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Genotypic difference in spikelet sterility and grain-filling response to air temperature during reproductive stage of rice

BY

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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

Grain yield of rice is expected to decrease under the projected future climate of global warming. The decrease of rice grain yield would be caused by spikelet sterility and decreased grain weight due to high temperature during reproductive stage. The objective of this study was to

evaluate the varietal differences of spikelet sterility and grain filling characteristics response to air temperature during reproductive stage.

The experiments were conducted at the experimental farm of Seoul National University, Suwon, Korea in 2011 and 2012. Six rice varieties differing in maturity group (early maturing; Unkwangbyeo and Odaebyeo, medium-maturing; Andabyeo and Hwasungbyeo, and mid-late maturing; Donganbyeo and Chuchungbyeo) were transplanted in a 1/5000 Wagner pot with 15 days old seedlings and grown under ambient air temperature condition before transferred to the temperature-controlled plastic houses. For the synchronization of growth stage, 15 rice seedlings (2011) and 10 rice seedlings (2012) per pot were transplanted in a circle and only main stems were grown by removing tillers at early stage of their emergence. At the initial heading stage, pots for each variety were transferred to the four plastic houses that were controlled to ambient temperature (AT), AT+1.5℃, AT+3.0℃ and AT+5.0℃, respectively. Air temperature for each plastic house was monitored with data logger equipped with platinum resistor thermoprobe. Each variety was sampled 8 times at an interval of 5 - 7 days from heading to physiological maturity.

Grain filling duration and maximum grain weight were estimated by fitting the time course change of grain weight to a logistic function. Grain-filling duration was not statistically different among temperature treatments similarly in all the tested varieties, while maximum grain weight was decreased with the rise of air temperature above ambient during grain filling stage. The grain weight decrease in response to air temperature was different among varieties, being most sensitive in Chunchungbyeo and Donganbyeo and least sensitive in early maturing varieties, Unkwangbyeo and Odaebye. These results imply that the decreased grain-filling duration would not be major factor to decrease the grain weight under higher temperature than the current ambient temperature while it would be attributed to physiological factors such as decreased photosynthesis increased respiration, etc…

As compared to ambient temperature treatment (AT), spikelet fertility was significantly decreased due to high temperature-induced spikelet sterility at flowering time at the treatment of –AT+3.0 and/or AT+5.0℃ in 2011. In 2012 spikelet fertility was much lower than in 2011 even at the ambient temperature treatment because spikelet sterility occurred due to high temperature at micosporogenesis stage. Critical temperature (Tc) that induces 50% spikelet sterility at flowering time was estimated by fitting the temperature response of spikelet fertility to a logistic function. Tc was estimated to range from 34.6℃(Odaebyeo) to 39.7℃(Hwasungbyeo), Odaebyeo being significantly more sensitive to high temperature-induced spikelet sterility than the other varieties.

In conclusion, the grain weight and spikelet sterility responded differentially to higher temperature according to rice varieties, leaving

enough rooms for establishing adaption strategies to warming air temperature through of crop management and variety improvement. And the method developed in this study would be applicable effectively to screening germplasm for the physiological responses to high temperature during reproductive stage of rice.

Key words: high temperature, grain-filling duration, grain weight, spikelet sterility, reproductive stage.

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Introduction

According to the IPCC report in 2007, the global surface temperature is likely to rise a further 2.4 to 6.4℃ during the 21st century, and the linear warming trend over the last 50 years is nearly twice that for the last 100 years. Especially, the temperature increase is greater at higher northern latitudes including Korea. In Korea, the average temperature was increased by 1.5℃ from 1904 to 2000, and IPCC A1B scenario predicted that average temperature would be increased by 4℃ in 2100 (Korea climate change assessment report 2010).

It is widely well-known that global warming is caused by increase of atmospheric greenhouse gases and excessive deforestation, and elevated CO_2 is one of the most major factors. Direct increase of CO_2 affects crops positively, but the problem is that it makes temperature increased. Such global warming has physiologically affected rice growth environments and caused reduction of rice production in many regions. Peng (2004) reported that the grain yield declined by 10% for each 1℃ increase in growing-season minimum temperature in the dry season.

Rice is one of the most important staple foods in the world. Over 50 percent of the world population depends on rice for about 80 percent of its food requirements (FAO, 2012). So the impact of high temperature on rice has become a serious problem under projected future climate of global warming.

Generally, the heat stress effect on grain yield is greater during reproductive stage than vegetative stage (Yoshida et al, 1981). High air temperature during reproductive stage has been reported to induce spikelet sterility and affect negatively to grain-filling characteristics. The spikelet sterility and grain-filling characteristics are main factors to determine the actual rice yield capacity.

Many studies for investigating the impact of high temperature on rice plant growth were conducted under various conditions. However, the evaluations of varietal differences about growth response to high temperature in rice are rarely studied.

For minimizing loss of rice production caused by high temperature, yield prediction with accurate grain growth model and developing high temperature resistance rice variety have become proposed alternatives, and they require a complete understanding of genetics and physiological parameters. Therefore it is worth that evaluating the varietal differences of physiological response to high temperature in rice.

The objective of this study is to evaluate the varietal differences of spikelet sterility and grain filling characteristics response to air temperature during reproductive stage so that obtain basic information for evaluating the effect of global warming on rice production in Korea.

Literature review

Yield loss as a result of high temperature would be explained as high temperature-induced spikelet sterility and changes in grain-filling characteristics during reproductive stage.

1. Effect of high temperature on grain-filling characteristics

Temperature during the grain-filling period is one of the most meaningful factors to determine the grain yield because it affects the grain-filling rate, duration, and the other physiological processes. Generally, the optimum temperature during grain-filling period in japonica rice has been reported to range from 20 to 22℃ in the average air temperature during 40 days after heading and the high temperature above this optimum temperature to decrease the grain weight of rice (Murata, 1964; Kim, 1983).

Yoshida (1981) also reported that high temperature accelerates the rate of grain growth and reduces the grain-filling duration. Reduced grain-filling duration and faster grain-filling rate cause the decrease of maximum grain weight. This phenomenon can be explained with the relationship between temperature and photosynthesis. The reduced grain-filling duration affects the maximum amount of solar energy available for grain-filling (Yoshida and

Hara, 1976) and the loss of grain weight in high temperature is caused by the decrease of net photosynthesis rate in, accompany with increasing respiration.

According to Yamada (1955), net photosynthesis dropped rapidly in high temperature above 38℃ but there was no significant difference in the range of 18.5~33.5℃. Generally in Korea, the maximum temperature in grain-filling season is not over 38℃ in the field. Therefore it can be considered that there are other physiological factors, which affect grain weight under high temperature condition.

Lee et al(2009) reported that high night temperature (32℃) increased respiration rates and decreased membrane thermal stability. The increased respiration can produce reactive oxygen species (ROS) (McDonald and Van Lerberghe, 2005). The ROS can cause increasing cell damage and decrease membrane thermal stability (Kreiner et al, 2002). Thus, increasing respiration due to high temperature negatively affects carbon production and transport to grain.

