Response of Leaf Photosynthesis to Vapor Pressure Difference in Rice (*Oryza sativa* L) Varieties in Relation to Stomatal and Leaf Internal Conductance

Akihiro Ohsumi[1]*, Akihiro Hamasaki[1], Hiroshi Nakagawa[2], Koki Homma[1], Takeshi Horie[1] and Tatsuhiko Shiraiwa[1]

(*[1]Division of Agronomy, Graduate School of Agriculture, Kyoto University, Sakyo, Kyoto 606-8502, Japan; [2]Ishikawa Prefectural University, Nonoichi, Ishikawa-gun, Ishikawa 921-8836, Japan*)

Abstract : In the afternoon when air humidity decreases, leaf photosynthetic rate (P_n) often declines in rice grown under irrigated conditions. To clarify the genotypic difference of P_n in response to humidity, we measured P_n and stomatal conductance (g_s) for nine rice varieties with diverse genetic backgrounds, at various vapor pressure differences (VPD) and developmental stages. P_n and g_s of all the varieties decreased with VPD increase from 1.0 to 2.3 kPa of VPD. The variety with high g_s at low VPD exhibited a greater decline of g_s with VPD increase than the variety with low g_s, but cv. Takanari showed the highest g_s under altered VPD conditions. Significant logarithmic relations were found between the decreased P_n and g_s at the respective developmental stages, suggesting that g_s is the dominant factor determining P_n and its response to VPD change. To explicate the effect of decreased g_s on P_n, we analyzed the relations by using the model that accurately estimated the genotypic difference in P_n at a low VPD with g_s and leaf nitrogen content per unit leaf area in the previous study. The model assuming that leaf internal conductance (g_w) remains unchanged well explained the decreased P_n at high VPDs by g_s change alone. The analysis also suggested the constancy of g_w and carboxylation capacity at high VPD. It is concluded that the genotypic difference in the decrease of P_n at a high VPD is brought mainly by that in decreased g_s, and the varieties with a high g_s always exhibit a high P_n owing to their relatively high g_s at either high or low VPD environments.

Key words : Genotypic difference, Internal conductance, Leaf photosynthesis, Rice (*Oryza sativa* L), Stomatal conductance, Vapor pressure difference (VPD).

Improvement of yield potential of rice (*Oryza sativa* L) is a major concern for Asian food security. As a consequence of breeding rice cultivars for a higher yield potential, recent high-yielding cultivars commonly possess large sink size. However, the yield of these cultivars has been reported to be restricted by carbohydrate accumulates available for grain filling due to their large sink size (Kusutani et al., 1999; Nagata et al., 2001). This suggests that improvement of biomass productivity can stabilize the yields of high-yielding rice.

Photosynthesis is influenced by various environmental factors such as temperature, irradiance and air humidity (Singh and Sasahara, 1981; Brooks and Farquhar, 1985; Makino et al., 1988). Decreased humidity in the fine afternoon causes midday depression of leaf photosynthetic rate (P_n, μmol m^{-2} s^{-1}) even in rice grown under well-irrigated conditions, although increased atmospheric vapor pressure deficit does not usually exceed 2.0 kPa in Japan (Hirai et al., 1984; Ishihara and Kuroda, 1986). This leads to reduction of cumulative carbohydrates and biomass productivity of the day. A decrease in P_n can be associated with the decrease of CO_2 supply from outside to the intercellular airspaces of leaves, which is controlled by stomatal function, CO_2 diffusion from intercellular airspaces to the carboxylation site and/or biochemical processes. Numerous studies have shown that decreased stomatal conductance (g_s, mol m^{-2} s^{-1}) strongly limits P_n at low humidity conditions (Morison and Gifford, 1983; Grantz, 1990; Dai et al., 1992). Franks and Farquhar (1999) reported that the responses of g_s to the change of the difference between ambient and leaf vapor pressure (VPD, kPa) differed among species and that greater reduction of g_s was found in tree species than in herbaceous species. The sensitivity of g_s to P_n differs among herbaceous C_3 and C_4 species in temperate areas (El-Sharkawy et al., 1984;

Kawamitsu et al., 1993). In rice, however, there are few studies on the difference in the g_s sensitivity among diverse genotypes, since Tsunoda and Singh (1986) compared P_n and transpiration for three indica and one japonica varieties.

