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# Stage-dependent temperature sensitivity function predicts seed-setting rates under short-term extreme heat stress in rice

Ting Sun[a,b], Toshihiro Hasegawa[b], Liang Tang[a], Wei Wang[a], Junjie Zhou[a], Leilei Liu[a], Bin Liu[a], Weixing Cao[a], Yan Zhu[a,*]

[a] *National Engineering and Technology Center for Information Agriculture, Key Laboratory for Crop System Analysis and Decision Making, Ministry of Agriculture, Jiangsu Key Laboratory for Information Agriculture, Jiangsu Collaborative Innovation Center for Modern Crop Production, Nanjing Agricultural University, Nanjing, Jiangsu, 210095, PR China*

[b] *Agro-Environmental Research Division, Tohoku Agricultural Research Center, National Agricultural and Food Research Organization (NARO), 4 Akahira, Shimokuriyagawa, Morioka, 020-0198, Japan*

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ABSTRACT

Seed-setting rate of rice (*Oryza sativa* L.) significantly decreases under high temperatures during the reproductive period largely due to heat-induced spikelet sterility. The effects depend largely on the timing and severity of heat stress, but the variation in the sensitivity of seed-setting rate in response to heat stress at different growth stages is not yet well simulated by most of the present crop models. To investigate the quantitative relationships between seed-setting rates of rice and various exposures of heat stress, we conducted four-year phytotron experiments with four different temperature regimes (the target maximum/minimum temperatures, 32 °C/22 °C, 35 °C/25 °C, 38 °C/28 °C and 41 °C/31 °C in 2011 and 2012; 32 °C/22 °C, 36 °C/26 °C, 40 °C/30 °C and 44 °C/34 °C in 2014 and 2015) with factorial combinations of durations (2, 4 and 6 days in 2014 and 2015; 3, 5 and 7 days in 2011; 3, 6 and 9 days in 2012) and the timings (0, 6 or 12 days after flowering), using three japonica cultivars. The duration and intensity of heat stress were quantified by the heat degree-days (HDD), defined as the temperature sum above a critical temperature value, which varied from 35 to 36 °C, depending on the cultivars. The observed seed-setting rates were well expressed as a logistic function of HDD, but the temperature sensitivity parameter varied with the timing of heat stress and the spikelet positions on the panicle. The variation in timing of flowering was apparent among upper, middle and lower parts of the panicles: 1 and 3-day delay of flowering for the spikelets on the middle and lower parts of the panicles, respectively, compared with upper ones. We therefore developed a simulation model that reflects the changes in the sensitivity of seed-setting rate to HDD to estimate the effects of heat stress with different intensities or durations at any time from flowering onward. The model with the stage-dependent parameters improved substantially the root mean square error (RMSE) and mean bias error (MBE) of seed-setting % from 20.1 and 6.0 to 7.6 and 0.2, respectively, compared to that with the stage-independent parameters. The proposed model needs to be tested under field conditions, but will be an important basis for accurate prediction of seed-setting rates in rice, which is critical for reliable estimates of crop production under climate change.

## 1. Introduction

Rice is one of the world's most important cereals as the staple food for the majority of the world population. Heat stress events, which caused large negative impacts on rice yields, have been reported in main global rice production areas such as Southern Asia (Aggarwal and Mall, 2002; Ishimaru et al., 2016; Matsushima et al., 1983; Osada et al., 1973), East Asia (Hasegawa et al., 2009; Yawei and Hua, 2006) and Southeast Asia (Wassmann et al., 2009). Therefore, rice plants are potentially at high risk of exposure to heat stress because the short episodes of extreme temperature will become more frequent with the increasing variability and intensity of global warming (IPCC, 2013; Tebaldi et al., 2006).

Crop growth model is the most important tool to predict rice productivity under different climate scenarios, but recent multi-models comparisons demonstrated that large uncertainties are involved in predictions by individual crop models (Asseng et al., 2013; Li et al., 2015). The uncertainties are largely associated with predictions under

* Corresponding author.
*E-mail address:* yanzhu@njau.edu.cn (Y. Zhu).

