Differences in the Photosynthetic Response to Air Humidity among Rice Varieties with Special Reference to the Xylem-vessel Size

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Photosynthetic response to air humidity and leaf characters were observed in fourteen rice varieties. In the *indica* type varieties the water-conduction system relative to their specific leaf weight and leaf nitrogen content was found to be more developed than in the *japonica* type varieties. The water-conduction system in the leaf was evaluated based on the ratio of the total cross-sectional area of xylem-vessels at the leaf blade base to the leaf area (RVA). Higher positive correlations between the photosynthetic rates and the RVA, and specific leaf weight were detected under dry than humid air conditions. The present study suggests that RVA may be related to varietal differences in the photosynthetic rate, at least under low air humidity conditions, and that RVA can be used as an index for evaluating the development of the water supply system. The well-developed water conduction system of *indica* type varieties may have evolved as an adaptation to high temperature conditions.

KEY WORDS : *Oryza sativa*, rice varieties, photosynthesis, water stress, air humidity.

Introduction

Rice plants cultivated in paddy fields are supplied with a large quantity of water. However, atmospheric factors, such as high air temperature and low air humidity, may offer the water status of the leaves resulting in water stress. ISHIHARA *et al.* (1978) and HIRAI *et al.* (1984) reported the effect of air humidity on the leaf photosynthetic rate of rice plants. KISHITANI and TSUNODA (1974) studied the effect of air temperature, and reported a significant positive correlation between the photosynthetic rate and the water content of the leaves of twelve rice varieties pretreated with a high temperature. HORIE (1979) evaluated the interrelation of air temperature and humidity with leaf photosynthesis and transpiration in rice.

We observed the photosynthetic response to air humidity of fourteen rice varieties in relation to their leaf characteristics, especially the water-conduction system in the leaf blade.

Materials and Methods

Fourteen varieties listed in Table 1 were investigated. Among them thirteen lowland varieties were taken, regarding the native district of varieties, from twenty five varieties which had been tested in both the temperate and tropical zones in the International Biological Programme, Section UM (Use and Management of Biological Resources) (TANIGUCHI and YOKOYAMA, 1975). An upland variety, Sensho, was included to compare its characteristics with those of the lowland varieties.

Plants sown on 22 April were grown singly in pots (10cm diameter and 20cm in height)

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Table 1. List of varieties used

Plant Number	Variety Name	Origin	Grain Type ¹⁾	Symbol in Figure
1	Culture 340	India	C	● ¹
2	N. 22	India	C	● ²
3	Rafaello	Italy	B	□ ³
4	Fujiminori	Japan	A	● ⁴
5	Sasanishiki	Japan	A	● ⁵
6	Nongkwang	Korea	A	● ⁶
7	Panbira	Bangladesh	C	● ⁷
8	IR 8	Philippines	C	● ⁸
9	Hsinchu 56	Taiwan	A	● ⁹
10	Taichung Native 1	Taiwan	C	● ¹⁰
11	Tainan 3	Taiwan	A	● ¹¹
12	Bluebelle	U. S. A.	C	● ¹²
13	Caloro	U. S. A.	A	● ¹³
14	Sensho ²⁾	Japan	B	□ ¹⁴

¹⁾ Grain Type : A—small grain or *japonica* type
 B—large grain or *javanica* type
 C—slender grain or *indica* type
 according to TANIGUCHI and YOKOYAMA (1975)

²⁾ upland variety

containing river clay silt for about 60 days in a glasshouse. The water level was kept at 1–2cm above the surface of the soil. A nutrient solution (47g ammonium sulphate, 10g sodium phosphate dibasic, and 12g potassium chloride per liter) was supplied weekly at a rate of 6–10ml per pot according to the stage of plant growth.

