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Effects of Temperature, Solar Radiation, and Vapor-Pressure Deficit on Flower Opening Time in Rice

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Abstract: Flower opening in the early morning helps to avoid sterility of rice (*Oryza sativa* L.) caused by heat stress at anthesis. Although flower opening time (FOT) is under genetic control, it is also affected by weather, particularly by air temperature (T_a). However, the effects of T_a, solar radiation (R_s), and vapor-pressure deficit (VPD) on rice FOT are unclear, making it difficult to predict FOT. Therefore, we investigated the correlation of FOT with T_a, R_s, and VPD during various periods before anthesis under field conditions. By photographing spikelets at 10-min intervals, we determined the FOT of five cultivars. To evaluate the individual effects of cultivar, T_a, R_s, and VPD on FOT, we constructed general linear models (GLMs) and calculated mean T_a, R_s, and VPD every 3 hr from 0000 to 1200. The GLMs revealed that the average T_a, R_s, and VPD between 0600 and 0900 significantly affected FOT (adjusted R^2=0.399; P<0.001). The standardized partial regression coefficients of T_a and R_s were negative and those of VPD were positive, indicating that higher T_a, higher R_s, and lower VPD in the early morning result in earlier FOT. Moreover, multiple-regression analysis showed that the period affecting FOT the most, and the relative contributions of T_a, R_s, and VPD to FOT differ with the cultivar.

Key words: Flower opening in the early morning, Flower opening time, Heat-induced sterility, *Oryza sativa*, Rice cultivars, Solar radiation, Temperature before anthesis, Vapor-pressure deficit.

Global climate change will pose a serious challenge to crop production around the world. In rice (*Oryza sativa* L.), temperatures >34°C at the time of flowering may induce floret sterility and decrease yield, even in temperate regions such as southern Japan, if the cropping season is not changed to avoid such temperatures (Horie et al., 1996; Kim et al., 1996; Nakagawa et al., 2003). Using crop simulation models, Horie et al. (1996) suggested that yields of currently grown rice varieties in southern Japan would be reduced by up to 40% under future climate scenarios. In the summer of 2003, the Yangtze River rice-growing region in China experienced temperatures above 39°C, leading to a large reduction in rice production resulting from a low seed-set (30 to 70%; Wang et al., 2004).

Opening of rice flowers in the early morning is a beneficial response to avoid sterility caused by heat stress at anthesis because the sensitivity of rice flowers to high temperatures decreases during the 1-hr period after flower opening (Satake and Yoshida, 1978). Thus, a flower opening time (FOT) 1 hr earlier than normal may reduce sterility, because it may lead to anthesis before the air temperature reaches the critical level; air temperature can rise at a rate of >3°C hr^{-1} starting around 1000 (Nishiyama and Blanco, 1980). A controlled-environment experiment revealed that flowers of ‘Milyang 23’ that opened earlier in the morning and at a lower temperature had higher seed-set than those that opened later (near midday) and at higher temperatures (Imaki et al., 1987).

Selection of cultivars with an early FOT is thus an important method for reducing heat-induced sterility (Nishiyama and Blanco, 1980; Jagadish et al., 2008). For example, the flowers of *Oryza glaberrima* Steud. open earlier than those of *Oryza sativa* L. (Nishiyama and Blanco, 1980; Jagadish et al., 2008), and the flowers of interspecific hybrids between *O. glaberrima* and *O. sativa* open earlier than those of *O. sativa* (Nishiyama and Satake, 1981). Imaki et al. (1983, 1987) reported that flowers of some cultivars of *O. sativa* opened 1 to 2 hr earlier than those of ‘Koshihikari’, a standard Japanese cultivar. Under controlled conditions, ‘Milyang 23’ exhibited heat tolerance because of the earlier opening of its flowers

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Abbreviations: FOT, flower opening time; GLM, general linear model; JST, Japan Standard Time; R_s, solar radiation; T_a, air temperature; VPD, vapor-pressure deficit.

Table 1. Seeding dates, measurement periods, and variations in daily mean air temperature (T_a) and flower opening time (FOT; expressed as Japan Standard Time, JST) for five *Oryza sativa* cultivars.

Cultivar	Seeding date	Measurement period	Daily mean T_a (°C)	FOT (JST)
'IR72'	9, 19, 29 May	5, 6, 10, 12–14, 16–18, 20–22 Sept.	23.6–28.3	0913–1200
'Hanaechizen'	11, 19 April; 18 June	20, 24, 28–30 July; 7, 8, Aug. 5–6 Sept.	22.3–28.7	1041–1404
'Fujihikari'	11, 19 April; 1, 9 May	9 July to 1 Aug.	22.1–27.6	1020–1606
'Shinriki'	29 May; 8, 28 June	5–10, 12–14, 16–23 Sept.	23.6–28.3	1107–1346
'Asahi'	29 May; 8, 28 June	1–4, 7–14, 16–23 Sept.	23.6–28.3	1120–1406

(Imaki et al., 1983).

