Varietal Range in Transpiration Conductance of Flowering Rice Panicle and Its Impact on Panicle Temperature

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Abstract: Transpiration from rice (Oryza sativa L.) panicles can help lower the temperature of the panicle \( T_p \), which is the susceptible organ for high temperature-induced spikelet sterility (HISS). By increasing the transpiration, the heat damage to the panicle predicted to occur due to global warming may be avoided. To examine the possibility of genetic improvement in transpiration conductance of intact rice panicles \( (g_{pI}) \), we measured \( g_{pI} \) at the time of flowering in the open field in 21 rice varieties of widely different origins. We observed a difference in \( g_{pI} \) among the varieties and three series of experiments, ranging from 0.15 to 0.67 cm s\(^{-1}\). We also estimated its impact on the difference between \( T_a \) and air temperature \( (\Delta T_p, T_p - T_a) \) using a micrometeorology model, where \( T_a \) was given as 28°C or 35°C. The varietal range in \( g_{pI} \) was estimated to correspond to the range of 2.1°C in \( \Delta T_p \) under a humid atmospheric condition and the range of 3.5°C in \( \Delta T_p \) under a dry atmospheric condition. The estimated \( \Delta T_p \) ranges due to varieties may be useful for improving heat avoidance capacity under excessive heat at the critical stage. The sensitivity analysis of \( \Delta T_p \) to ranging \( g_{pI} \) suggested that \( g_{pI} \) higher than the highest \( g_{pI} \) observed in this study may not be effective for additional cooling of \( T_p \). Thus, the target of improvement in \( g_{pI} \) against HISS should be set at the level of the existing varieties with the highest \( g_{pI} \).

Key words: High temperature-induced spikelet sterility, Panicle transpiration, Transpiration cooling, Varietal difference.

High temperature-induced spikelet sterility (HISS) in rice at flowering (Satake and Yoshida, 1978; Kim et al., 1996; Matsui et al., 2001; Matsui, 2009) is gathering concern because of the ongoing and predicted climate change. The extreme heat in midsummer 2007 resulted in the occurrence of HISS in rice grown in the open field in Japa (Hasegawa et al., 2011). The organ susceptible to high temperature is the panicle (Nishiyama and Satake, 1981) and the panicle temperature \( (T_p) \) is critically important for the heat damage (Jagadish et al., 2007; Weerakoon et al., 2008). Previous studies have shown that panicle temperature can be different from air temperatures \( (T_a) \) depending on the climatic conditions such as vapor pressure deficit \( (VPD) \) and wind speed; for example, Matsui et al. (2007) reported that under dry and windy conditions in New South Wales, the major rice growing region in Australia, \( T_p \) was 6°C lower than \( T_a \). On the other hand, Tian et al. (2010) reported that \( T_p \) was as much as 4°C higher than \( T_a \) under humid windless conditions in Jianghan Basin, China. These differences can be a source of large uncertainties in estimating the heat damage on rice.

Biotic factors can also affect \( T_p \) in addition to the meteorological conditions in the vicinity of panicles, such as \( T_a \), humidity, radiation and wind velocity. The biotic factors involve the transpiration from panicles and leaves. Compared to the abiotic factors which are difficult to manipulate in the field, the biotic factors which can be manipulated by breeding and/or cultural practice will be more promising options to lower \( T_p \).

Because transpiration from the plant surface causes latent heat loss, transpiration from the rice panicles directly lowers \( T_p \). Thus, it is a cooling system to maintain \( T_p \) low and avoid HISS (Roberts and Batchelor, 1983;
Weerakoon et al., 2008). By identifying the varietal difference of panicle transpiration as the strategic key trait, we can develop rice varieties with the ability to avoid heat damage.

To date, however, only limited information has been available on the varietal difference in rice panicle transpiration. Miyagawa et al. (1999) measured the transpiration rate of the cut panicles of the 24 varieties in a controlled environment and showed a range from 2 to 7 mg cm\(^{-2}\) h\(^{-1}\) at 5 and 10 d after panicle emergence. Other investigators showed values of panicle transpiration conductance \((g_p)\) in a few varieties on days of flowering (not necessarily at the time of flowering which starts from the opening of glumaceous flower and ends at its closure); in IR36, \(g_p\) of cut panicles while drying without water supply was reported to be 0.67 cm s\(^{-1}\) (O’toole et al., 1984). There were a few measurements in intact panicles of Nipponbare (0.4 cm s\(^{-1}\); Ishihara et al., 1990) and in Akitakomachi (0.2 to 0.6 cm s\(^{-1}\); Yoshimoto et al., 2011), but no direct comparisons between varieties have been made on the intact panicles under the field conditions. The genotypic variability is the key information to be targeted in the breeding program.