At the maximum tiller number stage, the second-upper fully expanded and intact leaf which was attached to the main stem was inserted into the acrylic air-sealed chamber (3mm interior thickness, 20mm width) and the net carbon dioxide exchange was estimated with an infra-red gas analyzer (Hitachi-Horiba EIA-1) consecutively at two levels of air humidity. The relative humidity of the air was maintained in the range of 60–65% and 34–38% at the entrance of the leaf chamber by circulating the air through a water bath with variable temperatures and a silica gel column, respectively. The average relative humidity in the leaf chamber, estimated from the humidity of the air entering and leaving the chamber, was in the range of 68–72% (about 70%) and 46–54% (about 50%), respectively. During the measurement of leaf photosynthesis, the transpiration rate was simultaneously determined from the difference in water vapour concentration calculated by measuring the dry-bulb and wet-bulb temperatures of the air entering and leaving the leaf chamber with a high-sensitive thermister thermometer (Iio Mic-165). The temperature of the air passing through the leaf chamber was maintained at $29 \pm 2^\circ\text{C}$ and the flow rate kept at 42 cm s^{-1} . The leaf was irradiated with six 500-W incandescent lamps through a 25cm flowing water filter. The light intensity was $1800\mu\text{E m}^{-2} \text{ s}^{-1}$ at the top surface of the leaf chamber.

After the completion of the photosynthesis and transpiration measurements, the leaf was cut off and its fresh weight and area were determined. Then, the leaf was placed

in an air blast at 80°C to determine its dry weight and water content. In the dry material, nitrogen content was measured by the semimicro-Kjeldahl method.

Thereafter, the base of the leaf blade adjacent to the lamina joint was fixed in a formalin-acetic-alcohol mixture (FAA solution), dehydrated with tertiary butyl alcohol, embedded in paraffin, sectioned at 20 μ in thickness, and stained with phloroglucin. The total cross-sectional area of the xylem-vessels was calculated from the figure of the cross section projected on the magnifying-screen of a profile projector (Nikon Model V-14). The development of the xylem-vessels was expressed as the ratio of the total cross-sectional area of the vessels to the leaf area (RVA).

Observations were repeated with five leaves and the average values are presented in this paper.

Results

Fig.1 shows the varietal differences in the specific leaf weight (leaf dry-weight per unit leaf area, SLW) (A), and the leaf nitrogen content per unit of leaf area (B) in relation to the ratio of the total cross-sectional area of xylem-vessels at the leaf blade base to the leaf area (RVA). In, at least, six *indica* type varieties, positive correlations were observed between RVA and SLW, and leaf nitrogen content (correlation coefficient $r=+0.915$, $P<0.05$ in A and $r=+0.964$, $P<0.01$ in B, respectively). The varietal scatter pattern (Fig.1) indicated that *indica* type varieties tended to have a higher RVA relative to their SLW and leaf nitrogen content as compared with the *japonica* type varieties. This finding suggests that in the *indica* type varieties the water-conduction system is more developed than in the *japonica* type varieties. The upland variety, Sensho, also had a higher RVA relative to its SLW and leaf nitrogen content.

The photosynthetic rates at about 70% R.H. in the air (P_{WET}) and at about 50% R.H. in the air (P_{DRY}) are shown in relation to SLW (Fig.2), leaf nitrogen content (Fig.3) and RVA (Fig.4). Although the number of varieties used was limited, P_{DRY} was positively correlated with the SLW ($r=+0.539$, $P<0.01$), the leaf nitrogen content ($r=+0.524$)

Fig.1. Relationship between the ratio of the total cross-sectional area of xylem-vessels to the leaf area (RVA) and specific leaf weight (SLW) (A), and leaf areal nitrogen content (B). Symbols of varieties are described in Table 1.

Fig. 2. Relationship between the specific leaf weight (SLW) and leaf photosynthetic rate under wet air (P_{WET}) and under dry air (P_{DRY}). Symbols of varieties are described in Table 1.