Although FOT is under genetic control, it is also affected by weather, and particularly by air temperature (Nishiyama and Satake, 1981; Imaki et al., 1983; Hoshikawa, 1989; Jagadish et al., 2007, 2008; Nakagawa and Nagata, 2007). The response of flower opening to high temperature differs among rice cultivars. FOT is earlier at high temperatures in 'Milyang 23', whereas it is later in 'Nipponbare' (Imaki et al., 1983). In a study of indica cultivars, FOT occurred about 45 min earlier at higher temperatures (Jagadish et al., 2007). However, most studies on FOT (Nishiyama and Blanco, 1981; Imaki et al., 1983; Jagadish et al., 2007, 2008) have been conducted under controlled environments, and rice plants grown in a glasshouse or a growth chamber have been reported to open flowers 1 to 2 hr later than those grown outdoors (Imaki et al., 1982).

In addition to temperature, other weather factors such as solar radiation (R_s) and relative humidity may affect FOT. For example, Nakagawa and Nagata (2007) found that R_s from 0400 to 0800 influenced FOT in 'Koshihikari', but not in EG0. Strong winds (Tsuboi, 1961), as well as low atmospheric pressure and rain (Hoshikawa, 1989), also affect FOT. Light conditions can also influence FOT, since the duration of anthesis increases under continuous light or dark conditions (Hoshikawa, 1989). Both the light intensity and the cycle of light and dark may affect FOT.

However, the combined effects of temperature, R_s, and humidity on the FOT of various rice genotypes remain unclear, particularly under field conditions, and this limits our ability to predict FOT. In the present study, we compared the effects of air temperature (T_a), R_s, and humidity (expressed as the vapor-pressure deficit, VPD) at various periods before anthesis on rice FOT under field conditions. First, we analyzed the correlations of FOT with T_a, R_s, and VPD averaged hourly from 0000 to 1000. Second, we used general linear models (GLMs) to separately evaluate the effects of cultivar, T_a, R_s, and VPD on FOT. In the second analysis, we used two kinds of 3-hr time span: a 3-hr time span based on Japan Standard Time (JST), and a 3-hr time span based on the time of sunrise that eliminated the seasonal effects of the light-dark cycle. Finally, because the period most sensitive to the effects of T_a, R_s, and VPD may differ among cultivars, we used multiple regression to evaluate the relative contributions of T_a, R_s, and VPD to FOT for each cultivar.

Materials and Methods

1. Field sites, plant materials, and culture methods

The study was conducted at an experimental field of Shimane University in Matsue, Shimane Prefecture, Japan (35°29′N, 133°04′E, 4 m asl) in 2007. We used five rice cultivars in this study: the indica cultivar 'IR72', and the japonica cultivars 'Hanaechizen', 'Fujihikari', 'Shinriki', and 'Asahi'. We used 'Hanaechizen' and 'Fujihikari' because they have weak sensitivity to photoperiod, and by shifting the transplanting dates, we can obtain flowering plants over a long period. We used 'Shinriki' and 'Asahi' to obtain flowering plants in September, when average daily temperatures are typically decreasing and a wide range of weather may be experienced. Although indica cultivars are rarely planted in Japan, we used 'IR72', one of the most popular indica cultivars, because flowers of this and several other indica cultivars open earlier than those of japonica cultivars (Imaki et al., 1987).

The soil at the study site was an alluvial sandy clay. On several occasions, 30 d old seedlings grown in nursery boxes were manually transplanted into the experimental field of Shimane University to obtain flowering plants under different weather conditions. Table 1 shows the seeding dates. The planting density was 22.2 hills m^{-2} (one seedling per hill, 15-cm hill spacing, and 30-cm row spacing). The area of each plot ranged from 2.25 to 3.6 m^2. A basal dressing of 5 g m^{-2} of N, 5.6 g m^{-2} of P_2O_5, and 4.4 g m^{-2} of K_2O was applied. No top dressing was used. Culture methods such as irrigation and pesticide use followed the standard local practices for rice production in Shimane Prefecture.

