Impacts of prolonged high temperature on heavy-panicle rice varieties in the field

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ABSTRACT

Although enhancement of sink capacity with heavy-panicle is an important approach to the improvement of yield potential in super rice (*Oryza sativa* L.) breeding, environmental fluctuations may greatly affect fertilization and grain filling of heavy-panicle rice. Here, we investigated the response of heavy-panicle rice varieties to high temperature at flowering and grain filling stages under field conditions, with a focus on spikelets positions on the panicle. Six varieties each with four staggered sowings were grown under various climatic conditions, and thus their flowering stages and grain filling stages experienced high or normal temperature weather scenarios. When rice varieties grown under high temperature, spikelet fertilities increased in all tested varieties. Grain weights of varieties CW2221, K106 and R-2 under high temperature stress showed an average of 10.81% increase compared with normal temperature, whereas 'C418', 'J1307' and 'Xianghui210' decreased by 15.21%. Head milled rice rates significantly decreased, but chalky grain rates and chalkiness degrees significantly increased under high temperature. We further demonstrated that the effects of high temperature on spikelet fertility, grain weight and grain qualities were correlated with grain positions. These results indicate that understanding effects of high temperature on grain weight and quality in heavy-panicle rice varieties is a key factor for super rice breeding in the future.

Key words: Chalky grain rate, grain position, grain weight, head milled rice rate, heavy-panicle rice, *Oryza sativa*, spikelet fertility.

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INTRODUCTION

As one of the staple food crops, rice (*Oryza sativa* L.) has been widely cultivated in the world, providing 35%-75% calories for approximately three billion people in Asia (Khush, 2005). Global warming is projected to continue, causing temperature to rise 0.3-4.8 °C at the end of this century compared to 1986-2005 (Stocker et al., 2013). Such drastic elevation in temperature is occurring more frequently in China (Rosenzweig et al., 2001). Large reductions in yield and rice quality caused by high temperature stress were documented, resulting in serious economic losses (Peng et al., 2004; Lanning et al., 2011).

Yield losses under high temperature were attributed to spikelet sterility and reduction of grain weight (Prasad et al., 2006; Shi et al., 2013). Flowering is the growth stage most susceptible to high temperature in rice, and poor germination of pollen grains on stigma is partially responsible for the spikelet sterility (Satake and Yoshida, 1978). The decrease of grain weight is related to the formation of imperfect grains and the reduction in dry mass accumulation and translocation (Tashiro and Wardlaw, 1991).

Rice quality is mainly evaluated by several traits, including milling, appearance, cooking, eating and nutritional qualities and other indicators. In addition to genetic factors, these traits are also affected by the grain positions on the rachis and environmental factors. Previous studies showed that grain quality was significantly affected by the different positions of grains, which is particularly relevant to heavy-panicle rice varieties (Cheng et al., 2003). During the grain filling stage, high temperature worsens transparency, increases chalky rice, and reduces head rice rate (Ambardekar et al., 2011; Lanning et al., 2011).

Heavy-panicle rice possesses high-yield potential and may provide an ideal way for development of new high-yielding varieties (Yuan, 2012). China initiated super rice breeding project in 1996 and has raised attainable rice yield record from 10.5 to 15 t ha^{-1} in succession with a large number of heavy-panicle varieties, which can demonstrate the importance of heavy-panicle rice (Cheng et al., 2007; Yuan, 2012). However, larger panicle rice varieties usually require longer flowering and grain-filling duration, and thus the positional differences among grains become more significant. When environmental fluctuations happen, their spikelet fertility, grain weight and quality are much more heavily affected than varieties with normal panicle size (Cheng et al., 2007; Mohammed and Tarpley, 2010). So far, studies on the effects of high temperature under

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field conditions on rice grain filling and quality are sparse (Ambardekar et al., 2011), even more limited for heavy-panicle rice varieties. Staggered sowing experiments in the field condition can provide a better way to reflect climate changes than those experiments conducted in the greenhouse. It can also test the adaptability of rice to the environmental change than the method of sowing in the same season of different years. High temperature occurs more frequently than before during rice growth season in China, especially during the flowering and grain filling period of time. It provides us an opportunity to test the effect of high temperature on rice development. The objectives of this study are: (i) to test the effects of high temperature on spikelet fertility, grain weight and grain quality of heavy-panicle varieties in field conditions; (ii) to determine if there are genotypic differences and grain position effects in response to high temperature; and (iii) to explore the possible responsive mechanisms underlying high temperature stress in heavy-panicle rice during the flowering and grain filling stages.