Recently, a simple micrometeorology model focusing on \(T_p\) and canopy temperature \((T_c)\) has become available (Yoshimoto et al., 2011). The model (Integrated Micrometeorology Model for Panicle And Canopy Temperature, IMP\(p\)\(\text{ACT}\)) predicts \(T_p\) and \(T_c\) from general surface weather parameters. In the model, \(g_p\) of intact panicles \((g_{pI})\) is the essential parameter, which is given based on the previous measurements for the single variety. We can use this model to interpret the genetic variability of \(g_{pI}\), obtained in the present experiment, in terms of \(T_p\).
under certain meteorological conditions.

Thus in this study, we quantified the $g_d$ of various rice varieties at the time of flowering under the field condition. Based on the obtained varietal range in $g_d$, we estimated the impact of ranging $g_d$ on $T_p$ by numerical experiments using the IM$^3$PACT model.

Materials and methods

1. Plant material

A total of 21 rice varieties of various origins, ecotypes, cultivation types and awnness shown in Table 1 were grown flooded in experimental paddy fields at the National Institute for Agro-Environmental Sciences (NIAES; Tsukuba, Ibaraki, Japan; 36°01′ N, 140°06′ E; elev. 22 m) in 2005 and 2006. The soil was classified as Upland Reformed soils according to the Comprehensive Soil Classification System of Japan (Obara et al., 2011), where the Fine-Textured Lowland soil appeared in the top 55 cm soil layer and the subsoil was Allophanic Andosols. This was also classified as the Regosols (Transportic) according to the World Reference Base for Soil Resources (FAO, 2006). The seedlings were transplanted on June 6 (Series 1) in 2005 and on June 6 (Series 2) and June 26 (Series 3) in 2006, all at a density of 23.8 hill m$^{-2}$ (28 × 15 cm). N, P$_2$O$_5$ and K$_2$O fertilizers were applied as basal application at a rate of 80, 40, 40 kg ha$^{-1}$ respectively; half of N was applied as ammonium sulfate and the rest of N was applied as polyolefin-coated urea which constantly exudates the urea for 70 d (LP70; Chisso Asahi Fertilizer Co., Ltd., Tokyo, Japan). The panicles were tested were selected evenly from the experimental panicles combination (Table 1). The typical time length which was required for the single measurement of $g_d$ was 1 to 2 minutes.

To ensure that the surface area of the measured part could be quantified later, we marked the bottom end of the measured part on one of the days of flowering as the representatives of each variety grown in each series-variety combination (Table 1). The typical time length which was required for the single measurement of $g_d$ was 1 to 2 minutes.

2. Measurement of panicle transpiration

On the days of flowering of each variety in each series (Table 1), we selected sample panicles the upper-middle part of which was going to bloom (usually on their second or third day of flowering sequence which occurs from top toward bottom of a panicle over several days), for the measurement of $g_d$ on each day of measurement. Although main culms and tillers were not discriminated in the selection, moderate panicles were selected as the sample panicles; precocious and late-emerging panicles were excluded from the sample panicles. While the upper-middle part of the sample panicles was flowering (i.e., during glumaceous flowers opening), $g_d$ was measured by using a steady-state porometer (LI-1600; Li-Cor Inc., Lincoln, NE, USA) equipped with an optional cylindrical chamber (1600-07; Li-cor Inc.). The chamber was originally designed to measure broad-leaves with high stomatal resistances and highly dissected or irregular shaped leaves; it had a circular-shaped sampling aperture the diameter of which was 5 cm (Fig. 1). For every measurement, the leaf temperature thermocouple for the 1600-07 chamber (1600TC-07; Li-cor Inc.) was carefully placed to touch the surface of a glume composing a flowering part of a sample panicle so that the temperature of the glume could be accurately measured to ensure that $g_d$ can be calculated accurately. The measurements were made during the time of flowering (0913 − 1313) for 425 panicles in total, consisted of 4 to 40 panicles in each series-variety combination (Table 1). The typical time length which was required for the single measurement of $g_d$ was 1 to 2 minutes.