Internal conductance (g_w, mol m^{-2} s^{-1}) as well as g_s limits P_n under non-stressed conditions, and the variation in g_w is proportional to that in g_s among plant species with similar leaf functions (von Caemmerer and Evans, 1991; Lauteri et al., 1997; Hanba et al., 2003). However, it has not been proven whether g_w responds to a short-term environmental change (Warren and Adams, 2006), since inconsistent results were reported for the nature of g_w; von Caemmerer and Evans (1991) showed that g_w remains unchanged during the day, but Centritto et al. (2003) reported that g_w changed as quickly as g_s can, and coordinates with g_s under altered CO_2 concentrations. If g_w coordinates with g_s at different VPDs, g_w can be an important factor of midday depression of photosynthesis together with g_s.

The primary objective of this study was to clarify the difference of the responses of P_n and g_s to VPD in various rice varieties. For this purpose, we used nine rice varieties with diverse genetic backgrounds for gas-exchange measurements at different VPDs. We also tested the variability of g_w in response to VPD change and its effect on decreased P_n by a model analysis. The applied model is based on g_s and nitrogen content of leaf per unit leaf area (N, g m^{-2}) and was reported to explain both genotypic and ontogenetic variation of P_n under low VPD in our previous study (Ohsumi et al., 2007).

Materials and Method

1.   Plant materials and growth conditions

Nine rice varieties selected for genotypic diversity were used. The varieties Takanari, IR72, Shanguichao and Ch86, are indica genotypes, and Nipponbare and Koshihikari are temperate japonica genotypes. The variety Banten is a tropical japonica. IR65564-44-2-2 (NPT) was bred by crossing between tropical japonica and indica. WAB450-I-B-P-38-HB (WAB) is an interspecific hybrid genotype between O. sativa sub. japonica and O. glaberrima. Ch86 and Banten are traditional varieties, and the others are improved ones.

Each variety was sown on 30 April in 2002 and transplanted on 24 May into 3.8 L pots with two seedlings per pot at Kyoto, Japan (35°2'N, 135°47'E, 65 m altitude). Plants with 12 replicates for each cultivar were grown outside sparsely to receive full sunlight and well watered throughout the growth period. N, P and K were applied at a rate of 0.3 g per pot as basal dressing, and 0.1 g of N was top-dressed biweekly.
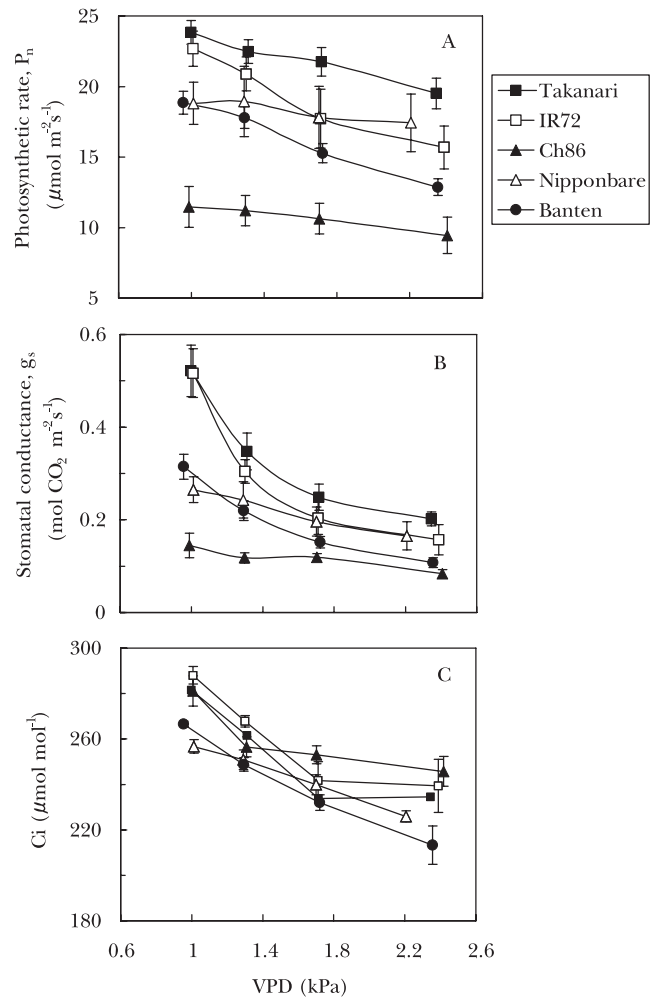