Sato and Inaba (1973) studied the effect of temperature on rice organs and found that the panicle contributes to the grain weight decrease rather than vegetative organs under high temperature during grain-filling period. This result suggested that early loss of sink activity under high temperature during grain-filling period causes the early termination of grain-filling and interrupt the starch accumulation. This early loss of sink activity is caused by reduction of translocation ability and a loss of activity of starch synthesis-related enzymes such as sucrose synthase and APGase.

Seo et al(1981) reported leaf senescence induces reduction of grain filling duration, while Kim et al(2011) reported that an early termination of grain filling in temperate rice under high temperature was not resulted from the lack of assimilate owing to the earlier leaf senescence but from earlier panicle senescence.

The grain-filling process could be estimated with various models. Yin et al (2003) reported ‘the beta growth function’ that calculates grain weight in dependence on time and estimates the time parameters such as time at the end of growth.

Kim (2010) also studied about estimation of temperature and radiation effect on grain-filling process, and developed single grain growth model. He suggested that grain growth model consisted of quantitative part and qualitative part. The model he developed could explain the effects of temperature and solar radiation through gap analysis between daily potential grain growth and daily attainable grain growth.

2. Spikelet sterility.

The spikelet sterility is one of the major factors that constraints grain yield of rice under the projected future climate of global warming.

The mechanism of sterility by high temperature was summarized well in previous studies (Matsui et al, 1999). High temperature-induced spikelet sterility is most sensitive at flowering time and followed by microsporogenesis stage that falls on 12 days before spikelet flowering (Satake et al, 1978). According to Matsui et al (2000), the swelling pollen grains is driving force for the opening of anther, and poor swelling of pollen grains as a result of high temperature is the main reason to induce the floret sterility. Decreased spikelet fertility at high temperature was due mainly to the decreased pollen production and pollen reception (pollen numbers on stigma) (Prasad et al, 2006). Thus, poor anther dehiscence and low pollen production that cause low numbers of germination are the main factor to induce the spikelet sterility. In rice, the reproductive processes that occur within 1 hour after anthesis such as anther dehiscence, pollen shedding, germination of pollen grain on stigma, and elongation of pollen tubes are most sensitive to high temperature (Satake and Yoshida, 1978).

Generally, the optimum temperature for the flowering of rice ranges from 30℃ to 33℃, and high temperature above 33.8℃ leads to spikelet sterility

(Satake and Yoshida, 1978). Jagadish et al (2006) studied about the effect of temperature on flowering pattern and the interactions between duration of exposure and temperature on spikelet fertility in IR64(*indica*) and Azucena (*japonica*), and reported that In both genotypes the peak of flowering occurred about 30-45 min earlier at 36.2℃, compared with 29.6℃ and 1hr exposure to above 33.7℃ at anthesis caused sterility. On the basis of these results, they suggested that high temperature affects the pattern of flowering and the number of spikelets that reach anthesis and 1h of exposure to high temperature is sufficient to induce sterility in rice. Yoshida (1978) also reported that spikelets at anthesis that are exposed to temperature above 35℃ for about 5 days during the flowering period were sterile and set no seed. The spikelets even on the same panicle are exposed to different temperature because they are not synchronous in flowering date and time. Nguyen (2012) reported that heading of panicles continued until about 12days after initial heading and reached peak around five days and three days after initial heading in *japonica* and *tongil-type*, respectively, and the individual spikelet flowering on a panicle peaked around five days after, and lasted until 11days after heading of panicle. These results suggested that flowering date distribution in *Japonica* and *Tongil-type* varieties closely followed the normal distribution.

As reviewed above, the timing of spikelet flowering is a key factor to determine the effect of high temperature on spikelet sterility.

Materials and methods

A series of experiments were conducted in temperature-controlled plastic houses at the experimental farm of Seoul National University, Suwon, Korea in 2011 and 2012.

1. Experimental set-up.

1.1 Variety and cultivation.

Six rice varieties differing in maturity group (Table 1) were transplanted in a 1/5000 Wagner pot with 15 days old seedlings on June, 1s (2011), May, 10th (2012) and grown with fertilization of 180-90-11.4kg/ha (N-P-K). Sixteen pots (2011) and twenty pots (2012) for each variety were grown under ambient air temperature condition before transferred to the temperature-controlled plastic houses. For the synchronization of growth stage, 15 rice seedlings (2011) and 10 rice seedlings (2012) were transplanted in a circle and only main stems were grown by removing tillers at early stage of their emergence.

Table 1. Maturity group and varieties employed for the experiments.

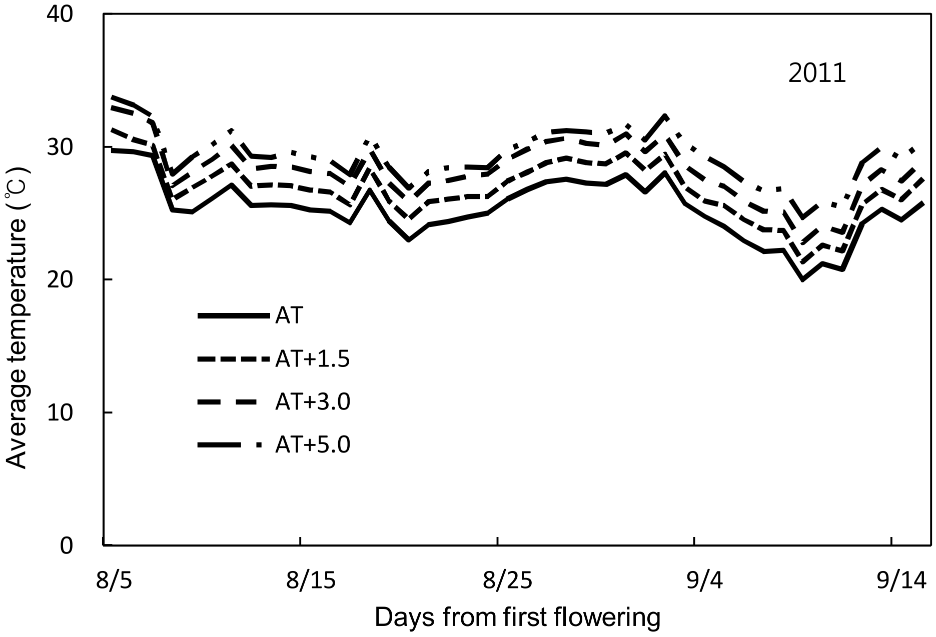
Maturity group	Variety
Early maturing	Unkwangbyeo, Odaebyeo
Medium maturing	Andabyeo, Hwasungbyeo
Mid-late maturing	Donganbyeo, Chuchungbyeo

1.2 Temperature treatment.

At the initial heading stage, four pots (2011) and five pots (2012) for each variety were transferred to the four plastic houses that were controlled to ambient temperature (AT), AT+1.5℃, AT+3.0℃ and AT+5.0℃. Air temperature for each plastic house was monitored with data logger equipped with platinum resistor thermoprobe (Fig. 1).

2. Measurement.

Each variety was sampled 8 times at an interval of 5 – 7 days from heading to physiological maturity. Dry weight, moisture contents, and the number of spikelet were investigated. Spikelet sterility was evaluated manually by pressing spikelet between thumb and index fingers.



