Dark panicle color and high panicle position increase spikelet temperature of rice (Oryza sativa L.)

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Abstract

Rice (Oryza sativa L.) quality and yield are degraded by high temperature, especially at the ripening stage after the heading of panicles. The effect is lethal when the panicle temperature ($T_p$) is excessively high; therefore, maintaining a low $T_p$ is important to avoid deleterious impacts on the grains. Microclimatic factors and plant physiological elements determine the $T_p$. One determining factor is the color (or reflectance) of spikelets that constitute the panicle because it determines the absorption of shortwave radiation energy. An additional factor is the panicle position because it influences heat exchange by the wind and input energy from downward shortwave radiation. In this study, inter-strain differences in spikelet color and panicle height at heading were assessed. The $T_p$ of strains differing in panicle color and panicle height were measured with thermocouples. In addition, to estimate the effect of each trait, we adopted a micrometeorological model. Panicle color was quantified using a hyperspectral sensor. Combining the spectral reflectance and spectral radiation, we assessed the effect of panicle color on $T_p$. The differences in panicle color and panicle position significantly affected $T_p$. The strain with a dark panicle had a maximum measured $T_p$ about 1.8°C higher than that of the strain with a light-colored panicle. The $T_p$ of a strain with panicles at higher positions was up to 2.0°C higher than that of a strain with panicles at lower positions. These relationships were consistent with the model estimates. When shortwave radiation was strong, the difference in $T_p$ between strains showed a positive correlation, suggesting that the temperature difference was associated with shortwave radiation. Therefore, we concluded that rice strains with a brighter panicle color and low panicle position are less prone to deleterious impacts of high temperature because net radiation is reduced.

Key words: High temperature deterioration, Micrometeorology, Panicle height, Panicle temperature, Spikelet reflectance

1. Introduction

The Intergovernmental Panel on Climate Change (IPCC) predicts an increase in global temperature of 4.4°C under the Shared Socio-economic Pathway 5 set at 8.5 W m⁻² of radiative forcing (SSP5-8.5) by 2100 (IPCC, 2021). Thus, an adaptive solution to global warming for rice (Oryza sativa L.) production is required. Rice is sensitive to high air temperature ($T_a$), which results in low quality and yield of grains (Arshad et al., 2017; Xiong et al., 2017). In particular, high $T_a$ in the heading and ripening stages causes marked deterioration in grain quality and yield. Two types of quality and yield loss are induced: development of chalky rice grains (CRGs) and heat-induced spikelet sterility (HISS). In Japan, CRGs incidence is predicted to increase in all regions, especially in western Japan (Takimoto et al., 2019). Because CRGs are inferior to normal grains in palatability (Wakamatsu et al., 2007), an economic loss of US$404.1 million y⁻¹ in the 2040s is predicted under RCP 8.5 (Masutomi et al., 2019). Thus, adaptation to global warming is important not only for rice production but also for economic well-being.

Deterioration of rice quality and yield is closely associated with the panicle temperature ($T_p$) in addition to $T_a$. Sato and Inaba (1973) revealed that high $T_p$ is a more important factor for development of CRGs than high leaf temperature. This finding indicates that one reason for occurrence of CRGs is decline in the panicle sink strength for starch accumulation. Proteomic and genomic studies have revealed that high temperature upregulates starch degradation enzymes, such as α-amylase (Kaneko et al., 2016; Yamakawa et al., 2007), which is considered to be an important factor because α-amylase degrades starch in the spikelet, resulting in loosely packed starch grains and, ultimately, opaque grains. In addition, high $T_p$ increases the risk of HISS, which arises at $T_a$ of approximately 35°C in the flowering stage (Matsui et al., 1997, 2007). However, HISS is not a serious problem in paddies in Australia, where $T_a$ in a paddy field may attain ~40°C. The stability in yield under such high $T_a$ was associated with the extremely dry atmosphere and strong wind above the canopy. Such conditions make it possible to maintain a low $T_p$ despite the high $T_a$ (Matsui et al., 2007). Therefore,
maintenance of low $T_p$ under high $T_a$ is important to secure high quality and yield of rice.