Fig. 1.   Changes in leaf photosynthetic rate (A), stomatal conductance (B) and CO_2 concentrations at intercellular airspaces (Ci) (C) at different VPD in five representative varieties of rice. Measurements were made at the heading stage. Each point and bar respectively represent the average and S.E. of four leaves in each variety.

2.   Measurements of photosynthetic rate, stomatal conductance and leaf nitrogen content of leaves

The exchange rates of CO_2 and water vapor in the youngest fully-expanded leaves were measured at panicle initiation (PI), heading, and 3 weeks after heading (3WAH) by an open-gas exchange system devised in our laboratory (Ohsumi et al., 2007). From the afternoon of the day before gas-exchange measurement, plants in the pots were kept in a black net (transmittance: 60%) and watered to ensure the leaves were hydrated. Four leaves from each variety were enclosed in an acrylic chamber (30×5.5×6.5 cm in L×W×H), and four chambers were used for one series of measurement. The leaves were irradiated at 1000 μmol m^{-2} s^{-1} PPF (photosynthetic photon flux) for half an hour with halogen lamps (JD500W-M, IWASAKI, Tokyo, Japan), and then gas exchange rates were measured at 1500 μ mol m^{-2} s^{-1} PPF. Leaf temperature and CO_2 concentration of the air

Table 1.   Stomatal conductance (g_s, mol CO_2 m^{-2} s^{-1}) in nine rice varieties measured at 1.0 kPa and 1.7 kPa VPDs at different developmental stages.

variety	Panicle initiation		Heading		3weeks after heading	
	1.0kPa	1.7kPa	1.0kPa	1.7kPa	1.0kPa	1.7kPa
Takanari	0.32±0.04	0.19±0.01	0.52±0.06	0.25±0.03	0.36±0.06	0.22±0.04
IR72	0.32±0.02	0.13±0.02	0.52±0.05	0.20±0.04	0.39±0.06	0.23±0.03
Shanguichao	0.22±0.01	0.13±0.01	0.36±0.02	0.25±0.01	0.20±0.02	0.11±0.01
Ch86	0.20±0.03	0.14±0.00	0.14±0.01	0.12±0.00	0.15±0.04	0.09±0.01
Nipponbare	0.17±0.01	0.16±0.01	0.26±0.03	0.20±0.03	0.11±0.01	0.08±0.00
Koshihikari	0.34±0.01	0.22±0.02	0.23±0.01	0.18±0.01	0.15±0.02	0.11±0.01
Banten	0.21±0.01	0.19±0.01	0.31±0.03	0.15±0.01	0.20±0.04	0.09±0.02
NPT[a]	0.17±0.01	0.17±0.01	0.26±0.03	0.20±0.02	0.14±0.01	0.10±0.01
WAB[a]	0.28±0.03	0.20±0.02	0.21±0.01	0.20±0.02	0.24±0.06	0.14±0.01
avg.	0.25	0.17	0.31	0.19	0.22	0.13
c.v.	0.27	0.20	0.41	0.21	0.46	0.43

[a] NPT and WAB denotes IR65564-44-2-2 and WAB450-I-B-P-38-HB, respectively.