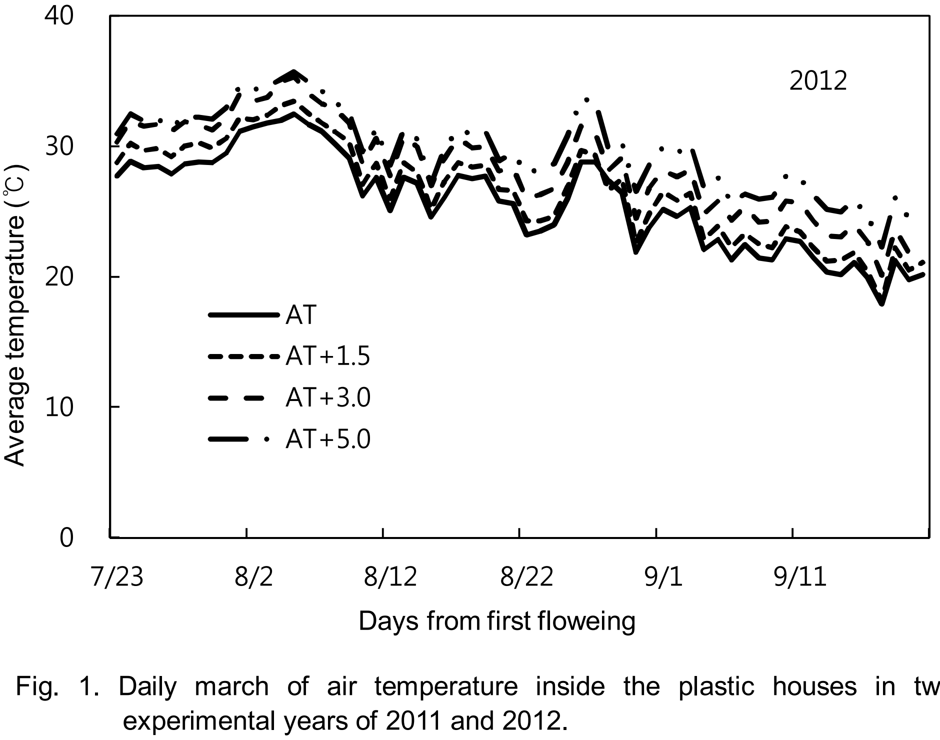


Fig. 1. Daily march of air temperature inside the plastic houses in two experimental years of 2011 and 2012.

3. Statistical analysis

3.1. Grain-filling characteristics.

The “beta growth function” is suitable for characterization of environmental and genotypic influences on growth processes (Yin, 2002), Grain growth as related to the days after flowering were fitted to the beta growth function (equation 1) to characterize grain-filling processes of each variety under different temperature regimes during grain filling period.

$$W = Wmax\left(1 + \frac{T_e - T}{T_e - T_m}\right)\left(\frac{T}{T_e}\right)^{\frac{T_e}{T_e - T_m}} \qquad with\, 0 \leq T_m < T_e \qquad [1]$$

where Wmax is grain weight at maturity, Tm is the time at the maximum grain growth rate in days after flowering and Te is the time at physiological maturity in days after flowering.

Parameters of equation [1] was estimated with NLIN procedure of statistical program SAS 9.3.

Mean grain developmental rate(DVR) could be represented by the reciprocal of grain filling period from flowering to physiological maturity (Te). Generally, DVR is the function of air temperature and its temperature response could be expressed the following equation [2].

$$DVR = \mu\,(T - Tb)^{a}\ \ (Tc - T)^{\beta} \qquad [2]$$

where T is daily average temperature, Tb is base temperature, Tc is critical temperature and μ, α, β are model parameters.

Grain developmental stage(DVS) is expressed as 0 (flowering time) to 1 (physiological maturity) and defined as the time integration of daily grain developmental rate (equation 3).

$$DVS = \int_{0}^{t} DVR\, dt \qquad [3]$$

In terms of DVS, grain weight growth can be expressed as the following logistic equation [4].

$$\mathrm{Grain\ weight} = \mathrm{Wmax}\left(1 + \exp\left(-(\mathrm{DVS} - \mathrm{DVSm})\left(\frac{\mathrm{RGR}}{\mathrm{DVR}}\right)\right)\right) \qquad [4]$$

where Wmax is the grain weight at DVS=1, DVS is grain development stage, DVSm is the time at 50% of the maximum grain weight, RGR[4] is relative grain growth rate, and DVR is grain development rate.

Relative grain growth rate (RGR) was expressed as the linear function of solar radiation(Sol) and the beta function of daily mean air temperature(T) [5];

$$RGR = K * Sol * (T - T_b)^{a} \ (T_c - T)^{\beta} \qquad [5]$$

where Sol is solar radiation (Mj/m^2), T is daily mean air temperature, Tb is base temperature, Tc (ceiling temperature) is the maximum temperature at which the development rate equals zero, and *K*, α, and β are model parameters.

All the parameters of equations of [2] to [5] were estimated with daily values of solar radiation and/or mean air temperature by Simplex method.

3.2 Spikelet sterility during reproductive stage.

Booting and flowering are the most susceptible stage of development to high temperature in rice and one hour exposure to high temperature is enough to induce sterility (Satake and Yoshida, 1978; Jagadish et al, 2007). Each spikelet on a panicle is differently affected by high temperature, because of its non-synchronized flowering dates and times even in the same panicle. It takes about 15 – 20 days for all the spikelets to complete anthesis. According to Nguyen (2012), individual spikelets flowering on a panicle reached peak around five days, and continued until 11days after initial heading of panicle. Flowering date distribution in a panicle of *Tongil*-type and japonica cultivar followed the normal distribution. Therefore, a normalized temperature was calculated by considering the probability distribution of the flowering date of spikelets on a panicle. Normalized temperature was calculated as equation [6].

$$\text{Normalized [T]} = \sum_{kk=0}^{15} p_k(k) * T_m \qquad [6]$$

where $P_k\ (k)$ is relative frequency that spikelet on a panicle flower on the K^{th} date after panicle heading, and T_m is maximum temperature.

Normalized temperature and spikelet fertility were fitted to a logistic equation [7].

$$\text{Fertility} = \frac{100}{1 + \exp[a(T - Tc)]} \qquad [7]$$

where T is normalized temperature, Tc is the critical temperature that induces 50% spikelet sterility, and α is parameter of nonlinear regression.

Parameters of equation [7] was estimated with NLIN procedure of statistical program SAS 9.3.

Results

1. Grain-filling characteristics

As in Table 2 and Fig. 2, the grain-filling duration and maximum grain weight of each tested variety under different temperature treatments were well fitted to beta growth function (equation 1). ‘Te’ representing grain-filling duration ranged from 30.6 to 36.5(days). The duration of grain-filling period was not statistically different among temperature treatments similarly in all the tested varieties. This result is different from the observation of Yoshida(1976) and Morita(2005) that the higher the temperature, the faster the grains filled and matured.

The maximum grain weight was decreased with the rise of temperature above ambient temperature, except Donganbyeo.

In Donganbyeo, there was a little different in maximum grain weight among temperature treatments and even its maximum grain weight of AT+3.0 was higher than AT+1.5. This abnormal phenomenon is probably due to extreme heat stress at booting stage in year 2012. The booting stage of Donganbyeo started from the beginning of August and the maximum temperature rose up to 40℃ even in AT house, being exposed to extreme heat stress before transferred to the temperature treatments.

