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A DISSERTATION

FOR THE DEGREE OF MASTER OF SCIENCE

Responses of spikelet fertility to air, spikelet, and panicle temperatures and vapor pressure deficit in rice

BY

WOO-SUNG JUNG

AUGUST, 2015

MAJOR IN CROP SCIENCE AND BIOTECHNOLOGY

DEPARTMENT OF PLANT SCIENCE

THE GRADUATE SCHOOL OF SEOUL NATIONAL UNIVERSITY

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UNDER THE DIRECTION OF DR. BYUN-WOO LEE
SUBMITTED TO THE FACULTY OF THE GRADUATE SCHOOL
OF SEOUL NATIONAL UNIVERSITY

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Abstract

Along with the rapid temperature rise anticipated in the future, high temperature-induced spikelet sterility is expected to expose a serious problem in rice production. High relative humidity (RH) or small vapor pressure deficit (VPD) that suppresses transpirational cooling of rice panicle is reported to increase high temperature-induced spikelet sterility.

For delineating the responses of spikelet sterility to those environmental variables and panicle/spikelet temperature, a series of experiments were conducted in four plastic houses that were controlled to the target temperatures of ambient (AT), AT+1.5℃, AT+3.0℃ and AT+5.0℃ at the experimental farm of Seoul National University (37.27˚N, 126.99˚E), Korea in 2013 and 2014. Three rice (*oriza sativa* L.) cultivars differing in maturity were grown under ambient temperature plastic house until transferred to different temperature-controlled plastic houses at initial heading stage of each cultivar. Air temperature, solar radiation, VPD, internal temperature of spikelet, and surface temperature of panicle were monitored at an interval of one minute and, for subsequent analysis, averaged over flowering time (09:00-14:00) during seven days after initial heading of panicle.

The spikelet fertility showed wide range of variation from 97.3% to 4.6% depending on temperature treatments, years, and cultivars. The standardized partial ridge regression revealed that not only air temperature but also VPD was negatively associated with spikelet fertility. The spikelet fertility was well fitted to logistic equations not only of air temperature, internal temperature of spikelet, and surface temperature of panicle but also of VPD. The model performances showed no clear differences among temperatures employed to the model equations, while the bi-logistic equation model employing air temperature and VPD as independent variables showed the best performance.

Our result was contrary to the previous reports that the increase of VPD (low humidity) reduced high temperature-induced spikelet sterility by increasing

transpirational cooling of panicle. However, it was inferred that increased VPD under high temperature conditions would accelerate desiccation of anther or pollen during flowering and result in the decline of pollen viability and germination, leading to lower spikelet fertility. Further detailed study is needed to verify VPD effects on spikelet fertility under high temperature conditions.

Keyword: rice, spikelet fertility, high temperature, panicle temperature, vapor pressure deficit.

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Introduction

According to IPCC fifth Assessment Report, mean surface temperature has increased by 0.89℃ from 1901 to 2012, and it is projected to increase by 1.0℃ - 3.7℃ by the end of 21st century depending on the greenhouse gas emission scenarios. Moreover, extreme events will become more frequent than before. Korea is projected to experience even faster mean surface temperature rise of over 5.9℃ by the end of 21st century(IPCC, 2014b). The vast majority of climate change impacts and the overall impact of climate change on rice production are likely to be negative (IPCC, 2014a).

Rice is one of the fundamental principal food for about half of the world's population, and it supplies 20% of the calories consumed worldwide. Rice consumption increases with population increase. Most of the large population increase anticipated in the 21st century will occur in Asia and Africa, where majority of the population lives on rice. The food problem will become as important as the environmental problem (Kubo, 2004).

Rice (*oriza sativa* L.) is vulnerable to high temperature. Especially flowering and microsporogenesis stages are the most susceptive period to heat stress during growth and development of rice (Satake and Yoshida, 1978). High temperature at flowering stage causes spikelet sterility, resulting in the reduction of rice yields. The major causes of high temperature-induced spikelet sterility were generally known for disturbed pollen shedding and decreased viability of pollen grains, resulting in a decreased number of germinated pollen grains on the stigma (Matsui, 1997). Spikelet sterility was reported to be affected by not only air temperature but also vapor pressure deficit (Matsui et al., 2007; Tian et al., 2010; Julia and Dingkuhn, 2013; Van Oort et al., 2014). However, there have been some controversies on the humidity effects on high temperature-induced spikelet sterility of rice. High vapor pressure deficit have been reported to force transpirational cooling of panicle and lead to avoiding heat damage (Matsui et al., 2007). On the contrary to this positive cooling effects on spikelet fertility, excessive low relative humidity or high vapor pressure deficit that drives rapid transpiration have been reported to desiccate anther or pollen and result in disturbing anther dehiscence, low pollen viability, and low number of germinated pollen as well (Matsushima et al., 1982; Ekanayake et al., 1989; Matsui et al., 1999; Abeysiriwardena et al., 2002).

The objective of this study was to find out the effects of air temperature, solar radiation and vapor pressure deficit on rice panicle temperature and evaluate the spikelet fertility responses to air temperature, internal temperature of spikelet, surface temperature of panicle, and vapor pressure deficit.

Literature review

Rice (*oriza sativa* L.) is vulnerable to high temperature. Especially, flowering stage is the most susceptive period to heat stress during growth and development of rice (Satake and Yoshida, 1978). Spikelet sterility of japonica rice was induced at the air temperature of above 36℃ during flowering time and a large cultivar difference existed in spikelet sensitivity to high temperature damage (Matsui et al., 1997; Prasad et al., 2006). The major cause of cultivar difference is referred to the difference of number of germinated pollen grains on stigma (Matsui et al., 1997; Prasad et al., 2006; Jagadish et al., 2011; Das et al., 2014). High temperature which lasts for over one hour at flowering time can lead to increased spikelet sterility (Satake and Yoshida, 1978; Jagadish et al., 2007) and result in yield losses (Satake and Yoshida, 1978; Nishiyama 1984; Prasad et al., 2006).

Most of spikelet sterility in high temperature condition is caused by male sterility. High temperature at the flowering time disturbs anther dehiscence which is the first step of fertilization process (Satake and Yoshida, 1978; Matsui et al., 1999; Matsui et al., 2000; Matsui et al., 2002). Basal pore length of the anther decreased with increasing temperature. Dehisced thecae and length of basal dehiscence were highly related to the number of swelling pollen (Matsui et al., 2002; Kobayasi et al., 2011). Therefore, these processes resulted in low number of germinating pollen grains on the stigma which was well known as main cause of male sterility in high temperature condition (Satake and Yoshida, 1978; Matsui et al., 2000; Matsui et al., 2001; Jagadish et al., 2007; Endo et al., 2009; Jagadish et al., 2011; Shah et al., 2011). Pollen which was exposed to high temperature condition could be viable as short as 10 minutes (Song et al., 2001), and the proportion of germinated pollen also was reduced under high temperature condition (Jagadish et al., 2010).