2. Measurements of flower opening time and weather

Physical stimuli such as touch may promote flower opening in rice (Tsuboi, 1961). To avoid this phenomenon, we used digital photographs of the panicles instead of physical inspections. The panicles were photographed at

10-min intervals with waterproof digital cameras (Optio W30, Pentax, Tokyo, Japan) to determine the FOT of the five cultivars. The photographs were recorded automatically in the cameras. We put the camera on a tripod and used a built-in electronic timer to control the measurement intervals. We recorded the time of anther extrusion of all observable flowers (more than 30% of flowers in a panicle) on the obverse side of 2 to 8 panicles per day per cultivar. Medians of anther extrusion time among all observed flowers in each panicle were calculated. FOT was defined as the mean of the medians per day. Recording anther extrusion time of flowers behind panicles and leaves was sometimes difficult.

We measured T_a, relative humidity, and R_s every 5 min using a wireless weather station (Wireless Vantage Pro, Davis Instruments, Hayward, CA, USA) located at Shimane University (http://www.ipc.shimane-u.ac.jp/weather/station/i/home.html). The weather station was installed at a distance of approximately 30 m from the observation plots. The ground surface below the station was covered with grass. We installed a thermometer, a hygrometer, a solarimeter, a barometer, and an anemometer at a height of 150, 150, 180, 150, and 300 cm, respectively. At our study site, the sun rose at 0500 (9 July) to 0556 (23 Sept.), so we did not measure R_s before twilight. Vapor-pressure deficits were calculated from T_a and relative humidity using the method of Buck (1981).

3. Statistical analysis

We analyzed our data by means of GLMs and multiple-regression procedures using SPSS (Version 14J for Windows, SPSS Japan Inc., Tokyo, Japan). We used Pearson's correlation analysis to identify relationships between weather factors (T_a, R_s, and VPD) and FOT. In this analysis, we used average hourly T_a, R_s, and VPD values for each hour between 0000 and 1000. The period of the correlation analysis was restricted to between 0000 and 1000 because flowers of 'IR72' usually started to open before 1000.

As there are inherent relationships among weather factors, there may be relatively high correlations among T_a, R_s, and VPD. Therefore, to evaluate their individual effects as well as the cultivar effects on FOT, we used GLMs. In this analysis, T_a, R_s, and VPD values were averaged over four 3-hr periods (0000–0300, 0300–0600, 0600–0900, 0900–1200) based on JST and over four 3-hr periods based on the sunrise time (successive 3-hr periods from 6 hr before sunrise until 6 hr after sunrise).

We analyzed the differences in sensitivity of FOT to T_a, R_s, and VPD and in the relative contributions of T_a, R_s, and VPD to FOT among the cultivars using multiple regressions. The relative contribution of each weather component to FOT was determined using their standardized partial regression coefficients, and the overall strength of the relationships was quantified using the multiple-correlation coefficients (i.e., adjusted R^2).

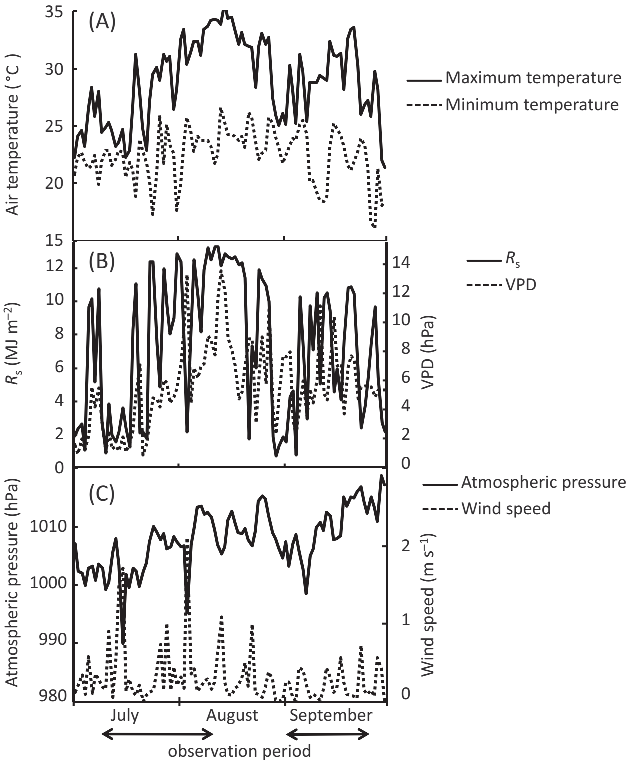

Fig. 1. Meteorological variables during the observation period.
(A) Maximum and minimum temperatures between 0000 and 1200.
(B) Total solar radiation (R_s) and average vapor-pressure deficit (VPD) between 0000 and 1200.
(C) Average atmospheric pressure and average wind speed between 0000 and 1200.

In all tests, the minimum level of statistical significance was set at a probability level of $P<0.05$.

