture conditions. Moreover, rice varieties also have been grown in a diverse range of latitude and altitude, where they encountered high and low temperatures. Thus, soil water and temperature conditions would affect the development of water-saving systems differently among rice varieties, during the processes of establishment and improvement as crops.

It has been reported that indica rice consumes a larger amount of water per unit leaf

* The parts of this work were presented in the 181st and 189th Meetings of the Crop Science Society of Japan, Utsunomiya, April, 1986 and Sendai, October, 1989, respectively.

** Present address ; Biological Engineering Laboratory, Asahi Industries Co., LTD., Kamikawa-machi, Kodama-gun, Saitama 367-02, Japan.

area than japonica rice[4,6,10,13]. However, it is not clear what mechanism(s) causes the varietal difference. It is important to investigate the difference and its causes from the viewpoint of crop physiology, because indica varieties have recently been introduced for breeding high-yielding varieties in Japan. Therefore, we conducted a study of morphological and physiological characteristics related to water-transport pathway in rice varieties. In the present study, we measured size, frequency, and aperture of stomata of japonica, indica, and japonica-indica hybrid, and evaluated the relative importance of these factors to the differences in leaf conductance among these variety groups.

Materials and Methods

Plant materials

Experiments were conducted using 55 (1982) and 51 (1985) rice varieties, at a paddy field of National Institute of Agrobiological Resources, Tsukuba, Ibaraki, Japan. The varieties were selected on the basis of similar heading date in Tsukuba, including japonica, indica, and japonica-indica hybrid (Table 1). The seeds were sown early in May in "Kabumaki pot" filled with soil, which was a plastic tray with square compartments of 16 mm in the dimension. Seedlings of each variety at the fifth or sixth leaf stage were transplanted to the paddy field early in June, at 35 cm in row space and at 15 cm hill space within a row, resulting in 19 plants per square meter. The paddy field was basally fertilized with 7 g m^{-2} of nitrogen, phosphate, and potash, respectively, and topdressed with 1.5 g m^{-2} of nitrogen twice, at most active tillering stage, late in July, and at spikelet differentiation stage, early in August. The plants were grown under submerged conditions up to around 2 cm from soil surface in the water, until flowering stage.

For measurement of cuticular conductance, three seedlings were transplanted into a 9 liter pot filled with soil, which was fertilized with 1 g pot^{-1} of nitrogen, phosphate, and potash, respectively. The plants in the pot were grown under similar conditions to the field, until panicle formation stage.

Leaf conductance

Leaf diffusive resistance was measured with Steady State Porometer (LI-COR, LI-1600) on clear days at tillering and panicle formation stages. Measurements were carried out on the middle part of the abaxial surface of the second fully developed leaf on the main culm, and two leaf blades were used for measurements of each variety, unless otherwise described. The inverse value of diffusive resistance was defined as leaf conductance.

Cuticular conductance

Cuticular conductance was estimated according to Yoshida and de los Reyes[15] by measuring leaf conductance with Steady State Porometer in a dark room, where the temperature and the humidity were controlled at 27°C and 60% RH, respectively. The plants grown

Table. 1. Varieties used in the field experiments. ([a]), ([b]): varieties used only in the experiment for stomatal morphology and that for leaf conductance and stomatal aperture, respectively.

Japonica, native
Joushu[a], Ginbouzu, Sen-ichi, Sekitori, Tamanishiki, Takenari, Kokuryoumiyako, Araki, Kameji, Fusaku Shirazu, Asahi, Kotobuki[a], Hiroshima Shinpo[a]
Japonica, improved
Kinmaze, Nakate Shin Senbon, Yamabiko[a], Manryou, Kusabue, Nipponbare, Mangetsu Mochi, Reihou, Akitsuho[a], Tsukushibare, Akinishiki, Kochihibiki, Wakagoma[a]
Japonica-indica hybrid
Tongil, Yeongnamjosaeng, Yushin, Raekyung, Milyang 21, Milyang 22, Milyang 23, Milyang 30, Milyang 44[b], Suweon 258, Suweon 262, Akenohoshi
Indica, semidwarf
Chen-chu-ai, Nanjing 11, Ai-chiao-nan-teh, Dee-geo-woo-gen, Lu-tou, Gue-chao 2[b], Taichung-xian 10[b], BG 34-8, RP 9-3, Bae-md-3-3, IR 2061, IR 24[a]
Indica
Yin-nian, Guan-yin-xian, Gai-liang-dong-wan-bai, Yan-jian-ke, Boro I, Basilanon, Lady Wright, Agulha

in pots were transferred to the dark room at 10 a.m., and leaf conductance was determined at 5 h later. Measurements were made on the middle part of the abaxial surface of the second fully developed leaf on the main culm.