Table 2. Estimated parameters of Beta growth function (equation 1) of each variety. under different temperature treatments during grain filling period.

Maturity group	Variety	Treatment	Parameters			*F*-value	*P*
			Wmax (mg/grain)	Te(day)	Tm(day)		
Early maturing	Unkwangbyeo	AT	23.3	35.1(5.3)	4.8	474.0	<.0001
		AT+1.5	22.9	35.4(3.9)	8.8	714.7	<.0001
		AT+3.0	21.8	34.3(2.9)	8.0	675.7	<.0001
		AT+5.0	-	-	-	-	-
	Odaebyeo	AT	25.7	34.3(5.9)	2.3	435.6	<.0001
		AT+1.5	24.2	34.2(10.3)	0.1	249.9	<.0001
		AT+3.0	24.3	33.9(8.8)	1.8	230.2	<.0001
		AT+5.0	13.5	34.1(6.9)	1.1	437.8	<.0001
Medium maturing	Andabyeo	AT	25.5	32.5(1.9)	6.0	763.5	<.0001
		AT+1.5	24.0	32.4(3.6)	4.6	765.6	<.0001
		AT+3.0	23.1	33.6(3.4)	4.2	373.6	<.0001
		AT+5.0	19.3	34.4(9.4)	4.6	90.3	<.0001
	Hwasungbyeo	AT	23.8	32.7(1.4)	6.7	858.0	<.0001
		AT+1.5	23.6	31.7(1.2)	5.6	1203.5	<.0001
		AT+3.0	22.9	33.1(2.0)	3.8	1082.3	<.0001
		AT+5.0	19.0	32.0(2.4)	3.2	324.0	<.0001
Mid-late maturing	Donganbyeo	AT	22.7	33.7(5.3)	10.6	173.3	<.0001
		AT+1.5	19.8	30.6(3.8)	10.5	126.2	<.0001
		AT+3.0	21.6	34.6(4.9)	10.9	168.9	<.0001
		AT+5.0	19.4	36.5(6.5)	10.6	445.6	<.0001
	Chuchungbyeo	AT	23.2	32.4(2.4)	13.1	414.7	<.0001
		AT+1.5	20.9	34.3(4.5)	13.2	320.6	<.0001
		AT+3.0	18.3	33.0(5.4)	8.5	314.3	<.0001
		AT+5.0	15.7	32.7(5.6)	7.5	219.6	<.0001

( ) is ±95% confidence limits, Tm is time of maximum grain growth rate in days after flowering and Te is time at physiological maturity in days after flowering.

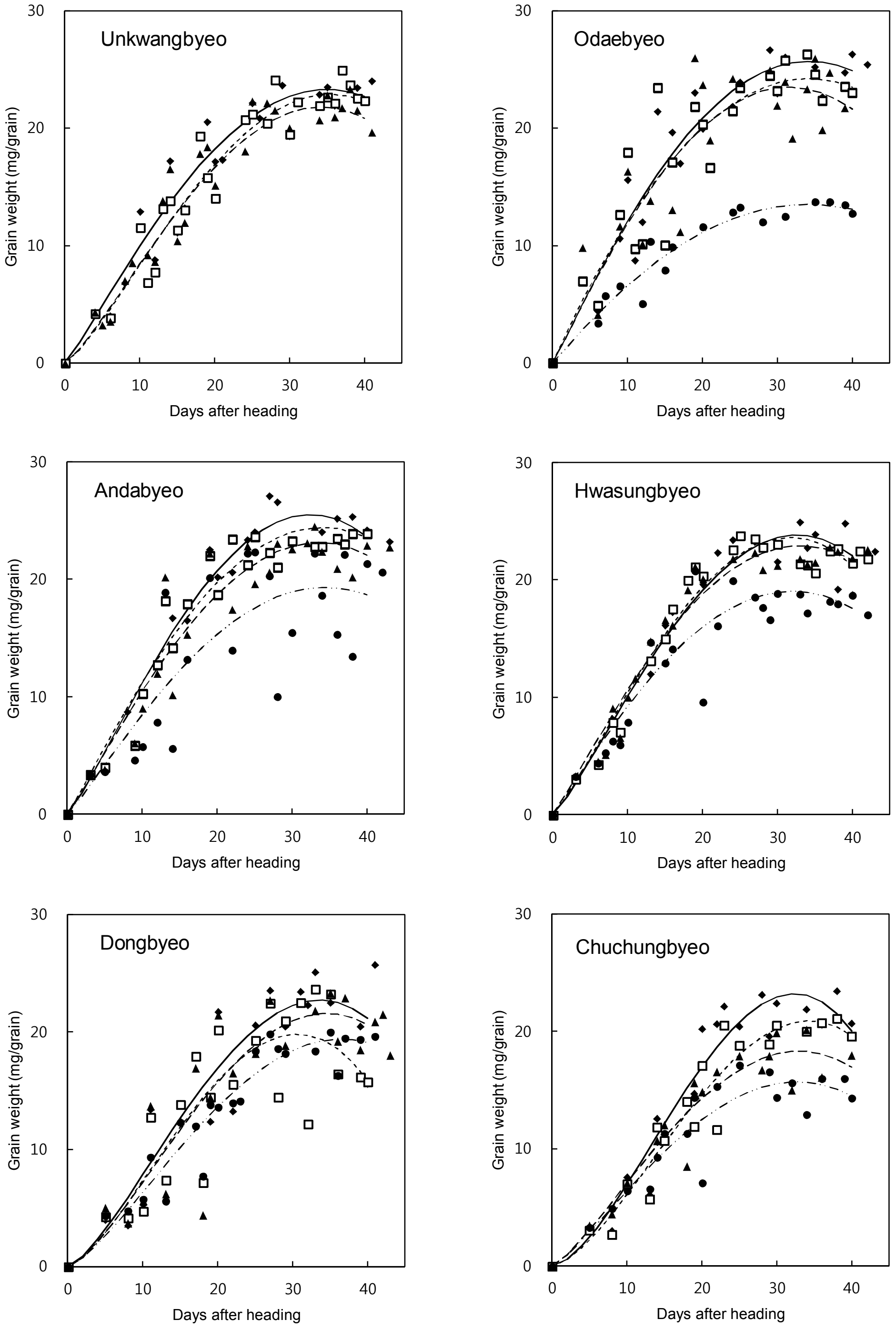


Fig. 2. Grain growth as affected by different air temperature regimes during grain-filling period. In six rice cultivars.

—◆— is AT treatment, ---□--- is AT+1.5℃ treatment,– –▲– – is AT+3.0℃ and –··–●–··– is AT+5.0℃

Table 3 shows the estimated parameters of grain development rate (DVR) function (Eq. 2) that relates the temperature dependence of DVR. As the parameter Tb, Tc, α, and β were not significantly different among tested varieties, the parameter μ was estimated with the fixed values of the other parameters. The parameter μ that means the DVR constant per thermal time ranged from 0.00039(Chuchungbyeo) to 0.00051(Andabyeo). The greater value of μ means the shorter grain filling duration at the same temperature. The temperature that accelerates most the grain senescence and reaches the physiological maturity earliest was estimated to be 29.2℃. Below this temperature the grain filling duration increases curve-linearly. At this temperature the grain filling duration was estimated to be from 28 days (Andabyeo) to 36 days (Chuchungbyeo).