Several studies reported the effect of water deficits under reproductive stage on maize. Luna et al. (2001) reported that pollen viability was related with exposed time in the drying conditions and pollen death was due mainly to dehydration. Aylor et al. (2003) reported that depending on the VPD, the water contents of maize pollen could change from being fully hydrated to being nearly dehydrated in 1- 4 hour. When maize pollen were exposed to drying condition, the shape of pollen were changed from prolate spheroid to prismatic, and it led to decreased pollen viability (Aylor et al., 2003; Marceau et al., 2012).

In rice, low relative humidity in high temperature condition (40.0℃~42.1℃) reduced spikelet fertility in the field experiment of Sudan (Matsushima et al., 1982). Sato et al. (1960) observed that high temperature and low relative humidity induced 100% spikelet sterility in Cambodia. Both of studies implied low relative humidity in high temperature accelerated spikelet sterility induction by desiccation of pollen. Ekanayake et al. (1989) conducted the experiment about the relation of spikelet sterility with water deficit. In this experiment, water deficit at anthesis were led to the decrease of water potentials, caused desiccation and death of anther and panicle, and spikelet sterility. Matsui et al. (1999) reported that low relative humidity might have negative effect on spikelet fertility caused by disturbing septum rupture and pollen dispersal. Abeysiriwardena et al. (2002) conducted chamber experiment to observe the influence of temperature and relative humidity on spikelet sterility. The results were shown that spikelet sterility in low relative humidity (35%) were lower than normal condition (65%) of that at 30℃, They regarded the increase of spikelet sterility in low relative humidity as loss of pollen viability or reduction of pollen germination on stigma.

However Matsui et al. (2007, 2014) reported that even though extreme dried and hot conditions were observed in Australia during the 2004-2006 growing seasons, spikelet sterility of rice did not occur as much as what they expected. They mentioned that strong transpirational cooling by low relative humidity (<20%) lowered panicle temperature and it helped avoiding heat damage.

High relative humidity (>80%) in high-temperature conditions accelerates spikelet sterility induction (Matsui et al., 1999; Abeysiriwardena et al., 2002; Weerakoon et al., 2008; Julia and Dingkuhn, 2013). Tian et al. (2010) reported that humid conditions (>80%) and low wind speed (<1m/s) might contribute to induce spikelet sterility, indicating that the two factors led to increase of panicle temperatures.

Strong wind velocity disturbed fertilization caused by pollen viability of water loss or decreasing number of pollen number on stigma. Matsui et al. (1997) reported that the number of pollen grains shed on stigma drastically decreased at 0.85m/s of wind velocity and percentage of germinated pollen grain gradually reduced by higher wind velocity. Ishimaru et al. (2012) also reported that spikelet sterility increased as wind velocity increased.

Sheehy et al. (1998) reported that thermal damage occurred by multiplicative factors such as high air temperature, high solar radiation, low wind speed, low vapor pressure deficit, etc. Recently, it is regarded that panicle temperature is better predictor variable of spikelet sterility than air temperature, because the calculated spikelet sterility with air temperature was overestimated compared to the observed (van Oort et al., 2014). Yoshimoto et al. (2011) presented IM^2PACT model using an energy balance to predict panicle temperature.

Materials and methods

1. Experimental set-up

1.1. Cultivar and cultivation

Three rice cultivars differing in maturity group were used in 2013 and 2014 (Table 1). 10 rice seedlings were transplanted in a circular pattern into 1/5000a Wagner pot with 15 days old seedlings on May 14th in 2013 and May 16th in 2014 and grown in flooded condition. Only main stems were grown by removing tillers during the vegetative stage as soon as they appeared. Fertilizer application included 0.78-0.9-0.38 g/pot (N-P_2O_5-K_2O) and nitrogen fertilizer was supplemented in case that rice showed nitrogen deficiency symptom. Twenty pots for each cultivar were grown under ambient air temperature plastic house until temperature treatments.

Table 1. Flowering and temperature treatment date of each cultivar in 2013 and 2014

Year	Maturity Group	Cultivar	Flowering Date	Treatment Date
2013	Early	Odaebyeo	July 17 – July 24	July 17
	Medium	Hwasungbyeo	August 2 – August 15	August 4
	Mid-late	Chuchungbyeo	August 14- August 19	August 13
2014	Early	Odaebyeo	July 15 – July 25	July 15
	Medium	Hwasungbyeo	August 4 – August 16	August 4
	Mid-late	Chuchungbyeo	August 15 – August 24	August 6

1.2. Temperature treatment

Plants were grown under ambient temperature plastic house before initial heading stage, and five pots for each cultivar was transferred to each temperature-controlled plastic house when first heading was observed. The four plastic houses were controlled to the target temperature of ambient temperature (AT), AT+1.5℃, AT+3.0℃ and AT+5.0℃ (Fig. 1).

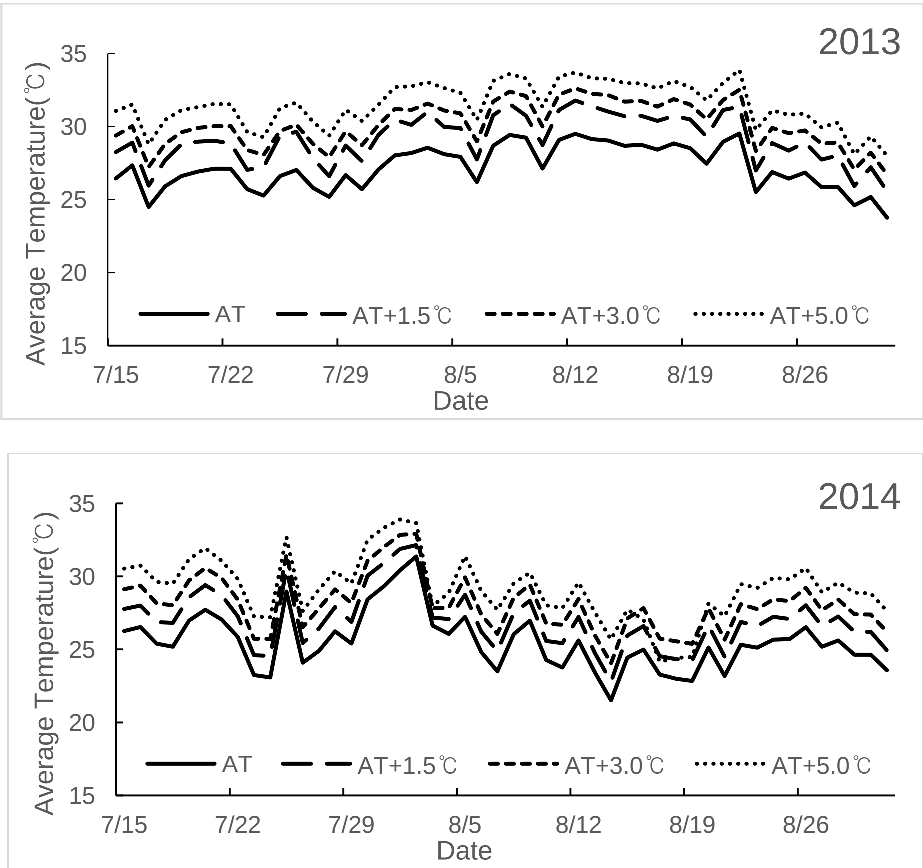

Fig. 1. Mean daily air temperature during flowering stage in 2013 and 2014

2. Measurement

2.1. Spikelet fertility

Flowering date was recorded by observing initial heading of each plant. Spikelet fertility was determined manually by pressing the spikelet between thumb and index finger at harvest. Both partially and fully filled spikelet were categorized as filled spikelet. Spikelet fertility was calculated as following equation.