Size and frequency of stomata

In the experiment of varietal differences in 1982, the blade of flag leaf was sampled at heading stage, fixed with FAA solution containing formalin, acetic acid, ethanol, and water (5 : 5 : 45 : 45, v/v) immediately after sampling, and then stored until observations. Leaf sample was cleared by the whole-leaf clearing technique according to Koga and Kobayashi[5], and the cleared leaf surface was observed with a microscope (Nikon Biophot HFX-II). Three leaf blades were used for measurements of size and frequency of stomata in each variety. Six stomata were selected in each leaf sample at random, and the length of the guard cells of stoma was measured at 600-fold magnification. The number of stomata was counted in each field at 400-fold magnification, and measurements were repeated in two different fields in each leaf sample.

In the experiment on relation between leaf conductance and stomatal frequency in 1985, the part of the blade of second fully developed leaf, used for the measurements of leaf conductance and stomatal aperture, was quickly sampled into alcoholic lactophenol solution for clearing the tissue, and the number of stomata was determined as described above.

Stomatal aperture

Infiltration technique[1] was employed for measurement of stomatal aperture. Infiltration solutions were applied on the middle part of the abaxial surface of the second fully expanded leaf on the main culm, on clear days in tillering and panicle formation stages. In the experiments on stomatal aperture in relation to leaf conductance, stomatal aperture was measured, after the measurements of leaf conductance, on the same part of the leaf blade.

Stomatal aperture was also observed with a scanning electron microscope, according to Shiraishi et al[12]. Briefly, the second fully developed leaf blade was sampled, immediately immersed into Karnowsky's fixative, stained with 2% (w/v) of tannic acid solution, washed with distilled water, and dehydrated with ethanol and acetone. After the acetone was replaced with isoamylacetate, the sample was dried in a critical point drier (Hitachi HCP-2), and coated with gold by an ion-coater (Hitachi IB-3). The stomata on the abaxial surface were photographed with a scanning electron microscope (Hitachi-Akashi MSM-102) with a 15 kv accelaration voltage, and width of ten stomata on each leaf blade was determined on the photograph. Four leaf blades were used for measurements in each variety.

Results

Leaf conductance

Leaf conductance of 51 rice varieties was measured by the porometer method on clear days at panicle formation stage in field conditions. Leaf conductance of the adaxial surface was similar to that of the abaxial in three varieties tested (data not shown). Therefore, measurements of leaf conductance of the abaxial surface were performed using 51 varieties, as shown in Table 2. Values of leaf conductance were similar in semidwarf and tall indica varieties, and slight difference was observed betweeen these variety groups and japonica-indica hybrid. However, leaf conductance of the three variety groups was clearly larger than that of native and improved japonica, indicating that the former variety groups transpired a larger amount of water per unit leaf area than the latter groups.

Cuticular conductance

Cuticular conductance of Nipponbare (japonica), Dee - geo - woo - gen (indica,

Table. 2. Varietal differences in leaf conductance of rice. Leaf conductance was measured with a porometer between 9 and 11 a.m. on August 8, 1985, and values are expressed as mean±S.D. in each variety group. Figures followed by a different letter are significantly different at the 5% level.

	No. of variety	Leaf conductance (cm s^{-1})
Japonica, native	10	0.65±0.09[d]
Japonica, improved	10	0.75±0.11[c]
Japonica-indica hybrid	12	1.13±0.12[b]
Indica, semidwarf	11	1.25±0.15[a]
Indica	8	1.27±0.08[a]

semidwarf), and Boro I (indica) was estimated at panicle formation stage by measuring leaf conductance in darkness, where the transpiration through stomata would be negligible. As shown in Table 3, the values of cuticular conductance were 4 to 7% of those of leaf conductance, suggesting most of the water transpires through stomata under light conditions. No significant difference was observed among the three varieties used.