The integrated micrometeorology model for panicle and canopy temperature (IM$^3$PACT) is advocated to predict the occurrence of HISS by estimating $T_p$ (Yoshimoto et al., 2011). This model estimates $T_p$ by considering meteorological variables ($T_a$, air humidity, wind speed, and radiation) and plant physiological factors (leaf transpiration rate, leaf area index, panicle transpiration conductance, and panicle reflectance). By consideration of these factors, low $T_p$ traits can be predicted. Fukuoka et al. (2012) studied the varietal range of panicle transpiration conductance and estimated the impact on $T_p$. The panicle transpiration conductance differed among strains, thus strains varied in transpiration rate. The varietal range in panicle transpiration conductance corresponded to the range of 3.5 $^\circ$C in ($T_p$ - $T_a$) under a dry atmosphere to 2.1 $^\circ$C in ($T_p$ - $T_a$) under a humid atmosphere. Although many traits may impact on $T_p$, a limited number have been studied to date.

The panicle reflectance affects $T_p$ but has not been well investigated. The panicle color differs among many rice strains, some of which are used in rice paddy art in Japan (Voltaire, 2018). Generally, a dark color perceived by human vision indicates low reflectance in the visible spectral region. Given that approximately half of the total energy of sunlight is in the visible wavelengths, such dark-colored panicles are expected to attain a high temperature owing to the elevated radiation absorbance. Moreover, the traits of direct and diffuse solar radiation differ depending on the wavelength (Kume et al., 2018). At noon, the maximum energy of direct radiation is ~550 nm, whereas that of diffuse radiation is ~450 nm. Such differences in radiation traits contribute to the green color of photosynthetic plant tissue. Therefore, such features of solar radiation should be considered to evaluate the effects of panicle color on $T_p$.

The panicle position is an additional factor that affects $T_p$ because micrometeorological parameters (e.g., wind speed and solar radiation) differ considerably when the panicle enters the canopy (Jones, 2013; Yoshimoto et al., 2005). The number of studies on panicle position has increased in recent years, and the optimal panicle position and panicle inclination for maximizing pollination frequency are gradually being clarified (Matsui et al., 2020; Win et al., 2020). Although panicle height affects pollination frequency, and pollination percentage increases when the panicle is at a lower position relative to the canopy (Matsui et al., 2021), few studies have investigated the relationship between panicle height and $T_p$.

In this study, the impact of differences in panicle reflectance and panicle position on $T_p$ was evaluated. To quantitatively evaluate panicle reflectance, the spectral reflectance of the spikelets constituting the panicle was measured. The $T_p$ of panicles of different color and different panicle position were measured using thermocouples in the field. To integrate spectral reflectance and radiation, energy absorption was calculated. The results were combined in the IM$^3$PACT model to estimate $T_p$. The findings of this study are expected to provide valuable information to improve future rice breeding and cultivation strategies.

## 2. Materials and Methods

### 2.1 Plant materials

Six strains were cultivated, of which four strains were used for further measurements, in the experimental paddy field of the Kyushu University Ito Campus (Fukuoka, Japan; 33.6031°N, 130.2308°E) in 2021. The details and panicle phenotype of these strains are summarized in Table 1 and Figure 1. HO353, HO835, and HO189 were provided by the Institute of Genetic Resources, Faculty of Agriculture, Kyushu University, and FL175 was provided by the National BioResource Project. The seeds were sown on 11 May, 2021, and transplanted randomly on 15 June, 2021. The transplantation density was 25 cm × 25 cm. The strains were fertilized with $\text{P}_2\text{O}_5;\text{Si(OH)}_3;\text{Mg}:\text{KCl} = 6, 6, 3.6, \text{and } 6 \text{ (g m}^{-2}\text{)}$.