$$Ferility(\%) = 100 \times \frac{number\ of\ filled\ spikelet}{total\ number\ of\ spikelet} \quad [1]$$

2.2. Meteorological data

General meteorological elements such as air temperature, relative humidity and solar radiation were measured at 1 minute intervals and averaged over flowering time (09:00-14:00) during seven days after initial heading of each plant (Table 2). Air temperature was measured by platinum resistor thermoprobe that was housed in a naturally aspirated 6-plated radiation shield (Campbell Sci., USA). Relative humidity was measured by HMP45a (Vaisala, Finland) and Watchdog 200 (Spectrum, USA). And solar radiation was measured by Li-200 pyranometer (Li-COR, USA).

2.3. Panicle/ Spikelet temperature

Internal temperature of spikelet was measured by inserting 0.147mm k-type thermocouples (Omega, USA) into the selected spikelet and recorded every one minute using DT80 (Datataker, Australia). Surface temperature of panicle was measured using infrared camera (Vario cam hr head, Infratec, Germany). Infrared Camera were installed against the panicle one hour before flower opening. The images were taken at a distance of approximately 40cm apart from the panicle and recorded every one minute. Most of images were taken on the north face. Images were digitized using thermal image analysis program (IRBIS3 plus, Infratec, Germany).

3. Panicle temperature estimation using energy balance model

Surface temperatures of panicle which could not be measured were estimated using the following energy balance equation [2] (Campbell and Norman, 1998).

$$R_{abs} = \left(\varepsilon \times \sigma \times T_p^4\right) + \left\{g_H \times \rho \times C_p \times \left(T_p - T_a\right)\right\} + \left(g_E \times \rho \times C_p \times VPD/\gamma\right) \quad [2]$$

Observed environmental variables were used for estimating, except wind speed. In this equation, ε is emissivity (0.985), σ is Stefan-Boltzmann constant (5.67×10^{-8} $W/m^2/K^4$), γ is psychrometer constant (66.5 pa/℃), ρ is density of air (1.2 kg/m^3), C_p is specific heat of air (1010 J/Kg/℃), R_{abs} is incoming net radiation (W/m^2), T_p is surface temperature of panicle (℃), T_a is air temperature (℃), VPD is vapor pressure deficit (kpa), g_E is latent heat conductance, and g_H is sensible heat conductance, respectively.

$$\mathrm{R}_{abs} = (R_S \times 0.7) + (1.24 \times \sigma \times (T_a + 273.15)^4 \times e_a \times 10 \div \left((T_a + 273.15)^{1/7}\right) \quad [3]$$

We used equation [3] for calculating incoming net radiation. Where R_S is measured data by pyranometer, σ is Stefan-Boltzmann constant, T_a is air temperature in centigrade, e_a is actual vapor pressure (kpa) as calculated by equation [4].

$$e_a = (RH/100) \times (0.6108 \times exp(17.27 \times T_a/(T_a + 237.3)) \quad [4]$$

Sensible heat conductance (g_H) was calculated by using equation [5] (Campbell and Norman, 1998). In equation [5], dimension is set to 0.01m, wind speed is set to 0.7m/s during ventilation on and 0.5m/s during ventilation off.

$$g_H = 0.0125/(dimension/wind\ speed)^{0.5} \quad [5]$$

Latent heat conductance (g_E) was calculated by using equation [6]. Panicle transpiration conductance (g_P) was calculated by using equation [7] (Yoshimoto et al., 2011).

$$g_E = (g_H \times g_P)/(g_H + g_P) \quad [6]$$

$$g_P = 0.0055 \times \exp(0.052 \times RH) \quad [7]$$

4. Statistical analysis

Averaged temperature over seven days during the time of flowering (09:00-14:00) and spikelet fertility were fitted to a logistic equation [8]. Where T is averaged temperature, *Tc* is the critical temperature that induces 50% spikelet sterility, and α is parameter of nonlinear regression.

$$Spikelet\ fertility = \frac{100}{1+\exp\left(\alpha \times (T-Tc)\right)} \quad [8]$$

The bi-logistic equation [9] was used for estimating two environment variables together. Where *T* is averaged air temperature, *VPD* is averaged vapor pressure deficit, *Tc* and *Vc* are the critical air temperature and vapor pressure deficit inducing 50% of spikelet sterility, respectively. α and β are parameters of nonlinear regression.

$$Spikelet\ Fertility = \frac{100}{(1+\exp(\alpha \times (T-Tc))) \times (1+\exp\left(\beta \times (VPD-Vc)\right))} \quad [9]$$

Parameters of equations [8] and [9] were estimated with NLIN procedure of a statistical program SAS 9.3.

We used three indexes of *Willmott's index of agreement* [10], *RMSEn* [11], and *BiasF* [12] for the evaluation of model performances. Where *Pi*, *Oi*, and $\bar{O}$ is model predictions, observations, and the observed mean, respectively.

$$Willmott's\ Index = 1 - \left[\frac{\sum_{i=1}^{n}[(P_i-\bar{O})-(O_i-\bar{O})]^2}{\sum_{i=1}^{n}(|P_i-\bar{O}|+|O_i-\bar{O}|)^2}\right] \quad [10]$$

$$RMSE_n = \frac{\sqrt{\frac{\sum_{i=1}^{n}(O_i-P_i)^2}{n}}}{\bar{O}} \quad [11]$$

$$BiasF = \frac{\sum_{i=1}^{n}(P_i - O_i)}{n \times \bar{O}} \quad [12]$$

High *Willmott's index of agreement and* Low *RMSEn* represent good model performance. And *BiasF* indicates the average value of absolute difference between simulations and observations. A positive *BiasF* indicates overestimation by the model, while a negative value indicates underestimation.

