

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



Dongliang Xiong, Xiaolia Ling, Jianliang Huang, Shaobing Peng*

National Key Laboratory of Crop Genetic Improvement, MOA Key Laboratory of Crop Ecophysiology and Farming System in the Middle Reaches of the Yangtze River, College of Plant Science and Technology, Huazhong Agricultural University, Wuhan, Hubei 430070, China

ARTICLE INFO

Keywords:

Dose-response analysis
High day and night temperature
Grain quality
Grain yield
Meta-analysis
Rice

ABSTRACT

Global warming is one of the biggest challenges for improving the productivity of rice crop in the future. In this study, a meta-analysis and a dose-response analysis were conducted to evaluate the effects of high day and night temperature on rice yield and quality. Overall, grain yield decreased by 39.6% (95% CI from -42.9% to -35.6%) under high temperature, which was primarily caused by the decrease of seed number per panicle. Yield reduction was also caused by high temperature through a decrease in photosynthesis and an increase in respiration. High temperature affected grain quality by decreasing head rice percentage and increasing chalkiness. The reduction of grain yield under high day temperature was primarily caused by the reduction in seed number per panicle, grain length, and biomass production in addition to decreased seed number per panicle, grain length, and biomass production in addition to decreased seed number per panicle. The results suggest that the differential effects of day and night warming on the process have contributed to the formation of rice yield loss. It should be considered when rice varieties are developed as a crop adaptation strategy for future global warming.

1. Introduction

Climate change represents an continual challenge for agricultural production and food security (IPCC in Core Writing Team, 2014). Global warming is an important aspect of climate change that has largely driven the increasing atmospheric concentration of greenhouse gases, stratospheric ozone depletion, aerosol emission and land-use change (Schneider, 2001; Shackleton 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 the 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 Auer, 2003), and many studies have shown the significant influence of elevated temperature on crop yield. According to Lobell and Auer (2003), both corn and soybean yield 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 temperature must be determined to develop adaptation strategies to achieve sustainable crop production to meet the demand of a growing population (Hodden et al., 2007). Previously, the high temperature response of rice to high temperature varies with genotype (Jagadi et al., 2010a, 2007; Mariani et al., 2013; Zik and Ordonez, 1996). Moreover, the reproductive stage is likely more sensitive to high temperature than the vegetative stage in rice (Schnepf et al., 2014; Welch et al., 2010). When temperature exceeds critical thresholds, anther dehiscence, pollen germination on the stigma, and/or pollen tube growth are affected, and consequently, pollen sterility increases dramatically (lower seed percentage), which results in a reduction of grain yield (Jagadi et al., 2010a, b, 2007, 2011; Prasad et al., 2006; Sasaki and Yoshida, 1978).

Atmospheric warming, with a greater increase in night than in day temperature, has been observed (Dona and Alexander, 2012) and may have an impact on the equilibrium for ecological and agricultural (Peng et al., 2013). Both high day and night temperature affect growth, development, and yield formation of crop species

* Corresponding author.

E-mail address: peng@mail.hzau.edu.cn (S. Peng).

(Krihnan et al., 2011). Studies report high and high temperature negative effect on rice biomass production and grain yield (Cooper et al., 2008; Krihnan et al., 2011; Mohammed and Tarple, 2009; Rang et al., 2011). High day temperature and relative humidity affect rice reproductive process (Tao et al., 2009; Jagadhi et al., 2007, 2010b; Madan et al., 2012; Rang et al., 2011), particularly pikele fertility, here high temperature lead to an increase in dark respiration and consequent reduction in biomass production and grain yield (Cooper et al., 2015; Peng et al., 2004; Shi et al., 2013, 2016). However, the die height has increased pikele fertility in the primary reaction for yield under high temperature (Mohammed and Tarple, 2009, 2011). Hence, the general pattern of temperature response and the differential effect of high day and high temperature on rice yield and yield attributes may be determined.

Grain quality is an important criterion for acceptance of an arable farmer and consumer. 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; Sreeniwal et al., 2015). Chalkiness results from the abnormal formation of starch granules, high silica effect, starch accumulation during the early grain filling stage, and the process are enhanced in high temperature (Fitzgerald and Reardon, 2009; Madan et al., 2012; Sreeniwal et al., 2015). Increased chalkiness and decreased head rice percentage are common outcomes of high temperature during the ripening phase of rice crop (Krihnan et al., 2011). Additionally, high temperature during the grain filling period causes a significant reduction in grain yield and moisture content (Yamaka et al., 2010; Yamaka et al., 2007).