Results

1. Meteorological variables and FOT during the observation period

Daily mean T_a during the FOT observation period ranged from 22.1 to 28.7°C (Table 1). Cultivar 'IR72' opened flowers more than 1 hr earlier (0913–1200) than the other cultivars. The FOT range was greater than 2.5 hr in all five cultivars.

The maximum and minimum T_a between 0000 and 1200 during the FOT observation period ranged from 22.3 to 33.5°C and from 17.3 to 25.9°C, respectively (Fig. 1). The maximum and minimum T_a increased rapidly from mid-July to early August. The total R_s and average VPD between 0000 and 1200 during the FOT observation period ranged from 0.8 to 12.9 MJ m^{-2} and from 0.9 to 13.3 hPa, respectively. Average wind speed and atmospheric pressure between 0000 and 1200 during the FOT observation period ranged from 0.0 to 2.1 m s^{-1} and from

Table 2. Correlation matrix showing the relationships among air temperature (T_a), solar radiation (R_s), vapor-pressure deficit (VPD), wind speed, and atmospheric pressure between 0000 and 1200 during the observation period.

	T_a	R_s	VPD	Wind speed
R_s	0.664***			
VPD	0.856***	0.748***		
Wind speed	0.386***	0.271***	0.361***	
Atmospheric pressure	0.091***	0.208***	0.142***	–0.296***

***, significant at P<0.001.

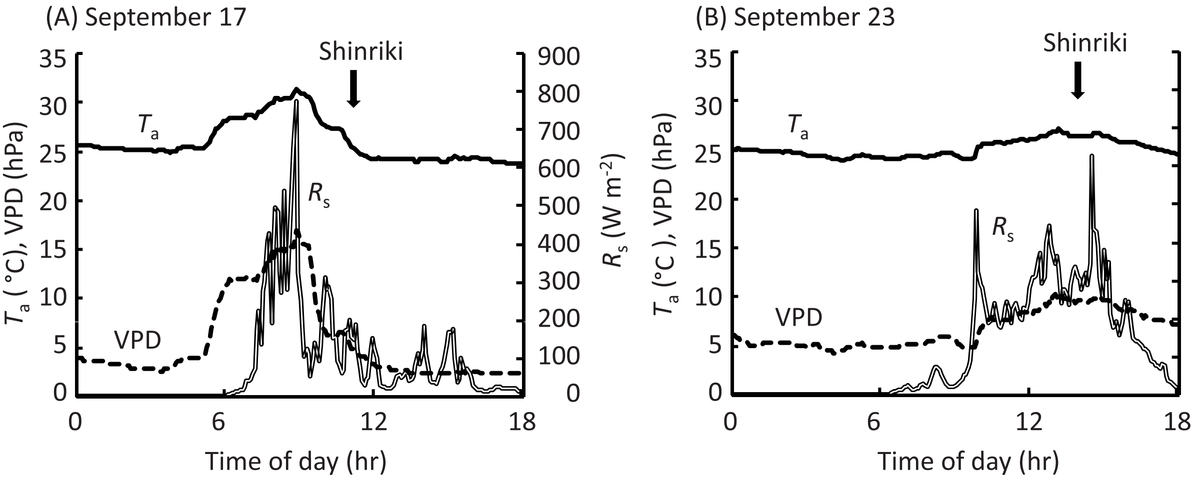

Fig. 2. Flower opening time (FOT) of rice cultivar ‘Shinriki‘ and meteorological variables during 0000 and 1800 on 17 September (A) and 23 September (B). Arrows in the figures show FOT of ‘Shinriki’.
T_a: Air temperature, R_s: Solar radiation, VPD: Vapor-pressure deficit.

989.9 to 1016.8 hPa, respectively.

There were significant correlations among the meteorological variables (Table 2). In particular, the correlation between T_a and VPD was high (r=0.856, P<0.001). The correlations of R_s with T_a and VPD were also relatively high. Wind speed and atmospheric pressure had relatively weak correlations with other meteorological variables.

2. An example of the effect of weather factors on FOT

On 17 September, T_a increased rapidly after 0600 (Fig. 2). However, T_a on 23 September was lower and changed little during the day although R_s increased after 0900. Accordingly, the FOT of ‘Shinriki’ on 17 September (1108) was earlier than that (1347) on 23 September . The trends of VPD on both days were similar to those of T_a.