3. Data processing

As shown in Fig. 1, the rice panicles tested had cylindrical shapes and did not cover the entire aperture of the circular-shaped chamber, making it impossible to assume that the area of transpiring surface was equal to the area of the chamber aperture. In addition, the surface area of the part measured for transpiration differed panicle to panicle. The raw data of conductance ($g_{cm}$, cm$^{-2}$), which were output by the porometer based on the assumption that the area of transpiring surface was a constant value (10 cm$^2$), were compensated with the surface area of each panicle measured for $g_d$ ($S_p$, cm$^2$) to obtain the actual value of $g_d$ for each tested panicle.

To quantify $S_p$, we sampled moderately grown panicles on one of the days of flowering as the representatives of each variety grown in each series. The number of the
representative panicles was 8 in Series 1 and 9 in Series 2 and 3. Immediately after the sampling, a side view image was scanned for each representative panicle in color (24-bits per pixel) at a resolution of 300-dots per inch with a flatbed image scanner (CanoScan N1240U; Canon Inc., Tokyo, Japan). The scanned images were handled in lossless image format for further processing.

The panicle images in color were converted to binary to segregate the panicle and background by the supervised classification technique using an image analysis software (LIA for Win32 version 0.376, http://www.agr.nagoya-u.ac.jp/~shinkan/LIA32/index-e.html). One of the panicle images for each variety in each series was randomly selected for use as a training image for the supervised classification technique; 150 pixels each designating either the panicle body or the background were sampled from each training image on the software to make a discriminant for the automated segregation of the panicle and the background.

In the process of the conversion to binary, the glume pubescence tended to be classified as the background because of its shininess. The small particles of the pixel classified as the background derived from the glume pubescence were corrected as the panicle body by another image analysis software (ImageJ version 1.34, http://rsweb.nih.gov/ij/), using “Process>Binary>CLOSE” command to prevent underestimation of the panicle surface area.

The binarized and closed images were then processed by “Analyze> Analyze Particles” command of ImageJ, obtaining the sideways projected areas of each representative panicle. Assuming that the panicles were double-sided, double the values of the projected areas were considered as surface areas of each whole panicle \( (S_{pW} \text{ cm}^2) \). The \( S_{pW} \) values for each representative panicle were then divided by the corresponding number of grains in the panicle, obtaining the surface areas per grain \( (S_p \text{ cm}^2) \). The \( S_p \) values were averaged for each variety in each series.

The \( S_p \) values in each panicle measured for transpiration were calculated by multiplying corresponding \( S_p \) value by the grain number in each part measured for transpiration, which was counted after the measurement for transpiration. The \( g_{pm} \) values were compensated with the thus calculated \( S_p \) values to obtain \( g_{pt} \) values using the following equation.

\[
g_{pt} = \frac{1}{\left( \frac{1}{g_{pm}} + 0.15 \right) \times \frac{S_p}{10}}
\]

In the above equation, the value 0.15 was given to compensate boundary layer resistance which was uniformly subtracted from the bulk resistance measured by LI-1600 to output stomatal conductance. In the present study, we did not subtract it again after the compensation of measure because we calculate \( g_{pt} \) as bulk conductance.

4. Acquisition of meteorological parameters

On the days of flowering of the varieties tested, meteorological parameters were observed above rice plant communities (‘Hatsuboshi’ and ‘Akitakomachi’ in 2005; ‘Hinohikari’ in 2006) which were grown adjacent to the communities used for the panicle transpiration measurements. \( T_a \) and relative humidity (RH) were measured at 1.5 m above the soil surface (i.e. 0.4 to 0.7 m above the canopy surface) with an integrated temperature and humidity sensor (HMP45D; Vaisala Oyj, Vantaa, Finland) which was sheltered by a double-hulled forced-ventilated radiation shield built-in-house from PVC pipes. The raw data of \( T_a \) and RH were sampled at 10-s intervals and averaged over every 10-min. Based on the 10-min average of \( T_a \) (°C) and RH (%), we calculated the vapor pressure deficit (VPD) (hPa), which is the index of the evaporative demand of the atmosphere, at 10-min intervals using the following equation.

\[
\text{VPD} = 6.1078 \times \left( \frac{T_a+237.3}{7.5} \right) \times (100−\text{RH})
\]

Each piece of the \( g_{pt} \) data was related to the nearest piece of preceding VPD data.