Values are expressed as mean ± S.E. of 3-4 leaves in each variety.

surrounding leaf were 27.7±0.3°C and 346.8±9.8 μmol CO_2 mol^{-1}, respectively, during the measurements. VPD was initially maintained at 1.0±0.04 kPa, and stepwise increased to 1.3±0.04, 1.7±0.08 and 2.3±0.12 kPa. Steady-state gas-exchange rate at each VPD was determined after CO_2 and water vapor concentrations stabilized. It took about 2.5 hours to complete the entire cycle of gas-exchange measurements with varying VPDs. When P_n showed a marked drift, the sample was discarded. Thus, gas-exchange rates in 3–4 leaves were obtained for each variety at each developmental stage. From these measurements, leaf gas-exchange parameters were calculated according to von Caemmerer and Farquhar (1981).

After the gas-exchange measurement, leaf area enclosed in a chamber was measured with a LI-3000 (LI-COR, USA). The leaf samples were oven-dried at 80°C for at least 72 hours, weighed, and then subjected to determination of the nitrogen concentrations by the Kjeldahl method. The nitrogen concentration was multiplied by the specific leaf weight to calculate the nitrogen content of leaf on an area basis for the individual leaf.

3.   Simulation method

P_n was obtained from the difference between CO_2 concentration on the leaf surface (Ca, μmol mol^{-1}) and CO_2 compensation point in the absence of mitochondrial dark respiration (Γ^*, μmol mol^{-1}), divided by total limitation, which consists of reciprocals of carboxylation capacity, g_s and g_w (Ohsumi et al., 2007).

$$P_n = \frac{k_1 \cdot g_s (N-N_0)}{g_s + k_1 (1+g_s/g_w)(N-N_0)} (Ca-\Gamma^*) \qquad (1)$$

where N_0 and k_1 are empirical parameters; N_0 is

N when the amounts of Rubisco reached zero, and k_1 represents the amount of active Rubisco per ($N-N_0$) and its kinetics. Thus, carboxylation capacity is expressed as the product of k_1 and ($N-N_0$) in Eqn 1. Γ^* was assumed to be 43.8 μmol mol^{-1} for rice leaves at 30°C (Horie, 1981).

On the basis of previous reports showing that g_w varies with g_s (Loreto et al., 1992; Lauteri et al., 1997; Hanba et al., 2003), g_w was assumed to be proportional to g_s with little variation in the proportionality constant among plant species. In this case,

$$g_w = k_2 g_s \qquad (2)$$

where k_2 is an empirical parameter. Using Eqns 1 and 2, we regressed P_n of the nine varieties over developmental stages against their g_s, N and Ca measured at a low VPD (1.0 kPa) to obtain best estimates for the values of parameters k_1, k_2 and N_0 on the assumption that these parameter values are independent of genotypes and developmental stages. A least square method for non-linear functions was applied for this regression to minimize the sum of squared errors between measured and estimated P_n values. These estimated parameters represent the average of the attributes of all the individual leaves.

Eqn 1 with the three parameters obtained for a low VPD was applied to the simulation of P_n at higher VPDs. We made two simulations based on the following different assumptions for the response of g_w to VPD. The first was based on the assumption that g_w coordinates with g_s change for a short term (Centritto et al., 2003). If such coordination was applicable for rice g_w, the ratio of g_s/g_w, k_2, obtained at a low VPD should be maintained at higher VPDs. The second assumption was that g_w remains unchanged during the day (von Caemmerer and Evans, 1991). If this is applicable, the g_w values estimated by k_2 and g_s in

Eqn 2 at a low VPD for the individual leaves should be maintained at a higher VPD. Their goodness of fit to the measured P_n at higher VPDs was compared to examine the variability of g_w at different VPDs.

