



# Meta-analysis and dose-response analysis of high temperature effects on rice yield and quality



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## ABSTRACT

Global warming is one of the biggest challenges for improving the productivity of rice crops in the future. In this study, a meta-analysis and a dose-response analysis were conducted with data collected from 95 publications to study the differential responses of physiological traits, yield components, and grain quality to high day and night temperatures in rice. Overall, grain yield was reduced by 39.6% (with 95% CI from  $-42.9\%$  to  $-35.6\%$ ) under high temperatures, which was primarily caused by the decrease of seed set percentage. Yield reductions caused by high temperatures were associated with a decrease in photosynthesis and an increase in respiration. High temperatures affected grain quality by decreasing head rice percentage and increasing chalky rice rate and chalkiness. The reduction of grain yields under high day temperature was primarily caused by the reduction in seed set percentage. However, under high night temperature, the combination of decreased spikelet number per panicle, grain weight, and biomass production in addition to decreased seed set percentage contributed to the decline of grain yields. These results suggest that the differential effects of day and night warming on the processes that contribute to formation of rice yield should be considered when new rice cultivars are developed as a crop adaptation strategy for future global warming.

## 1. Introduction

Climate change represents a continual challenge for agricultural production and food security (IPCC in Core Writing Team, 2014). Global warming is an important aspect of climatic change that is largely driven by increasing atmospheric concentrations of greenhouse gases, stratospheric ozone depletion, aerosol emissions and land-use changes (Schneider, 2001; Shakun et al., 2012). The frequency and intensity of extreme weather events such as regional drought and heat waves are predicted to increase with global warming (Dale et al., 2001). Most climate models predict that the global temperature will increase from 0.3 to 6.4 °C at the end of this century depending on the mitigation of atmospheric greenhouse gas emissions (IPCC in Core Writing Team, 2014; Meehl et al., 2007). Such an increase in air temperature will profoundly affect crop production (Lobell and Asner, 2003), and many studies show a significant influence of elevated temperatures on crop yield. According to Lobell and Asner (2003), both corn and soybean yields will decrease approximately 17% for each degree increase in air temperature in the USA. Coincidentally, Peng et al. (2004) found that a 1.13 °C increase in night temperature over a period of 25 years (1979–2003) markedly decreased rice grain yield in the Philippines.

Rice (*Oryza sativa* L.) is produced under a wide range of climatic conditions and is a staple food crop for more than 50% of the world's population (Maclean et al., 2002). Hence, the response of rice to high temperatures must be determined to develop adaptation strategies to achieve sustainable crop production to meet the demands of a growing population (Howden et al., 2007). Previous studies show that the growth response of rice to high temperatures varies with genotypes (Jagadish et al., 2010a, 2007; Maruyama et al., 2013; Ziska and Odonez, 1996). Moreover, the reproductive stage is likely more sensitive to high temperature stress than the vegetative stage in rice (Sánchez et al., 2014; Welch et al., 2010). When temperatures exceed critical thresholds, anther dehiscence, pollen germination on the stigma, and/or pollen tube growth are affected, and consequently, spikelet sterility increases dramatically (lower seed set percentage), which results in a serious loss of grain yield (Jagadish et al., 2010a,b, 2007, 2011; Prasad et al., 2006; Satake and Yoshida, 1978).

Asymmetric warming, with a greater increase in night than in day temperatures, has been observed (Donat and Alexander, 2012) and some attention focused on subsequent consequences for ecology and agriculture (Peng et al., 2013). Both high day and night temperatures affect growth, development, and yield formation of crop species

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(Krishnan et al., 2011). Studies report that high day and night temperatures negatively affect rice biomass production and grain yield (Cooper et al., 2008; Krishnan et al., 2011; Mohammed and Tarpley, 2009; Rang et al., 2011). High day temperature severely affect rice reproductive processes (Ito et al., 2009; Jagadish et al., 2007, 2010b; Madan et al., 2012; Rang et al., 2011), particularly spikelet fertility, whereas high night temperatures lead to an increase in dark respiration and consequent reductions in biomass production and grain yield (Coast et al., 2015; Peng et al., 2004; Shi et al., 2013, 2016). However, other studies show that increased spikelet sterility is the primary reason for yield loss under high night temperature (Mohammed and Tarpley, 2009, 2011). Hence, the general patterns of temperature response and the differential effects of high day and night temperatures on rice yields and yield attributes must be determined.

Grain quality is an important criterion for acceptance of any variety by farmers and consumers. Rice is consumed primarily as an intact kernel, and a high proportion of broken rice leads to a reduction in market price from 40% to 50% (Cooper et al., 2008; Sreenivasulu et al., 2015). Chalkiness results from the abnormal formation of starch granules, which ultimately affects starch accumulation during the early grain filling stage, and these processes are sensitive to high temperature (Fitzgerald and Resurreccion, 2009; Madan et al., 2012; Sreenivasulu et al., 2015). Increased chalky rice rate and decreased head rice percentage are common outcomes of high temperature stress during the ripening phase of rice crops (Krishnan et al., 2011). Additionally, high temperature during the grain filling period cause a significant reduction in grain size and amylose content (Yamakawa and Hakata, 2010; Yamakawa et al., 2007).

Many studies have investigated the potential effects of high temperatures on physiological traits, yield components and grain quality in rice. These studies provide a large database for evaluating the general response of rice crops to high temperatures using a meta-analysis. This approach has been used to study the overall response of rice to elevated CO<sub>2</sub> and O<sub>3</sub> (Ainsworth, 2008) and has also been successfully used to summarize crop responses to elevated CO<sub>2</sub> in free-air CO<sub>2</sub> enrichment (FACE) experiments (Ainsworth et al., 2002). However, the general response of rice to high temperatures has not been quantitatively assessed to date using a meta-analysis, which might be due to the different studies using different high temperature treatment methods in terms of the intensity, timing, and duration. Therefore, in this study, we used both meta-analysis and dose-response analysis to summarize the effects of high day and night temperatures on rice physiological processes, grain yields, yield components, and grain quality. More specifically, the goal was to answer the following questions: (i) What are the responses of rice physiological processes, grain yields, yield components and grain quality to elevated temperatures? (ii) Do elevated day and night temperatures have different effects on grain yield and yield attributes in rice crops?