### 2.2 Spectral reflectance measurement

On 30 August, 2021, we sampled two panicles each from three rice strains—a normal cultivated strain with green panicles (HO353), a strain with dark panicles (HO835), and a strain with relatively light green panicles (FL175) — and measured the panicle spectral reflectance. The imaging system was essentially identical to that of a previous study (Matsuda et al., 2012; Wakabayashi et al., 2021) except that the light source comprised a pair of DC halogen lamps. A line-scanning hyperspectral camera (VNIR-200R, Themis Vision Systems, Bay St Louis, MO, USA) sensitive to visible to near-infrared wavelengths (450–980 nm) was used. The camera was equipped with a silicon charge-coupled-device (CCD) detector and was capable of acquiring 1,392 × 1,000 pixel images with 12-bit digitization and at 1.3 nm spectral resolution (with a 12-μm-wide entrance slit). The reflectance was obtained based on a white filter paper placed beside the panicle as a reflector. The visible (450–780 nm) and near-infrared (780–980 nm) reflectance of the filter paper was 93.0% and 97.8%, respectively, and the obtained reflectance was calibrated with a PFTE standard reflector. After capturing the images, the area of the spikelet was extracted manually from each image. The spectral reflectance of each spikelet was determined by averaging the spectral reflectance of each pixel. Panicle reflectance was determined by averaging the spectral reflectance of all spikelets in a panicle.

### 2.3 Field experiment

Spectral solar irradiance was measured on the roof of the West 5 building at Kyushu University. This building was located 2 km from the paddy field.

| Strain name | Hull color (heading) | Panicle height (m) | Canopy height (m) | Heading date |
|-------------|---------------------|-------------------|------------------|-------------|
| HO353       | Green               | 0.8               | 0.85             | 2021/8/25   |
| HO835       | Dark Purple         | 1.2               | 1.1              | 2021/8/19   |
| HO189       | Green               | 1                 | 1                | 2021/8/19   |
| FL175       | Light Green         | 1.2               | 1.1              | 2021/8/26   |
from the field. The measurement was conducted using a SP-500 pyranometer (Apogee Instruments, Inc., Logan, USA) and MS-711 spectroradiometer (EKO Instruments Co., Ltd, Tokyo, Japan) with a rotating shadow band (MB-22, EKO Instruments Co., Ltd, Tokyo, Japan). Because this system was equipped with a rotating shadow band, which casts a shadow on the sensor, direct radiation and diffuse radiation were measured separately. These data were recorded at 5 min intervals. Downward longwave radiation was approximated as a black body 20°C lower than the atmospheric temperature (Jones, 2013).

Air temperature and relative humidity were measured by a Thermo Recorder TR-72wf (T&D Co., Tokyo, Japan) with a manually generated forced draft. Measurements were recorded at 30 s intervals and averaged over 10 min. Wind speed was measured with a sonic anemometer (ATMOS-22, METER Group, Inc. Pullman, USA). The parameters were measured in the experimental paddy at 1.9 m height above the ground.

The T\textsubscript{d} of the rice strains was measured using T-type thermocouples (copper−constantan) of 0.12 mm diameter. The thermocouples were attached directly to the spikelets with a cyanoacrylate adhesive. The ground (depth = 0.1 m) and water (depth = 0.1 m) temperature were also measured by a T-type thermocouple with sunshade. Data from the thermocouples and the anemometer were recorded with a CR1000X datalogger (Campbell Scientific, Inc., Logan, USA). In the experiment for evaluation of panicle color effect, thermocouples were attached to 3−5 panicles (HO353: n = 5, HO835: n = 3, FL175: n = 4). The reason for the different sample sizes was that some thermocouples malfunctioned during the experiment. In the experiment for evaluation of the effect of panicle position, each sample size was 7. All data were recorded by the datalogger at 30 s intervals and averaged over 10 min.