Size and frequency of stomata

Size and frequency of stomata were determined on the flag leaf of 55 rice varieties. In the preliminary experiments, differences of stomatal frequency within a leaf blade were studied using nine varieties selected from them. Stomatal frequency of the middle part was larger than that of the tip or the base of the leaf blade, and stomatal frequency around the midrib and the leaf margins was smaller than that in the part between them. On the other hand, stomatal frequency of adaxial surface was less than that of abaxial surface. However, the ratio of adaxial to abaxial was around 80%, although there were large differences in stomatal frequency among the nine tested varieties (data not shown). Therefore, one can estimate total stomatal frequency by measuring that of abaxial surface. As there was not clear difference in stomatal size, defined as the length of the guard cells, between adaxial and abaxial surface of the leaf blade (data not shown), we measured stomatal size and frequency in the middle part of the abaxial surface of the flag leaf, except leaf veins and margins.

Table. 3. Varietal differences in cuticular conductance of leaf blade of rice. Cuticular conductance was estimated by the leaf conductance in darkness, and values are expressed as mean±S.D. of 5 replicates. Figures followed by a different letter are significantly different at the 5% level.

Variety	Cuticular conductance (cm s^{-1})
Nipponbare (japonica)	0.049±0.005[a]
Dee-geo-woo-gen (indica, semidwarf)	0.067±0.021[a]
Boro I (indica)	0.047±0.004[a]

only slight differences were observed in stomatal size among the five variety groups (Table 4). To assure the result, the actual length of the pore was observed with a scanning electron microscope. The value was 10.6μm in Nipponbare (japonica) and 10.5 μm in Dee-geo-woo-gen (indica, semidwarf), and the difference between the two varieties was small. On the other hand, there were clear varietal differences in stomatal frequency. Japonica-indica hybrid had the highest stomatal frequency, which was followed by semidwarf indica, and native and improved japonica and tall indica varieties had a lower frequency of stomata. The product of stomatal size (A) and stomatal frequency (B) was calculated and compared within the five variety groups (Table 4). The value of the product (A×B), which is a measure of stomatal transpiration potential, was larger in japonica-indica hybrid and semidwarf indica than that in native and improved japonica or tall indica.

Stomatal aperture

Stomatal aperture was measured by the infiltration method on clear days in maximum tillering stage. Figure 1 shows diurnal changes

Table. 4. Varietal differences in size and frequency of stomata of leaf blade in rice. Size and frequency of stomata were determined on the abaxial surface of the flag leaf on the main culm, and values are expressed as mean±S.D. in each variety group. Figures followed by a different letter are significantly different at the 5% level.

	No. of variety	Stomatal size (A) (μm)	Stomatal frequency (B) (mm^{-2})	A×B ($mm\ mm^{-2}$)
Japonica, native	13	22.4±0.7[ab]	557±44[c]	12.4±0.9[c]
Japonica, improved	13	22.2±0.7[b]	514±33[d]	11.5±0.6[d]
Japonica-indica hybrid	11	21.5±0.9[c]	730±66[a]	15.7±1.2[a]
Indica, semidwarf	10	22.0±1.6[ab]	647±60[b]	14.2±1.0[b]
Indica	8	23.0±0.7[a]	549±72[cd]	12.6±1.8[cd]