5. Sensitivity analysis of the impact of varying \( g_{pt} \) on \( T_p \)

To estimate the impact of the varietal range of \( g_{pt} \) on \( T_p \), we conducted a sensitivity analysis of \( T_p \) to the range of \( g_{pt} \) between 0.01 cm s\(^{-1}\) and 1.50 cm s\(^{-1}\), which sufficiently covers the range of observed \( g_{pt} \), in 0.01 cm s\(^{-1}\) step using the IMPACT model (Yoshimoto et al., 2011). Three pairs of \( T_a \) and RH above canopy were given as [28°C, 70%], [35°C, 70%] and [35°C, 30%]. The pair [28°C, 70%] was a typical atmospheric condition under which we measured \( g_{pt} \). \( T_a \) of 35°C was given because it was reported to be a threshold temperature for the occurrence of HISS (Matsui, 2009) and two contrasting levels of RH of 70% simulating the humid atmospheric condition such as that in Japan and 30% simulating the dry atmospheric condition such as that in Australia, were given to test if RH affects the sensitivity of \( T_p \) to \( g_{pt} \). The other meteorological parameters above canopy which were required for the calculation were given as fixed typical values as follows: wind velocity=2 m s\(^{-1}\), downward shortwave radiation=700 W m\(^{-2}\), downward longwave radiation=440 W m\(^{-2}\). Based on the calculated \( T_p \), \( \Delta T_p \) was obtained by subtracting \( T_p \) from \( T_a \). By combining the varietal ranges of \( g_{pt} \) with which we quantified and the relationship between \( g_{pt} \) and \( T_p \), we obtained the varietal ranges of \( T_p \).

Results

1. Varietal difference and range of \( g_{pt} \) at time of flowering

The VPD of the 21 varieties ranged from 4.0 to 17.4 hPa, but with no significant difference among three series of \( g_{pt} \) measurements (Fig. 2). We observed a difference in \( g_{pt} \)
Plant Production Science

were ranked by the mean $g_p$ averaged over the series at the highest and the lowest, respectively. The tropical japonica representatives of IR65598-112-2 and IR67966-44-2-3-2 were ranked by the mean $g_p$ averaged over the series at the fifth highest and the second lowest, respectively. The awned varieties were ranked by the mean $g_p$ averaged over the series at the third highest, the midst and the third lowest, respectively. The series-to-series difference in the $g_p$ of each variety was generally greater in the varieties which had relatively high mean $g_p$ over the series.

2. Sensitivity analysis on the impact of $g_p$ on $\Delta T_p$

Figure 4 shows the predicted $\Delta T_p$ as a function of the $g_p$ given. In each pair of $T_a$ and $RH$, the $\Delta T_p$ decreased with

among the varieties and with the series of experiments, ranging from 0.15 to 0.67 cm s$^{-1}$. Moderate to strong negative correlations were observed between $VPD$ and $g_p$ in each series and over the series with a statistical significance. From the regression over the series, we found that $g_p$ was dependent on $VPD$ at a rate of $-0.0457$, $-0.0128$, $-0.0173$ and $-0.0183$ cm s$^{-1}$ hPa$^{-1}$ in Series 1, 2 and 3 and over the series, respectively. However, $g_p$ was not uniquely determined by a certain value of $VPD$; $g_p$ varied largely even at similar $VPD$.