2.4 Calculation of radiation absorption and \( T_p \)

To compare the effects of panicle color on radiation absorption by the panicle, absorptance was calculated in the measured wavelength range. This calculation was conducted by simply integrating the radiation and reflectance spectra from 450 nm to 980 nm. Global radiation was obtained by summing the direct radiation and diffuse radiation.

To simulate \( T_p \) for different plant and environmental conditions, a modified IM\textsuperscript{PACT} model was adopted. To estimate \( T_p \), radiation absorption was calculated using the following formula:

\[
A_{\text{id}} = F_p \text{ (sec a A}_{\text{差}} + d_1 A_{\text{diff}}) 
\]

where \( A_{\text{差}} \) is absorption from the downward shortwave radiation, \( F_p \) is the inclination factor of the panicle, \( a \) is the solar zenith angle, \( d_1 \) is the diffusive factor for diffuse radiation, and \( A_{\text{差}} \) and \( A_{\text{diff}} \) are the absorption from direct radiation and diffuse radiation, respectively. For calculation of \( A_{\text{差}} \) and \( A_{\text{diff}} \) the following formulas are used:

\[
A_{\text{差}} = \left(1 - \frac{\rho_{\lambda}}{100}\right) \int_{450}^{980} R_{\text{diff}}(\lambda) \, d\lambda + \int_{450}^{980} R_{\text{差}}(\lambda) \times \left(1 - \frac{\rho(\lambda)}{100}\right) \, d\lambda 
\]

\[
A_{\text{diff}} = \left(1 - \frac{\rho_{\lambda}}{100}\right) \int_{280}^{450} R_{\text{diff}}(\lambda) \, d\lambda + \int_{450}^{980} R_{\text{差}}(\lambda) \times \left(1 - \frac{\rho(\lambda)}{100}\right) \, d\lambda
\]
where $R_{\text{dir}}$ and $R_{\text{diff}}$ are direct radiation and diffuse radiation, respectively; $R_{\text{res}}$ is the residual global radiation obtained by subtracting radiation measured by the MS-711 from radiation measured by the SP-500; $\rho(\lambda)$ is reflectance at a given wavelength; and $\rho_{p}$ and $\rho_{\text{an}}$ are the reflectance in the 280–450 nm and 980–1100 nm regions, which are set to 10% and 28%, respectively (Croft and Chen, 2018). The calculated values were used as inputs to estimate $T_p$.

In this paper, we used a modified IM$^3$PACT model as described earlier. The main changes implemented were that we did not perform the iterations necessary to calculate canopy temperature ($T_c$), water temperature was obtained by actual measurements, and air temperature adjacent to the panicle ($T_{\text{an}}$) was predicted from the air temperature, shortwave radiation, and wind speed.

We adopted these methods because the fetch in the experimental environment was not secured and was more similar to an isolated canopy than a paddy canopy. Therefore, the original IM$^3$PACT model did not fit well. The IM$^3$PACT model is based on solving the heat budget between the panicle and its surrounding environment ($T_{\text{an}}$) to estimate $T_p$, which is obtained from a two-layer model. The accuracy of the estimation is shown in Supplemental data 1. The formula used to estimate $T_{\text{an}}$ was:

$$T_{\text{an}} = 0.88 \times T_c - 0.0027 \times R_{\text{dir}} + 0.389 \times u_d + 2.4 \quad (4)$$

where $R_{\text{dir}}$ is downward shortwave radiation and $u_d$ is wind speed. The model coefficient of determination, RMSE, and bias were 0.93, 0.73°C, and 6.1 × 10^{-5} °C, respectively.