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extreme temperatures, because most of the current crop models were developed under current temperature ranges. Although some crop models were tested under extreme high temperature conditions, variation in crop yield under largely varying temperatures is still difficult to predict (Liu et al., 2016; Shi et al., 2015a, b; Wang et al., 2017). It is therefore imperative to improve the quantitative understandings on the crop responses to extreme temperatures, which are projected to increase greatly under projected changes in climate.

Heat stress occurs when the temperature rises above a threshold value and persists over a certain period of time, and results in an irreversible damage on crop plants (Wahid et al., 2007). Various growth processes can be affected by heat stress, but the sensitivity and severity of the stresses changes depending on the growth stages and processes (Sánchez et al., 2014). Among them, the seed-setting rate is highly sensitive to heat stress, and directly influences grain yield via reduced number of filled grains (Siebert et al., 2014). A pioneering study by Satake and Yoshida (1978) identified the most sensitive stage for seed-setting as around flowering. Horie (1993) showed that the seed-setting rate decreases sharply above around 35 °C using temperature gradient chambers. Since then, this threshold temperature has been widely used in rice growth models (Bouman, 2001; Shi et al., 2015a, b; Tang et al., 2009). However, as shown in many chamber and field studies, 35 °C is not an unequivocal threshold temperature for failure in seed-setting (Hasegawa et al., 2011; Jagadish et al., 2007; Satake and Yoshida, 1978; Tian et al., 2010), which needs further examination (Sánchez et al., 2014).

Duration of high-temperature exposure is another important determinant of the effects of heat stress. For instance, seed-setting rate was almost linearly decreased as duration of high-temperature exposure increased from 0 to 5 h, because of increased spikelet sterility (Jagadish et al., 2007). At higher temperatures, the critical duration to induce equal sterility became shorter (Satake and Yoshida, 1978). This suggests that a cumulative temperature above a threshold value seemed to be more reasonable because of the interaction between temperature intensity and duration (Liu et al., 2014; Prasad et al., 1999; Shi et al., 2015a, b). Nevertheless, heat-induced spikelet sterility was generally quantified with the daily maximum temperature (Bouman, 2001; Horie et al., 1996; Krishnan et al., 2007; Matthews, 1995; Nakagawa et al., 2003; Shi et al., 2016; Tang et al., 2009). This may be because determination of the threshold temperatures and/or the response of seed-setting to the heat dose have not been well documented.

Early studies clearly demonstrated that susceptibility to heat damages peaks at the heading stage and decreases sharply from then onward for an individual panicle (Satake and Yoshida, 1978). The rice community, however, includes panicles and spikelets at different growth stages. Timing of panicle exertion varies among tillers in the field by 10–14 days and flowering time of spikelets even on the same panicle can vary by 7–10 days (Yoshida, 1981). On the other hand, heat events with different intensities and duration can occur at any time during reproductive stages (Hasegawa et al., 2009; Redden et al., 2013; Shi et al., 2015a, b). The effects of the variation in the growth stages of the panicles and spikelets on seed-setting rates have often been overlooked or averaged in crop models (Bouman, 2001; Tang et al., 2009; Yoshida and Horie, 2009), which can be an important source of uncertainties.

Recently, new models have been developed which consider the flowering pattern in the field to estimate heat-induced spikelet sterility (Barlow et al., 2015; Nguyen et al., 2014; Shi et al., 2007). These models account for the distribution of the flowering events from a single panicle to the crop population, which is an important improvement in application to the field situation. However the sensitivity changes in the response of seed-setting to heat stress are not fully taken into account. Seed-setting involves a series of processes to complete in a short period, including dehiscence of anther, pollen shedding, germination of pollen grains and elongation of pollen tubes, which are susceptible to heat stresses (Mackill et al., 1982; Matsui et al., 2000; Prasad et al., 2006). The effects of heat events at different growth stages should therfore be better quantified.