## 2. Materials and methods

### 2.1. Data collection

The PRISMA flow diagram (Fig. S1) shows the procedure used for the selection of research papers for this study. Research papers were searched from the Web of Science, Scopus, and the China Knowledge Resource Integrated Database using four search terms: 'Rice AND elevated temperature', 'Rice AND high temperature', 'Rice AND increased temperature', and 'Rice AND warming' in December 2015. An initial search resulted in 29,428 articles (total results from the three databases), which were reduced to 4264 by limiting research to agriculture, plant science, ecology, and environmental science. After duplicate studies were removed by comparing the article titles, author lists, publication years, and journal names, the article number was reduced to 1307 records. Then, the abstracts were examined to judge their relevance, and 262 articles were considered relevant. The full text of the

262 articles was checked to determine the suitability for meta-analysis based on the following criteria: (i) at least two temperature (control and high) treatments; (ii) for grain yield (GY) and yield components (panicle number, PN; spikelet number per panicle, SN; seed set percentage, SPP; grain weight, GW; and biomass, BM), only the studies that contained information on treatment means, sample size, and data variability [standard deviation (SD) or standard error of the mean (SE)] were included; (iii) for grain quality traits, the studies without information on data variability were also included, because few studies were available on the temperature responses of rice grain quality traits in the literature; (iv) wild-type phenotypes were selected and mutants were excluded; and (v) other treatments (i.e., CO<sub>2</sub> and drought) were excluded. The studies selected for dose-response analysis met the following criteria: (i) for physiological traits (light-saturated photosynthesis and respiration), the growth temperature and measurement temperature were reported, with at least two measurement temperatures; (ii) for grain yield (GY) and yield components, at least two temperature treatments; and (iii) mutants and other treatments were excluded. As a result, 95 peer-reviewed articles were included for both meta- and dose-response analyses (Appendix S1).

Grain quality parameters referred to gel consistency, protein content, amylose content, chalkiness, chalky rice rate, grain length, grain width, brown rice percentage, milled rice percentage, and head rice percentage. Chalky rice rate is defined as a ratio of grains with opaque parts in the endosperm to total number of grains, whereas chalkiness is defined as the percentage of chalky area to projected grain area (Lisle et al., 2000).

The data were extracted directly from the tables and text in the original papers or indirectly from figures using WinDIG 2.5 (<http://www.unige.ch/sciences/chifi/cpb/windig.html>). When the variances were reported as SEs, they were then converted into total variances using the number of replicates of each volatile collection, summed, and finally converted to SDs for grouped volatiles. Other information, when available, such as experimental duration, cultivar name, types of high temperature treatments (day, night or whole day), growing conditions (pot or field), and ecotypes of the genotypes, was also extracted for further analysis.

### 2.2. Meta-analysis

A meta-analysis was performed using R 3.2.2 (<https://cran.r-project.org>). The meta-analysis consisted of two primary steps: (1) calculate individual effect sizes and their associated variances for each study to place the data from the primary studies on a common scale, and (2) assess the accumulative effects size. In the current study, the individual effect sizes of rice traits were calculated using a natural log-transformed response ratio ( $\ln R = \ln \frac{X_e}{X_c}$ ), where  $X_e$  and  $X_c$  are the mean values of all comparisons in the control and high temperature treatments, respectively. The random-effects model analysis, which was based on the assumption of random variation in responses among studies, and a weighted parametric analysis were used for grain yields and components. In the weighted analysis, the variance of  $\ln R$  ( $v$ ) was approximated using the following formula:  $v = \frac{(SD_c)^2}{N_c X_c} + \frac{(SD_e)^2}{N_e X_e}$

where  $SD_c$  and  $SD_e$  are the standard deviations for all comparisons in the control and high temperature treatments, respectively;  $N_c$  and  $N_e$  are the sample sizes for the control and high temperature treatments, respectively. For each study, the weighting factor  $w$  was calculated as the inverse of the pooled variance ( $1/v$ ). The final weight ( $w^*$ ) used in the analyses was:  $w^* = w/N$ , where  $N$  is the number of observations from the same study. To quantify the accumulative effect, the weighted mean response ratio  $\left( \ln RR = \frac{\sum_{i=1}^k w_i^* R_i}{\sum_{i=1}^k w_i^*} \right)$  and its 95% CI were calculated by the reciprocal of the mixed-model variance (Curtis and Wang, 1998; van Groenigen et al., 2011). An unweighted analysis was conducted for grain quality parameters for which a lack of information

on data variance allowed only a re-sampling calculation (McGrath and Lobell, 2013; Morgan et al., 2003). Response effects were estimated as a percentage change relative to the control (%), using the equation  $A = (e^{\ln RR} - 1 \times 100\%)$ . When the 95% CI did not overlap with zero, the temperature effects were considered statistically significant.

Beyond testing whether the accumulative effect sizes for each group are significantly different from zero, whether the groups differed from one another is also of interest (Heterogeneity). In the current study, a homogeneity test was applied in which total heterogeneity ( $Q_T$ ) was partitioned into within-group ( $Q_w$ ) and between-group ( $Q_b$ ) heterogeneities. These partitions were calculated as:

$$Q_b = \sum_{j=1}^m \sum_{i=1}^{k_j} w_{ij} (\ln RR_j - \ln RR_i)^2$$

$$Q_w = \sum_{j=1}^m \sum_{i=1}^{k_j} w_{ij} (\ln R_{ij} - \ln RR_j)^2$$

where  $m$  is the number of groups,  $k_j$  is the number of studies in the  $j^{\text{th}}$  group,  $w_{ij}$  is the weight for the  $i^{\text{th}}$  study in the  $j^{\text{th}}$  group,  $\ln RR_j$  is the cumulative effect size for the  $j^{\text{th}}$  group and  $\ln R_{ij}$  is the effect size for the  $ij$  study in the  $j^{\text{th}}$  group. According to Gurevitch and Hedges (1999),  $Q_b$  rather than  $Q_w$  may be of considerable scientific interest. A comparison against the critical value of the  $\chi^2$  distribution tested the significance of  $Q_b$ . A significant  $Q_b$  implies that there are differences among cumulative effect sizes between groups (Fonturbel et al., 2015; Koricheva and Gurevitch, 2014). Differences were considered statistically significant when  $P < 0.05$ .