Table 2 summarizes the environmental parameters used in this model calculation. These values were obtained from Yoshimoto et al. (2005), (2011) and Kondo and Watanabe (1992). The panicle height and canopy height were defined as the upper limit of panicles and leaves in the paddy, respectively. For evaluation of the effect of color differences, panicle height and canopy height were 1 m for all strains. For evaluation of the effect of panicle position, the panicle height and canopy height were 1 m for HO189, and 0.8 m and 0.85 m for HO353, respectively.

### 2.5 Statistical analysis

Analysis of covariance (ANCOVA) was used to evaluate the difference of $T_p$ in each strain and was performed with R software version 4.0.2 (R Core Team, 2020). The R packages used for data analysis were nleqslv (Hasselman, 2018), suncalc (Benoit and Elmarhraoui, 2019), and NLopt (Johnson, n.d.).

### 3. Results

#### 3.1 Spectral reflectance of the panicle

The panicles of all three strains showed high reflectance in the near-infrared region (from 780 nm) (Figure 2). The typical strain, HO353, had low reflectance in the blue (approximately 450–500 nm) and red regions (approximately 570–700 nm), and high in the green range (approximately 500–570 nm) because of the green color of the panicle. HO835 had consistently low reflectance in the visible range (450–780 nm) and relatively low reflectance in the near-infrared range. FL175, which produces a relatively light green panicle, had an overall higher reflectance in the visible spectrum compared with that of HO353.

#### 3.2 Difference in $T_p$ with panicle color in the field

Figure 3 compares $T_p$ among strains with a different panicle color. For most of the experimental period, HO835 with dark panicles showed higher $T_p$ than those of the other two strains, and FL175, which showed relatively high panicle reflectance, showed lower $T_p$. The difference in $T_p$ between HO835 and FL175 was larger during the daytime when the solar radiation intensity was strong; the mean and maximum differences were 0.19°C and 1.8°C, respectively. In contrast, the difference in $T_p$ was small at night.

ANOVA revealed that in FL175 the effect of radiation and wind on $T_p$ was significant, and that the effects of radiation differed significantly among the three strains (Table 3). Intercepts among strains were not significantly different (HO353 and HO835 rows). $T_p$ increased significantly with radiation and wind. The interaction between radiation and strains was significant (HO353:Radiation and HO835:Radiation rows), suggesting the effect of radiation differed among strains. Therefore, the difference in $T_p$ was large under high shortwave radiation and negligible in the absence of shortwave radiation (Figure 4). Because the interaction between wind effect and strains was not significant (HO353:Wind and HO835:Wind rows), the difference in regression slope among the strains was small (Figure 5).

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**Table 2. Values used for the panicle temperature ($T_p$) estimation**

| Name of each variation | Value |
|------------------------|-------|
| Leaf area index (LAI: m² m⁻²) | 4.38 |
| Attenuation coefficient for shortwave radiation and wind velocity in canopy (C) | 0.35 |
| Panicle reflectance for model calibration ($a_p$) | 0.3 |
| Diffusivity factor of longwave radiation ($d_l$) | 1.66 |
| Bulk transfer coefficient for sensible heat ($c_h$) | 0.05 |
| Drag coefficient of an individual leaf element ($c_d$) | 0.2 |
| Inclination factor of panicle ($F_p$) | 0.35 |

**Fig. 2. Differences in spectral reflectance of the panicle among the three strains.**
3.3 Difference in $T_p$ with panicle position in the field

In the strain HO189 the panicle and canopy are both 1 m high, whereas in HO353 the panicle is 0.8 m high and the canopy is 0.85 m high. The $T_p$ of HO189 was higher than that of HO353 at most time points, and the difference was larger during the day and smaller at night (Figure 6). The $T_p$ of HO189 was higher by 0.18°C on average and was higher by a maximum of 2.0°C across all measurement time points.