Table 3. Parameter estimates of the DVR function (equation 2)

Maturity group	Variety	Tb	Tc	α	β	μ	R^2
Early maturing	Unkwangbyeo	10.8	46.4	0.78	0.73	0.00047	0.96
	Odaebyeo					0.00044	0.97
Medium-maturing	Andabyeo					0.00051	0.98
	Hwasungbyeo					0.00045	0.99
Mid-late maturing	Donganbyeo					0.00045	0.98
	Chuchungbyeo					0.00039	0.99

Air temperature and solar radiation are the main factors to determine the grain filling process and the final grain weight. The estimated parameters of the grain growth function (equation 4 and 5) are presented in table 4. In all the varieties the grain growth process was well fitted to the logistic function in which relative grain growth rate (RGR) was parameterized with daily mean air temperature and total solar radiation (Table 4 and Fig. 3).

Table 4. Parameter estimates of grain growth model functions (equation 4 and 5).

Maturity group	Variety	Parameters							R^2
		Wmax (mg/grain)	k	alpha	beta	Tb (℃)	Tc (℃)	DVSm	
Early maturing	Unkwangbyeo	24.9	0.0020	0.061	0.731	11.0	37.6	0.64	0.95
	Odaebyeo	27.6	0.0018	0.254	0.429	10.5	39.5	0.56	0.96
Medium-maturing	Andabyeo	26.2	0.0015	0.627	0.082	10.0	40.1	0.52	0.98
	Hwasungbyeo	24.2	0.0010	0.039	1.053	10.9	38.6	0.46	0.98
Mid-late maturing	Donganbyeo	25.0	0.0027	-0.028	0.755	9.7	40.4	0.39	0.97
	Chuchungbyeo	23.4	0.0096	0.175	0.063	12.3	30.5	0.75	0.98

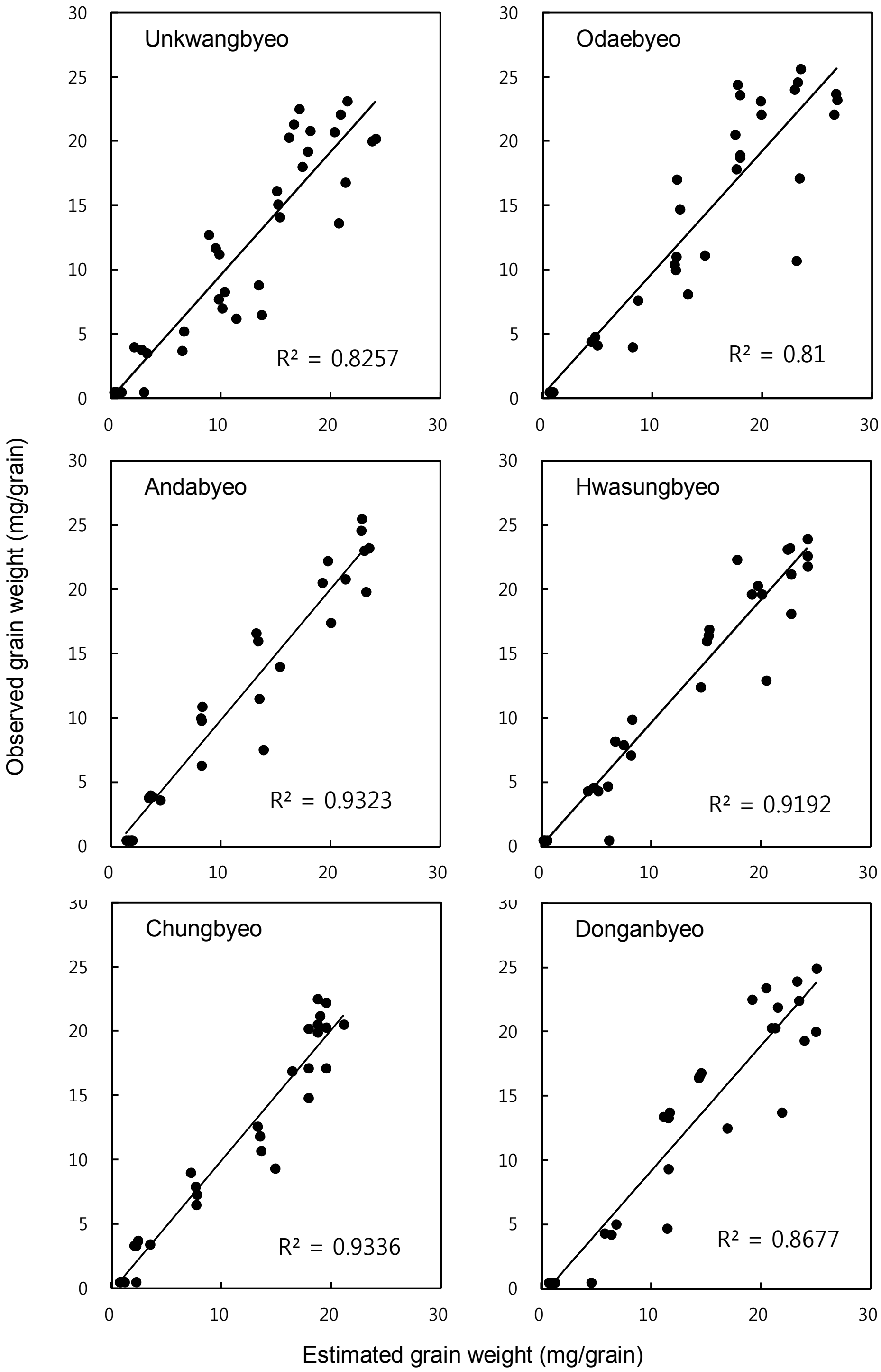


Fig. 3. Relationship between estimated and observed grain weight.

The maximum grain weight in year 2011 was related to the average air temperature during the grain filling period from flowering to physiological maturity as presented in fig. 4. The maximum grain weight showed decreasing trends with temperature rise differentially according to varieties. Chuchungbyeo and Andabyeo showed the most sensitive decrease of maximum grain weight with the rise of average air temperature above about 23℃ and followed by Donganbyeo and Hwasungbyeo. Early maturity varieties, Odaebyeo and Ubkwangbyeo, showed the least and gradual decrease up to about 29℃ while sharp decrease above in this temperature.