### 2.3. Publication bias

Publication bias is a common problem for meta-analyses because nonsignificant results are often not published, and this problem is usually investigated by estimating data correlations. In this study, four methods were used to evaluate the potential publication bias. (1) Using the funnel plot approach, effect sizes were plotted against sample size (number of observations). A plot that shows no publication bias should have a triangular or funnel shape that is symmetric around the mean effect size. (2) Kendall's tau correlation with continuity correction was used to determine whether the magnitude of effects and sample size were correlated. (3) Because studies reporting null effects are unlikely to be published and hence not included in literature surveys (potentially overestimating positive or negative effects), we estimated the Rosenthal's fail-safe number that indicates the number of unpublished case studies with null effects required to reverse the observed effects (Rosenthal, 1979). This calculation indicates a robust result when the fail-safe number is equal to or greater than  $5N + 10$ , where  $N$  is the number of case studies. (4) Additionally, because most cases had more than one treatment temperature adopted in the same study, we ran an analysis using the article ID as a moderator variable to determine a potential bias toward negative or positive effects. Then, we calculated the Spearman rank correlation coefficient and its bias-corrected and accelerated confidence intervals to determine whether the number of cases and the magnitude of the effect were correlated. We expected an unbiased sample to be heterogeneous and the number of cases per article to not be correlated with the effect magnitude.

### 2.4. Dose-response curves

As described above, meta-analyses generally only distinguish between 'high' and 'low' levels of temperature for a given trait and fail to scale for the level of the temperatures across experiments. To investigate the responses of rice traits to the scale of temperature changes, dose-response curves were used in this study. Dose-response curves capture the relationship between a biological trait and an environmental factor in a continuous manner, thereby providing an excellent

way to quantify the strength, sign and form of the effect of a given factor on the trait of interest over the full relevant range of that factor (Poorter et al., 2012). Recently, methodology has become available to derive dose-response curves from a range of different experiments (Poorter et al., 2010, 2012). We used this approach here to establish general dose-response curves of rice physiological traits, yields and yield components to high temperatures; however, these curves were not applied to grain quality traits because of the limited data points for those traits in our database.

Photosynthesis and respiration in plant ecophysiology are regularly investigated by instantaneous measurements. Hence, the responses of photosynthesis and respiration to temperature may be affected by both growth and measurement (the leaf temperatures during the measuring) temperatures. Because most studies included in our database determined the response of photosynthesis/respiration to measurement temperatures, the dose-response curves were based on the measurement temperature. When more than 10 data points were available for a given growth temperature, the dose-response curves for the measurement temperature at the growth temperature were also performed. In this study, we also performed dose-response curves for the grain yields and yield components for day or night temperatures but not for whole day temperatures. The whole day temperature treatment in our database was usually set as different day-night temperature combinations and identifying the temperature values for dose-response curves was difficult.

To develop the dose-response curves, a two-step procedure was used according to (Poorter et al., 2010). In step one, to extract relative (normalized) values for each trait, we chose the values at reference temperatures (photosynthesis and respiration response to measurement temperature at 30 and 25 °C, respectively; yield and its components response to day and night temperature at 30 and 24 °C, respectively). We selected those values because most experiments covered a range of temperatures that included those values; however, in some cases, the value of those traits was not found exactly at the value of the reference temperature. In those cases, we linearly interpolated a reference value from the two adjacent temperature levels (Poorter et al., 2010). In step two, the scaled values were calculated by dividing the value at reference temperature ( $V_{i\text{scaled}} = V_i/V_{\text{ref}}$ ;  $V_i$  and  $V_{\text{ref}}$  represent the values at temperature  $i$  and at the reference temperature, respectively).

Before determining dose-response curves, descriptive statistics and the distributions of variables were analyzed, and the error distributions of scaled responses did not follow a normal distribution (Fig. S11). There are two general strategies to fit the response curves: parametric and non-parametric fitting. Parametric fitting is an effective way to summarize a relationship when the structure in the data conforms to the type of function that is fitted by the smoothing algorithm. However, the functional forms of rice yield and its components scaled responses to temperature were unclear. Therefore, a later generalization of *locally* weighted regression (*loess*) was used for dose-response curves fitting in R 3.2.2 (<https://cran.r-project.org>). The theory and step-by-step protocol for *loess* fitting can be found in Cleveland et al. (1988) and Jacoby (2000), respectively.

## 3. Results

In our database for meta-analysis, the mean of control and high temperatures was 28.5 and 34.7 °C, 22.9 and 28.0 °C, and 27.2 and 32.5 °C for day, night, and whole day temperatures, respectively (Table 1). The difference between high and control temperatures ranged from 1 to 15 °C, 2 to 12 °C, and 1 to 12 °C for day, night, and whole day temperature treatments, respectively. The temperature range was greater for dose-response analysis than for meta-analysis because some studies in the 95 articles included other temperature treatments in addition to control and high temperatures.

**Table 1**

The temperature range and means of three high temperature types included in meta-analysis.

HT type	No.	CK range (°C)	CK mean (°C)	HT range (°C)	HT mean (°C)	$\Delta T$ range (°C)	$\Delta T$ mean (°C)
Day	407	21–39	28.5	24–44	34.7	1–15	6.1
Night	882	18–28	22.9	24–35	28.0	2–12	5.1
Whole	246	19–35	27.2	28–41	32.5	1–12	5.3
All	1535	18–39	25.1	24–44	30.5	1–15	5.4

Day, high day temperature; Night, high night temperature; Whole, high day and high night temperature; CK, control check; HT, high temperature;  $\Delta T$ , the difference between HT and CK; CK range, the temperature range of all control checks included in meta-analysis; CK mean, the mean temperature of all control checks included in meta-analysis; and No., the number of data points included in meta-analysis. The whole day temperature was calculated as the average of day and night temperatures for each study.

