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Modeling and validation of high-temperature induced spikelet sterility in rice

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ABSTRACT

Spikelet sterility due to heat stress during reproductive stage would be one of the prominent factors to reduce rice yield under the projected global warming climate. A simulation model that was comprised of equations to estimate the probability distributions of heading date of panicles in the field, flowering date of spikelets on a panicle, and flowering time of spikelets during the day time and the two sterility response functions to the temperature on the day of meiosis and at the flowering time of a spikelet was constructed, calibrated, and validated to predict high-temperature induced spikelet sterility in rice.

The model was calibrated and validated against the data collected from a series of experiments conducted in the plastic houses controlling the temperature to ambient, ambient + 1.5 °C, ambient + 3.0 °C, ambient + 5.0 °C, and ambient + 7.0 °C in 2009 and 2010. Heading, flowering habit, and spikelet sterility of rice exposed to different temperatures during two periods from 20 days before heading and initial heading to 20 days after heading were recorded on panicle basis for model calibration. For model validation spikelet sterility data were collected on hill (pot) basis from rice plants exposed to different temperatures from transiting to maturity in 2009 and 2010.

The heading of panicle reached peak on four to six days after and lasted until 12 days after initial heading and the heading date distribution of panicles was well fitted to Poisson's equation. The flowering peak of spikelets on a panicle occurred at about 5 days after heading and lasted 11 days regardless of temperature and cultivars and the flowering distribution was well fitted to the normal distribution function. The anthesis in a day started from 8:00 h, reached peak around 11:00 h, and lasted until 15:00 h regardless of temperature treatments, the flowering peak being a little earlier in a *japonica* cultivar "Hwaseongbyeo" than in a *Tongil* type one "Dasanbyeo". The flower opening time followed the normal distribution with standard deviation of about one hour. The fertility responses to high temperature on the day of spikelet meiosis and at the time of spikelet anthesis were well fitted to logistic functions of heating degree hour above 31 °C on 12 days before spikelet anthesis and air temperature at the time of spikelet flowering, respectively. The heating degree hour causing 50% spikelet sterility at meiosis was higher in a *japonica* cultivar "Hwaseongbyeo" than in a *Tongil* type one "Dasanbyeo", while the air temperature causing 50% spikelet sterility at spikelet flowering time was higher in *Tongil* type cultivars than in *japonica* ones.

The model integrating the above equations predicted the spikelet sterility/fertility response to air temperature with reasonable precision and accuracy.

1. Introduction

Global warming is unequivocal and surface air temperature is projected to rise by 1.4–5.8 °C at the end of this century (IPCC, 2007). The projected climate change characterized by the increase in both frequency and intensity of high temperature along with its large variability is expected to become a major detrimental factor to rice production in most rice growing regions including temperate region in the future. Generally, high temperature stress effect on grain yield is greater during reproductive stage than during vegetative stage (Yoshida, 1981). High temperature during reproductive stage reduces the number of spikelets produced per unit dry weight or nitrogen absorbed (Yoshida, 1983), the spikelet fertility (Satake and Yoshida, 1978; Tashiro and Wardlaw, 1991; Kim et al., 1996; Matsui et al., 1997), and grain weight by accelerating the panicle senescence (Kim et al., 2011), leading to the decrease of grain yield. High temperature-induced spikelet sterility has been an

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important factor to decrease rice yield and its variability only in tropical Asia (Osada et al., 1973) and Africa (Matsushima et al., 1982), but would become a prominent detrimental factor even in temperate rice growing regions in the future (Horie et al., 1995).

Sterility induction by high temperature is most sensitive at flowering time and next at meiotic stage of spikelet that falls on 12 days before flowering (Satake and Yoshida, 1978). During microsporogenesis the processes close to the meiotic stage are most sensitive to high temperature (Yoshida, 1981). A significant decrease in pollen production was found at 5 °C above ambient temperature (Prasad et al., 2006) that was attributed to impaired cell division of pollen mother cell (Takeoka et al., 1992). In rice, the reproductive processes that occur within one hour after anthesis–dehiscence of anther, shedding of pollen, germination of pollen grains on stigma, and elongation of pollen tubes, are most sensitive to high temperatures and are disrupted at day temperatures above 33.8 °C, leading to spikelet sterility (Satake and Yoshida, 1978). Therefore, an hour exposure of high temperature during flowering is enough to induce spikelet sterility (Jagadish et al., 2007; Satake and Yoshida, 1978) and spikelet opened beyond ±1 h of the high temperature exposure are not affected (Satake and Yoshida, 1978; Wassmann et al., 2009). Among these reproductive processes occurring within one hour after anthesis, anther dehiscence is the most susceptible process under high temperature (Matsui et al., 1999b). High temperatures at flowering inhibit swelling of the pollen grains (Matsui et al., 2000), which is the driving force for anther dehiscence in rice (Matsui et al., 1999a,b). Sterility is caused by poor anther dehiscence and low pollen production, and hence low numbers of germinating pollen grains on the stigma (Matsui et al., 2000, 2001; Prasad et al., 2006). Weerakoon et al. (2008) reported that grain sterility increased with increased humidity under high temperature above the critical value that induces spikelet sterility in rice. Similarly, Matsui et al. (1997b) found that spikelet sterility was further aggravated with higher air humidity and higher wind velocity through disturbance of pollination process. He observed that the fertility of spikelets flowered at 37.5 °C was highest at 45% relative humidity (RH), followed by that at 60% RH, and lowest at 80% and wind speed over 0.85 m s^{-1} decreased spikelet fertility at 37.5 °C.