MATERIALS AND METHODS

Rice cultivars and crop husbandry

Six heavy-panicle rice varieties, screened from 21 heavy-panicle *indica* varieties in previous studies, were used in this research. C418, J1307 and CW2221 are heat tolerant varieties, and Xianghui210, K106 and R-2 are heat-intolerant varieties. For these varieties, the average panicle weight is about 5.1 g. The experiment was conducted on the Yangtze University farm (112°31' E, 30°21' N), located in the western part in Jianghan Basin in China, in 2013. The soil type is paddy soil with 11.00 g kg^{-1} organic matter, 1 g kg^{-1} total N, 82.03 mg kg^{-1} available N, 33.25 mg kg^{-1} available P, and 57.11 mg kg^{-1} available K. The trial was conducted in a randomized complete block design with three replicates. Seeds of six rice varieties were sown in seedling nursery as four sowing batches with a 10-d interval, starting 16 April to 15 June. The sowing dates of these varieties were adjusted according to accumulative temperatures to ensure similar heading dates in the hottest season (late-July to mid-August) and normal condition. The plot dimensions were 2 m × 1 m, with a distance of 16.7 cm between plants within a row, and 20 cm between rows (one seeding per hill). The quantity of chemical compound fertilizer as basal application was 120 kg N ha^{-1} ($N:P_2O_5:K_2O$ = 25:10:15). Regular irrigation, disease and pest control were conducted during rice growth period. All the information about rice growth and development is listed in Table 1.

Sampling and measurements

The growth and development of rice was recorded daily. Rice plants with uniform development were tagged at heading stage in each plot. At physiological mature stage, six hills of rice plants were harvested from tagged plants where 20 rice plants were randomly selected to determine spikelet fertility, grain weight and grain quality. The main-stem panicles were divided equally into three parts from the top to the base of the panicle based on panicle length: upper, middle, and lower parts (Mohammed and Tarpley, 2010). Grains were dried naturally to 13.5% seed water content and placed under constant temperature and humidity conditions for 3-mo for quality test.

To evaluate spikelet fertility, briefly, the grains were squeezed using index finger and thumb together to determine filled or not. Both completely and partially filled grains were recorded as fertile grains; only empty grains were recorded as sterile grains (Prasad et al., 2006). Specific calculation formula is as follows:

Spikelet fertility (%) = number of fertile grains × 100/ total number of florets = (number of completely filled grains + number of partially filled grains) × 100/total number of florets.

To obtain 1000-grain weight, three replicates with 500 grains each one were chosen from filled grains at random and weighted.

Grain quality included milling quality (head milled rice rate) and appearance quality (chalky grain rate and chalkiness degree), which were measured with exterior quality tester (FD.02-JMWT 12, Beijing Zhuochuan Electronic Science and Technology Co., Ltd, Beijing, China) in accordance with the national standard of People's Republic of China, High Quality Paddy (GB/T17891-1999).

Weather conditions

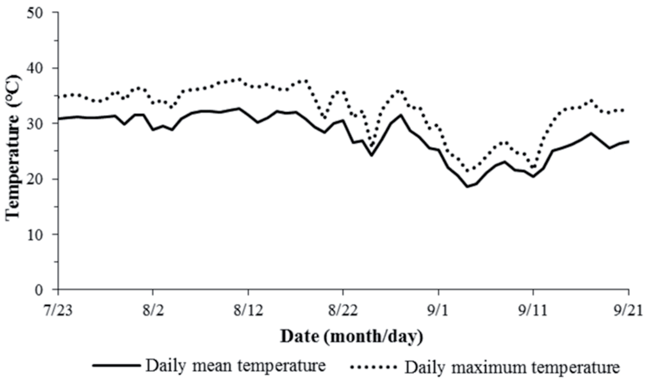
The threshold of high temperature assumed to cause damage to spikelet fertility is set at 30 °C for daily mean temperature or at 35 °C for daily maximum temperature for three consecutive days (Tian et al., 2007). Daily mean temperature ≥ 26 °C was defined as threshold temperature of heat injury for grain filling (Yoshida and Hara, 1977). Measured daily mean temperature and daily maximum temperature during the flowering stage and grain filling stage are shown in Figure 1. All the meteorological data involved in this study

Table 1. Planting dates (PD) and heading dates (HD) of six heavy-panicle rice varieties with four batches of sowing (2013).