3. Correlations between weather factors and FOT

In ‘IR72’, there were significant negative correlations between FOT and mean hourly T_a for every hour between 0000 and 0900 (Fig. 3). No significant correlations were detected between FOT and mean hourly T_a between 0000 and 0800 in any of the other cultivars. However, ‘Shinriki’ had a significant negative correlation between FOT and

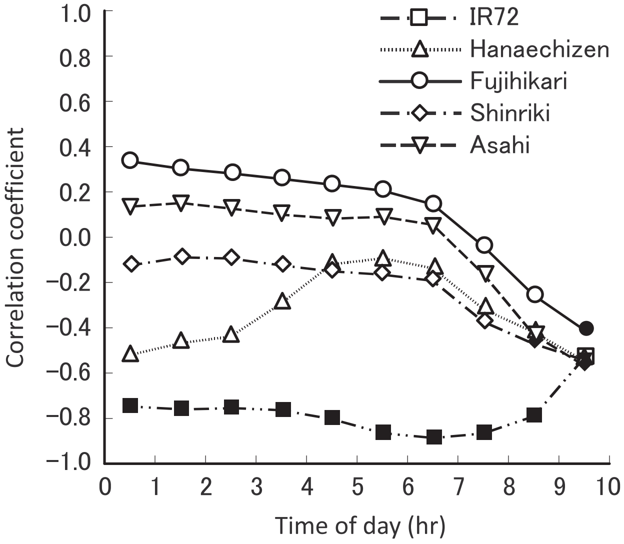

Fig. 3. The correlation coefficients (r) between flower opening time (FOT) and average air temperature (T_a) for each hour between 0000 and 1000 in five *Oryza sativa* cultivars.
Black and white symbols represent the correlation coefficients that are significant and nonsignificant, respectively (P<0.05).

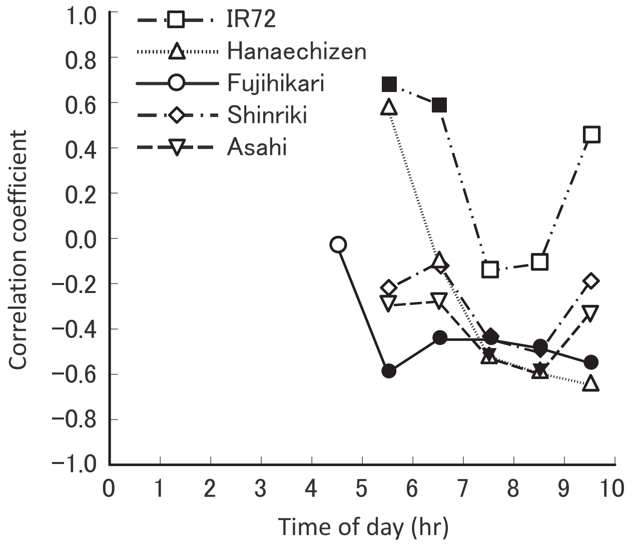

Fig. 4. The correlation coefficients (r) between flower opening time (FOT) and average solar radiation (R_s) for each hour from 0400 to 1000 in 'Fujihikari' and from 0500 to 1000 in the other four *Oryza sativa* cultivars.
At our study site, the sun rose at 0500 (9 July) to 0556 (23 Sept.), so we did not measure R_s before twilight. Black and white symbols represent the correlation coefficients that are significant and nonsignificant, respectively ($P<0.05$).

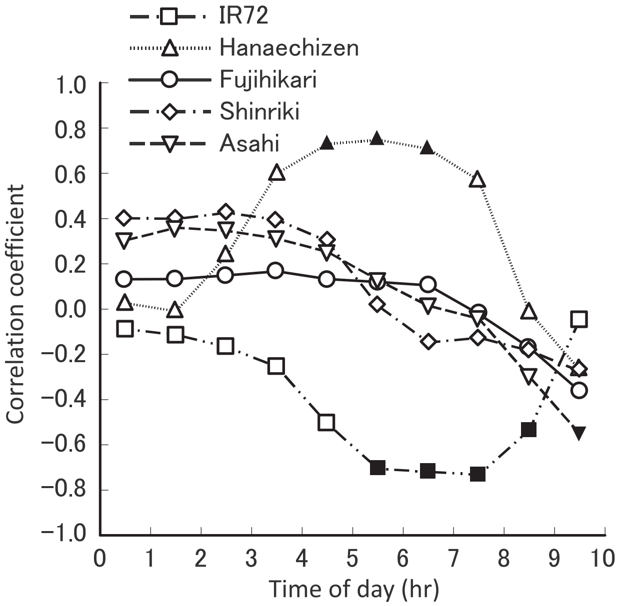

Fig. 5. The correlation coefficients (r) between flower opening time (FOT) and hourly vapor-pressure deficit (VPD) for each hour from 0000 to 1000 for the five *Oryza sativa* cultivars.
Black and white symbols represent the correlation coefficients that are significant and nonsignificant, respectively ($P<0.05$).

mean hourly T_a in the two 1-hr periods between 0800 and 1000. 'Fujihikari' and 'Asahi' showed significant negative correlations between FOT and mean T_a only during the final hour (between 0900 and 1000).