Figure 3 shows the $g_p$ at the time of flowering in the varieties tested. Statistically significant differences were found in $g_p$ among the varieties in each series, as determined by one-way ANOVA followed by Tukey's HSD test. Three series composite of the mean $g_p$ for each variety ranged from the lowest of 0.15 cm s$^{-1}$ in Dular in Series 3 to the highest of 0.67 cm s$^{-1}$ in IR72 and IR65598-112.2 both in Series 1 (hereafter, the “Composite Varietal Range”) with a width of 0.52 cm s$^{-1}$. The indica representatives of IR72 and Dular were ranked by the mean $g_p$ averaged over the series at the highest and the lowest, respectively. The tropical japonica representatives of IR65598-112.2 and IR67966-44-2.3-2 were ranked by the mean $g_p$ averaged over the series at the fifth highest and the second lowest, respectively. The awned varieties were ranked by the mean $g_p$ averaged over the series at the third highest, the midst and the third lowest, respectively. The series-to-series difference in the $g_p$ of each variety was generally greater in the varieties which had relatively high mean $g_p$ over the series.

2. Sensitivity analysis on the impact of $g_p$ on $\Delta T_p$

Figure 4 shows the predicted $\Delta T_p$ as a function of the $g_p$ given. In each pair of $T_a$ and $RH$, the $\Delta T_p$ decreased with
the increase in $g_{pI}$, with the curves which had the greatest slope at the lowest end (0.01 cm s$^{-1}$) of the given $g_{pI}$ range and continuously reduced their slopes along with the increase in $g_{pI}$. At [28ºC, 70%], the $\Delta T_p$ ranged from 2.84ºC to 0.77ºC with a width of 2.07ºC for the Composite Varietal Range of the $g_{pI}$, and from 2.39ºC to 1.08ºC with a width of 1.31ºC for the Averaged Varietal Range of the $g_{pI}$. As for the pair of [35ºC, 70%] and [35ºC, 30%], we estimated the impact of $g_{pI}$ on $\Delta T_p$ on the assumption that the Composite Varietal Range and the Averaged Varietal Range of $g_{pI}$ were not affected by the increment of VPD. At [35ºC, 70%], the $\Delta T_p$ ranged from 1.39ºC to −0.73ºC with a width of 2.12ºC for the Composite Varietal Range of the $g_{pI}$, and from 0.92ºC to −0.42ºC with a width of 1.34ºC for the Averaged Varietal Range of the $g_{pI}$. At [35ºC, 30%], the $\Delta T_p$ ranged from −2.63ºC to −6.18ºC with a width of 3.54ºC for the Composite Varietal Range of the $g_{pI}$, and from −3.38ºC to −5.63ºC with a width of 2.25ºC for the Averaged Varietal Range of the $g_{pI}$.

However, the analysis revealed that only a marginal cooling would be expected by the additional $g_{pI}$ beyond the highest end of the Composite Varietal Range of the $g_{pI}$ (0.67 cm s$^{-1}$) because the slopes of the curves are already small at the highest level observed and get even smaller as the $g_{pI}$ increases. For example, if the upper end of the Composite Varietal Range of $g_{pI}$ is extended from 0.67 cm s$^{-1}$ to 1.19 cm s$^{-1}$ by doubling the range, the contribution of increment to the additional decrease in the $\Delta T_p$ is estimated to be merely 0.67ºC at [28ºC, 70%], 0.63ºC at [35ºC, 70%] and 1.17ºC at [35ºC, 30%]; they are 33%, 30% and 33%, respectively, of cooling capacity which can be attained by the increment of the $g_{pI}$ from the lower end to the upper end of the Composite Varietal Range.

**Discussion**

Our results showed a difference in $g_{pI}$ among the 21 widely different varieties and three series of experiments, ranging from 0.15 to 0.67 cm s$^{-1}$. Previously, varietal differences in panicle transpiration during the grain filling period were reported using the cut panicles in the controlled environment (Miyagawa et al., 1999), but the present study is the first study that has revealed a large varietal difference in the intact panicle transpiration conductance at the time of flowering in the open field.

The width of 0.52 cm s$^{-1}$ for the Composite Varietal Range of $g_{pI}$ were observed (Fig. 3) with the difference in VPD of 3.0 hPa (Table 1) which is estimated to be equivalent to the difference in $g_{pI}$ of 0.14 cm s$^{-1}$ using the slope of the regression for the Series 1 (−0.0457 cm s$^{-1}$ hPa$^{-1}$) which estimates the influence of VPD on $g_{pI}$ most severely (Fig. 2). Thus, at least 73% of the Composite Varietal Range of $g_{pI}$ can be attributed to the ‘true’ varietal difference. Similarly, the width of 0.92 cm s$^{-1}$ for the Averaged Varietal Range of $g_{pI}$ was observed (Fig. 3) with the difference in VPD of 3.2 hPa (Table 1) which is estimated to be equivalent to the difference in $g_{pI}$ of 0.06 cm s$^{-1}$ using the slope of the regression over the series (−0.0183 cm s$^{-1}$ hPa$^{-1}$). Thus, more than 80% of the Averaged Varietal Range of $g_{pI}$ can be attributed to the ‘true’ varietal difference.