### 3.1. Effects of high temperatures on rice physiological traits

Generally, light-saturated leaf photosynthetic rate increased with temperature before the optimal temperatures and decreased with temperature after optimal temperatures (Fig. 1A). Overall, the optimum temperature for rice photosynthesis was approximately 30 °C. However, the optimum temperature for photosynthesis varied with growth temperature (Fig. 1C). Plants grown at low temperatures showed greater photosynthetic capacity at lower temperatures, whereas plants grown at high temperatures showed greater capacity for photosynthesis at higher temperatures. We also found that leaf respiration rate increased

**Table 2**

Between-group heterogeneity ( $Q_b$ ) for high temperature effect size across different categorical variables.

Variable	No.	HT type	Growth condition	Ecotype	Genotype	Treat stage
Yield	232	35.19***	109.5***	8.49 <sup>†</sup>	331.0***	19.93***
PN	161	0.91	3.87 <sup>†</sup>	1.27	47.21	0.67
SN	161	9.70**	0.06	18.80***	75.58***	3.95
SSP	211	35.88***	74.62***	1.30	300.4***	43.37***
GW	124	3.31	7.86**	2.58	20.17	0.01
BM	112	12.98**	0.41	4.79	18.12	7.87 <sup>†</sup>

HT, high temperature; GY, grain yield; PN, panicle number; SN, spikelet number per panicle; SSP, seed set percentage; GW, grain weight; BM, biomass; and No., data point included. HT type included day, night, and whole day high temperature treatments; Growth condition included field and pot conditions; Ecotype included *indica* and *japonica*; and Treatment stage included high temperature treatments before heading, after heading, and entire growth season.

<sup>†</sup>  $P < 0.05$ .

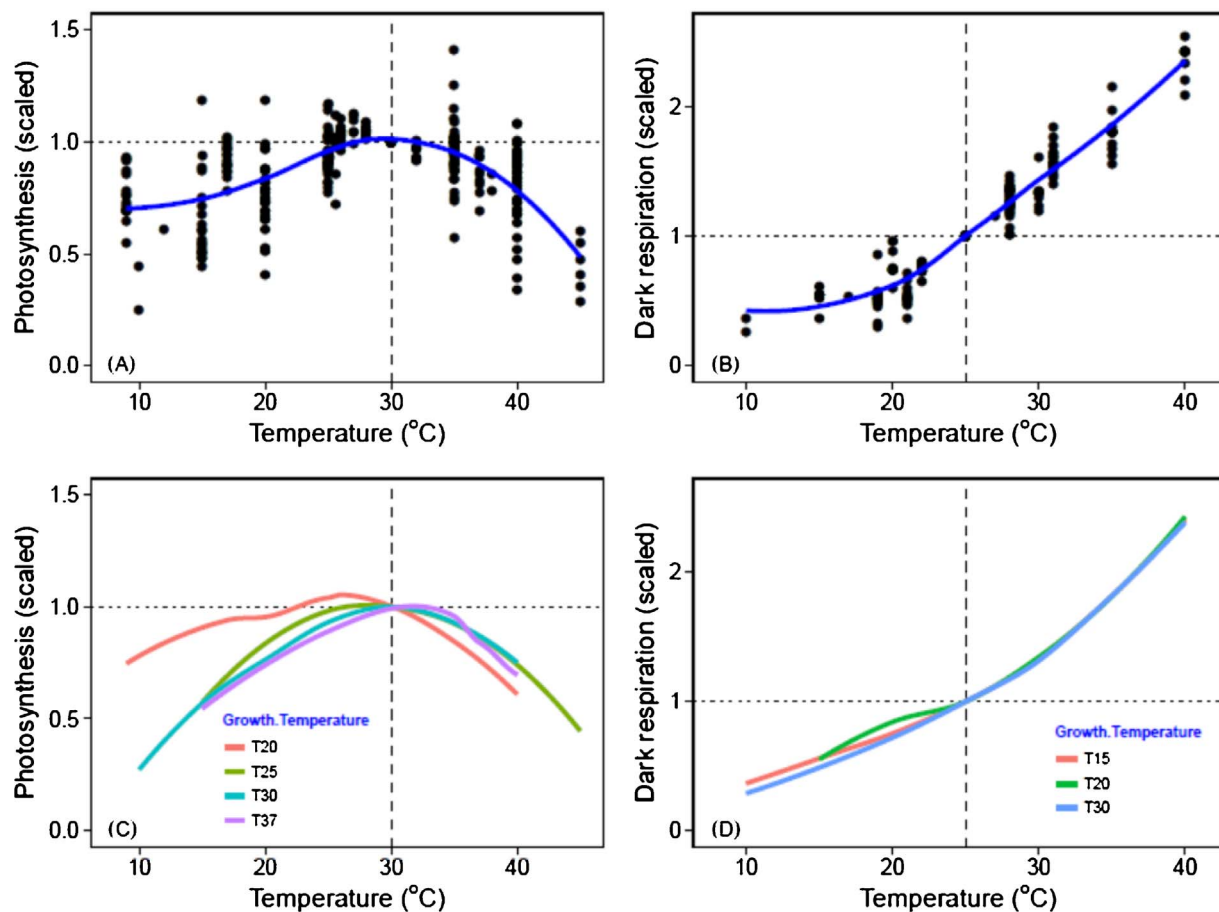
\*\*  $P < 0.01$ .

\*\*\*  $P < 0.001$ .

significantly with high temperatures (Fig. 1B and D). The respiration increased with temperature exponentially. Unlike photosynthesis, the response of respiration to temperature was independent from growth temperature (Fig. 1D).