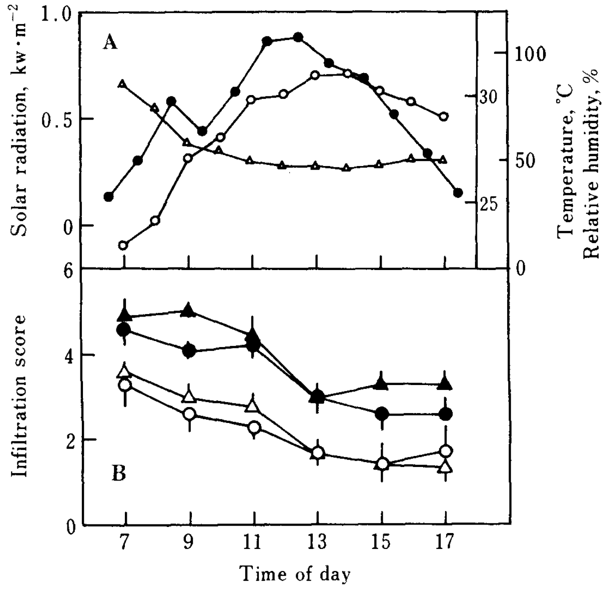

Fig. 1. Diurnal changes in meteorological conditions (A) and stomatal aperture of leaf blade in rice varieties (B), on July 26, 1985. Stomatal aperture was measured by infiltration method and expressed as infiltration score, according to Ishihara et al[1]. A : ○, Temperature ; △, relative humidity ; ●, solar radiation. B : ○, Nipponbare (japonica) ; △, Manryou (japonica) ; ●, Dee-geo-woo-gen (indica, semidwarf) : ▲, RP 9-3 (indica, semidwarf). Each vertical bar indicates standard deviation of 6 replicates.

in meteorological conditions and stomatal aperture of leaf blade of 4 varieties, Manryou (japonica), Nipponbare (japonica), Dee-geo-woo-gen (indica, semidwarf), and RP 9—3 (indica, semidwarf). The stomatal aperture showed similar diurnal changes among the four varieties. It was high early in the morning and gradually decreased from around noon to early in the afternoon, and remained at the same level thereafter. The stomatal aperture of semidwarf indica, Dee-geo-woo-gen and RP 9—3, was clearly larger than that of japonica varieties, Manryou and Nipponbare, at every time of day.

Relationsphip between leaf conductance and frequency or aperture of stomata

Stomatal aperture and leaf conductance of Nipponbare (japonica) and Dee-geo-woo-gen (indica, semidwarf) were measured precisely, and the relationship between these characteristics was analyzed. The values of stomatal frequency of Nipponbare and Dee-geo-woo-gen were 471 and 631 mm^{-2}, respectively. Diurnal changes of stomatal aperture were determined by both the infiltration method and the scanning electron microscopy, and those of leaf conductance were measured by the porometer method, and then, obtained data were plotted as shown in Fig. 2A and 2B. Linear correlation was observed between

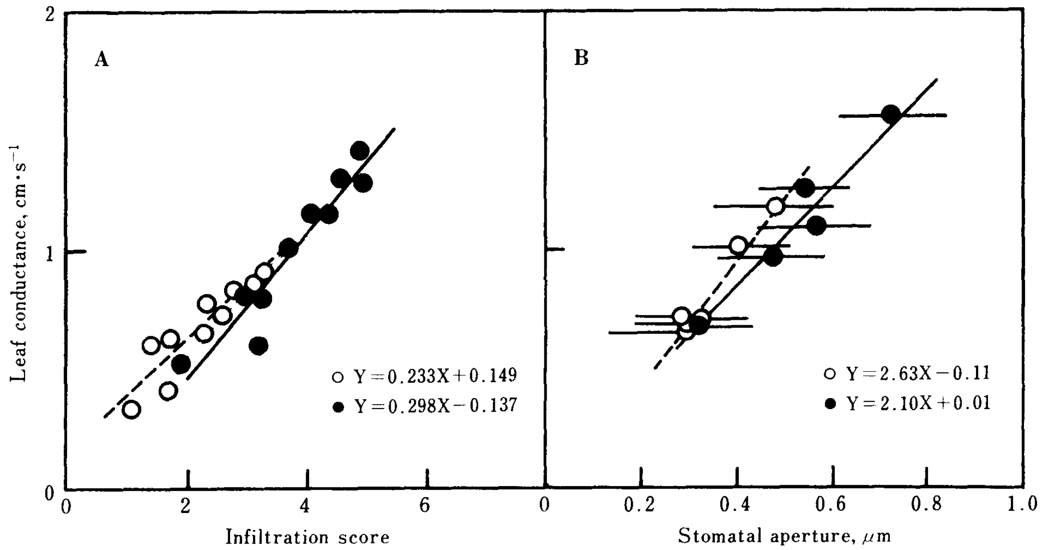

Fig. 2. Relationships between stomatal aperture and leaf conductance using infiltration method (A) or scanning electron microscopy (B). Diurnal changes in leaf conductance and stomatal aperture were measured on July 26 and 31 for A, and August 2 for B, in 1985, and those data are plotted on the figure. ○, Nipponbare (japonica) ; ●, Dee-geo-woo-gen (indica, semidwarf). Each horizontal line in B indicates standard deviation of 40 replicates.