	Sowing 1		Sowing 2		Sowing 3		Sowing 4	
	PD	HD	PD	HD	PD	HD	PD	HD
C418	26 Apr	1 Aug	10 May	9 Aug	26 May	21 Aug	7 June	30 Aug
J1307	16 Apr	2 Aug	6 May	8 Aug	13 May	19 Aug	27 May	31 Aug
CW2221	22 Apr	3 Aug	6 May	10 Aug	19 May	20 Aug	1 June	2 Sept
Xianghui210	4 May	30 July	18 May	9 Aug	2 June	21 Aug	15 June	1 Sept
K106	22 Apr	4 Aug	6 May	10 Aug	19 May	21 Aug	1 June	1 Sept
R-2	22 Apr	31 July	6 May	9 Aug	19 May	22 Aug	1 June	30 Aug

Seeds of six rice varieties were sown in seedling nursery as four batches and 25 d-old seedlings were transplanted into a paddy field.

Figure 1. Daily mean temperature and daily maximum temperature during the flowering and grain filling stages in 2013.



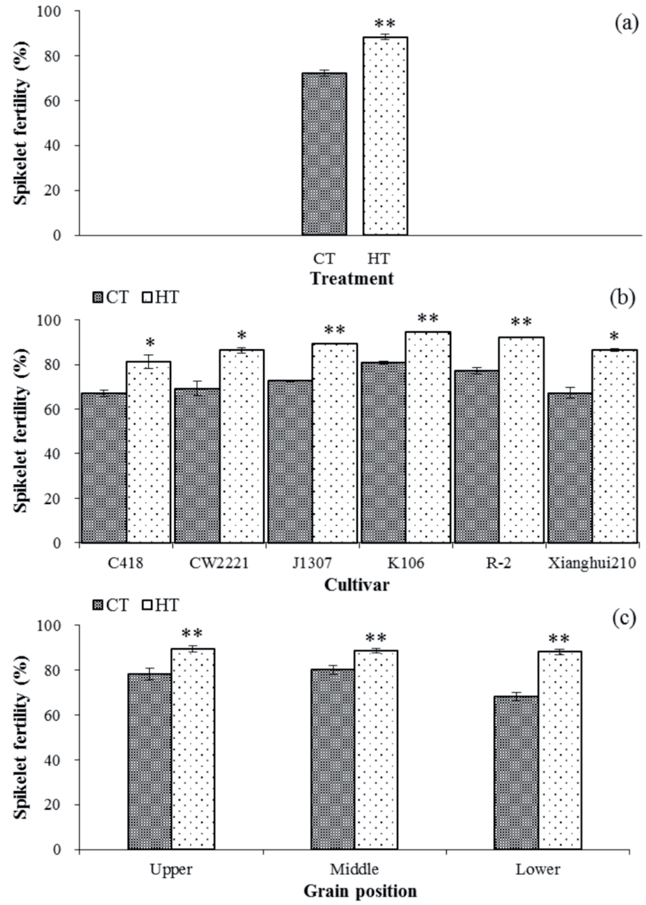
Under high temperature treatment and control treatment, the flowering stage was 24 July-4 Aug and 24 Aug-2 Sept, moreover, the grain filling stage was 30 July-2 Sept and 22 Aug-20 Sept. The meteorological data were provided by Agro-meteorological Experimental Station in Jingzhou, Hubei Province, 500 m away from the experimental farm.

were obtained from Agro-meteorological Experimental Station (national-level ecological agriculture test station in China) in Jingzhou, Hubei Province, 500 m away from the experimental farm (Figure 1).

Data analysis

Statistical analysis was conducted with the SPSS software, version 17.0 (IBM, Armonk, New York, USA). Differences between treatments were analyzed using Tukey's Least Significant Difference (LSD) at $p < 0.01$ and $P < 0.05$. Correlation analysis of spikelet fertility with temperature was conducted after arcsine conversion.