In 'Fujihikari', there were significant negative correlations between FOT and mean R_s for every hour between 0500 and 1000 (Fig. 4). On the other hand, 'IR72' had significant positive correlations between FOT and mean R_s for the two hours between 0500 and 0700. 'Shinriki' and 'Asahi' had significant negative correlations between FOT and mean R_s for the two hours between 0700 and 0900.

There were few significant correlations between FOT and the averaged hourly VPD values (Fig. 5). Significant negative correlations between FOT and averaged hourly VPD were detected in 'IR72' (from 0500 to 0900), versus significant positive correlations in 'Hanaechizen' (from 0400 to 0700) and a significant negative correlation in 'Asahi' (from 0900 to 1000).

4. Evaluation of the effects of cultivar, T_a, R_s, and VPD on FOT

Among the four 3-hr time spans based on JST, the adjusted R^2 value determined by the GLMs (Table 3) was highest (adjusted $R^2=0.399$, $P<0.001$) for the 0600–0900 period. During this period, all four factors (cultivar, T_a, R_s, and VPD) were significant at $P<0.05$ or better. The standardized partial regression coefficient for T_a was −0.480, indicating that a higher T_a during this period resulted in an earlier FOT. Similarly, the standardized partial regression coefficient of R_s was −0.540, indicating that a higher R_s during this period also resulted in an earlier FOT. However, the standardized partial regression coefficient of VPD was +0.346, indicating that a lower VPD (i.e., more humid conditions) resulted in an earlier FOT.

Table 3. Results of multiple-regression analysis using general linear models (GLMs) for the correlations between three weather factors (T_a, air temperature; R_s, daily total solar radiation; VPD, daily mean vapor-pressure deficit) and flower opening time (FOT) for the 3-hr periods based on Japan Standard Time (JST), and the significance of the rice cultivar.

Period (JST)	Adjusted R^2	F values in the GLMs				Standardized partial regression coefficient		
		Cultivar	T_a	R_s	VPD	T_a	R_s	VPD
0000–0300	0.160*	4.156**	1.529 ns	–	4.023*	−0.164	–	0.282
0300–0600	0.351***	9.454***	13.124***	19.743***	14.653***	−0.488	−0.666	0.475
0600–0900	0.399***	2.580*	9.408**	27.204***	4.850*	−0.480	−0.540	0.346
0900–1200	0.392***	2.526*	16.368***	9.603**	8.986**	−1.009	−0.531	0.935

ns, not significant. *, **, and ***, significant at $P<0.05$, $P<0.01$, and $P<0.001$, respectively.

Table 4. Results of multiple-regression analysis using general linear models (GLMs) for the correlations between three weather factors (T_a, air temperature; R_s, daily total solar radiation; VPD, daily mean vapor-pressure deficit) and flower opening time (FOT) for the 3-hr periods based on the time of sunrise, and the significance of the rice cultivar.

Period	Adjusted R^2	F values in the GLMs				Standardized partial regression coefficient		
		Cultivar	T_a	R_s	VPD	T_a	R_s	VPD
6BSR–3BSR	0.173**	4.736**	1.608 ns	–	3.185 ns	–0.163	–	0.242
3BSR–SRH	0.282***	4.960**	9.904**	9.512**	7.556**	–0.436	–0.353	0.328
SRH–3ASR	0.393***	2.610*	8.901**	27.536***	5.139*	–0.432	–0.618	0.326
3ASR–6ASR	0.385***	3.217*	16.011***	11.793**	9.677**	–0.904	–0.536	0.867

ns, not significant. *, **, and ***, significant at $P<0.05$, $P<0.01$, and $P<0.001$, respectively.
6BSR, 6 hr before sunrise; 3BSR, 3 hr before sunrise; SRH, sunrise hour; 3ASR, 3 hr after sunrise; 6ASR, 6 hr after sunrise.

Table 5. Adjusted R^2 values and standardized partial regression coefficients from multiple-regression analyses for the correlation of flower opening time (FOT) of each rice cultivar with air temperature (T_a), solar radiation (R_s), and vapor-pressure deficit (VPD), averaged for 3-hr periods from 0000 to 1200 (based on Japan Standard Time, JST).