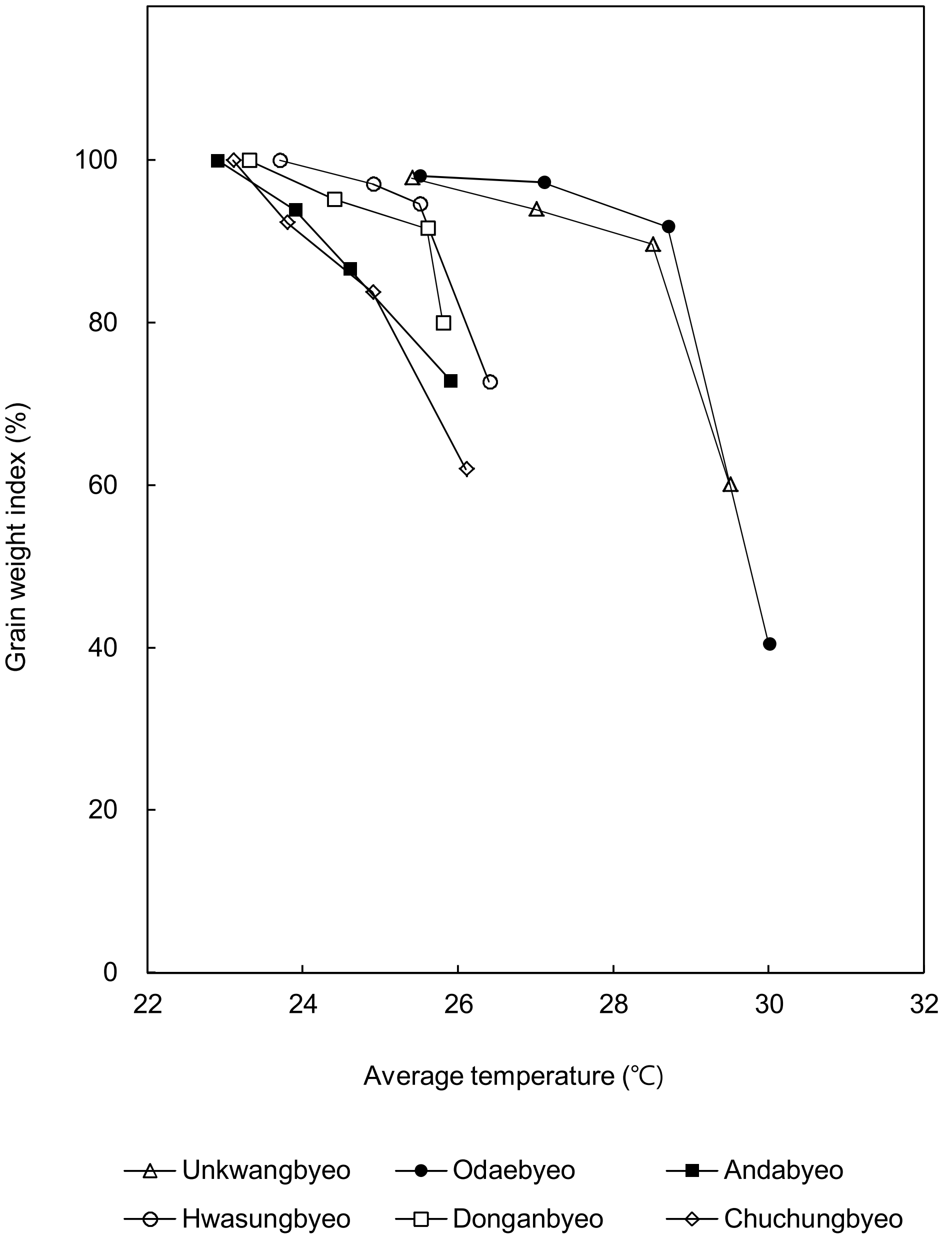


Fig. 4. Effect of temperature on the grain dry weight of each variety in year 2011. Horizontal axis is average air temperature during grain-filling period and vertical axis is grain weight index as represented by the percentage of the potential maximum grain weight of each variety.

2. Spikelet fertility.

Spikelet fertility of each variety under different temperature treatments was presented for year 2011 and 2012 in table 5. As compared to ambient temperature treatment (AT), spikelet fertility was significantly decreased due to high temperature-induced spikelet sterility at flowering time at the treatment of –AT+3.0 and/or AT+5.0℃ in 2011. In 2012 spikelet fertility was much lower than in 2011 even at the ambient temperature treatment because spikelet sterility occurred even before high temperature from initial heading stage due to high temperature at microsporogenesis stage. As shown in Table 6, the average maximum temperature at booting stage of medium and mid-late maturity cultivars ranged from 28.7℃ to 29.5℃ in year 2011, but it was 34.5℃ to 37.0℃ in year 2012 (Table 6).

Table 5. Spikelet fertility as affected by different temperature regimes exposed from the initial heading stage in six rice cultivars.

Maturity group	Variety	Spikelet fertility (%)							
		2011				2012			
		AT	AT+1.5	AT+3.0	AT+5.0	AT	AT+1.5	AT+3.0	AT+5.0
Early maturing	Unkwangbyeo	93.9	91.1	93.7	61.6	95.4	87.5	83.9	25.0
	Odaebyeo	95.6	92.9	91.8	53.3	-	-	-	-
Medium maturing	Andabyeo	90.6	85.2	72.5	52.7	44.0	43.7	39.4	35.7
	Hwasungbyeo	95.1	95.2	95.1	85.3	73.3	80.7	71.5	60.7
Mid-late maturing	Donganbyeo	94.6	97.0	96.0	73.3	64.8	31.2	29.3	24.9
	Chuchungbyeo	95.3	90.3	85.9	62.5	71.5	66.7	60.8	59.1
F-value	Temp	8.84	0.0001						
	MG	9.25	<.0001						
	Var(MG)	14.79	<.0001						

Temp: Temperature treatments, MG: Maturity groups, Var(MG): Varieties within maturity groups

Table 6. Average maximum temperature at booting stage in 2011 and 2012.

	Average maximum temperature (℃)	
	2011	2012
Andabyeo	28.8	35.3
Hwasungbyeo	28.7	34.5
Donganbyeo	28.6	37.0
Chuchungbyeo	29.5	37.0

This extreme heat stress occurred at booting stage in 2012 and induced spikelet sterility before anthesis. Therefore, spikelet fertility of panicle was calculated by considering the effect of high temperature at both booting and flowering stage (Equation 8).

$$\text{Fertility} = 100/[(1+\exp(a_b(T_b\text{-}Tc_b))) \text{ x } (1+\exp(a_f(T_f\text{-}Tc_f)))] \quad [8]$$

where a_b is parameter of nonlinear regression at booting stage, T_b is normalized maximum air temperature at booting stage, Tc_b is critical temperature that induces 50% spikelet sterility at booting stage, a_f is parameter of nonlinear regression at flowering stage, T_f is normalized maximum temperature at flowering stage, and Tc_f is critical temperature that induces 50% spikelet sterility at flowering stage.

Temperature-induced spikelet fertility of panicle during the flowering stage was well fitted to a logistic function of normalized temperature in all the tested varieties and presented in table 7 and fig. 4. Critical temperature (Tc) that induces 50% spikelet sterility at flowering time was estimated by fitting the temperature response of spikelet fertility to a logistic function. Tc was estimated to range from 34.6℃(Odaebyeo) to 39.7℃(Hwasungbyeo), Odaebyeo being significantly more sensitive to high temperature-induced spikelet sterility than the other varieties.

Table 7. Estimated parameters of spikelet fertility response function (equation 7) at flowering time.