Results

1. Measurements of gas exchange

Fig. 1 shows the P_n, g_s and CO_2 concentrations in the intercellular airspaces (Ci, μmol mol^{-1}) at different VPD in the five representative varieties at the heading stage, when the rice varieties showed the highest P_n. All the varieties excepting Ch86 reduced P_n and g_s
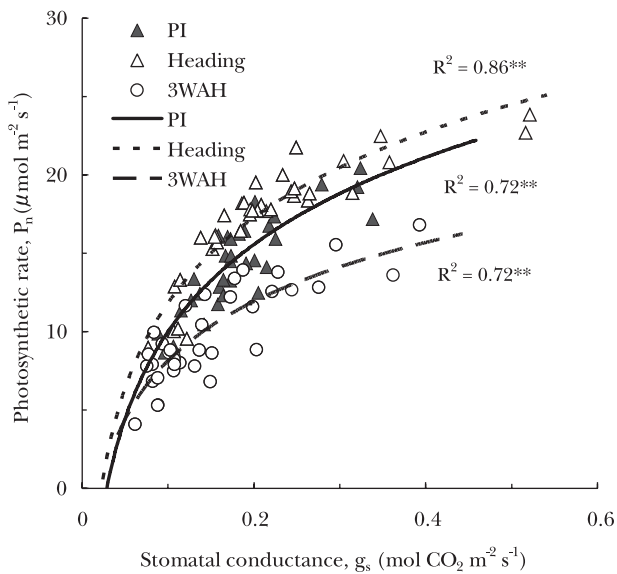

Fig. 2. Relationships between stomatal conductance and leaf photosynthetic rate at different VPD in nine rice varieties at panicle initiation (PI), heading and 3 weeks after heading (3WAH). All the relations are significant at 1% level. Each point represents the average of 3–4 leaves.

with increased VPD. Takanari and IR72 exhibiting a high g_s at a low VPD tended to reduce g_s sharply as VPD increased from 1.0 to 1.3 kPa and maintained moderate g_s values at higher VPDs, while Ch86 with the lowest g_s decreased g_s at a high VPD only slightly. Ci tended to decrease linearly with increasing VPD, but was maintained at 1.3 kPa VPD, despite the concurrent decreases of P_n and g_s at a VPD of 2.3 kPa in Takanari and IR72 (Fig. 1C). Ch86 having low sensitivity of P_n and g_s to VPD showed small change in Ci. The pattern that the variety with a high g_s at a low VPD decreases g_s largely with the increase in VPD was observed similarly at all developmental stages (Table 1). However, the varieties with a high g_s at a low VPD tended to show higher g_s even at increased VPDs. Takanari had a high g_s at a high VPD than Ch86, Nipponbare and NPT at all the stages, although g_s of some varieties changed their ranks depending on the stages. Genotypic differences in g_s became smaller as VPD increased; coefficients of variance at 1.0 and 1.7 kPa VPDs were 27 and 20%, respectively, at PI, 41 and 21% at heading, and 46 and 43% at 3WAH.

When g_s values of the nine varieties at different VPDs were aggregated at each developmental stage, the responses of P_n to a change in g_s could be well approximated by logarithmic curves with determination coefficients of 0.71, 0.88 and 0.71 for the stages of PI, heading, and 3WAH, respectively (Fig. 2). These relations indicate that the leaves with high g_s at a low VPD has low sensitivity of P_n to a decreased g_s, while the leaves showing a low g_s at a low VPD largely decreases P_n with the decrease in g_s. The regression curves differed with the stages. These differences might reflect the differences in N, and the average N values of the nine varieties were 1.35, 1.39 and 1.02 g N m^{-2} at PI, heading and 3WAH, respectively (Table 2).