Many studies have shown that there are varietal differences in the tolerance to high temperature-induced sterility during flowering (Osada et al., 1973; Satake and Yoshida, 1978; Yoshida, 1981; Jagadish et al., 2007; Matsui et al., 2001, 2005). For instance, Matsui et al. (2001) reported that difference of the temperature causing 50% spikelet sterility was about 3 °C between the tolerant variety "Akitakomatch" (40 °C) and the susceptible variety "Hinohikari" (37 °C). Although heat tolerant varieties have been found in both indica and japonica subspecies, it has been suggested that indica types are more tolerant to higher temperatures than japonica ones (Satake and Yoshida, 1978; Matsui et al., 2001).

Generally, spikelet sterility response to high temperature has been modeled using daily mean maximum temperature during 10 day period close to heading (Matsui and Horie, 1992; Horie et al., 1995), number of days with maximum temperature above 34 °C (Challinor et al., 2007), and daily maximum and minimum temperature (Krishnan et al., 2007). These models have taken into account the genotypic difference in the critical temperature causing sterility while they have not considered the temperature x duration interaction effect on spikelet sterility and the non-synchrony of the dates of panicle heading and thus flowering date and time in the field. However, Jagadish et al. (2007) reported an interaction between high temperature and duration of exposure was found in a heat-sensitive genotype "Azucena" but not in a moderately tolerant genotype "IR 64", and the linear relationship between the logits of percent spikelet fertility and the accumulated hourly temperature above 33 °C.

As reviewed above, the effect of high temperature on spikelet sterility is seems to be limited only to the time of spikelet flowering and microsporogenesis and also spikelets in the field are exposed to different temperature at flowering time because flowering of rice in the field and even on the same panicle occurs over an extended time period of 15–20 and 7–10 days, respectively, due to the non-synchrony of tillering and thus heading date of panicles (Yoshida, 1981). Therefore, the accuracy of modeling the temperature effects on spikelet sterility depends on the diurnal time course of temperature and on the accuracy of the model in predicting the probability distribution of flowering date and time in the field. This is particularly true when temperature varies considerably from day to day. However, only a model (Shi et al., 2007) considered this flowering habit in predicting high temperature–induced sterility of rice, but this model also did not include high temperature-induced sterility at meiosis.

In this regards, a simulation model considering the flowering habit was constructed, calibrated, and validated for predicting spikelet sterility induced by high temperature during meiosis and flowering time of spikelet in the rice field.

2. Materials and methods

2.1. Model description

Based on the literature review, we assumed that high temperature-induced sterility of spikelet is sensitive at meiotic stage and spikelet opening time (Satake and Yoshida, 1978; Yoshida, 1981), high temperature at one hour before and after flower opening does not induce sterility (Satake and Yoshida, 1978; Wassmann et al., 2009), and one hour exposure to high temperature during spikelet opening is enough to induce sterility (Jagadish et al., 2007; Satake and Yoshida, 1978). As assumed, not only high temperature effect on spikelet sterility is limited only to the time of spikelet flowering and meiosis but also spikelets in the field are exposed to different temperatures at flowering time because of non-synchrony in flowering dates and times of spikelets in the field. Therefore, it is the first step to model the probability distribution of flowering date and time of spikelets in the field for the accurate prediction of high temperature-induced sterility of spikelets.

It is reported to take about 15–20 days for all the spikelets to complete anthesis in the field because it takes 10–14 days to complete heading in the field and 7–10 days for all the spikelets on the same panicle to complete anthesis (Yoshida, 1981). However, their probability distribution patterns have not been well documented. The probability distribution of flowering date was estimated by modeling the probability distributions of heading dates of panicles in a field and flowering dates of spikelets on a panicle. The probability density distribution of heading dates of panicles in a field was fitted to the following Poisson probability distribution equation;

$$P_h(j) = \frac{e^{-m} m^j}{j!} \quad (1)$$

where $P_h(j)$ is relative frequency of panicles that headed on the jth day after the start of heading, and m is constant.

The date of anthesis of individual spikelet varies with the positions of spikelets on the same panicle. The probability density distribution of flowering date on a panicle was fitted to the following normal distribution function;

$$P_f(k) = \frac{1}{\sqrt{2\pi}\sigma} \exp\left[-\frac{(k-k_m)^2}{2\sigma^2}\right] \quad (2)$$

where $P_f(k)$ is relative frequency of spikelets on a panicle that flowers on the kth day after heading of panicle, k_m is peak (mean) date