Maturity group	Variety	alpha	Tc(℃)	F-value	Pr > F
Early maturing	Unkwangbyeo	1.19	39.7 (0.3)	715.5	<.0001
	Odaebyeo	1.10	34.6 (0.5)	840.6	<.0001
Medium-maturing	Andabyeo	0.51	38.1 (0.5)	864.8	<.0001
	Hwasungbyeo	0.47	39.9 (3.3)	2095.1	<.0001
Mid-late maturing	Donganbyeo	1.19	39.6 (2.4)	389.5	<.0001
	Chuchungbyeo	1.59	39.2 (0.4)	1905.0	<.0001

( ) is ±95% confidence limits, and Critical temperature (Tc) that induces 50% spikelet sterility at flowering.

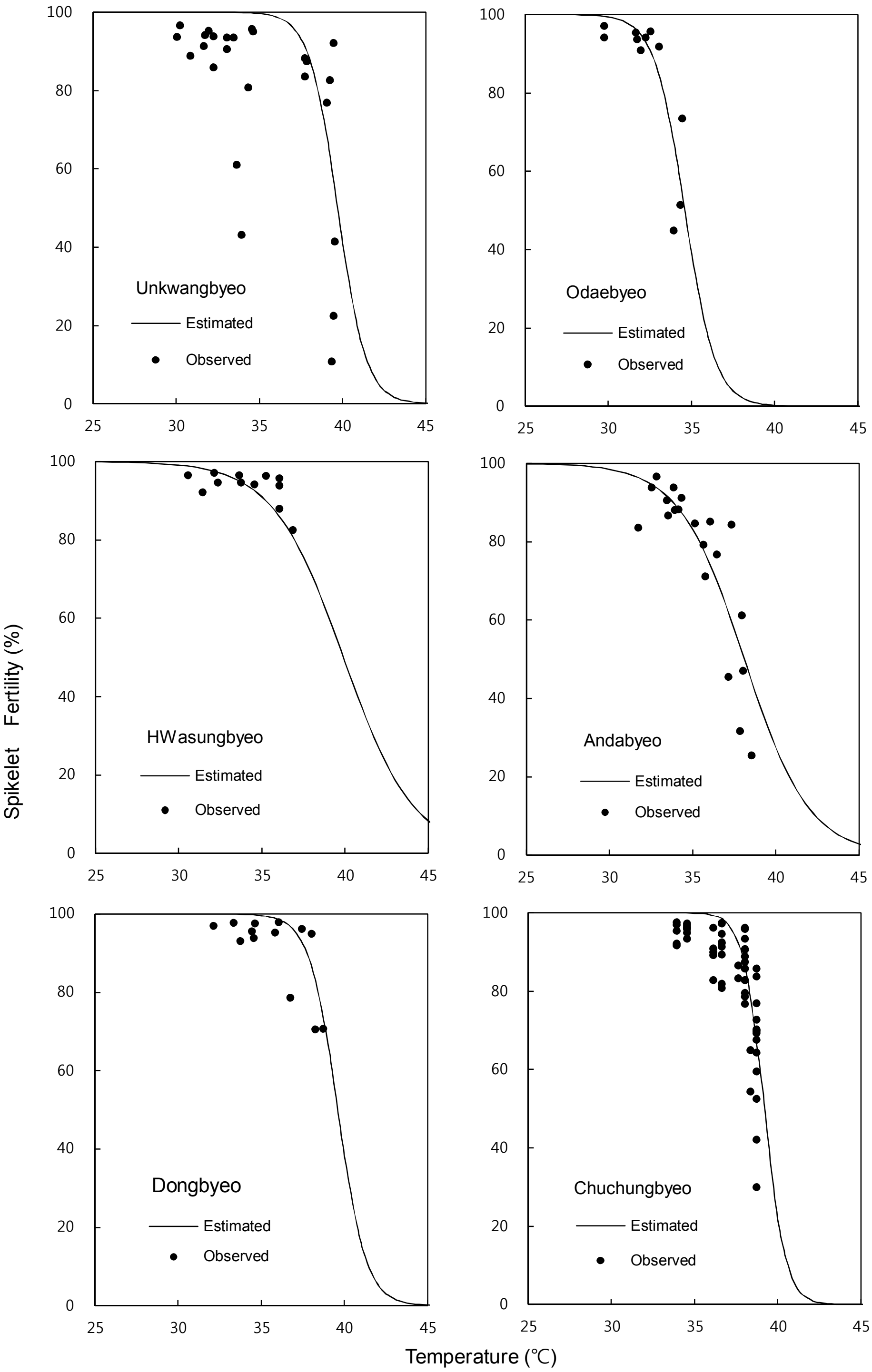


Fig. 5. The fertility response of each variety to the normalized maximum temperature at spikelet flowering.

Discussion

Grain-filling characteristic changes and high temperature-induced spikelet sterility during reproductive stage are reported to be the major factors that constraint grain yield of rice under the projected future climate of global warming. The objective of this study was to evaluate the varietal differences of spikelet sterility and grain filling characteristics response to air temperature during reproductive stage.

1. Grain-filling characteristics.

Grain-filling duration and maximum grain weight were estimated by fitting the time course change of grain weight to a logistic function (Table 2 and Fig. 2). No statistical difference in grain-filling duration were found among temperature treatments in all the tested varieties while maximum grain weight was decreased significantly with the rise of temperature above ambient during grain-filling stage. This result is different from the previous studies that high temperature causes the faster panicle senescence the earlier grain maturity, and thus decrease grain-filling duration (Kim, 2010, Sato and Inaba, 1973; Yoshida, 1981). This discrepancy of temperature response in grain filling duration might have resulted from the experimental condition. In this experiment only the temperature regimes higher than the ambient temperature were treated, the treated average air temperature ranging from 23℃ to 26℃ in medium and medium-late maturity cultivars and from 25℃ to 30℃ in early maturity cultivars (Fig. 4).

Meanwhile, grain developmental rate (DVR) was well fitted to beta-function of daily average temperature with the same base and ceiling temperatures in all the tested cultivars (Table 3). The temperature that accelerates most the grain senescence and reaches the physiological maturity earliest was estimated to be 29.2℃. Below this temperature the grain filling duration increases curve-linearly. Calculating from the DVR function in Table 3, the difference of grain filling duration were only within one day in early maturity cultivars and three days in the other cultivars under this experimental condition, matching well with the statistical inference.

According to Yoshida and Hara (1976), decreased length of grain-filling duration causes the reduction of the maximum grain weight because it affects the maximum amount of solar energy available for grain filling. However, the grain-filling duration was not significantly decreased but the maximum grain weight was substantially decreased by high temperature in this study. This result suggests that the decreased grain-filling duration would not be the major factor to decrease the grain weight under higher temperature than the current ambient temperature while it would be attributed to physiological factors such as decreased photosynthesis, increased respiration, etc. …

Optimum temperature for grain-filling stage in japonica rice has been reported to range from 20℃ to 22℃ in the average temperature and the high temperature above this optimum temperature reduce grain weight of rice (Murata, 1964; Kim, 1983). In this experiment, the maximum grain weight showed decreasing trends with temperature rise differentially according to varieties (Fig. 4). Chuchungbyeo and Andabyeo showed the most sensitive decrease of maximum grain weight with the rise of average air temperature above 23℃ and followed by Donganbyeo and Hwasungbyeo. Early maturity varieties, Odaebyeo and Unkwangbyeo, showed the least and gradual decrease up to about 29℃ while sharp decrease above this temperature. Few results have been reported about the varietal differences in maximum grain response to high temperature.