ANCOVA revealed that the effects of radiation, wind, and interactions between the strains were significant (Table 4). In detail, this result based on HO189 and the values of the intercept differed between the strains (HO353 row in Table 4). The effects of radiation and wind were significant (Radiation and Wind rows). Because the interaction between radiation and strains was significant (HO353:Radiation row), the difference in $T_p$ tended to be larger under high shortwave radiation (Figure 7). The effect of radiation and wind were significant (Radiation and Wind rows). Because the interaction between radiation and strains was significant (HO353:Radiation row), the difference in $T_p$ tended to be larger under high shortwave radiation (Figure 7). The effect of radiation and wind were significant (Radiation and Wind rows). Because the interaction between radiation and strains was significant (HO353:Radiation row), the difference in $T_p$ tended to be larger under high shortwave radiation (Figure 7).

![Graph](image)

**Fig. 3.** Typical daily $T_p$ variation measured in the strains with different panicle color. The results were recorded on 6 September, 2021.

**Fig. 4.** Linear regressions between the mean $T_p$ and radiation for strains with different panicle color. Circles and solid line represent the $T_p$ of FL175 with radiation (formula: $24.66 + 1.872 \times 10^{-3} \times \text{Radiation}$, $R^2 = 0.35$). Triangles and dashed line represent that of HO353 (formula: $24.57 + 3.178 \times 10^{-3} \times \text{Radiation}$, $R^2 = 0.18$). Crosses and dotted-dashed line represent that of HO835 (formula: $24.75 + 3.140 \times 10^{-3} \times \text{Radiation}$, $R^2 = 0.32$).

**Fig. 5.** Linear regressions between the mean $T_p$ and wind speed for strains with different panicle color. Circles and solid line represent the $T_p$ of FL175 with wind speed (formula: $24.66 + 1.491 \times 10^{-1} \times \text{Wind}$, $R^2 = 0.12$). Triangles and dashed line represent that of HO353 (formula: $24.57 + 4.779 \times 10^{-2} \times \text{Wind}$, $R^2 = 0.09$) and crosses and dotted-dashed line represent that of HO835 (formula: $24.75 + 5.619 \times 10^{-2} \times \text{Wind}$, $R^2 = 0.11$).

**Table 3.** Results of ANCOVA among the different panicle color strains

|          | Estimate | Std.Error | t-value | Pr (>|t|) |
|----------|----------|-----------|---------|-----------|
| Intercept| 2.47E+01 | 7.62E-02  | 323.677 | <2e-16    | ***       |
| HO353    | -9.69E-02| 9.64E-02  | -1.006  | 3.15E-01  |           |
| HO835    | 8.28E-02 | 1.01E-01  | 0.821   | 4.12E-01  |           |
| Radiation| 1.87E-03 | 1.78E-04  | 10.536  | <2e-16    | ***       |
| Wind     | 1.49E-01 | 5.66E-02  | 2.636   | 8.43E-03  | **         |
| HO353:Radiation| 1.31E-03 | 2.25E-04  | 5.81    | 6.75E-09  | ***       |
| HO835:Radiation| 1.27E-03 | 2.35E-04  | 5.396   | 7.21E-08  | ***       |
| HO353:Wind| -1.01E-01| 7.15E-02  | -1.416  | 1.57E-01  |           |
| HO835:Wind| -9.29E-02| 7.48E-02  | -1.241  | 2.15E-01  |           |
of wind differed significantly between the strains (HO353:Wind row); the $T_p$ of HO189 was larger than that of HO353 across different wind speeds (Figure 8).

### 3.4 Model estimation of $T_p$

First, we verified the accuracy of the model. To create the model, we used the data recorded on 23 August and from 20 to 24 September. Then, we estimated $T_p$ on 9 September. The final coefficient of determination, RMSE, and bias were 0.90, 1.59 °C, and −0.31 °C, respectively (Supplemental data 2). This estimation was performed using the meteorological environment on 6 September.