Many studies have investigated the potential effect of high temperature on physiological traits, yield components and grain quality in rice. The die provides a large database for evaluating the general response of rice crop to high temperature using a meta-analysis. This approach has been used to determine the overall response of rice to elevated CO₂ and O₃ (Ainsworth, 2008) and has also been used to estimate the response of rice to elevated CO₂ in free-air CO₂ enrichment (FACE) experiments (Ainsworth et al., 2002). However, the general response of rice to high temperature has not been quantitatively evaluated using a meta-analysis, which might be due to the different die using different high temperature treatments method in terms of height, timing, and duration. Therefore, in this die, we evaluated both meta-analysis and dose-response analysis to estimate the effect of high day and high temperature on rice physiological process, grain yield, yield components, and grain quality. More specifically, the goal is to answer the following questions: (i) What are the responses of rice physiological process, grain yield, yield components and grain quality to elevated temperature? (ii) Do elevated day and high temperature have different effects on grain yield and yield attributes in rice crop?

2. Materials and methods

2.1. Data collection

The PRISMA flow diagram (Fig. S1) shows the procedure for the selection of research papers for this die. Research papers were searched from the Web of Science, Scopus, and the China Knowledge Infrastructure Database using the following 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 agricultural, plant science, ecology, and environmental science. After duplication, the die removed by comparing the article title, author list, publication year, and journal name, the article number was reduced to 1307 records. Then, the abstract 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) a leaf temperature (control and high) treatment; (ii) for grain yield (GY) and yield components (panicle number, PN; pikele number per panicle, SN; seed percentage, SPP; grain weight, GW; and biomass, BM), only the die has contained information on treatment mean, amplitude, and data variability [standard deviation (SD) or standard error of the mean (SE)] were included; (iii) for grain quality traits, the die provides information on data variability were also included, because the die were available on the temperature response of rice grain quality traits in the literature; (iv) yield-phenomena were elected and moisture content was excluded; and (v) other treatments (i.e., CO₂ and drought) were excluded. The die elected for dose-response analysis were the following criteria: (i) for physiological traits (high-temperature and respiration), the growth temperature and mean temperature were reported, the leaf temperature and mean temperature; (ii) for grain yield (GY) and yield components, a leaf temperature treatment; and (iii) moisture and other treatments were excluded. A total of 95 peer-reviewed articles were included for both meta- and dose-response analysis (Appendix S1).

Grain quality parameters referred to gel content, protein content, amylose content, chalkiness, chalkiness, grain length, grain width, broken rice percentage, milled rice percentage, and head rice percentage. Chalkiness is defined as the ratio of grain in opaque part in the endosperm to the total number of grains, here chalkiness is defined as the percentage of chalk area to projected grain area (Lilley et al., 2000).

The data were extracted directly from the available and in the original paper or indirectly from figures using WinDIG 2.5 (<http://www.nige.ch/cience/chifi/cpb/indig.html>). When the variance was reported as SE, the error was converted into overall variance using the number of replicates of each data collection, pooled, and finally converted to SD for grouped data. Other information, when available, such as experimental duration, climate name, type of high temperature treatment (day, night or hole day), growing condition (pot or field), and genotype of the genotype, were also extracted for further analysis.

2.2. Meta-analysis

A meta-analysis was performed using R 3.2.2 (<http://cran.r-project.org>). The meta-analysis consisted of two primary steps: (1) calculate individual effect size and heteroscedastic variance for each die to place the data from the primary die on a common scale, and (2) evaluate the accumulated effect size. In the current die, the individual effect size of rice traits were calculated using a natural logarithm transformed response ratio ($\ln R = \ln \frac{X_e}{X_c}$), where X_e and X_c are the mean value of all comparisons in the control and high temperature treatments, respectively. The random-effect model analysis, which is based on the assumption of random variation in response among die, and a weighted parametric analysis were used for grain yield 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 deviation for all comparisons in the control and high temperature treatments, respectively; N_c and N_e are the amplitude for the control and high temperature treatments, respectively. For each die, the weighting factor was calculated as the inverse of the pooled variance ($1/v$). The final weighted die in the analysis was: $w^* = 1/v$, where N is the number of observations from the same die. To quantify the accumulated effect, the weighted mean response ratio ($\ln RRR = \frac{\sum_{i=1}^k w_i^* R_i}{\sum_{i=1}^k w_i^*}$) and its 95% CI were calculated as the reciprocal of the mixed-model variance (Cribari 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). Reproduction effect size is measured 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 empirical effect size considered statistically significant.