2. Spikelet sterility.

Spikelet sterility due to heat stress during reproductive stage would be one of the primary factors to decrease rice yield in the future climate change.

As compared to ambient temperature treatment (AT), spikelet fertility was significantly decreased due to high temperature-induced spikelet sterility at flowering time at the treatments of –AT+3.0 and/or AT+5.0 in 2011. In 2012 spikelet fertility was much lower than in 2011 even at the ambient temperature treatment because spikelet sterility occurred even before high temperature exposure from initial heading stage due to high temperature at microsporogenesis stage (Table 5). Especially spikelet fertility of AT treatment in medium and mid-late maturity groups in 2012 was lower than AT and even AT+5.0 in 2011. This abnormal phenomenon seems to be caused high temperature stress at booting stage in 2012 when their booting stages started from the beginning of august. The mean maximum temperature inside AT house rose up to 37℃ during this time (Table 6). The booting stage that microsporogenesis occurs is sensitive to low and high temperature stress (Endo et al., 2009; Nishiyama, 1984; Satake an Yoshida, 1978). High temperature treatment above 35℃ at microspore stage was reported to have caused significant spikelet sterility (Endo et al., 2009; Satake and Yoshida, 1978). Such extremely high temperature at booting stage even in ambient condition (Table 6) should have induced spikelet sterility of medium and mid-late varieties before flowering. These results suggested that spikelet sterility by high temperature at microsporogensis stage was not problem in the past, but it become a serious problem in future climate change condition.

The accurate assessment for effect of global warming on spikelet sterility is fastidious due to the non-synchrony of flowering time that is caused by non-synchronous-panicle heading and spikelet flowering on panicles (Yoshida 1981). Nguyen(2012) also reported that as spikelets even on the same panicle are exposed to different temperatures due to their non-synchrony of meiosis date, flowering date and time, it is not reasonable to relate the spikelet fertility of a panicle to the temperature of specific date or time of a day. On the basis of these results, he suggested that a normalized temperature be calculated by considering the probability density distribution of flowering date and time of spikelets. In this study, the normalized temperature was calculated according to equation 6 and was related to spikelet fertility using equation 8 for assessing varietal differences in spikelet sterility response to temperature at spikelet flowering. The critical temperature (Tc) that induces 50% spikelet sterility were estimated to range from 34.6℃ to 39.9℃, differing according to cultivars (Table 8). Odaebyeo with Tc of 34.6℃ was most sensitive among the tested cultivars. Nguyen (2012) also reported the similar observation that a critical temperature(Tc) was estimated at 38.5℃ in a japonica cultivar, Hwasungbyeo. Matsui et al (2001) reported a 3℃ difference in critical temperature between the tolerant variety Akitakomatch(40℃) and the susceptible variety Hinokikar(37℃). He suggested that *Indica* types are more tolerant to higher temperature than *japonica* types. However, a indica cultivar, Andabyeo showed similar or higher Tc than japonica varieties in this experiment.

In conclusion, the grain weight and spikelet sterility responded differentially to higher temperature according to rice varieties, leaving enough rooms for establishing adaption strategies to warming air temperature through crop management and variety improvement. And the method developed in this study would be applicable effectively to screening germplasm for the physiological responses to high temperature during reproductive stage of rice. However, further study should be done to arrive at the concrete conclusion.

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생식생장기 온도 변화에 따른 벼 품종별 임실률 및 등숙특성 차이에 관한 연구

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초 록

지구온난화로 인한 지구의 평균기온상승은 벼 수량성 저하로 이어지고 있다. Peng (2004)에 따르면, 최저온도가 1℃ 상승 할 때 마다 벼 수량은 10%감소한다고 하였다. 벼 수량성 저하는 생식생장기 고온에 따른 임실률 저하와 등숙특성 변화에 따른 입중저하가 주요인으로 알려져 있다. 따라서 본 연구에서는 생식생장기에 온도변화에 따른 벼 품종별 불임률과 등숙특성의 변화를 연구하였다.

본 실험은 2011년과 2012년 서울대학교 부속농장에서 실시하였으며, 실험에는 조생종인 운광벼, 오대벼, 중생종인 안다벼, 화성벼 그리고 중만생종인 동안벼, 추청벼를 사용하였다. 모든 품종들은 1/5000a

Wagner pot에 원형으로 15주(2011년), 10주(2012년)를 심어 등숙기 온도처리 전까지 야외 기상 조건에서 키웠으며, 생육단계와 출수기를 동기화 시켜주기 위해 분얼은 나오는 대로 제거하여 주간만을 키웠다. 각 품종은 출수기에 실외기온(AT, ambient temperature), AT+1.5℃, AT+3.0℃, AT+5.0℃로 조절되는 Plastic house에 옮겨 온도처리를 하였다. 온도처리 후 5일에서 7일마다 처리 및 품종별로 샘플을 채취하여 주당 영화수, 종실의 수분함량, 건물중 및 불임률을 조사하였다.

생식생장기 온도변화에 따른 등숙특성을 보면 모든 품종에서 현재 외기온보다 고온으로 처리된 조건에서도 등숙기간이 유의하게 단축되거나 연장되지않았으나, 최고입중은 고온조건으로 갈수록 감소하는 경향이었다. 따라서 온난화에 따른 입중 저하는 등숙기간 단축에 의한 것이라기 보다는 평균 온도 상승으로 인한 광합성 감소, 호흡량 증가 와 같은 생리적 요인들에 의한 것으로 판단된다. 온도 상승에 따른 최고입중 저하는 품종간에 유의한 차이가 있었다. 조생종인 운광벼와 오대벼가 고온에 따른 입중 저하가 가장 둔감하였으며, 중만생종인 추청벼와 통일계 중생종인 안다벼가 가장 민감하였다.

생식생장기 고온조건에 따른 벼 품종별 임실률은 50%불임을 나타내는 최고온도 Tc (℃)값을 기준으로 판단 할 수 있으며, 오대벼가 Tc값 34.6℃를 나타내어 고온에 가장 취약한 품종으로 판단되었으며,

그 외의 품종들은 38.1℃ ~ 39.7℃로 품종간에 차이가 없었다. 2012년 중생종과 중만생종의 수잉기 평균최고온도는 36℃로 2011년 28.9℃ 보다 높아 출수기 이전 벼 임실률에 영향을 주었다. 이는 수잉기 온도가 과거에는 크게 문제가 되지 않았으나 평균온도가 상승하는 미래 기후조건에서는 벼 임실률저하에 영향을 줄 것으로 판단된다.

전체적으로 고온에 따른 벼 입중 과 임실률 저하는 품종간 다르게 반응하여 재배법 및 품종 개량을 통한 온난화 적응의 여지가 있는 것으로 사료되며, 또한, 본 실험에서 사용된 등숙특성과 임실률 평가방법은 다량의 유전자원평가에 유효적으로 이용될 수 있을 것으로 판단된다.

주요어 : 고온, 등숙기, 최고입중, 불임률, 생식생장기