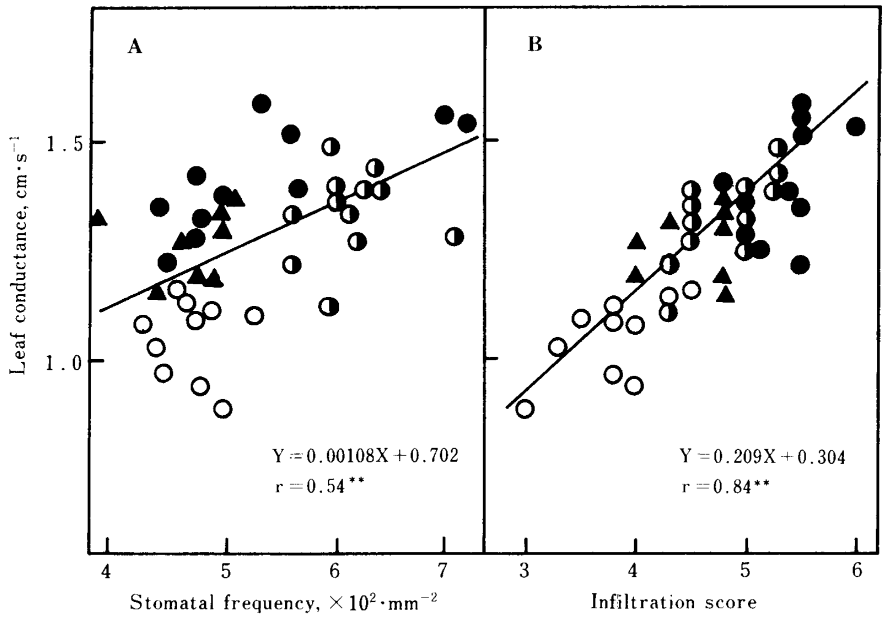

Fig. 3. Relationship between leaf conductance and stomatal frequency (A) or stomatal aperture (B) in rice varieties. Measurements were made between 9 and 11 a.m. on July 30, 1985. Two leaf blades were used for measurements in each variety. ○, Japonica, improved; ◑, japonica-indica hybrid; ●, indica, semidwarf; ▲, indica. **Significant at the 1% level.

stomatal aperture and leaf conductance, regardless of the method of measurement of stomatal aperture. The regression lines in Dee-geo-woo-gen were similar to those in Nipponbare, although Dee-geo-woo-gen had 34% more stomata per leaf area than Nipponbare.

Effects of frequency and aperture of stomata on leaf conductance were studied using 41 rice varieties, as shown in Fig. 3A and 3B. Leaf conductance was correlated with both frequency and aperture of stomata. The correlation coefficient between leaf conductance and stomatal frequency was 0.54, and that between leaf conductance and stomatal aperture was 0.84 (both significant at the 1% level). However, as stomatal aperture correlated with stomatal frequency ($r=0.46$, significant at the 1% level), calculated partial correlation coefficient between leaf conductance and stomatal freguency decreased to 0.30, and not significant at the 1% level. In contrast, the partial correlation coefficient between leaf conductance and stomatal aperture was 0.79 (significant at the 1% level), which was similar to the single correlation coefficient.

Discussion

Transpiration per unit leaf area in indica was reported to be larger than that in japonica[4,6,10,13], and the present study confirms the previous result. The present results also suggest that the leaf conductance of both semidwarf and tall indica, and japonica-indica hybrid was larger than that of japonica (Table 2). Kawamitsu and Agata[3], however, failed to detect the reported difference in their study by a chamber method. They measured transpiration of the first fully developed leaf blade, whereas others used the second fully extended leaf blade or whole plant for measurements. Thus, the inconsistent results perhaps come from the difference of the leaf age for measurements. In addition, Kishitani and Tsunoda[4] observed the difference in leaf conductance between those variety groups only at higher temperatures. They found that the transpiration rate of indica was even smaller than that of japonica at low temperatures. Thus, indica rice would transpire more water vapor than japonica in particular physiological and environmental conditions. However, it should be addressed that the difference was observed in field conditions, where rice plant actively grew, in the present study.