### 3.2. Effects of high temperatures on rice yield attributes

Overall, high temperatures significantly reduced rice grain yield (–39.6%, with a 95% CI of –42.9% to –35.6%) and seed set percentage



**Fig. 1.** Effects of high temperature on rice physiological traits. General response of light-saturated photosynthesis (A) and dark respiration (B) to measuring temperature, and the growth temperature depended response of light-saturated photosynthesis (C) and dark respiration (D) to measuring temperature. To demonstrate the responses of physiological traits to temperature under different growth temperature more clearly, the data points in (C) and (D) were not shown. The reference value for temperature is indicated by dotted line (30 °C for photosynthesis and 25 °C for respiration).



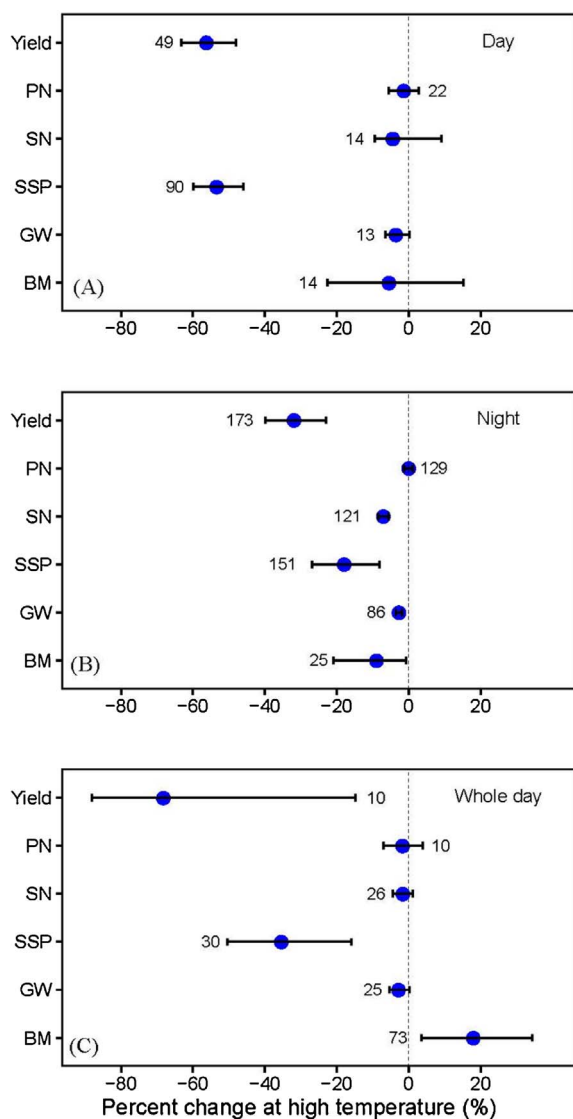


Fig. 2. Effects of high temperature on rice yield attributes varied with type of high temperature treatment. Percent change in grain yield (GY), panicle number (PN), spikelet number per panicle (SN), seed set percentage (SSP), grain weight (GW), and biomass (BM) under high day (A), night (B) and whole day (C) temperature. Error bars represent 95% confidence intervals. The values near the error bars indicate the number of data points for meta-analysis.

(−33.3%, with a 95% CI of −36.9% to −29.5%) (Fig. S2). However, the effect of high temperatures on panicle number (−0.69%, with a 95% CI of −7.54% to 6.67%), spikelet number per panicle (−6.83%, with a 95% CI of −13.30% to 0.09%), grain weight (−4.92%, with a 95% CI of −12.36% to 3.15%) and biomass (8.07%, with a 95% CI of −0.91% to 17.86%) was not significant.

Significant differences in temperature responses were observed among the three types of high temperature treatments for grain yield ( $Q_b = 35.19$ ,  $P < 0.001$ ), spikelet number per panicle ( $Q_b = 9.70$ ,  $P < 0.05$ ), seed set percentage ( $Q_b = 35.88$ ,  $P < 0.001$ ), and biomass ( $Q_b = 12.98$ ,  $P < 0.01$ ) (Table 2). However, temperature responses in panicle number ( $Q_b = 0.91$ ,  $P = 0.738$ ) and grain weight ( $Q_b = 3.31$ ,  $P = 0.184$ ) were not significantly different among the types of high temperature treatments. Drastic reductions in grain yield and seed set percentage occurred in the high day (−56.3% and −53.4%, respectively), night (−31.9% and −18.0%, respectively), and whole day (−68.3% and −35.4%, respectively) temperature treatments (Fig. 2). Biomass decreased under high night temperature, whereas an opposite response was observed under high whole day temperature and no

response under high day temperature. Spikelet number per panicle and grain weight decreased only under high night temperature but not under high day and whole day temperatures. Moreover, panicle number did not respond to any of the high temperature treatments. To better understand the response pattern of grain yield and its components to high temperature, we analyzed their dose-response curves to day temperature (Fig. 3) and night temperature (Fig. 4). Our result shows that the optimum day temperature for rice grain yield was approximately 28 °C. When the temperatures were lower than the optimal day temperature, grain yield was increased with day temperature by increasing biomass and spikelet number per panicle, while the panicle number decreased with day temperature. When the temperatures were higher than optimal day temperature, the decrease in grain yield was caused by the reduction of seed set percentage and biomass (Fig. 3). However, grain yield decreased with night temperature ranging from 22 to 35 °C, and almost all yield components contributed to the yield loss under high night temperature (Fig. 4).

As observed the type of high temperature treatment, the growth condition, ecotype, genotype and stage of temperature treatment significantly influenced the response of grain yield to high temperatures (Table 2). The response of panicle number, seed set percentage and grain weight to high temperatures varied with growth condition (Fig. S3). In addition to grain yield, the response of spikelet number per panicle to high temperatures also varied with ecotype (Fig. S4). To determine the effects of temperature treatment on the stage in the response of grain yield and its components to high temperatures, we divided our data into three groups of treatment stages: before heading, after heading, and entire season (Fig. S5). Grain yield and grain weight were significantly reduced for the entire season and before and after heading in high temperature treatments. Additionally, the response of grain yields to high temperatures varied significantly among genotypes (Tables 2 and S1).