Figure 2. Effects of high temperature treatment (HT) during the flowering stage on spikelet fertility of the whole panicle (a), six rice varieties (b) and different grain positions (c).



CT: Control treatment, ns: nonsignificant.
Each bar represents the mean ± standard error of three replicates.
*, ** Significant at the 0.05 and 0.01 probability levels, respectively.

RESULTS

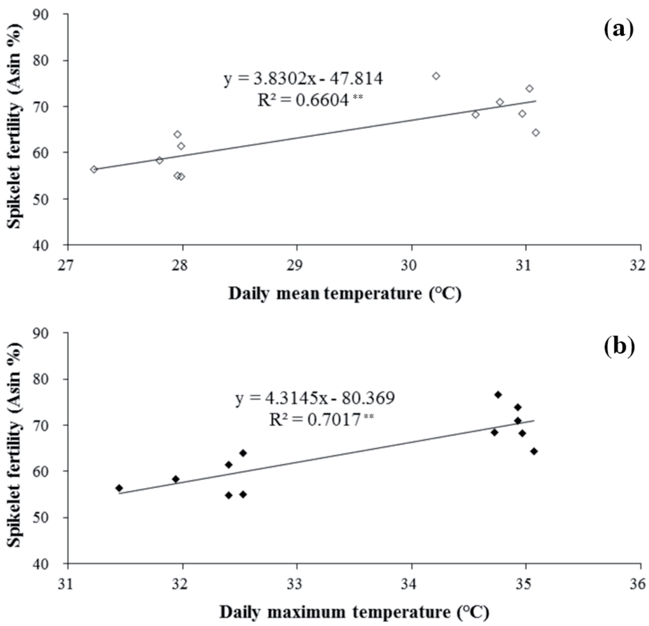
During the flowering stage, sowings 1, 2 and 3 endured high-temperature stress for about 7 d for the six varieties, while sowing 4 was placed under normal temperature. Consequently, sowing 1 was chosen as high-temperature treated and sowing 4 as control. Daily mean temperature and daily maximum temperature were 26.9 and 31.0 °C under control treatment (24 August-2 September), and 30.6 and 34.7 °C under high temperature treatment, respectively (24 July-4 August).

During the grain filling stage, sowings 1 and 2 endured high-temperature stress for about 26-29 d and 20-22 d, respectively, for the six varieties; sowings 3 and 4 were placed under normal temperature. Consequently sowing 1 was chosen as high-temperature treated and sowing 3 as control. Daily mean temperature and daily maximum temperature were 24.9 and 29.3 °C under control treatment (22 August-20 September), and 29.6 and 34.3 °C under high temperature treatment, respectively (30 July-2 September) (Figure 1).

The heavy-panicle varieties fertilized significantly higher under high temperature treatment than under control treatment (Figure 2a). All the tested varieties showed the same trend in which they all had significantly higher spikelet fertilities under high temperature than under control treatment (Figure 2b). Regardless of the position of spikelets (upper, middle or lower part of the panicle), they also showed a better fertility rate under high temperature than under control treatment (Figure 2c). Among these three types of spikelets, the fertility rate of the lower part ones, which are usually referred to as inferior spikelets, was particularly improved by high temperature treatment (Figure 2c). Correlation analysis (Figure 3) showed that spikelet fertility rates were positively and significantly related with daily mean temperature and daily maximum temperature ($R^2 = 0.6604$ and 0.7017, $P < 0.01$), suggesting that high temperature increases spikelet fertility.

On average, 1000-grain weight significantly decreased by high temperature weather scenarios (Figure 4a). Nevertheless, different heavy-panicle varieties showed different patterns, or even trends completely opposite to each other under high temperature treatment and control treatment. Among them, 'C418', 'J1307' and 'Xianghui210' showed a decrease in 1000-grain weight under high temperature. In contrast, 'CW2221', 'K106' and 'R-2'

Figure 3. Correlation between spikelet fertility and daily mean temperature (a) or daily maximum temperature (b).