Fig. 3. Relationship between leaf areal nitrogen content and leaf photosynthetic rate under wet air (P_{WET}) and under dry air (P_{DRY}). Symbols of varieties are described in Table 1.

and the RVA ($r=+0.741$, $P<0.01$). These results show that the photosynthetic rate under conditions of low air humidity is related with leaf characters concerning not only leaf thickness but also the water-conduction system in the leaf. Under conditions of high air humidity, the following four varieties, Bluebelle (variety number 12), Sensho (14), IR 8 (8) and Panbira (7), showed higher photosynthetic rates than the other varieties. At a low level of humidity, among these four varieties, the photosynthetic rates of IR 8 and Panbira which had a relatively low RVA, declined, whereas the photosynthetic rates of varieties which had a relatively high RVA, such as Bluebelle, Sensho, Taichung Native 1 (10) and Culture 340 (1), showed almost no reduction. On the other hand, the photosynthetic rates of the *japonica* type varieties showed a clear reduction at a low level of humidity (Fig. 4).

Fig. 5 shows the relationship between the photosynthetic rate and the leaf water content. Bluebelle, from the southern part of the United States of America, which had the highest RVA, also had the highest leaf water content. Furthermore, Raffaello (3) from Italy, which apparently did not show a reduction of the photosynthetic rate at a low level of

Fig. 4. Relationship between the ratio of total cross-sectional area of xylem vessels to the leaf area (RVA) and leaf photosynthetic rate under wet air (P_{WET}) and under dry air (P_{DRY}). Symbols of varieties are described in Table 1.

Fig. 5. Relationship between leaf water content and leaf photosynthetic rate under wet air (P_{WET}) and under dry air (P_{DRY}). Symbols of varieties are described in Table 1.

Fig. 6. Relationship between transpiration rate and photosynthetic rate. (A) represents under wet air and (B) under dry air. Symbols are described in Table 1.

humidity, had a relatively higher leaf water content.

Fig. 6 illustrates the relationship between the leaf photosynthetic rate and the transpiration rate, estimated simultaneously during the measurement of leaf photosynthesis. Two *indica* type varieties, Panbira and IR 8, and a very old *japonica* type variety from California, Caloro (13), showed high rates of transpiration relative to their photosynthetic rates at a low level of humidity. Culture 340 and N. 22 from India showed low rates of transpiration at a low level of humidity.

Discussion

Several authors have reported on the effect of air humidity on leaf photosynthesis. HORIE (1979) observed the relationship between the leaf photosynthetic rate of rice and the air humidity, and reported that the stomatal resistance increased gradually with the decrease in humidity from 60% downwards and that the photosynthetic rate tended to decrease. HIRAI *et al.* (1984) also observed the effect of air humidity on the photosynthetic rate of rice seedlings. But they did not supply data on the varietal differences in the response of the leaf photosynthetic rate to the air humidity. The results shown in Fig.2, 3 and 4 suggest that the varietal differences are likely to be related with the degree of development of the water-conduction system which can be evaluated from the difference in RVA, in addition to the SLW and leaf nitrogen content.

Among the varieties included in this study, *indica* type varieties, particularly Bluebelle released in Texas, U.S.A., showed a well developed xylem-vessel system relative to their SLW and leaf nitrogen content. This property of *indica* type varieties may have evolved as an adaptation to high temperature conditions in the region where they are cultivated. High temperature often causes low relative humidity of the air. In taking into account the conditions of cultivation of the *indica* type varieties, the physiological significance of the results shown in Figs. 1 and 4 is readily recognized. Therefore, the present study suggests that RVA may be related to varietal differences in the photosynthetic rate under the atmospheric conditions which cause a water deficit inside the leaf, and that RVA can be used as an index for evaluating the development of the water supply system in the leaf. On the other hand, as pointed out by YOSHIDA and ONO (1978) since the stomatal frequency of the *indica* type varieties is expected to be higher than that of the *japonica* type varieties, this characteristic in the *indica* type varieties may induce a transpiratory cooling effect under hot and humid climatic conditions (TSUNODA, 1984), as reflected by the high RVA observed in such varieties.