Estimation of $T_p$ in strains that differed in panicle color (Figure 9) was done under conditions in which only the color of the panicle varied. Compared with HO353, $T_p$ was higher in HO835, in which the panicle was dark, and lower in FL175, in which the panicle was relatively light. The maximum difference in $T_p$ between FL175 and HO353 was −0.13 °C, between HO835 and HO353 was 0.17 °C, and between HO835 and FL175 was 0.3 °C.

The estimated $T_p$ when only the panicle height varied is shown

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**Table 4. Results of ANCOVA for the strains with different panicle positions relative to canopy height**

|                       | Estimate | Std.Error | t-value | Pr (>|t|) |
|-----------------------|----------|-----------|---------|-----------|
| Intercept             | 2.28E+01 | 2.60E-02  | 876.509 | <2e-16    |
| HO353                 | -1.41E-01| 3.67E-02  | -3.831  | 1.28E-04  |
| Radiation             | 6.24E-03 | 7.91E-05  | 78.854  | <2e-16    |
| Wind                  | 6.63E-02 | 2.39E-02  | 2.774   | 5.55E-03  |
| HO353:Radiation       | -1.04E-03| 1.12E-04  | -9.299  | <2e-16    |
| HO353:Wind            | 1.03E-01 | 3.38E-02  | 3.033   | 2.42E-03  |

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**Fig. 6.** Typical daily $T_p$ variation measured in the strains with different panicle positions relative to canopy height. The results were recorded on 9 September, 2021.

**Fig. 7.** Linear regressions between the mean $T_p$ and radiation for the strains with different panicle positions relative to canopy height. Circles and solid line represent the $T_p$ of HO189 with radiation (formula: $22.76 + 6.237 \times 10^{-3} \times$ Radiation, $R^2 = 0.51$). Crosses and dashed line represent that of HO353 (formula: $22.62 + 5.200 \times 10^{-3} \times$ Radiation, $R^2 = 0.43$).

**Fig. 8.** Linear regressions between the mean $T_p$ and wind speed in the strains with different panicle positions relative to canopy height. Circles and solid line represent the $T_p$ of HO189 with wind speed (formula: $22.76 + 6.631 \times 10^{-2} \times$ Wind, $R^2 = 0.10$). Crosses and dashed line represent that of HO353 (formula: $22.62 + 1.689 \times 10^{-1} \times$ Wind, $R^2 = 0.11$).
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in Figure 10. The $T_p$ of HO189, for which the panicles and canopy were of the same height, was higher than that of HO353, in which the panicles were lower than the canopy. The maximum difference in $T_p$ was 0.16°C.

4. Discussion

4.1 Heat avoidance strategy for heat deterioration

With recent climate warming, there is an urgent need to develop heat-resistant strains of crops. There are two possible means of adapting to high temperature: maintaining high performance under high $T_a$ or $T_p$, and maintaining low $T_p$ under high $T_a$. With regard to the former solution, a number of quantitative trait loci have been identified as heat-tolerant traits, for example, anther dehiscence and pollen viability (Jagadish et al., 2010; Wada et al., 2020). These heat-tolerant quantitative trait loci are especially associated with reproductive organs (Raza et al., 2020). With respect to the latter solution, it is important to avoid excessive heat effectively. This strategy can be roughly divided into reducing net radiation and dissipating heat into the atmosphere. In this study, we investigated the effect of panicle color, which is considered to affect net radiation, and panicle position, which is considered to affect heat dissipation by wind. The results showed that both traits have a significant impact on $T_p$. Therefore, more attention should be paid to heat avoidance strategies.