Table 2. Meteorological data averaged over flowering time (09:00-14:00) during seven days after first flowering observed

Odaebyeo		2013				2014			
		AT	AT+1.5℃	AT+3.0℃	AT+5.0℃	AT	AT+1.5℃	AT+3.0℃	AT+5.0℃
Air Temperature (℃)	Average	28.1	30.9	31.4	33.0	28.3	30.3	31.6	32.7
	Max	32.5	38.2	36.5	37.9	36.4	38.8	40.3	41.6
	Min	23.5	24.9	26.2	27.8	21.0	22.4	23.5	25.2
Vapor Pressure Deficit (kpa)	Average	1.24	1.88	2.21	2.34	1.35	1.69	2.03	2.32
	Max	2.22	3.20	3.54	3.71	2.10	2.59	2.93	3.19
	Min	0.38	0.76	1.02	1.10	0.29	0.54	0.71	1.01
Solar Radiation (W/m^2)	Average	200.6				256.3			
	Max	591.8				545.0			
	Min	11.9				35.1			

Hwasungbyeo		2013				2014			
		AT	AT+1.5℃	AT+3.0℃	AT+5.0℃	AT	AT+1.5℃	AT+3.0℃	AT+5.0℃
Air Temperature (℃)	Average	31.5	34.5	35.0	36.4	26.8	28.6	29.8	30.8
	Max	36.1	40.8	39.7	40.9	32.9	34.7	36.4	36.8
	Min	23.8	25.3	26.3	28.0	21.5	22.9	24.0	23.7
Vapor Pressure Deficit (kpa)	Average	1.69	2.31	2.56	2.96	1.09	1.38	1.67	1.91
	Max	2.68	3.40	3.99	4.10	2.90	3.16	3.80	3.96
	Min	0.40	0.69	0.81	1.20	0.19	0.42	0.60	0.74
Solar Radiation (W/m^2)	Average	268.1				222.3			
	Max	577.1				634.8			
	Min	0.9				9.1			

Chuchungbyeo		2013				2014			
		AT	AT+1.5℃	AT+3.0℃	AT+5.0℃	AT	AT+1.5℃	AT+3.0℃	AT+5.0℃
Air Temperature (℃)	Average	32.0	34.9	35.6	36.9	28.8	30.9	32.2	33.2
	Max	35.8	39.6	39.4	40.5	32.0	34.6	35.8	36.9
	Min	25.8	27.5	28.9	30.4	24.1	25.4	26.8	28.3
Vapor Pressure Deficit (kpa)	Average	2.09	2.68	2.98	3.31	1.30	1.62	1.94	2.16
	Max	2.68	3.40	3.99	4.10	2.23	2.69	3.16	3.44
	Min	0.65	0.91	1.06	1.37	0.19	0.42	0.60	0.74
Solar Radiation (W/m^2)	Average	321.9				313.0			
	Max	577.1				584.4			
	Min	53.3				71.4			

Results

1. Response of panicle temperature under different environments

Temperature differences (TDs) between air temperature and surface temperature of panicle varied widely in the range of -4℃ to +7.4℃ depending on environments. Generally surface temperature of panicle was lower than air temperature when air temperature/VPD rises over 25℃/1kPa and TD increased with increasing air temperature and VPD. TDs were positively correlated with air temperature and vapor pressure deficit, but there was no significant correlation with solar radiation (Table 3). Genotypic differences were observed in TDs under environment changes (Fig. 2).

Estimated surface temperatures of panicle showed high coefficients of determination (Fig. 3). Panicle temperature tended to be overestimated in all cultivars as temperature increases.

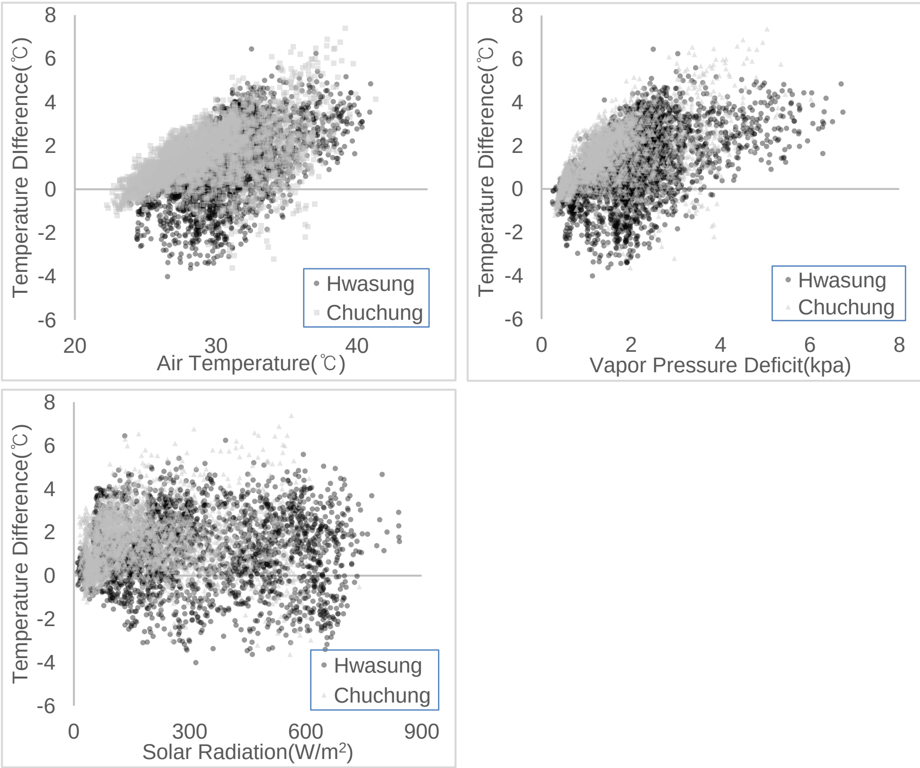

Fig. 2. Correlation between temperature differences (TDs) and environmental factors (air temperature, vapor pressure deficit, and solar radiation)

Table 3. Correlation of temperature difference between air and panicle surface temperatures (TDs) with three meteorological elements

Cultivar	Air temperature	Solar radiation	Vapor pressure deficit
Odaebyeo	0.6889**	0.2656**	0.6332**
Hwasungbyeo	0.5755**	-0.0024^{NS}	0.5084**
Chuchungbyeo	0.5087**	0.0613**	0.4910**
Pulled	0.4847**	0.0131^{NS}	0.4484**

^{NS}, *, **, *not significant, significant at the 0.05, 0.01 probability levels, respectively.*