### 3.3. Effects of high temperatures on rice grain quality

High temperatures significantly affected head rice percentage (−22.5%, with a 95% CI of −34.8% to −8.0%), chalky rice rate (118%, with a 95% CI of 49% to 218%) and chalkiness (179%, with a 95% CI of 151% to 210%) (Fig. 5). However, high temperatures did not significantly affect other grain quality traits, including gel consistency, protein content, amylose content, grain length, grain width, brown rice percentage, and milled rice percentage (Fig. 5). Then, we examined the effects of each type of high temperature treatments on grain quality traits. Chalkiness increased by 222% (with a 95% CI of 174% to 278%) under high day temperature, by 61% (with a 95% CI of 46% to 79%) under high night temperature, and by 331% (with a 95% CI of 201% to 518%) under high whole day temperature (Fig. S6). Head rice percentage decreased significantly under high night and whole day temperatures, but not under high day temperature. The responses of chalkiness to high temperatures were affected by growth condition ( $Q_b = 7.26$ ,  $P < 0.01$ ). The responses of milled rice ( $Q_b = 18.51$ ,  $P < 0.001$ ) and brown rice ( $Q_b = 15.83$ ,  $P < 0.001$ ) to high temperatures were affected by ecotype (Table S2). Likewise, the responses of some grain quality traits to high temperatures were also affected by genotypes.

### 3.4. Publication bias

Funnel plots revealed a relative asymmetry in effect size for the sample size (Figs. S7 and S8). We found no correlation between effect size and sample size for the total data (Kendall's tau = 0.0019,  $P = 0.92$ ), which was consistent with the Spearman-rank correlation ( $\rho = 0.002$ ,  $P = 0.92$ ). Moreover, the fail-safe number (5,522,049) was much higher than the threshold value ( $5 \times 1536 + 10 = 7690$ ), indicating that these results were relatively robust. Studies from the last 10 years dominated this analysis, and therefore changes in the

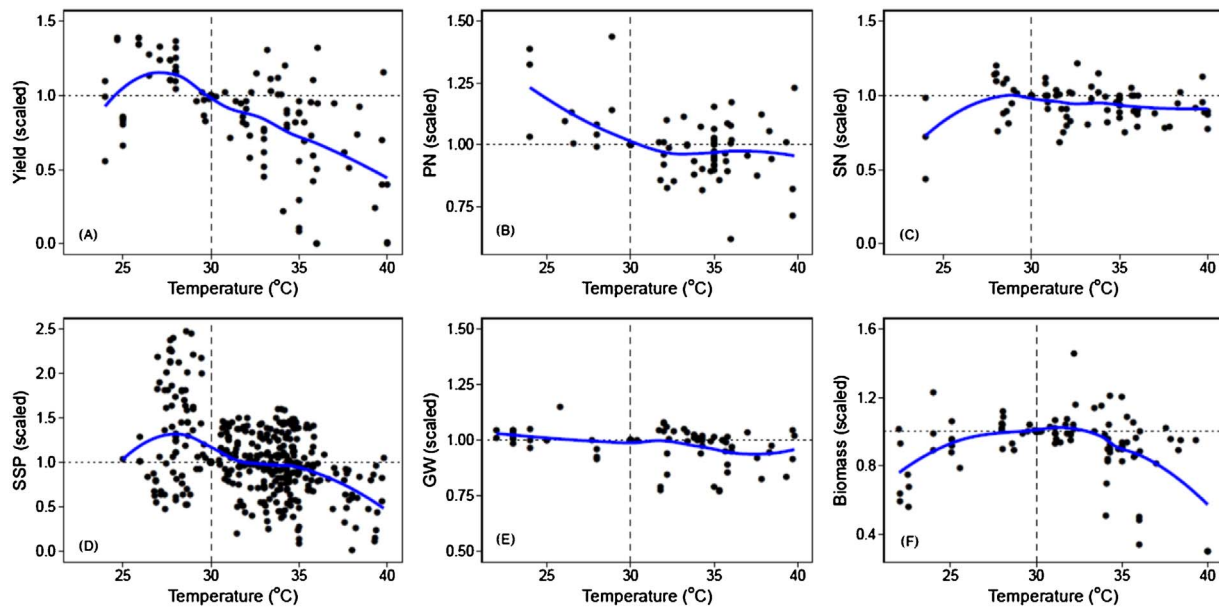


Fig. 3. Dose-response analysis of high day temperature effects on rice yield attributes. General response of (A) grain yield (GY), (B) panicle number (PN), (C) spikelet number per panicle (SN), (D) seed set percentage (SSP), (E) grain weight (GW), and (F) biomass (BM) to high day temperature. The reference value for temperature is indicated by dotted line (30 °C).