Values of spikelet fertilities in the figure were arcsine conversed. Linear regression analysis was adopted.
**Significant difference at the 1% probability level.

exhibited an opposite trend (Figure 4b). When the spikelets at different positions on a panicle were compared for 1000-grain weight after different temperature treatments, spikelets of all three positions evenly decreased for their 1000-grain weights in varieties whose 1000-grain weight decreased under high temperature. However, for those varieties whose 1000-grain weights increased under high temperature, the increase was mainly attributed to spikelets at the middle and lower positions (Figure 4c and 4d).

High temperature induced an evident decrease in head milled rice rate, with a 35.74% reduction in comparison with control treatment (Figure 5a). Specifically, among six varieties tested, five varieties showed a sharp decrease in head milled rice rate, but not 'J1307' (Figure 5b). With respect to spikelet positions, all of them were reduced in head milled rice rate under high temperature, particularly those at the upper position (Figure 5c).

Similarly, high temperature led to a marked increase in chalky grain rate, with a 2.41 times increase compared to control treatment (Figure 6a). Among the varieties tested, 'R-2', 'CW2221', 'K106' and 'Xianghui210' showed an increase ranging 1.12-10.26 times in chalky grain rate, whereas 'C418' and 'J1307' showed nonsignificant impact under high temperature (Figure 6b). Considering spikelet positions, all three positions responded to high temperature almost in the same way, all had a significant increase (Figure 6c).

High temperature induced a clear increase in chalkiness degree, with an average increase of 8.89 times compared to control treatment (Figure 7a). However, different varieties showed diversified chalkiness degrees in response to various temperature scenarios: 'Xianghui210', 'K106', 'R-2', 'J1307' and 'C418' increased greatly, while 'CW2221' showed almost no change (Figure 7b). In addition, spikelets at various positions on the panicle responded almost the same to high temperature (Figure 7c).