Rafaello (3), a *javanica* type varieties from Italy, that had an even lower RVA and preserved a higher water content on either leaf area or dry-weight basis did not show a reduction in the photosynthetic rate at a low level of humidity and its transpiration rate was not very high (Fig.6). Probably, leaf conductance for gas exchange was lower in Rafaello than in the four other varieties; Panbira, IR 8, Bluebelle and Sensho, which showed higher photosynthetic rates under humid atmospheric conditions. Among the latter four varieties Bluebelle and Sensho in which the water content and RVA were relatively higher, showed a higher photosynthetic rate at a low level of humidity. Thus the ability to maintain a high water content under dry air conditions is important for the plants, although in this study plant-water relationships were not analysed in detail.

The characteristics of the upland variety Sensho were closer to those of the *indica* type varieties than to the *japonica* type varieties.

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イネ品種の空気湿度に対する葉光合成反応と導管断面積の大きさ

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イネは一般に湛水条件下で栽培されているが, 大気の空気湿度の低下によって, 葉光合成速度が低下することが報告されている (ISHIHARA *et al.* 1978, HIRAI *et al.* 1984). また, HORIE (1979) は葉光合成と蒸散に及ぼす気温と空気湿度の相互作用を評価している. しかし, いずれもイネの品種間差異についての知見はなく, 葉形質との関連も葉室素含量や葉面当り葉身重 (SLW) を除いて明らかではない. そこで, 葉形質として葉身への水分供給系の大きさ (ここでは葉身基部の総導管断面積とした) を取り上げ, これと空気湿度に対する光合成反応との関係を世界に栽培されている品種でみて, 適応性の観点から考察した.

供試品種 (Table 1) は国際生物学事業計画 (IBP) の生殖質の保存と利用に関する研究 (UM) 部門のイネの適応性試験に用いられた共通品種の中から 13 品種を選び, それに日本の陸稲 6 品種を加えた計 14 品種とし, 最高分けつ期に 2 段階の空気湿度 (同化箱内平均相対湿度, 約 70% と 50%) 条件下で葉身の光合成及び蒸散速度を測定した. 測定葉身について, 葉面積, 乾物重, 室素含量, 含水量, 葉身基部の導管断面積等を観察した.

供試品種のうち, インド型品種では SLW および葉身室素含量と葉面積に対する葉身基部の導管断面積比 (RVA) との間に有意の正の相関関係が認められ, 日本型品種に比べて, インド型品種はその SLW と葉身室素含量の割によく発達した導管断面積を持っていた (Fig. 1). この RVA と低湿度空気下で観察した光合成速度との間には高い正の相関関係が見られた (Fig. 4). 同様に, SLW と葉身室素含量も低湿度空気下で観察した光合成速度と正に相関していた (Fig. 2 と 3). このように, 低湿度空気下での光合成速度の品種間差異には, SLW や葉室素含量などの葉形質のみならず, 葉身への水分供給系の発達に関係した形質 (RVA) も関係することが示唆された.

高湿度空気下では, Bluebelle, Sensho, IR 8, Panbira は他の品種より高い光合成速度を示したが, これら 4 品種のうち, RVA の比較的小さい IR 8 と Panbira は低湿度空気下で光合成速度を低下させた. ところが, RVA の比較的大きい品種 (Bluebelle, Sensho, Taichung Native 1, Culture 340) や, RVA が比較的小さくても葉身の含水量を高く保った品種 (Rafaello) は低湿度空気下でもそれほど光合成速度を低下させなかった. 一方, 日本型品種は低湿度空気下で一様に光合成速度を低下させたが, その RVA は比較的小さかった.

この RVA は葉身への水分供給系の大きさを評価する一つの指標と考えることができるが, インド型品種に見られたその SLW の割に RVA の大きい葉特性はインド型品種の高温条件に対する一つの適応であると考えられる. 高温はしばしば空気の相対湿度を低下させる. そうした葉身に水分欠乏をもたらすような条件下では, 葉身への水分供給系の大きさが葉身の光合成速度に関係する要因となりうるということが指摘された.

唯一の供試陸稲品種 Sensho は全体として, 日本型品種群よりインド型品種群に近い特性を示した.