Between indica and temperate japonica, ecotype does not seem the key factor to determine the level of $g_{pI}$. IR72 and Dular as a representative pair of indica were ranked at the both ends of the Averaged Varietal Range with the pair being torn apart whereas the influence of the difference in corresponding VPD was negligibly small; japonica varieties were scattered between the indica representatives (Fig. 3). As for IR65598-112-2 and IR67966-44-2-3-2 as a representative pair of tropical japonica, and as for awnness, the difference in $g_{pI}$ and that in VPD were not conclusive evidence (Fig. 3 and Table 1). It was not easy to distinguish a high-$g_{pI}$ or low-$T_p$ pedigree without directly measuring $g_{pI}$.

![Fig. 4. The predicted temperature difference ($\Delta T_p$) between panicle temperature ($T_p$) and air temperature above canopy ($T_a$) as a function of $g_{pI}$, calculated by the micrometeorology model 'IM’PACT' (Yoshimoto et al. 2011). The curves were well approximated by the following 6th order polynomials with residuals of less than 0.07ºC.](image-url)
or \( T_p \). To manipulate \( g_{pl} \) genetically, it is mandatory to develop a methodology that enables high throughput screening for \( g_{pl} \) or \( T_p \) together with the elucidation of the mode of inheritance in \( g_{pl} \).

The significant varietal difference in \( g_{pl} \) observed in the present study (Fig. 3) and its predicted effectiveness as a means to lower \( T_p \) (Fig. 4) by the sensitivity analysis was evidence that introducing high-\( g_{pl} \) variety instead of low-\( g_{pl} \) variety can enhance heat avoidance capacity by lowering the \( T_p \). Thus genetic improvement of \( g_{pl} \) can be a promising option to lower \( T_p \), though its mode of inheritance is unknown. As illustrated by Weerakoon et al. (2008), fertility rate of rice declines exponentially above the threshold \( T_p \). According to their observation, the fertility rate started to decline from almost 100% with increasing \( T_p \) above 30°C and reached almost zero at about 36°C. It means that fertility rate declines at a rate of 17 percentage point \(^{°C}^{-1}\) on average within the critical range of \( T_p \). Therefore, although the efficiency of \( g_{pl} \) to lower \( T_p \) under the humid atmospheric conditions was estimated to be smaller than that under the dry atmospheric condition (Fig. 4), even such slight decrease in \( T_p \), which was conservatively estimated using the Averaged Varietal Range of the \( g_{pl} \) as 1.31°C for [28°C, 70%], 1.34°C for [35°C, 70%] and 2.28°C for [35°C, 30%] in the present study, can efficiently contribute to the increase in the fertility rate.

However, the result of the sensitivity analysis on \( T_p \) which extended the upper end of the Composite Varietal Range of \( g_{pl} \) by doubling the range (Fig. 4) predicts that the enhancement of \( g_{pl} \) beyond the Composite Varietal Range becomes increasingly inefficient to lower \( T_p \) in contrast with \( g_{pl} \) within the range. Considering that it is not confirmed whether there is a variety which has outstandingly higher level of \( g_{pl} \) than that in the varieties we tested, the improvement of \( g_{pl} \) with the aim to lower \( T_p \) should firstly seek to achieve the level of IR72 which exhibited the highest \( g_{pl} \) in the Averaged Varietal Range.

The series-to-series difference in the \( g_{pl} \) for each variety was generally greater in the varieties which had a relatively high mean \( g_{pl} \) over the series (Fig. 3). Further investigation on the determining mechanism of \( g_{pl} \) and on the methodology to keep \( g_{pl} \) of each variety at its highest is required to effectively utilize panicle transpiration to maintain \( T_p \) low.

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