4.2 Adaptive significance of dark panicle as a wild trait and proposal of high panicle reflectance as a trait for high temperature avoidance

Spikelet color is one factor that affects $T_p$. Normal colored strains produce spikelets that are green at the heading stage. This trait was intentionally selected because in *Oryza rufipogon*, the wild progenitor of *O. sativa*, the spikelet is dark (Gu et al., 2005; Sweeney et al., 2007; Zhu et al., 2011). The dark color might be owing to anthocyanins (Wang et al., 2020). Anthocyanins play important roles in plant tissues, such as in protection against oxidative damage, light attenuation, and thermoregulation (Chalker-Scott, 1999). In the present study, we quantitatively evaluated the effect of spikelet color on panicle temperature regulation. The spectral reflectance of ‘HO835’ at the heading stage at around 550 nm was low compared with that of ‘HO353’. Green plants tend to avoid absorbing radiation of this wavelength (Kume et al., 2018). Thus, the absorption of radiation in this wavelength range by photosynthetic pigments is low, but accumulated anthocyanins greatly increase the absorption. In addition, members of the Poaceae are anemophilous; therefore, pollen transport by wind is essential for pollination (McCombe and Ackerman, 2018), which simultaneously results in cooling of the flower. A dark spikelet color would be advantageous to maintain an elevated temperature during pollination and fertilization. In contrast to such wild traits, reduction in the spikelet temperature is needed for adaptation to high temperature.

The present results confirmed that a panicle with high reflectance tended to have a low $T_p$ because of the low absorption of downward shortwave radiation; therefore, high panicle reflectance is a candidate trait for development of heat-avoidance strains. The advantage of the high reflectance of the panicle is that it prevents temperature increase in environments with high solar radiation. Therefore, strains in which the panicle shows high reflectance may be more effective in wet, low-wind-speed environments where heat exchange is less likely to occur. However, when high reflectance occurs owing to low contents of photosynthetic pigments, low photosynthetic activity in reproductive organs and low productivity may result (e.g. Chang et al., 2020; Ferguson et al., 2021). Thus, incorporation of such traits in cultivars requires optimization of the advantages and disadvantages.
4.3 Relationship between $T_p$ and panicle position

In this experiment, we focused on the panicle position. The leaves and panicles of cultivated rice are generally preferred to be in a low position because it reduces the risk of lodging (Shah et al., 2017) and increases the pollination frequency (Matsu et al., 2020; Win et al., 2020). The present results suggest one reason for the reduction in $T_p$ when the panicle is in a low position is that the penetration of solar radiation to the panicle is attenuated by the canopy, which also decreases $T_m$. The relationship between solar radiation and $T_p$ at different panicle positions is indicated in Figure 7. Because the panicle color of HO189 and HO353 used in this experiment was identical, the absorptivity was not significantly different. However, a positive correlation between the difference in $T_p$ and shortwave radiation was observed, suggesting that the low panicle position may have reduced reception of shortwave radiation. Thus, $T_p$ was reduced by shading from the canopy. The $T_m$ in a paddy field is determined by various parameters, such as canopy characteristics and soil moisture content. In general, a paddy field often acts as a heat sink owing to high evapotranspiration. Therefore, the low position of the panicle may lead to a decrease in $T_p$ as air adjacent to the panicle is cooled by transpiration from the canopy and the water surface. However, given that the direction of sensible heat transport in a paddy field may differ depending on a number of factors, for example air humidity, transplantation density, and wind speed (Ishimaru et al., 2016; Matsui et al., 2007; Oue, 2003; Yoshimoto et al., 2012), further research on panicle temperature and panicle position is needed.

4.4 Conclusion

This study revealed that strains with high panicle reflectance and/or low panicle position are less likely to be affected by high temperature. The reason why the panicle color affects $T_p$ is that the difference in reflectance of the panicle results in differences in energy input from solar radiation, which reduces net radiation. The difference in panicle color indicates a difference in reflectance. Therefore, plant tissues pigmented by anthocyanins may assume a different temperature to that of non-pigmented tissues. When the height of the panicle is lower than that of the canopy, $T_p$ will be smaller because the canopy interrupts solar radiation, thus reducing interception of solar radiation by the panicle, and because the temperature within the canopy decreases. Combining these properties may be an effective solution in the development of rice strains resistant to high temperature.

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