Cultivar	Period (JST)	Adjusted R^2	Standardized partial regression coefficient		
			T_a	R_s	VPD
'IR72'	0000–0300	0.505*	–0.851*	–	0.367 ns
	0300–0600	0.636*	–0.562 ns	0.412 ns	–0.067 ns
	0600–0900	0.672*	–0.827*	–0.102 ns	–0.058 ns
	0900–1200	0.036 ns	–0.462 ns	0.496 ns	0.319 ns
'Hanaechizen'	0000–0300	0.123 ns	–0.646 ns	–	0.378 ns
	0300–0600	0.854**	–0.492 ns	0.277 ns	0.941**
	0600–0900	0.747*	–0.883*	–0.237 ns	0.953*
	0900–1200	0.491 ns	–1.050*	–0.635 ns	0.712 ns
'Fujihikari'	0000–0300	0.008 ns	0.307 ns	–	–0.010 ns
	0300–0600	0.393**	–0.539 ns	–0.864***	0.548*
	0600–0900	0.196 ns	–0.500 ns	–0.589**	0.564 ns
	0900–1200	0.549***	–1.394**	–1.404***	2.085**
'Shinriki'	0000–0300	0.228 ns	–0.467 ns	–	0.658*
	0300–0600	0.091 ns	–0.638 ns	–0.303 ns	0.461 ns
	0600–0900	0.282 ns	–0.467 ns	–0.592*	0.279 ns
	0900–1200	–0.038 ns	–0.712 ns	–0.272 ns	0.655 ns
'Asahi'	0000–0300	–0.015 ns	–0.091 ns	–	0.390 ns
	0300–0600	–0.110 ns	–0.191 ns	–0.259 ns	0.221 ns
	0600–0900	0.346*	–0.485 ns	–0.733**	0.397 ns
	0900–1200	0.033 ns	–0.496 ns	–0.180 ns	0.146 ns

ns, not significant. *, **, and *** indicate significant at $P<0.05$, $P<0.01$, and $P<0.001$, respectively.

As suggested by their standard partial regression coefficients, the relative contributions of these three factors to FOT were similar.

Among the four 3-hr time spans based on the time of sunrise, the adjusted R^2 value was highest (adjusted $R^2=0.393$, $P<0.001$) for the period between sunrise and 3 hr after sunrise (Table 4). During this period, all four factors (cultivar, T_a, R_s, and VPD) were significant at $P<0.05$ or better. The adjusted R^2 value for the period between sunrise and 3 hr after sunrise was slightly lower than the value for the 0600–0900 JST period.

5. Evaluation of the effects of T_a, R_s, and VPD on FOT in each cultivar

In 'IR72', the highest adjusted R^2 was obtained for the 0600–0900 period (0.672; Table 5). During that period, the only significant standardized partial regression coefficient was that for T_a (–0.827). In 'Hanaechizen', the highest adjusted R^2 (0.854) was obtained for the 0300–0600 period, and in that period, the only significant standardized partial regression coefficient was for VPD (0.941). In 'Fujihikari', the highest adjusted R^2 (0.549) was obtained for the 0900–1200 period. In that period, all three standardized partial regression coefficients were significant (−1.394 for T_a; −1.404 for R_s; +2.085 for VPD). No significant adjusted R^2 values were detected in 'Shinriki', whereas the highest adjusted R^2 in 'Asahi' (0.346) was obtained for the 0600–0900 period, in which the only significant standardized partial regression coefficient was for R_s (−0.733).

Discussion

We found that the values of T_a, R_s, and VPD averaged between 0600 and 0900 significantly affected FOT (adjusted R^2=0.399, $P<0.001$; Table 3). The standardized partial regression coefficients for the contributions of T_a, R_s, and VPD to FOT were similar. However, simple correlation analysis showed only a limited number of significant correlations of FOT and hourly averaged T_a (Fig. 3), R_s (Fig. 4), and VPD (Fig. 5), and some differences among cultivars in the direction (positive or negative) of the correlation. For example, the correlation of FOT with R_s was negative in 'Fujihikari', but positive in 'IR72'. Similarly, the correlation of FOT with VPD was negative in 'IR72', but positive in 'Hanaechizen'. These cultivar-specific differences indicate that it is necessary to consider all three weather factors (T_a, R_s, and VPD) when analyzing the effects of weather on FOT.

Air temperature had negative standardized partial regression coefficients for all time periods using both JST (Table 3) and the times before and after sunrise (Table 4). Thus, a higher T_a resulted in an earlier FOT using both time systems. Imaki et al. (1983) reported that high T_a in the morning was related to an early FOT in 'Milyang 23', a japonica–indica hybrid. Similarly, Jagadish et al. (2007, 2008) found that the flowers of rice plants, including indica, japonica, and hybrid varieties, open earlier at higher temperatures to avoid high midday temperatures. These results suggest that rice plants might be able to open their flowers under cooler conditions in the early morning by detecting and responding to high night temperatures. Typically, average T_a at 0900 in mid-August is more than 2°C lower than that at 1100 in Matsue, Japan. The combination of genetic control of FOT with the dependence of FOT on night temperatures may allow earlier flower opening in the morning to mitigate or avoid potential heat-induced sterility in rice.