Leaf conductance for water vapor is composed of two parallel conductances, stomatal and cuticular conductances. The value of cuticular conductance was remarkably lower than that of leaf conductance, and only slight differences were observed among the variety groups (Table 3), suggesting the difference of leaf conductance is in the stomatal path. In consequence, size, frequency, and aperture of stomata were investigated in order to analyze what factor(s) causes the difference in the leaf conductance.

Yoshida and Ono[17] reported that the stomatal frequency of indica or japonica-indica hybrid was larger than that of japonica. Their work, however, would not be sufficient, because they used only three indica varieties and a japonica-indica hybrid for measurements. Moreover, there were few investigations on varietal difference in pore size of stoma in rice. Thus, the present study is the first precise report on differences in size and frequency of stomata of variety groups in rice.

There were only small differences in the length of the pore and the guard cells in rice varieties. However, the stomatal frequency of japonica-indica hybrid and semidwarf indica was larger than that of japonica, whereas stomatal frequency of tall indica was similar to that of japonica (Table 4). The higher stomatal frequency in semidwarf indica and japonica-indica hybrid could cause larger leaf conductance, as Yoshida[16] observed an inverse relationship between stomatal frequency and stomatal resistance in barley.

On the other hand, the stomatal aperture of indica and japonica-indica hybrid was also larger than that of japonica (Fig. 1 and 3). Similar results were reported using japonica-indica hybrid and japonica varieties[2,7]. Thus, the difference of the stomatal aperture could also explain the difference in leaf conductance among those variety groups.

Two different experiments were conducted to clarify which factor influences leaf conductance strongly. In the first experiment, the relationship between stomatal aperture and leaf conductance was studied with two varieties which differ in stomatal frequency. If the stomatal frequency affected leaf conductance, the relationship would be different between two varieties. However, the regression lines between stomatal aperture and leaf conductance were similar in both varieties (Fig. 2), suggesting the stomatal frequency does not affect leaf conductance so large. In the second experiment, effects of frequency and aperture of stomata on leaf conductance were determined using 41 varieties (Fig. 3). According to the partial correlation coefficients from these relationships, it is suggested that stomatal aperture is the major factor that influences leaf conductance, whereas stomatal frequency affects it only slightly.

The reason why stomatal frequency scarcely affected leaf conductance is not clear at this moment. One of the possibilities could be non-uniform stomatal apertures within a leaf, and the number of opened stoma is similar in every variety group. However, the standard deviations of the width of the pore of the stoma of Dee-geo-woo-gen were similar to those of Nipponbare (Fig. 2B), suggesting the stomata opened uniformly on the leaf surface in these varieties.

The other possibility could be a mutual interference of pores of stomata, if the stomata are in small interstomatal spacing on a leaf surface[8,14]. Stomatal frequency in rice was in the range between 514 and 730 mm^{-2} (Table 4), therefore, the stomata are on the average at a distance of 37 to 44 μm from their neighbors. Stomata on leaf blade of rice are in rows along the length of stomata. As the length of the pore of stoma was 10 to 11 μm from the observations with a scanning electron microscope, the interstomatal spacing is 3.4 to 4.4 times larger than the pore length of stoma. At this situation, the stomatal interference could occur[14], and the effect of stomatal frequency on leaf conductance would be reduced. On the other hand, since the width of the stomatal pore opened only up to 0.73 μm in maximum (Fig. 2B), the interstomatal spacing is at least 50 to 60 time larger than the aperture width of stomata. Therefore, there would be almost no interference along stomatal width, and the influence of stomatal aperture to leaf conductance would perfectly exist. Thus, the mutual interference of stomatal pores is a possible cause to explain the relation between leaf conductance and frequency or aperture of stomata.