One of the major bottlenecks in modeling seed-setting under heat stress is lack of the high quality experimental datasets. Most of the previous controlled experiments were conducted in chambers, which usually specified panicles at specific timing to single out factors (Matsui et al., 1997; Matsui et al., 2001; Satake and Yoshida, 1978), leading to the variations among different flowers often been overlooked and the crop-level responses of seed-setting to heat stress difficult to test. During 2011–2012 and 2014–2015, we initiated a series of high quality experiments in the chambers to determine the effects of short-term heat stress at different growth stages on seed-setting rates of the whole plants. This study was conducted (i) to quantify the heat stress by taking account into the interaction of high temperature intensites and durations, and (ii) to develop a model that can quantify the variation of seed-setting rates of the whole plants under the heat events at different stages from flowering stage.

## 2. Materials and methods

### 2.1. Experimental design

Dataset were obtained from the environment-controlled phytotrons experiments conducted in Nanjing (118.78°E, 32.04°N) from 2011 to 2012 and in Rugao (120.33°E, 32.23°N) from 2014 to 2015 in Jiangsu Province of China. The experimental methods and details are described fully by Shi et al. (2016). Briefly, three japonica rice cultivars, Nanjing41 (grown in 2011, 2012, 2014 and 2015), Wuxiangjing14 (grown in 2011 and 2012) and Wuyunjing 24 (grown in 2014 and 2015) were used in the experiments. Seeds of these cultivars are sown in nearby field and raised on the dry seedbed. Three-leaf seedlings were transplanted into plastic pots (height = 35.6 cm, inner diameter = 29.8 cm, volume 25.0 L filled with a soil of 22.5 L) and kept submerged until one week before harvest. The pots were placed closely together at a density of about 11 pots per $m^2$ and the transplanting density was two plants per hill and three hills per pot, equivalent to 66 plants per $m^2$, which is similar to a typical density in farmers' practice for japonica rice cultivars in the region of 60 to 75 plants per $m^2$ (Jiangsu Province Commission of Agricutral, 2011). 1.5 g N, 1.5 g $P_2O_5$ and 2 g $K_2O$ were applied in each pot as basal fertilizer before transplanting, and the additional 0.3 g N and 1.2 g N were top-dressed at mid-tillering and panicle initiation, respectively. Irrigation, weed, and disease and pest control were carried out according to local standards of rice cultivation to avoid biotic and abiotic stresses.

The rice plants were grown under ambient condition before the heat stress treatments. We recorded the date when the first spikelet flowered on each panicle and determined the flowering date as 50% of panicles initiated flowering for each pot. Once the rice plants reached the target development stages of 0, 6 and 12 days after flowering (DAF), pots with plants of similar number of panicles and growth stage were transferred into each phytotron room (L × W × H; 3.4 m × 3.2 m × 2.8 m) for the designated treatments. Because there were about 4000 spikelets in a pot, the timings of flowering varied greatly. This resulted that the heat stress was imposed on spikelets of different growth stages including both pre-flowering and post-flowering depending on the positions of the panicles.

After the heat stress treatments were completed, the plants were moved out and grown outside until harvest. The heat stress treatments varied slightly from year to year, but four temperature regimes were set for all years; target daily maximum and minimum temperatures ($T_{max}$/$T_{min}$) were 32 °C/22 °C, 35 °C/25 °C, 38 °C/28 °C and 41 °C/31 °C in 2011 and 2012; 32 °C/22 °C, 36 °C/26 °C, 40 °C/30 °C and 44 °C/34 °C in 2014 and 2015. Durations were 2, 4 and 6 days in 2014 and 2015; 3, 5 and 7 days in 2011; 3, 6 and 9 days in 2012, which are summarized in Table 1. Air temperature (Ta, °C) and relative humidity (RH, %), soil volumetric water content (VWC, $m^3\,m^{-3}$) and photosynthetically active