It is unclear how high night temperatures can result in earlier FOT. Development of the embryo sac is completed the day before flowering, and the egg cells become physiologically capable of being fertilized (Hoshikawa, 1989). Pollen grains continue developing until flowering occurs, and fill with starch 1 day before anthesis (Koike and Satake, 1987). After the end of starch engorgement in the pollen grains, starch is rapidly digested at the end of the grain opposite to the germ poles, 3 to 4 hr before anther dehiscence, and more than 70% of pollen grains become sugar-type grains by the time of anther dehiscence (Koike and Satake, 1987). These findings suggest that high night temperatures may promote the digestion of starch in the pollen grains, thereby resulting in earlier FOT. However, the mechanism or mechanisms by which starch digestion triggers opening of the flowers remains unclear. When starch becomes sugar, the sugar would become an osmolyte, leading to imbibition of water, which in turn would cause swelling, leading to dehiscence. That could explain the effect of VPD: at low VPD, more moisture would be available.

Solar radiation was also significantly and negatively correlated with FOT: higher R_s resulted in earlier FOT (Tables 3, 4). In addition to R_s, other aspects of light conditions may influence FOT. Flowers of rice plants housed in a growth chamber tend to open 1 or 2 hr later than those grown outdoors (Imaki et al., 1982), and artificial dark or light treatments have been reported to affect FOT (Nishiyama and Blanco, 1981). Previous studies also showed that high R_s levels in the early morning lead to earlier FOT in 'Koshihikari', and that cultivars differ in their FOT response to R_s levels (Nakagawa and Nagata, 2007). Similar effects were observed in our study under field conditions, suggesting that there may be synergistic effects on FOT between temperature and light.

The adjusted R^2 values for the 3-hr time spans based on sunrise time were similar to those based on JST, so we did not detect an effect of the cycle of light and dark on FOT. Under field conditions, where light intensity varies, it may be difficult to separate the effects of light intensity (i.e., R_s) and the cycle of light and dark. It will be necessary to study the effect of the light cycle on FOT using growth chambers or supplementary light under field conditions to separate this factor from the effects of light intensity.

In the present study, we detected a significant positive contribution of VPD to FOT (Tables 3, 4), with a lower VPD resulting in earlier FOT. Transpirational cooling resulting from higher VPD (Matsui et al., 2007) in the early morning might decrease panicle tissue temperature and thereby delay FOT. However, on a rainy day, rice flowers usually open in the afternoon (Hoshikawa, 1989). It is also possible that T_a, R_s, and VPD synergistically affect FOT through their alteration of panicle tissue temperature.

We observed differences among cultivars in the period most sensitive to T_a, R_s, and VPD in affecting FOT (Table 5). The adjusted R^2 was highest for 'Hanaechizen' in the 0300–0600 period, but was highest in the 0900–1200 period for 'Fujihikari'. However, FOT was similar in both cultivars (Table 1). Under field conditions, where T_a, R_s, and VPD change gradually, it may be difficult to precisely detect the most sensitive period for FOT. Experiments under controlled conditions will be needed to obtain more accurate sensitivity results.

Based on our results, the contributions of T_a to FOT were largest in 'IR72' and 'Hanaechizen' (Table 5). On the other hand, the contribution of VPD was not significant in 'IR72' and 'Asahi' but was large in 'Hanaechizen' and 'Fujihikari'. These results suggest that the relative contributions of T_a, R_s, and VPD differ among cultivars. Imaki et al. (1983) found that high T_a before flowering delayed flower opening in japonica cultivars, but led to earlier flower opening in indica cultivars and indica-japonica hybrids. Overall, the present results and those of previous studies indicate that the effects of temperature and VPD might differ between indica ('IR72') and japonica ('Hanaechizen' and 'Fujihikari') cultivars. However, there are some limitations in detecting the difference in the effect of weather factors on FOT among cultivars from the data observed in different seasons such as July and September, because the cycle of light and darkness and day length would affect FOT (Nishiyama and Blanco, 1981; Hoshikawa, 1989).

The present results suggest that a higher T_a, higher R_s, lower VPD, or a combination of these conditions during the early morning resulted in an earlier FOT. However, the period when T_a, R_s, and VPD affected FOT most strongly and the relative contributions of these three factors differed with the cultivar. To predict FOT under field conditions, it will be necessary to collect more information on temperature, light, humidity, and other weather factors under both field and controlled conditions.

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* In Japanese with English summary.
** In Japanese.
*** In Japanese with English abstract.