By conducting the hierarchical analysis/effect size for each group are significantly different from zero, the hierarchical group differed from one another in order of heterogeneity. In the current study, a homogeneity test was applied in which overall heterogeneity (Q_T) was partitioned into within-group (Q) and between-group (Q_b) heterogeneity. The partition were calculated as:

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

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

Table 1

The emperature range and mean of three high emperatures (HT) included in meta-analysis.

HT type	No.	CK range (°C)	CK mean (°C)	HT range (°C)	HT mean (°C)	ΔT range (°C)	ΔT 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 emperatures; Night, high night emperatures; Whole, high day and high night emperatures; CK, control check; HT, high emperatures; ΔT, the difference between HT and CK; CK range, the emperatures range of all control check included in meta-analysis; CK mean, the mean emperatures of all control check included in meta-analysis; and No., the number of data points included in meta-analysis. The whole day emperatures calculated as the average of day and night emperatures for each day.

3.1. Effects of high temperatures on rice physiological traits

Generally, light-lowered leaf photosynthesis rate increased with emperatures before the optimal emperatures and decreased with emperatures after optimal emperatures (Fig. 1A). Overall, the optimal emperatures for rice photosynthesis is approximately 30°C. However, the optimal emperatures for photosynthesis varied with growth emperatures (Fig. 1C). Plant growth rate increased greater photosynthesis capacity at lower emperatures, whereas plant growth rate at higher emperatures showed greater capacity for photosynthesis at higher emperatures. We also found that leaf respiration rate increased

Table 2

Between-group heterogeneity (Q_b) for high emperatures effect across different categorical variables.

Variable	No.	HT type	Growth condition	Eco type	Genotype	Treatment
Yield	232	35.19***	109.5***	8.49 [†]	331.0***	19.93***
PN	161	0.91	3.87 [†]	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 [†]

HT, high emperatures; GY, grain yield; PN, panicle number; SN, spikelet number per panicle; SSP, seed percentage; GW, grain weight; BM, biomass; and No., data points included. HT type included day, night, and whole day high emperatures treatment; Growth condition included field and pot condition; Eco type included *indica* and *japonica*; and Treatment included high emperatures treatment before heading, after heading, and entire growth season.

[†] $P < 0.05$.
^{**} $P < 0.01$.
^{***} $P < 0.001$.