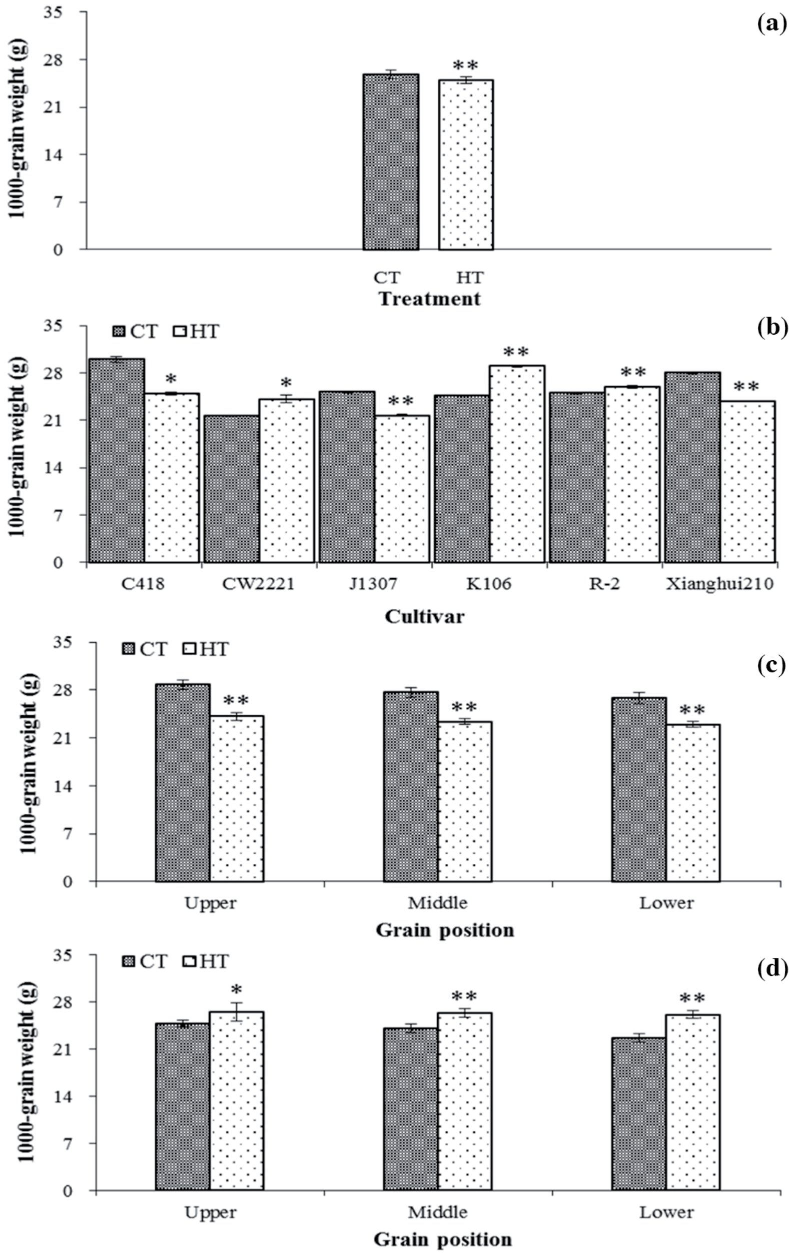
DISCUSSION

Given the greater capacity of assimilator storage and a more powerful drawing force for plant photosynthates, heavy or big panicles should be regarded as a trait favorable for further enhancement of yield potential in rice breeding. Meanwhile, heavy-panicle varieties require a longer period of flowering and grain-filling time, hence are more vulnerable to environmental fluctuations than conventional ones. Exploiting heavy-panicle rice varieties for genotypes or traits that retain high grain filling and good grain quality performances under stressful environments is a key step for super rice breeding in the future (Cheng et al., 2007).

In this research, high temperature accelerated spikelet fertilization to all tested heavy-panicle varieties (Figure 2b). This result was contradictory to some of previous studies with normal panicle rice varieties (Jagadish et al., 2007; Tian et al., 2010a). Meanwhile, Tian et al. (2010b) observed that the optimal grain filling temperature for super hybrid rice combinations was higher than for normal panicle rice in the field condition. These results may imply that heavy-panicle rice varieties adapt to hotter environment better than the normal panicle varieties in spikelet fertility. On the other hand, our result showed that the increase of spikelet fertility rate was higher for lower-position spikelets than for upper-position ones; thereby higher temperature shortened the differences among grain positions (Figure 2c). More research is needed to further investigate how higher temperature benefits fertilization of the inferior spikelets of heavy-panicle rice varieties.

Previous research with normal-panicle rice varieties indicates that grain weights decrease under high temperature treatment in general (Lin et al., 2010; Mohammed and Tarpley, 2010). In our study, however, different cultivars respond to elevated temperature in a diverse way (Figure 4b). Wassmann et al. (2009) reported that grain weight would not decrease if assimilates were sufficient for higher grain mass accumulation under high temperatures. Shimoda (2011) and Huang et al. (2016) found that grain weights did not decrease under high temperature due to a focused enhancement in translocation of pre-heading assimilates to the fertilized spikelets. Cao et al. (2015) reported an increase in grain weights under high temperature (38/28 °C) at anthesis, especially for the lower-position spikelets. The increase in grain weights in our research resulted from the increase in grain weights of each position, especially those of the middle and lower positions (Figure 4d). In short, the effects of high temperature on grain weight of heavy-panicle rice varieties are cultivar dependent and more beneficial to the grains at the middle and lower positions.

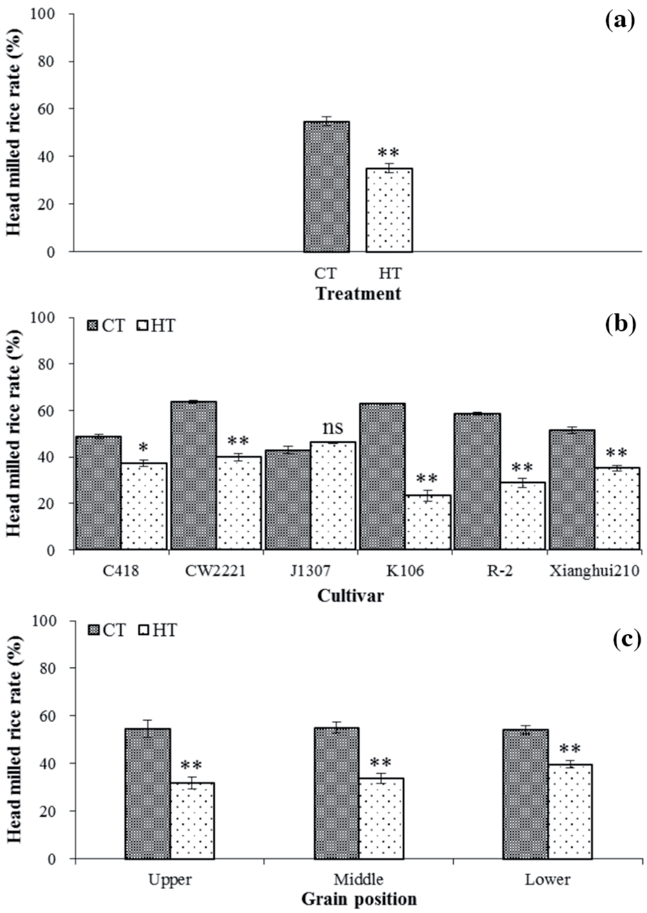
Figure 4. Effects of high temperature treatment (HT) during the grain-filling stage on 1000-grain weight of the whole panicle (a), six rice varieties (b) and different grain positions for 'C418', 'J1307' and 'Xianghui210' (c), and for 'CW2221', 'K106' and 'R-2' (d).