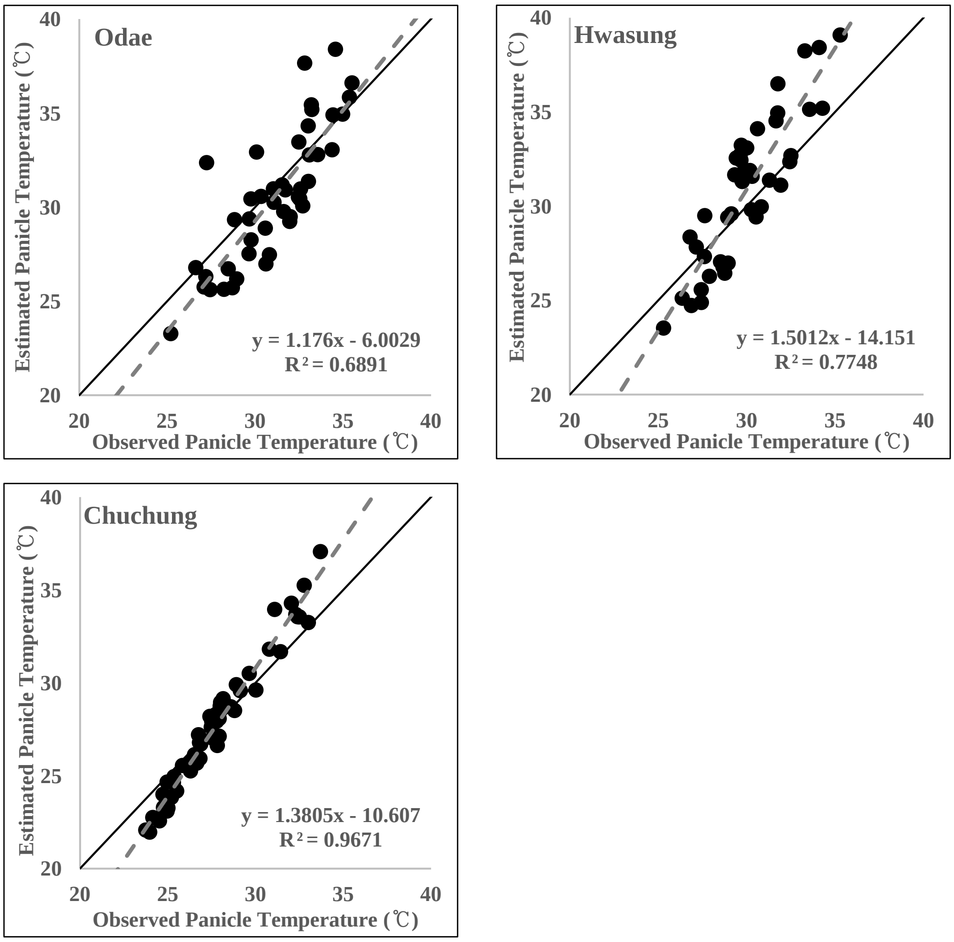

Fig. 3. Relationship between observed and estimated surface temperatures of panicle using energy balance equation [2] (Dotted line and solid line represented trend line and 1:1 line, respectively)

2. Response of yield components to the elevated temperature treatments

Yield components including spikelet fertility were investigated under different temperature treatments for two years. As shown in Table 4, yield components were significantly different among temperature treatments and years. Most of yield components were observed to decrease with the elevated temperature treatments except the number of spikelet. Yield components in 2013 showed larger variation than those in 2014. Spikelet fertility of Hwasungbyeo and Chuchungbyeo in 2013 was drastically decreased between AT+3.0℃ and AT+5.0℃. Similarly to the response of spikelet sterility, unfilled grain ratio of all cultivars was increased drastically at AT+5.0℃. Spikelet fertility and unfilled grain ratio in 2014 showed decreasing tendency with increasing temperature, but the variations were not substantial compared to 2013.

3. Response of spikelet fertility to different meteorological variables.

As in Table 5, spikelet fertility showed highly significant negative correlations with air temperature, internal temperature of spikelet, surface temperature of panicle, solar radiation, and VPD in Hwasungbyeo and Chuchungbyeo. However, early cultivar “Odaebyeo” showed significant negative correlations of spikelet fertility only with air temperature and internal temperature of spikelet.

Table 4. Yield components of three cultivars exposed to elevated temperature treatments after initial heading in 2013 and 2014

Treatments			No. of spikelet	**Spikelet fertility (%)**	Ripened grain ratio (%)	Unfilled grain ratio (%)	1000 grain weight (g)	Grain weight (g/panicle)
Cultivars	Year	Temperature						
Odae byeo	2013	AT+1.5℃	54.25	**94.53**	79.16	16.39	29.83	1.09
		AT+3.0℃	53.29	**95.07**	75.63	20.45	30.32	1.04
		AT+5.0℃	60.57	**83.98**	33.84	60.16	27.46	0.48
	2014	AT	83.99	**95.35**	90.59	5.01	30.54	1.98
		AT+1.5℃	77.78	**96.08**	92.60	3.62	30.93	1.90
		AT+3.0℃	87.17	**94.96**	88.47	6.85	30.48	2.00
		AT+5.0℃	84.04	**89.37**	84.13	5.90	30.72	1.86
	F-value	Year(Y)	338.95**	**18.92****	883.66**	1069.69**	27.69**	1228.47**
		Temperature(T)	4.43**	**80.12****	256.03**	201.85**	6.18**	37.52**
		Y*T	5.52**	**9.58****	207.19**	276.74**	10.20**	32.28**
Hwasung byeo	2013	AT	59.00	**93.49**	91.23	2.45	26.37	1.21
		AT+1.5℃	61.45	**87.58**	83.20	5.02	25.42	1.11
		AT+3.0℃	62.22	**81.22**	68.17	15.72	24.86	0.91
		AT+5.0℃	59.96	**35.14**	6.14	82.05	15.21	0.08
	2014	AT	75.84	**96.59**	94.90	1.75	28.21	1.74
		AT+1.5℃	77.53	**96.92**	94.91	2.07	28.68	1.81
		AT+3.0℃	75.73	**95.53**	91.26	4.48	28.84	1.70
		AT+5.0℃	81.91	**92.84**	85.19	8.27	28.02	1.68
	F-value	Year(Y)	365.48**	**608.85****	1954.03**	784.29**	0.47^{NS}	1926.47**
		Temperature(T)	3.01*	**270.25****	1031.44**	641.20**	1.10^{NS}	178.12**
		Y*T	3.62*	**205.70****	644.36**	467.71**	1.19^{NS}	128.58**
Chuchung byeo	2013	AT	48.87	**95.28**	94.37	0.96	25.69	1.02
		AT+1.5℃	48.79	**90.01**	86.51	4.05	24.98	0.90
		AT+3.0℃	46.54	**71.26**	67.83	4.85	25.07	0.68
		AT+5.0℃	50.16	**4.60**	0.98	76.94	5.16	0.01
	2014	AT	85.59	**96.66**	94.89	1.87	23.50	1.64
		AT+1.5℃	83.43	**97.28**	95.29	2.09	23.65	1.61
		AT+3.0℃	83.96	**95.18**	89.38	6.41	22.36	1.44
		AT+5.0℃	85.74	**94.84**	85.88	9.68	22.64	1.43
	F-value	Year(Y)	1410.27**	**2923.53****	800.72**	23.88**	54.03**	34.79**
		Temperature(T)	1.33^{NS}	**1370.26****	481.03**	48.55**	44.58**	7.22**
		Y*T	0.36^{NS}	**1251.40****	321.78**	24.34**	44.69**	3.96**

^{NS}, *, **, *not significant, significant at the 0.05, 0.01 probability levels, respectively.*

Table 5. Correlations among spikelet fertility with air temperature, internal temperature of spikelet, surface temperature of panicle, solar radiation, and vapor pressure deficit

Odae	Fertility	Air-Temp	Spi-Temp	Pan-Temp	S. Rad.	VPD
Fertility	1	-	-	-	-	-
Air-Temp	-0.3536**	1	-	-	-	-
Spi-Temp	-0.1268**	0.3092**	1	-	-	-
Pan-Temp	-0.0181^{NS}	-0.0358^{NS}	0.8987**	1	-	-
S. Rad.	0.1847**	-0.0407^{NS}	-0.2621**	-0.2956**	1	-
VPD	-0.0659^{NS}	0.0790^{NS}	0.9437**	0.9902**	-0.2907**	1