Table 2. Leaf nitrogen content per unit leaf area (g m^{-2}) in nine rice varieties at different developmental stages.

variety	Panicle initiation	Heading	3weeks after heading
Takanari	1.51±0.10	1.54±0.08	1.03±0.06
IR72	1.43±0.05	1.51±0.06	1.21±0.15
Shanguichao	1.31±0.04	1.39±0.06	0.65±0.08
Ch86	1.07±0.08	1.09±0.09	0.80±0.12
Nipponbare	1.53±0.06	1.46±0.05	0.96±0.01
Koshihikari	1.41±0.09	1.30±0.08	1.00±0.03
Banten	1.19±0.09	1.24±0.04	1.04±0.15
NPT[a]	1.19±0.08	1.52±0.08	1.18±0.04
WAB[a]	1.47±0.08	1.45±0.10	1.30±0.04
avg.	1.35	1.39	1.02
c.v.	0.12	0.11	0.20

[a] NPT and WAB denotes IR65564-44-2-2 and WAB450-I-B-P-38-HB, respectively.
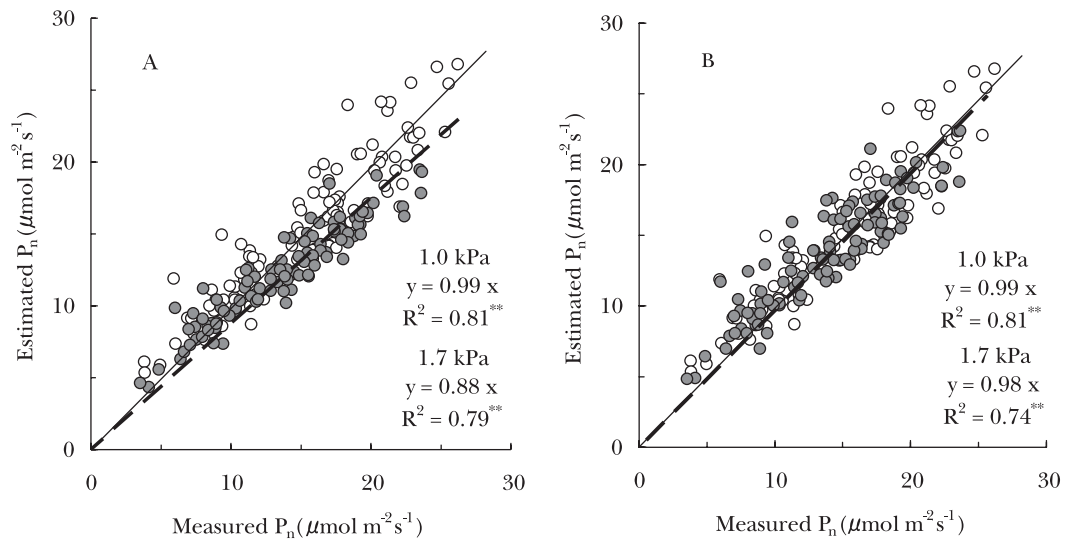Values are expressed as mean ± S.E. of 3-4 leaves in each variety.

Fig. 3.   Relationships between the photosynthetic rates (P_n) measured and estimated by Eqn.1 assuming that internal conductance coordinates with stomatal conductance (A) and is constant at different VPDs (B) in rice. Different remarks represent measurements at 1.0 kPa VPD (open circle, solid line) and 1.7 kPa VPD (closed circle, dashed line). All the relations are significant at 1% level.

Table 3.   Results of the two simulations of photosynthetic rate (P_n) at different VPDs by Eqns 1 and 2 assuming internal conductance to coordinate with stomatal conductance and to be constant at different VPDs in rice, respectively.

VPD(kPa)	coordinate		constant	
	bias	R^2	bias	R^2
1.0	0.99	0.81		
1.3	0.90	0.84	0.97	0.79
1.7	0.88*	0.79	0.98	0.74
2.3	0.85*	0.80	1.01	0.69

All of the relations are significant at 1% level.