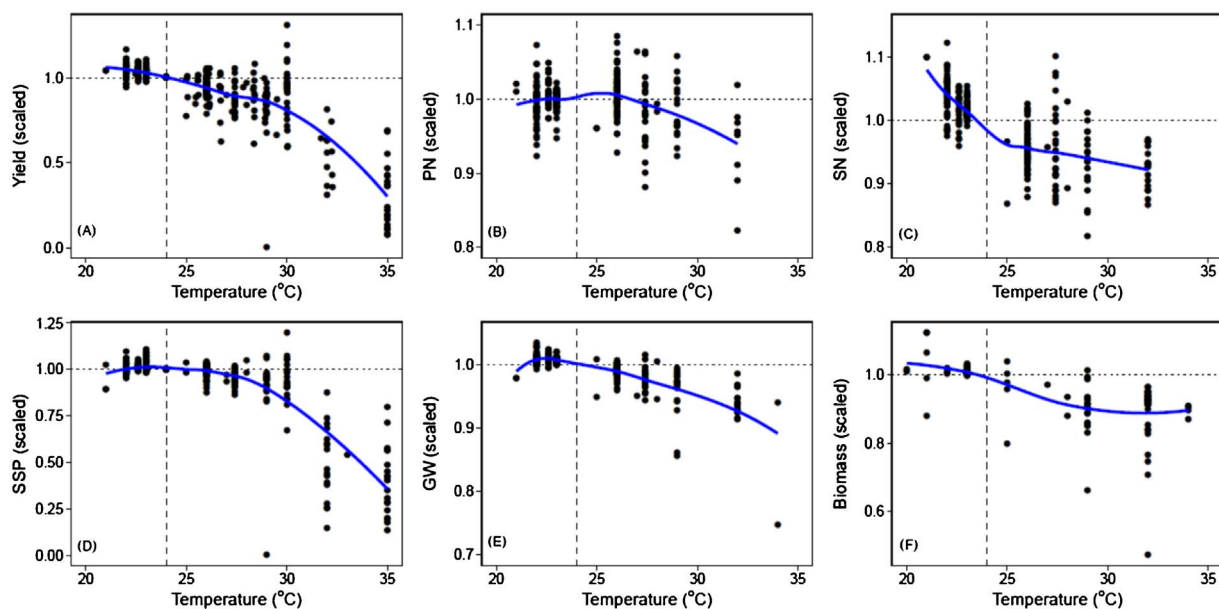


Fig. 4. Dose-response analysis of high night temperature effects on rice yield attributes. General response of (A) grain yield (GY), (B) panicle number (PN), (C) spikelet number per panicle (SN), (D) seed set percentage (SSP), (E) grain weight (GW), and (F) biomass (BM) to high night temperature. The reference value for temperature is indicated by dotted line (24 °C).

sensitivity of equipment were unlikely to have a strong effect on this study (Fig. S9).

## 4. Discussion

### 4.1. Photosynthesis and respiration are responsible for decreased biomass and grain yields under high temperatures

Similar to most  $C_3$  plants, rice leaf light-saturated photosynthesis increases from a base temperature to a lower optimum and then declines with increasing temperature from an upper optimum. Overall, the optimum temperature for photosynthesis was approximately 30 °C in rice. However, the optimum temperature could be shifted by the growth temperature: plants grown under relatively low temperatures showed greater photosynthetic capacity under lower temperatures, which resulted in a lower optimum temperature, whereas plants grown

under relatively high temperatures showed greater capacity for photosynthesis under higher temperatures, which resulted in a higher optimum temperature. An increase in the capacity of photosynthetic enzymes such as Rubisco is likely for photosynthetic acclimation to low temperatures, whereas photosynthetic acclimation to high temperatures may involve an increase in the heat stability of the photosynthetic apparatus (Sage and Kubien, 2007; Yamori et al., 2014, 2010). Here, we found that the dose-response curve of photosynthesis to temperature was inconsistent with the dose-response curve of biomass to day temperatures; thus, the decrease in biomass under high day temperatures might be primarily caused by the decline in photosynthesis. Moreover, biomass could decline because of an increase in photorespiration under high temperatures; however, photorespiration data are limited due to the technical limitations in its measurement. Dark respiration is considered the primary factor that affects rice biomass and yield under high night temperatures (Peng et al., 2004). Based on our results, dark

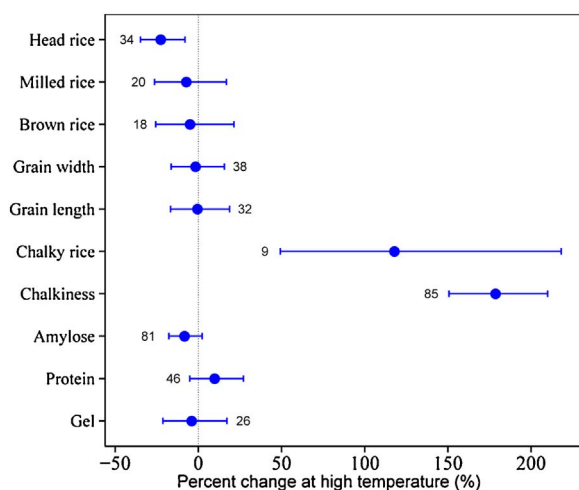


Fig. 5. Effects of high temperature on rice grain qualities. Error bars represent 95% confidence intervals. The values near the error bars indicate the number of data points for meta-analysis.

respiration increased drastically with increased temperatures (Fig. 1), which explained the decrease of biomass under high night temperatures. Meta-analysis indicated that biomass increased significantly under high whole day temperatures (Fig. 2C), because the high temperatures increased biomass production by several-fold when control temperatures were lower than 21 °C (Fig. S10). Additionally, dose-response analysis suggested that the increased temperatures might contribute positively to biomass when control day temperatures were lower than 30 °C (Fig. 3F).

#### 4.2. Effects of high temperatures on yield and its components

Rice yield is composed of panicle number, spikelet number per panicle, seed set percentage, and grain weight. In the current study, we found that grain yields were reduced significantly (−39.6%) under high temperatures (Fig. S2), with the reduction primarily caused by a decrease in seed set percentage (−33.3%). Additionally, spikelet number per panicle and grain weight decreased slightly but not significantly under high temperatures. These results suggested that reproductive processes and organs are more sensitive to high temperatures than vegetative growth. In fact, a significant effect of high temperatures after the heading stage was detected on seed set percentage, but not for the high temperatures before the heading stage (Fig. S5). The decrease in seed set percentage induced by high temperatures was most likely the result of the effects of temperature stress on meiosis and growth of the ovaries during the pre-anthesis period, in addition to temperature effects on anther dehiscence and production, transfer, viability, and germination of pollen during anthesis (Ito et al., 2009; Jagadish et al., 2007, 2010b; Madan et al., 2012; Rang et al., 2011).