Hwasung	Fertility	Air-Temp	Spi-Temp	Pan-Temp	S. Rad.	VPD
Fertility	1	-	-	-	-	-
Air-Temp	-0.6186**	1	-	-	-	-
Spi-Temp	-0.5324**	0.9062**	1	-	-	-
Pan-Temp	-0.7051**	0.8896**	0.9219**	1	-	-
S. Rad.	-0.1690**	0.5032**	0.5136**	0.5023**	1	-
VPD	-0.6123**	0.9149**	0.9271**	0.9574**	0.6706**	1

Chuchung	Fertility	Air-Temp	Spi-Temp	Pan-Temp	S. Rad.	VPD
Fertility	1	-	-	-	-	-
Air-Temp	-0.6734**	1	-	-	-	-
Spi-Temp	-0.7104**	0.9134**	1	-	-	-
Pan-Temp	-0.6103**	0.9700**	0.9414**	1	-	-
S. Rad.	-0.4565**	0.8696**	0.9071**	0.9474**	1	-
VPD	-0.6954**	0.9759**	0.9340**	0.9798**	0.8762**	1

^{NS}, *, **, *not significant, significant at the 0.05, 0.01 probability levels, respectively.*
Air-Temp, Spi-Temp, Pan-Temp, S. Rad., VPD, *represented air temperature, internal temperature of spikelet, surface temperature of panicle, solar radiation, and vapor pressure deficit, respectively.*

The ridge regression was used to analyze the relationship between spikelet fertility and environmental variables, avoiding the multicollinearity problems among meteorological elements as sown in Table 5. K-values were determined at the point of drastic decrease by inspection of ridge trace curve. Table 6 presented the result of ridge regression analysis at the K-value of 0.15 (Hwasungbyeo), 0.09 (Chuchungbyeo), and 0.11 (pulled). The coefficients of air temperature and vapor pressure deficit were negative, while the coefficients of solar radiation were positive, indicating that increasing air temperature or VPD resulted in decrease of spikelet fertility. The standard partial ridge regression coefficients of VPD were the greatest among the three meteorological elements.

Table 6. The results of ridge regression analysis between spikelet fertility and meteorological elements

Cultivar	Intercept		Air temperature			Solar radiation			Vapor pressure deficit			K value	RMSE
	Coef.	SEB	Coef.	SP Coef.	SEB	Coef.	SP Coef.	SEB	Coef.	SP Coef.	SEB		
Hwasung	143.85	4.982	-1.741	-0.295	0.177	0.096	0.236	0.012	-13.37	-0.436	0.923	0.15	14.265
Chuchung	176.13	7.955	-3.025	-0.372	0.327	0.165	0.348	0.021	-21.03	-0.585	1.430	0.09	20.371
Pooled	155.92	4.754	-2.023	-0.284	0.185	0.108	0.239	0.012	-17.75	-0.521	0.885	0.11	17.693

Coef., SP Coef., SEB, RMSE, *ridge regression coefficient, Standard Partial of ridge regression coefficient, Standard Error Band, Root mean square error, respectively*

As in Table 7 and Fig. 4, spikelet fertilities in the two cultivars were well fitted to logistic equations [8] of air temperature, internal temperature of spikelet, surface temperature of panicle, and VPD, When air temperature and VPD were employed as predictor variables spikelet fertility were well fitted to bi-logistic equation [9] (Table 8).

Critical air temperature (Tc) inducing 50% of spikelet sterility were estimated approximately at 36℃, and critical vapor pressure deficit (Vc) approximately at 3.0kPa in both of cultivars. Parameter of α in Chuchungbyeo was larger than that of Hwasungbyeo, indicating that spikelet fertility in Chuchungbyeo decreases more drastically with increasing air temperature and VPD compared to Hwasungbyeo. Critical spikelet/panicle temperatures ranged from 31.7℃ to 32.9℃ with little difference between the two cultivars. The critical air temperature was higher than the critical spikelet/panicle temperature by 3.5℃ to 4.3℃.

Model performances were analyzed using four statistical evaluation indexes (Table 9). Regardless of statistical evaluation indexes, the bi-logistic equation model employing air temperature and VPD as predictor variables showed the best performance in both cultivars. However, the best model could not be selected among the models using one predictor variable as their performances were varied according to cultivars.