* denotes a significant difference from the value at 1.0 kPa VPD at 5% level.

2.   Simulation of P_n at different VPDs

Considerable differences were observed in P_n, g_s at low VPDs and N among the nine rice varieties at different developmental stages, and the values of P_n, g_s and N ranged from 6.8 to 19.7 μmol m^{-2} s^{-1}, from 0.11 to 0.52 mol CO_2 m^{-2} s^{-1}, and from 0.69 to 1.59 g N m^{-2}, respectively. There was no correlation between g_s at a low VPD and N in the varieties examined. Applying the measured P_n, g_s and N values to Eqns 1 and 2, the model well explained the measured P_n at a low VPD (1.0 kPa) (Fig. 3). The parameter values of k_1, k_2 and N_0 estimated by the model were 0.09 mol CO_2 g N^{-1} s^{-1}, 1.05 and 0.32 g N m^{-2}, respectively. There was little difference in goodness of fit for 1.7 kPa VPD between the two different simulations that assumed g_w change and do not change with the VPD. However, the slopes between the estimated and measured P_n were different between the simulations at 1.7 kPa VPD. The slope in the model assuming constant g_w differed little at all VPDs, but the model assuming that g_w coordinates with g_s changes underestimated the P_n particularly at a high

VPD (Table 3). The slopes of the latter at 1.7 and 2.3 kPa VPDs significantly differed from that at 1.0 kPa VPD (P < 0.05).

Discussion

The responses of P_n and g_s to VPD were evaluated for the rice varieties with diverse genetic backgrounds in the present study. The change of P_n with the increase in VPD was related to the decrease of g_s (Fig. 2), and genotypic difference in g_s well accounted for that in P_n in the model analysis (Fig. 3). This confirmed that g_s is one of the major determinants of the genotypic difference in P_n and its response to VPD, as reported previously (Morison and Gifford, 1983; Hirasawa et al., 1988; Grantz, 1990; Dai et al., 1992; Kawamitsu et al., 1993). Therefore, clarification of the genotypic difference in sensitivity of g_s to VPD will help confirm the genotypic difference in the sensitivity of P_n to VPD in rice.

The sensitivity of g_s to VPD varied with the variety and developmental stage. A number of factors have

been suggested to affect the sensitivity of g_s before. Cunningham (2004) reported that, comparing eight tree species collected from a wide range in Australia, tropical species showed a higher g_s sensitivity than temperate ones. This indicates that the water environment affects the sensitivity of g_s. Tropical rice varieties in Southeast Asia experience a higher VPD during midday in the growing seasons than the temperate varieties bred in Japan. In our study, there was no consistent difference in the sensitivity of g_s to VPD between tropical varieties (IR72, Banten and NPT), and temperate varieties (Nipponbare and Koshihikari) at the three developmental stages. On the other hand, Ishihara and Kuroda (1986) showed that leaves with high nitrogen concentrations showed a greater decline of g_s with the increase in VPD than leaves with low nitrogen concentrations in a temperate japonica variety. However, the genotypic difference in the sensitivity of g_s to VPD was not related to the nitrogen concentrations in leaves (Table 2). This is because, while Ishihara et al. (1978) reported that high nitrogen concentrations in leaves enhanced g_s in a temperate japonica cultivar, there was no significant relation between genotypic differences of g_s and nitrogen concentration/content in the leaves at low VPDs among rice varieties in the present study, which has been suggested previously (Ohsumi et al., 2007). The variety with a high g_s at a low VPD showed a large decline of g_s with increasing VPD (Fig. 1B, Table 1), indicating that sensitivity of g_s to VPD depends on the g_s at low VPDs rather than nitrogen concentrations of the leaves in rice.