CT: Control treatment, ns: nonsignificant.
Each bar represents the mean ± standard error of three replicates.
*, ** Significant at the 0.05 and 0.01 probability levels, respectively.

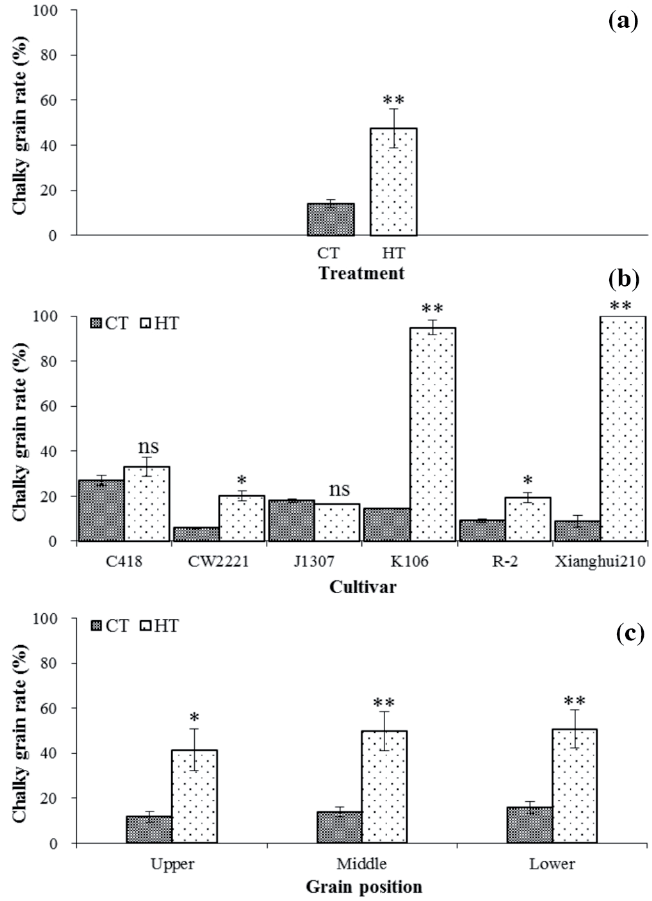
High temperature resulted in a fatal decrease of the appearance and milling quality in this experiment; especially, head milled rice rate decreased seriously, and chalky grain rate and chalkiness degree increased tremendously (Figures 5, 6 and 7). Such tendency is generally in agreement with previous studies (Lanning et al., 2011; Dong et al., 2014). On the one hand, it is worthy notice that some varieties performed well, retaining good grain quality under high temperature – a result also found in previous research with normal panicle rice varieties 'Cypree' and 'Bengal' (Cooper et al., 2008). This discovery may provide a valuable clue for breeders to improve resistance to high temperature. Spikelets at the upper rachis position, on the other hand, showed lower head milled rice rate than those at the middle and lower positions, differing from previous studies with normal panicle rice varieties (Cao et al., 2016). High temperature reduced head milled rice rate by 9.22% compared with normal temperature, but increased

Figure 5. Effects of high temperature treatment (HT) during the grain filling stage on head milled rice rate of the whole panicle (a), six rice varieties (b), and different grain positions (c).