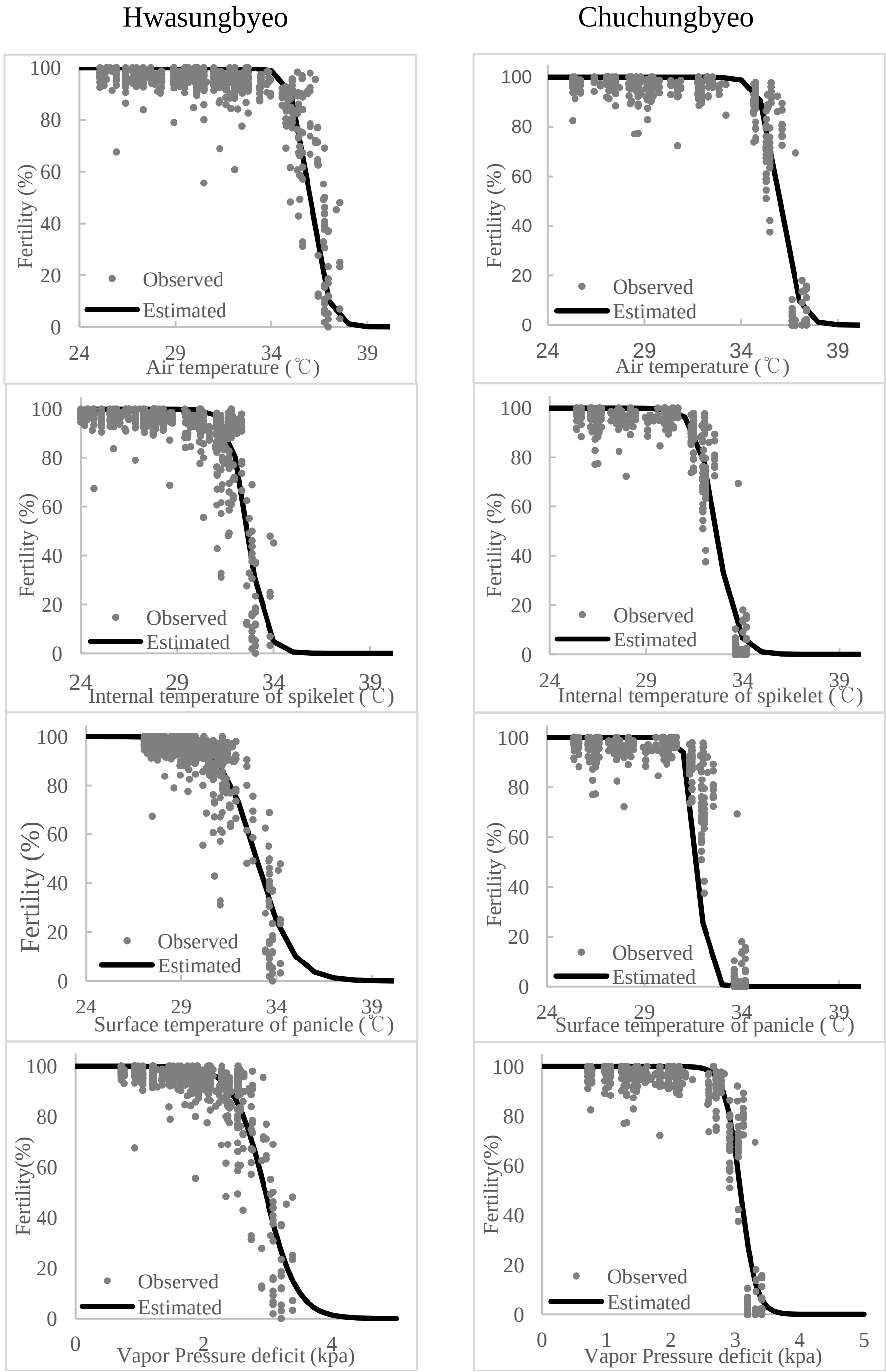

Fig. 4. Response of spikelet fertility to air temperature, internal temperature of spikelet, surface temperature of panicle, and vapor pressure deficit

Table 7. Estimated parameters of spikelet fertility response function [8] against air temperature, internal temperature of spikelet, surface temperature of panicle, and vapor pressure deficit at flowering time

Cultivar	Meteo. Factor	*α*		*Tc (Vc)*		F value	Pr>F	R^2
		PARM.	S.E.	PARM.	S.E.			
Hwasung	Air-Temp	1.2603	0.0639	36.3536	0.0392	23717.2	<.0001	0.4706
	Spi-Temp	2.2082	0.1184	32.6435	0.0297	17492.0	<.0001	0.5932
	Pan-Temp	1.0649	0.0350	32.9422	0.0456	27925.0	<.0001	0.7272
	VPD	4.0825	0.1610	2.9599	0.0126	23930.7	<.0001	0.6967
Chuchung	Air-Temp	2.2169	0.1125	36.0102	0.0306	12371.8	<.0001	0.8627
	Spi-Temp	1.9627	0.0870	32.6452	0.0325	17992.5	<.0001	0.9098
	Pan-Temp	3.8470	0.2972	31.7219	0.0197	5516.5	<.0001	0.6240
	VPD	8.3225	0.4860	3.0765	0.0080	11400.3	<.0001	0.8463

PARM. and S.E. *represented parameter and standard error, respectively*.

Air-Temp, Spi-Temp, Pan-Temp, S. Rad. VPD, *represented air temperature, internal temperature of spikelet, surface temperature of panicle, solar radiation, and vapor pressure deficit, respectively.*

Table 8. Estimated parameters of spikelet fertility response function [9] against air temperature and vapor pressure deficit at flowering time

Cultivar	*α*		*β*		*Tc*		*Vc*		F-value	Pr>F	R^2
	PARM.	S.E.	PARM.	S.E.	PARM.	S.E.	PARM.	S.E.			
Hwasung	0.2818	0.0338	6.9245	0.6365	41.352	1.0711	3.0546	0.0158	14303.9	<.0001	0.7470
Chuchung	23.145	221.7	1.7137	0.1393	36.491	1.3368	3.6899	0.0789	13253.8	<.0001	0.9377

PARM. and S.E. *represented parameter and standard error, respectively.*

Table 9. Statistical indices for evaluating the spikelet fertility model performances

Cultivar	Meteorological factor	***R-Square***	***$RMSE_n$***	***BiasF***	***Willmott's index***
Hwasungbyeo	Air temperature (Air-Temp)	0.4706	0.1369	0.0349	0.8771
	Internal temperature of spikelet	0.5932	0.1310	0.0424	0.8977
	Surface temperature of panicle	0.7272	0.1040	0.0193	0.9348
	Vapor pressure deficit (VPD)	0.6967	0.1446	0.0003	0.9261
	Air-Temp * VPD	0.7470	0.1019	0.0017	0.9434
Chuchungbyeo	Air temperature (Air-Temp)	0.8627	0.1356	0.0453	0.9648
	Internal temperature of spikelet	0.9098	0.1131	0.0371	0.9761
	Surface temperature of panicle	0.6240	0.2008	0.0353	0.9132
	Vapor pressure deficit (VPD)	0.8463	0.2668	-0.0425	0.9607
	Air-Temp * VPD	0.9377	0.0933	-0.0000	0.9845

Discussion

Climate change in the future is very likely to have negative effect on yields of rice (IPCC, 2014). Many studies proved about the decrease of rice yields under high temperature during reproductive stage, but the uncertainty exists in the crop models to predict yields under a wide range of climate conditions (Hasegawa et al., 2011; Tao et al., 2015). The aim of this study was to find out the response of spikelet fertility to different environment variables and evaluate spikelet fertility model performances against different meteorological factors.

Temperature differences between air temperature and panicle temperature (TDs) increased with increasing air temperature and/or vapor pressure deficit (Fig. 2). TDs showed wide range of variation depending on air temperature and VPD, but there was no significant correlation with solar radiation. These results suggested that transpirational cooling decreased panicle temperature similarly to the other reports (Abeysiriwardena et al., 2002; Matsui et al., 2007; Yan et al., 2010) that increasing air temperature and VPD resulted in large temperature differences in hot and arid conditions. Stomata do not exist on the spikelet glumes, and glume epidermis is composed of thin cuticle-silica double layer in early flowering stage (Ekanayake et al., 1993). Thin cuticle-silica layer made a large variation of transpirational cooling by environmental factors such as air temperature and vapor pressure deficit. Ishihara et al. (1990) reported that transpiration rate in the panicle increased linearly as vapor pressure deficit increased, and there was no significant difference between the light and dark. This result could explain that there was no or Hwasungbyeo and Chuchungbyeo showed large decreases in spikelet fertility with temperature elevation treatment above ambient in 2013, but not in 2014. Air temperature during flowering time of those cultivars were over 35℃ in AT+3.0℃ and AT+5.0℃ in 2013. Air temperature during flowering time of Odaebyeo were lower than 33.0℃ even at AT+5.0℃ treatments in both years, reflecting the mild decrease of spikelet fertility. Satake and Yoshida (1978) and Matsui et al. (2001) reported that air temperature over 35℃ induced spikelet sterility.

The ridge regression analysis revealed that air temperature and vapor pressure deficit exerted negative effects on spikelet fertility, indicating that increase of air temperature and VPD increased spikelet sterility induction. This result was contrary to the previous reports that the increase of vapor pressure deficit reduced high temperature-induced spikelet sterility by increasing transpirational cooling of panicle (Matsui et al., 2007; Jagadish et al., 2007; Weerakoon et al., 2008; Tian et al., 2010; Julia and Dingkuhn, 2013). On the other hands, there was a paucity of studies that low relative humidity under high temperature accelerated rice spikelet sterility induction by desiccating anther and/or pollen. Sato et al. (1960) observed that low relative humidity combined with high temperature provoked 100% of spikelet sterility in Cambodia, and Matsushima et al. (1982) also observed similar responses under the field experiments in Sudan. Matsui et al. (1999) reported that low relative humidity disturbed septum rupture and pollen dispersal.

