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

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Abstract: In the afternoon when air humidity decreases, leaf photosynthetic rate (Pn) often declines in rice grown under irrigated conditions. To clarify the genotypic difference of Pn in response to humidity, we measured Pn and stomatal conductance (gs) for nine rice varieties with diverse genetic backgrounds, at various vapor pressure differences (VPD) and developmental stages. Pn and gs of all the varieties decreased with VPD increase from 1.0 to 2.3 kPa of VPD. The variety with high gs at low VPD exhibited a greater decline of gs with VPD increase than the variety with low gs, but cv. Takanari showed the highest gs under altered VPD conditions. Significant logarithmic relations were found between the decreased Pn and gs at the respective developmental stages, suggesting that gs is the dominant factor determining Pn and its response to VPD change. To explicate the effect of decreased gs on Pn, we analyzed the relations by using the model that accurately estimated the genotypic difference in Pn at a low VPD with gs and leaf nitrogen content per unit leaf area in the previous study. The model assuming that leaf internal conductance (gw) remains unchanged well explained the decreased Pn at high VPDs by gs change alone. The analysis also suggested the constancy of gw and carboxylation capacity at high VPD. It is concluded that the genotypic difference in the decrease of Pn at a high VPD is brought mainly by that in decreased gs, and the varieties with a high gs always exhibit a high Pn owing to their relatively high gs 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 (Pn, 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 Pn can be associated with the decrease of CO₂ supply from outside to the intercellular airspaces of leaves, which is controlled by stomatal function, CO₂ diffusion from intercellular airspaces to the carboxylation site and/or biochemical processes. Numerous studies have shown that decreased stomatal conductance (gs, mol m⁻² s⁻¹) strongly limits Pn at low humidity conditions (Morison and Gifford, 1983; Grantz, 1990; Dai et al., 1992). Franks and Farquhar (1999) reported that the responses of gs to the change of the difference between ambient and leaf vapor pressure (VPD, kPa) differed among species and that greater reduction of gs was found in tree species than in herbaceous species. The sensitivity of gs to Pn differs among herbaceous C₃ and C₄ 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.

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 $\mu$mol 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 $\mu$ mol m$^{-2}$ s$^{-1}$ PPF. Leaf temperature and CO$_2$ concentration of the air.
surrounding leaf were 27.7 ± 0.3°C and 346.8 ± 9.8 μmol CO₂ mol⁻¹, respectively, during the measurements. VPD was initially maintained at 1.0 ± 0.04 kPa, and stepwisely 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 CO₂ and water vapor concentrations stabilized. It took about 2.5 hours to complete the entire cycle of gas-exchange measurements with varying VPDs. When Pₙ 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

Pₙ was obtained from the difference between CO₂ concentration on the leaf surface (Ca, μmol mol⁻¹) and CO₂ compensation point in the absence of mitochondrial dark respiration (Γ*, μmol mol⁻¹), divided by total limitation, which consists of reciprocals of carboxylation capacity, gₛ and gₙ (Ohsumi et al., 2007).

\[
Pₙ = \frac{k₁ • gₙ(N–N₀)}{gₛ+k₁(1+gₛ/gₙ)(N–N₀)} (Ca–Γ*)
\]  

where N₀ and k₁ are empirical parameters; N₀ is N when the amounts of Rubisco reached zero, and k₁ represents the amount of active Rubisco per (N–N₀) and its kinetics. Thus, carboxylation capacity is expressed as the product of k₁ and (N–N₀) 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 gₛ varies with gₙ (Loreto et al., 1992; Lauteri et al., 1997; Hanba et al., 2003), gₙ was assumed to be proportional to gₛ with little variation in the proportionality constant among plant species. In this case,

\[
gₙ = k₂ gₛ
\]  

where k₂ is an empirical parameter. Using Eqns 1 and 2, we regressed Pₙ of the nine varieties over developmental stages against their gₛ, N and Ca measured at a low VPD (1.0 kPa) to obtain best estimates for the values of parameters k₁, k₂ and N₀ 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 Pₙ 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 Pₙ at higher VPDs. We made two simulations based on the following different assumptions for the response of gₙ to VPD. The first was based on the assumption that gₙ coordinates with gₛ change for a short term (Centritto et al., 2003). If such coordination was applicable for rice gₙ, the ratio of gₛ/gₙ, k₂, obtained at a low VPD should be maintained at higher VPDs. The second assumption was that gₙ remains unchanged during the day (von Caemmerer and Evans, 1991). If this is applicable, the gₙ values estimated by k₂ and gₛ in

| variety         | Panicle initiation | Heading | 3 weeks 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 | 0.56±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*            | 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*            | 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 and WAB4504-B-P-38-HB, respectively.

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

Table 1. Stomatal conductance (gₛ, mol CO₂ m⁻² s⁻¹) in nine rice varieties measured at 1.0 kPa and 1.7 kPa VPDs at different developmental stages.
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 $g_s$ 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 ($C_i$, 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 $g_s$ 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. $C_i$ 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 $C_i$. 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 | 3 weeks 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.
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 $\mu$mol 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 $g_s$ differed little at all VPDs, but the model assuming that $g_s$ coordinates with $g_w$ 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 $C_i$ 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 $g_s$, $C_i$ should remain constant under altered VPD. However, it is not clear whether the carboxylation capacity and $g_w$ were stable under different VPD conditions: $C_i$ 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 $\mu$mol 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, $C_i$ 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, $C_i$ 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 $C_i$ 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 $C_i$ is affected by cuticular conductance ($g_c$) when $g_w$ decreased markedly. Boyer et al. (1997) precisely measured $g_w$ 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 $g_c$ 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 $g_w$ decrease without any marked changes in $g_s$ 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, in response to VPD in diverse rice genotypes should help improve the daily biomass productivity of rice.

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