Tsunoda and Singh (1986) showed that the variety ranks of P_n and transpiration remain constant at different VPDs comparing three indica lowland and one japonica upland varieties in rice. In our study with the diverse rice genotypes, the variety rank of g_s changed in some varieties under varied VPD conditions, but no difference in the sensitivity of g_s to VPD was observed at any developmental stage (Table 1). However, it is evident that Takanari that has the highest g_s at a low VPD exhibited the highest g_s at higher VPDs throughout development.

The decrease of Ci at a VPD below 1.7 kPa implies that g_w and carboxylation capacity did not vary with the VPD in most rice varieties (Fig. 1C). This is because, if g_w and carboxylation capacity decrease coordinately with decreased g_s, Ci should remain constant under altered VPD. However, it is not clear whether the carboxylation capacity and g_w were stable under different VPD conditions: Ci decreased, when the g_w and carboxylation capacity decreased at high VPDs, but not so much as that of g_s. Thus, the model simulation successfully demonstrated the constancy of g_w and carboxylation capacity under altered VPD conditions. The model assuming that g_w changes coordinately with the decrease of g_s underestimated the measured

P_n at higher VPDs (Fig. 3), and significant differences between the measured and estimated P_n were found at 1.7 and 2.3 kPa VPDs (Table 3). On the other hand, the model assuming that g_w remains unchanged at a high VPD well explained the measured P_n at different VPDs without noticeable biases. These results indicate that g_w and carboxylation capacity changed little in rice varieties depending on VPD, which agrees with the previous study on the nature of g_w by von Caemmerer and Evans (1991). The stability of carboxylation capacity is also supported by previous studies showing that Rubisco activation reached a maximum (higher than 1000 μmol m^{-2} s^{-1} PPF) after a 30-minute irradiation and does not change during the day (Vu et al., 1983; Servaites et al., 1984; Jiang et al., 1994).

In some varieties, Ci slightly increased with increasing VPD from 1.7 to 2.3 kPa (Fig. 1C), which would be reflected in the slight increase of the bias at the VPD of 1.7 and 2.3 kPa in the simulation assuming that g_w is constant due to the overestimated k_1 (Table 3). This suggests that carboxylation capacity decreases above 2.0 kPa VPD, as suggested by the previous report for rice (Morison and Gifford, 1983). However, Ci is overestimated when patchy stomatal closure occurred (Terashima, 1992). Patchy stomatal closure occurs in thin and amphi-stomatous leaves as in rice at severely high VPD, which might be also observed in the increases in Ci at 2.3 kPa in some leaves. Therefore, our analysis could not clarify if g_w and/or carboxylation capacity decreased at above 1.7 kPa VPD, but these effects on P_n appeared to be small (Table 3). There is also a possibility that calculation of Ci is affected by cuticular conductance (g_c) when g_s decreased markedly. Boyer et al. (1997) precisely measured g_c using grape leaves with no stoma at the upper surface. Their measured g_c-values for H_2O were about 0.004 mol m^{-2} s^{-1}, which were considerably lower than the measured g_s values at high VPD in our study. Thus, the effect of g_c on our analyses can be negligible.

In conclusion, we showed that the genotypic difference in P_n decrease with increasing VPD mainly by that in g_s decrease without any marked changes in g_w and carboxylation capacity. Our study also showed that the developed model is useful for analyses of the responses of P_n to environmental changes. The genotypic difference in the sensitivity of g_s to VPD was found in rice, and the variety with a high g_s at a low VPD reduced g_s sharply with increasing VPD. Takanari exhibited the highest g_s not only at a low VPD but also at high VPDs. As the genotypic variability of g_s is greater at a low VPD than at a high VPD, selection of genotypes with a high g_s at a low VPD would be effective for finding the plants with large daily CO_2 accumulates at a single leaf level. Since, we did not examine the changes of leaf water potential or water-absorbing ability relating to midday depression of g_s and P_n were not examined (Hirasawa et al., 1988;

Saliendra et al., 1995), clarification of their effects on the genotypic difference of g_s in response to VPD in diverse rice genotypes should help improve the daily biomass productivity of rice.

Acknowledgements

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