The spikelet fertility was well fitted to logistic equation [8] against not only air temperature, internal temperature of spikelet, and surface temperature of panicle but also vapor pressure deficit. The spikelet fertility model employing VPD were shown similar trend to the other models employing temperatures because of high correlations between air temperature and vapor pressure deficit (Table 5). And the model using panicle/spikelet temperature as predictor variable did not show better performance compared to the models using air temperature or VPD. Furthermore, the spikelet fertility was also well fitted to a bi-logistic equation [9] using air temperature and VPD as predictor variables at the same time and showed better performances than the other models using one environmental element or panicle/spikelet temperature in both cultivars (Table. 9). These results also indicate that not only the increased transpirational cooling under low humidity/large VPD may play positive role in reducing high temperature-induced spikelet sterility but also transpirational desiccation of anther/pollen may play positive role in inducing spikelet sterility under high temperature. Further detailed study is needed to verify the effect of VPD on spikelet sterility. Most of recent studies indicated that decreasing VPD under high temperature conditions decreased spikelet fertility (Abeysiriwardena et al., 2002; Matsui et al., 2007; Yan et al., 2008; Weerakoon et al., 2008; Tian et al., 2010; Yan et al., 2010; Julia and Dingkuhn, 2013; Van Oort et al., 2014). However many of these studies were conducted under high relative humidity conditions above 80% and compared with normal condition of 60% relative humidity. Paucity of studies indicated that increasing vapor pressure deficit under high temperature conditions decreased spikelet fertility. Excessive high vapor pressure deficit accelerated desiccation of anther and pollen, and resulted in disturbing anther dehiscence and low pollen viability (Sato et al., 1960; Matsushima et al., 1982; Ekanayake et al., 1989; Matsui et al., 1999). Strong wind velocity also aggravated spikelet sterility by dehydration of pollen and anther under hot and dry condition. Ishimaru et al. (2012) reported that increasing wind velocity reduced spikelet fertility. Matsui et al. (1997) revealed that wind velocity over 0.85m/s decreased the number of shedding pollen on stigma. Matsui et al. (2014) observed pollen from the windward edge of the rice showed extremely poor pollen germination. Stronger winds might have enhanced the induction of spikelet sterility, even though higher temperature could be main reason of spikelet sterility. In our experiment, the lowest of spikelet fertility were observed in AT+5.0℃ treatment house. We could infer that the plastic house controlled AT+5.0℃ was most often ventilated and the strongest winds were produced because of greatest temperature differences between inside and outside of plastic house, although we did not measured wind velocity.

Our result was contrary to the previous reports that the increase of VPD (low humidity) reduced high temperature-induced spikelet sterility by increasing transpirational cooling of panicle. It was considered that increased VPD in high temperature conditions would accelerate desiccation of anther or pollen during flowering and result in the decline of pollen viability and germination, leading to lower spikelet fertility. However, further detailed study is needed to verify VPD effects on spikelet fertility under high temperature condition during flowering.

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기온 및 이삭 온도에 대한 벼 임실률 반응 연구

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초 록

미래에는 지구 온난화로 인하여 현재보다 기온이 상승할 것으로 예측되며, 아시아 지역에서 널리 재배되고 있는 벼는 개화기간 중 고온에 의한 불임이 발생하여 수량이 감소할 것으로 예상된다. 고온 건조한 환경에서는 고온 다습한 환경에서보다 증산작용이 활발하여 식물체 온도를 낮추며, 고온 스트레스를 피할 수 있을 것으로 보고되었다. 이번 연구에서는 기온, 수증기압포차, 일사 등의 기상 요소들과 영화 내 온도, 이삭 표면 온도들의 변화에 따른 임실률의 반응을 분석하고자 하였다.

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부속실험농장의 플라스틱 하우스 4개동에서 수행되었으며, 공시 품종으로는 조생종인 오대벼, 중생종인 화성벼, 중만생종인 추청벼를 사용하였다. 파종 후 15일된 모를 1/5000a 와그너포트에 10주씩 환형으로 이식하였으며, 발생하는 분얼은 모두 제거하였다. 출수 전까지 외기온과 동일한 온실에서 재배되었으며, 품종마다 최초 출수가 관찰된 후 외기온보다 1.5℃, 3.0℃, 5.0℃ 높은 온실에 옮겨 고온 처리를 하였다. 각 개체의 개화일 및 임실률을 포함한 수량구성요소를 조사하였다. 기상 데이터의 수집은 온실 내의 온도, 습도, 일사를 1분 간격으로 관측하였으며, 열전쌍(thermocouple)을 사용하여 영화 내 온도를 측정하였고, 열화상 카메라를 사용하여 이삭 표면 온도를 측정하였다. 측정된 기상 데이터는 각 개체의 개화일부터 7일간, 개화시각에 해당하는 9시부터 14시까지의 평균 값을 구하여 분석에 사용하였다.

임실률은 처리에 따라 97.2%에서 4.6%까지 품종, 실험연도, 온도 처리에 따라 넓은 범위의 변이를 보였다. 2013년에는 2014년과 비교하여 화성벼와 추청벼의 임실률이 처리온도가 상승함에 따른 감소가 현저히 컸다. 조생종인 오대벼의 임실률은 처리 온도 상승에 따른 큰 변화가 나타나지 않아서 분석에서 제외하였다.

임실률과 각각의 기상 데이터들 사이에는 모두 높은 부의 상관을 보였으며, 기상 데이터 사이에도 매우 높은 상관을 보였다. 능형회귀를

통해 기상 요소들이 임실률에 미치는 영향을 분석한 결과, 기온과 포화수증기압차(VPD)가 증가함에 따라 임실률이 감소하는 것으로 나타났으며, 일사가 증가함에 따라 임실률이 증가하는 것으로 나타났다. 능형회귀의 표준편회귀계수는 VPD가 가장 큰 값을 보였으며, 기온, 일사 순으로 나타났다. 임실률은 기온, 영화 내 온도, 이삭 표면 온도, 및 VPD의 로지스틱 회귀식에 잘 적합되었으며, 모델 적합도 또한 모델 간에 차이를 보이지 않았다. 그러나 기온과 VPD를 동시에 추정 변수로 하는 bi-logistic model이 품종에 관계 없이 가장 높은 모델 적합도를 보였다.

본 실험 결과에서는 기온과 VPD가 증가할수록 영화온도가 기온보다 낮아지는 것을 관찰할 수 있었지만, 기존의 많은 연구 결과들과는 달리 VPD의 증가가 임실률을 감소시키는 것으로 분석되었는데, 이는 고온 조건에서 VPD의 증가가 증산을 촉진하여 개화한 영화의 약과 화분을 건조시킴으로써 화분의 활력과 이에 따른 화분 발아를 감소시키기 때문인 것으로 판단되나, 고온 불임에 있어서 VPD의 역할에 대해서는 보다 구체적인 연구가 필요한 것으로 사료된다.

주요어: 벼, 개화기, 고온불임, 영화온도, 포화수증기압차

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