CT: Control treatment, ns: nonsignificant.
Each bar represents the mean ± standard error of three replicates.
*, ** Significant at the 0.05 and 0.01 probability levels, respectively.

Figure 6. Effects of high temperature treatment (HT) during the grain-filling stage on chalky grain rate of the whole panicle (a), six rice varieties (b), and different grain positions (c).



CT: Control treatment, ns: nonsignificant.
Each bar represents the mean ± standard error of three replicates.
*, ** Significant at the 0.05 and 0.01 probability levels, respectively.

chalky grain rate and chalkiness degree by 69.6% and 4.10 times, respectively, for variety 'II You 128' (Dong et al., 2014). In summary, we observed that panicle type is directly correlated with rice quality, that grain qualities of heavy-panicle rice varieties are more seriously impacted by stressful high temperature than normal panicle rice varieties, and that some heavy-panicle rice varieties are more resistant to high-temperature stress, retaining good rice quality.

CONCLUSIONS

High temperature has a positive effect on spikelet fertility rate, particularly on the spikelets at the lower positions of the panicle, in heavy-panicle rice varieties. On the other hand, impacts by high temperature on grain weights of the heavy-panicle rice varieties are diversified. Generally, high temperature shows a detrimental effect in heavy-panicle rice varieties on main grain qualities, such as head milled rice rate, chalky grain rate and chalkiness degree; this impact is uniform on spikelets at different positions of the panicle. Similarly, some varieties, however, show resistance to the detrimental impact. These results indicate that exploitation of heavy-panicle rice germplasm resources in future rice breeding can not only enhance rice yield potential, but also improve their grain filling under high-temperature condition, offsetting the partial detrimental impact of global warming. Exploitation of genetic traits characterized with stable qualities under high temperature and positive increase in 1000-grain weight is a key task for future super rice breeding.

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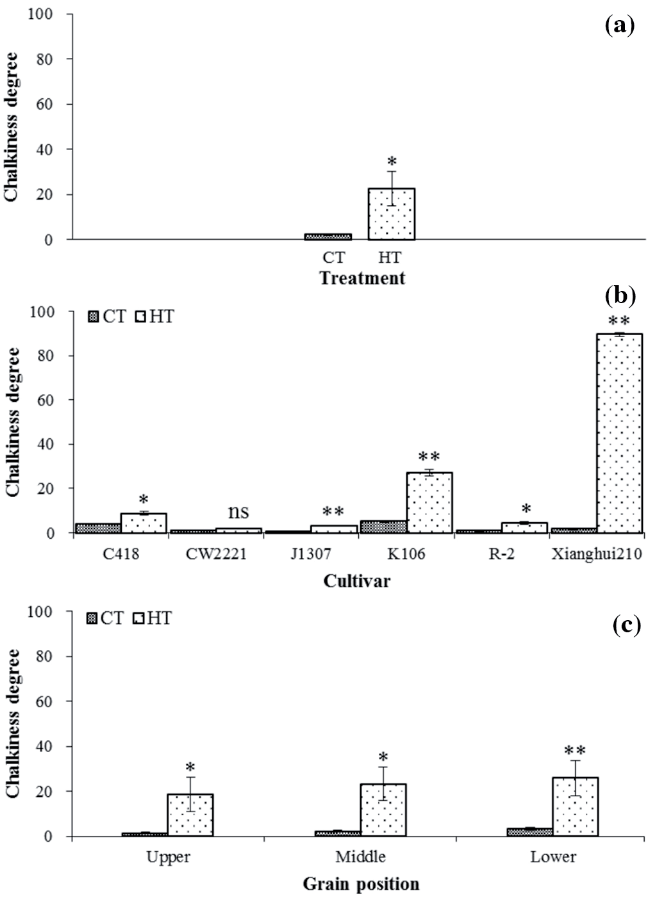
Figure 7. Effects of high temperature treatment (HT) during the grain filling stage on chalkiness degree of the whole panicle (a), six rice varieties (b), and different grain positions (c).



CT: Control treatment, ns: nonsignificant.
Each bar represents the mean ± standard error of three replicates.
*, ** Significant at the 0.05 and 0.01 probability levels, respectively.

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