Our analysis also showed that the response of grain yield and seed set percentage to high temperatures differed significantly with genotype and growth conditions (Table 2). The genotype-dependent response of seed set percentage to high temperatures is observed in many studies (Jagadish et al., 2010a, 2007; Maruyama et al., 2013 Ziska and Ordenez, 1996). The differences in high temperature tolerance among genotypes might be caused by several mechanisms. First, genotypic differences occur in pollination ability, characterized by traits such as pollen number, anther size and shape, and anther dehiscence (Jagadish et al., 2007; Madan et al., 2012). For example, Maruyama et al. (2013) found that genotypes with large anthers and more abundant pollen had better pollination abilities under high temperatures. Second, the thermal condition of the spikelet caused by transpiration ability could be different across genotypes (Xiong et al., 2015). Finally, the timing of flowering can be different among genotypes. For example, genotypes

with an early-morning flowering trait had less sterility due to the cooler morning air than at midday (Ishimaru et al., 2010). In the present study, we found that the reduction of yield in pots was more serious than that in the field (Fig. S3). Methodologically, creating a large temperature gradient under field conditions is more difficult than for pots in the laboratory and greenhouse. Moreover, extreme high temperatures were reached in few field studies. Additionally, other environmental factors are also difficult to control in the field, such as air humidity, and the interactions between high temperatures and other environmental factors under field conditions may contribute to this difference. Recent studies suggest that more open-field studies are required to confirm the temperature responses (Julia and Dingkuhn, 2012; Matsui et al., 2014).

Overall, grain yields decreased under both high day and night temperatures. This result is in contrast to those reported by Welch et al. (2010) who showed that farm field rice yield decreased with high daily minimum temperature but increased with high daily maximum temperature. The daily maximum temperatures of different sites and years in their study were very close to 30 °C; however, the maximum day temperatures in the current study is higher than 40 °C (Table 1; Fig. 3). In fact, our results also showed that a day temperature of approximately 28 °C had a positive effect on rice yield (Fig. 3A).

In this study, we observed the differential effects of high day and night temperatures on rice yield formation. The reduction of grain yield under high day temperatures was primarily caused by the reduction in seed set percentage. However, decreased spikelet number per panicle, grain weight, and biomass production in addition to decreased seed set percentage contributed collectively to the decline of grain yields under high night temperatures (Figs. 2–4Figure 2). The decrease in spikelet number per panicle and grain weight, which determine the sink capacity, might be caused by the decline in assimilation supply due to the increase in respiration under high night temperatures. In fact, spikelets are less competitive than the stem for available assimilates during panicle formation in wheat (Fischer and Stockman, 1980). During grain filling, carbohydrates are from either current photosynthesis directly or translocated from assimilates accumulated in the leaf sheath and culms before heading. Reduced grain weights under high night temperatures may be a result of the carbohydrate supply failing to meet the demand of an accelerated rate of grain filling (Shi et al., 2013).

The finding of differential effects of high day and night temperatures on rice yield formation is novel. However, such a conclusion could be confounded with different treatment methods between day and night in terms of the intensity, timing, and duration of high temperature treatments. In addition to the meta-analysis, the dose-response analysis also confirmed that high day and night temperatures had different effects on yield components. Therefore, the intensity of high temperature treatments should not be a confounding factor for the differential effects of high day and night temperatures on rice yield formation. Furthermore, the timing and duration of high temperature treatments were randomly variable across all studies (Table S3); thus, high day and night temperature treatments did not show consistent differences in timing and duration of the treatments. We also checked the timing of high temperature treatments for the observations of panicle number and spikelet number per panicle in the meta-analysis (Fig. 2) and found that all observations for both day and night received high temperature treatments before the heading stage (data not shown). It is well known that reactive oxygen species (ROS) can be generated under stress conditions including high temperatures and plant cells (e.g. membranes) injured by accumulated ROS (Asada, 2006). Recently, Lai et al. (2012) found that ROS-response genes exhibit a time-of-day-specific phase of expression under diurnal and circadian conditions, and the efficiency of ROS scavenging systems is high during the day. Byeon and Back (2014) observed that more detrimental effect of high night temperature than high day temperature in rice is well correlated with the production of melatonin – acting as a potent antioxidant which can efficiently scavenge ROS in the plant cells – under high night temperature.



Therefore, the less efficiency of ROS scavenging systems during the night is likely one of the reason that rice production is more sensitive to elevated night temperature. In addition, synthesis and accumulation of heat shock proteins (HSPs) and cold shock proteins (CSPs) also suggested playing an important in heat tolerance, however, mechanisms are still not certain (Grover et al., 2013; King and Macrae, 2015). Further studies will be necessary to reveal the mechanisms of rice yield response to asymmetric warming.

#### 4.3. High temperature effects on grain quality

Among grain quality traits, chalkiness, chalky rice rate, and head rice percentage showed significant responses to high temperature treatments, whereas the effects of high temperatures on other grain quality traits were not significant. High temperatures increased chalkiness and chalky rice rate but reduced head rice percentage. The effect of high temperature treatments on chalkiness was greater under high whole day temperatures than under high day and night temperatures alone. Chalkiness is one of the key factors in determining rice quality and commercial price and detracts from grain appearance and therefore decreases market acceptance. Head rice percentage is a decisive factor for measuring milled rice quality. Previous studies report that grain quality traits such as chalkiness and head rice percentage are very sensitive to high temperatures (Cooper et al., 2008; Fitzgerald and Resurreccion, 2009; Madan et al., 2012; Sreenivasulu et al., 2015). The high temperature stress during the filling stage triggers non-uniform filling and impairment in storage biosynthesis, which lead to chalk formation. The gaps formed due to aborted starch granule formation are thought to be responsible for making chalky grains more brittle and for forming fissures along the grain (Sreenivasulu et al., 2015). As a result, chalky grains crack easily during grain processing, which declined head rice percentage as a consequence of the increased amount of broken grains (Sreenivasulu et al., 2015).

#### 5. Conclusions

To identify, select, and breed suitable cultivars for a warming world, understanding the effects of high temperatures on rice yield formation is an urgent task. Here, we showed that high temperatures profoundly influenced rice physiology, grain yield and grain quality. The processes of rice yield formation were affected differently by high day and night temperatures. The reduction of yields under high day temperatures was primarily caused by a decrease in seed set percentage; however, decreased spikelet number per panicle, seed set percentage, grain weight and biomass production combined contributed to the decline of yields under high night temperatures. Our results suggest that adaptation strategies in crop breeding for global warming should consider asymmetric warming and that further studies are required to understand the differences in the physiological mechanisms underlying rice yield declines under high day and night temperatures.

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#### Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.envexpbot.2017.06.007>.

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