In the past, it seemed to be difficult to use stomatal aperture as a parameter to estimate leaf conductance or transpiration of different varieties or plants with different treatments, bacause stomatal frequency or some other morphological factors could cause some differences[13]. However, as stomatal aperture seems to be the major factor which affects leaf conductance in the present study, it would be possible to roughly estimate differences of leaf conductance by measuring stomatal aperture in rice. Infiltration method is useful to investigate stomatal aperture without any expensive equipments. Thus, stomatal aperture seems to be a good parameter to select a variety which have large or small leaf conductance.

It is not clear which factor(s) causes the differece in stomatal aperture between japonica and indica or japonica-indica hybrid. It has been recognized that water status and CO_2 concentration in leaf tissue would affect stomatal actions[9]. Further investigations are needed on physiological factor(s) that causes the differences in stomatal aperture among these variety groups.

References

1. Ishihara, K., T. Nishihara and T. Ogura 1971. The relationship between environmental factors and behavior of stomata in the rice plant. I. On the measurement of the stomatal aperture. Proc. Crop Sci. Soc. Japan 40 : 491—496*.
2. Jiang, C.-Z., T. Hirasawa and K. Ishihara 1988. Physiological and ecological characteristics of high yielding varieties in rice plant. II. Leaf photosynthetic rates. Japan. Jour. Crop Sci. 57 : 139—145*.
3. Kawamitsu, Y. and W. Agata 1987. Varietal differences in photosynthetic rate, transpiration rate and leaf conductance for leaves of rice plants. Japan. Jour. Crop Sci. 56 : 563—570*.
4. Kishitani, S. and S. Tsunoda 1974. Effect of low and high temperature pretreatment on leaf photosynthesis and transpiration in cultivars of *Oryza sativa*. Photosynthetica 8 : 161—167.
5. Koga, H. and T. Kobayashi 1980. A whole-leaf clearing and staining technique to observe the invaded hyphae of blast fungus and host responses in rice leaves. Ann. Phytopath. Soc. Japan 46 : 679—681.
6. Maruyama, S., N. Kabaki and K. Tajima 1985. Water consumptions in japonica and indica rice varieties. Japan. Jour. Crop Sci. 54 : 32—38.
7. Nishiyama, I., M.-H. Lee and Y.-D. Yun 1987. Varietal difference in stomatal aperture in rice seedlings in relation to the cool temperature susceptibility in Tongil group varieties. Japan. Jour. Crop Sci. 56 : 482—490*.
8. Parlange, J.Y. and P.E. Waggoner 1970. Stomatal dimensions and resistance to diffusion. Plant Physiol. 46 : 337—342.
9. Raschke, K. 1975. Stomatal action. Ann. Rev. Plant Physiol. 26 : 309—340.
10. Sakuratani, T. and T. Horie 1985. Studies on evapotranspiration from crops. I. On seasonal changes, varietal differences and the simplified methods of estimate in evaportranspiration of paddy rice. J. Agric. Meteorol. 41 : 45—55*.
11. Schulze, E.-D. 1986. Carbon dioxide and water vapor exchange in response to drought in the atmosphere and in the soil. Ann. Rev. Plant Physiol. 37 : 247—274.
12. Shiraishi, M., Y. Hashimoto and S. Kuraishi 1978. Cyclic variations of stomatal aperture observed under the scanning electron microscope. Plant Cell Physiol. 19 : 637—645.
13. Sugimoto, K. 1973. Studies on transpiration and water requirement of indica and japonica rice plants. I. Relationship of transpiration to leaf area and to meteorological factors. Japan. Jour. Trop. Agric. 16 : 260—264*.
14. Ting, I.P. and W.E. Loomis 1965. Further studies concerning stomatal diffusion. Plant Physiol. 40 : 220—228.
15. Yoshida, S. and E. de los Reyes 1976. Leaf cuticular resistance of rice varieties. Soil Sci. Plant Nutr. 22 : 95—98.
16. Yoshida, T. 1976. On the stomatal frequency in barley. I. The relationship between stomatal frequency and photosynthesis. Japan. J. Breed. 26 : 130—136*.
17. Yoshida, T and T. Ono 1978. Environmental differences in leaf stomatal frequency of rice. Japan. Jour. Crop Sci. 47 : 506—514*.

* In Japanese with English summary.