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

3.2. Effects of high temperatures on rice yield attributes

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

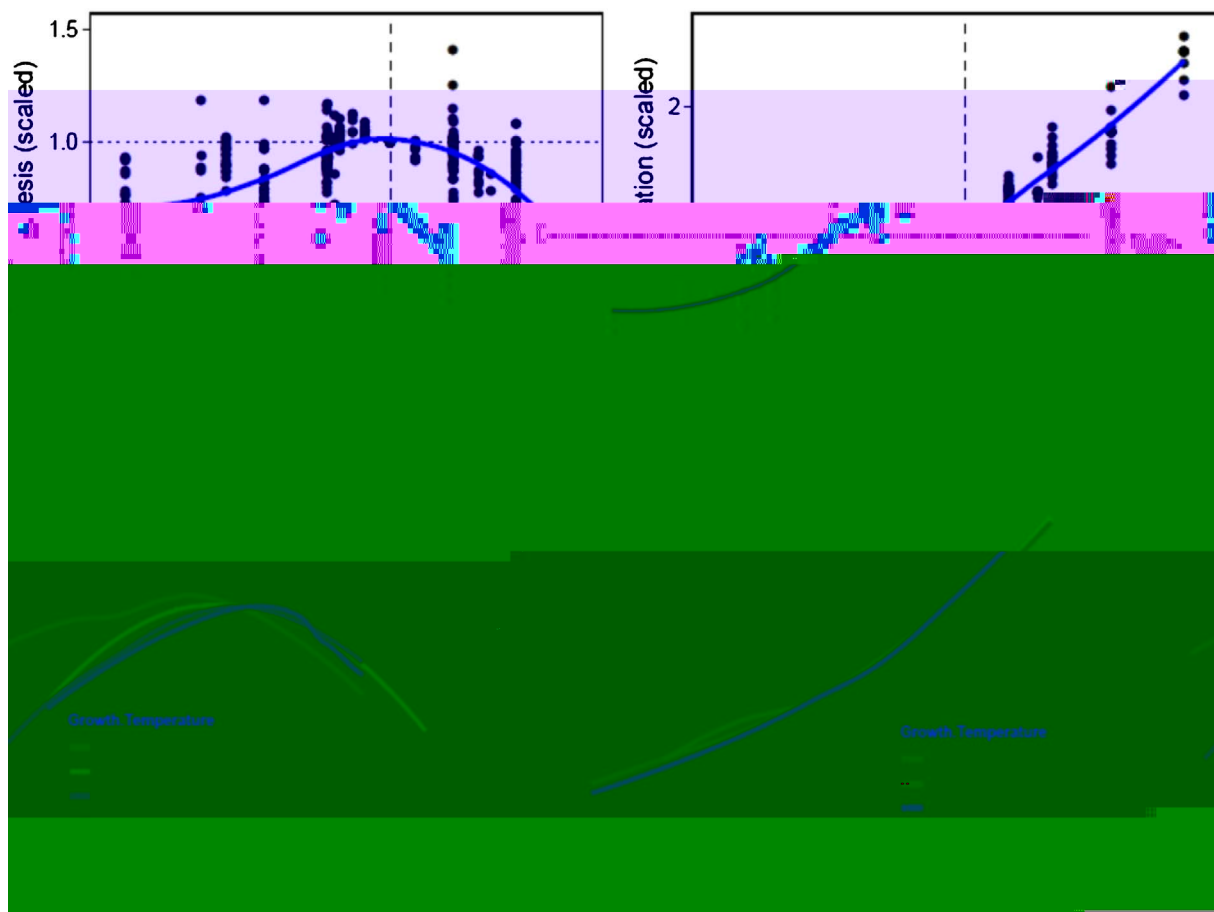


Fig. 1. Effect of high emperatures on rice physiological traits. General response of light-lowered photosynthesis (A) and dark respiration (B) to mean emperatures, and the growth emperatures depended response of light-lowered photosynthesis (C) and dark respiration (D) to mean emperatures. To demonstrate the response of physiological traits to emperatures under different growth emperatures more clearly, the data points in (C) and (D) were normalized. The reference value for emperatures is indicated by dotted lines (30°C for photosynthesis and 25°C for respiration).

repon e nder high da empera re. Spikele n mber per panicle and grain eigh decrea ed onl nder high nigh empera re b no nder high da and hole da empera re. Moreo er, panicle n mber did no re pond o an of he high empera re rea men. To be er nder and he repon e pa ern of grain ield and i componen o high empera re, e anal ed heir do e-repon e c r e o da empera re (Fig. 3) and nigh empera re (Fig. 4). O r re l ho ha he op im m da empera re for rice grain ield a appo ima el 28, C. When he empera re ere lo er han he op imal da empera re, grain ield a increa ed i h da empera re b increa ing bioma and pikele n mber per panicle, hile he panicle n mber decrea ed i h da empera re. When he empera re ere higher

(-33.3%, i h a 95% CI of -36.9% o -29.5%) (Fig. S2). Ho e er, he effec of high empera re on panicle n mber (-0.69%, i h a 95% CI of -7.54% o 6.67%), pikele n mber per panicle (-6.83%, i h a 95% CI of -13.30% o 0.09%), grain eigh (-4.92%, i h a 95% CI of -12.36% o 3.15%) and bioma (8.07%, i h a 95% CI of -0.91% o 17.86%) a no ignifican.

Significan difference in empera re repon e ere ob er ed among he hree pe of high empera re rea men for grain ield ($Q_b = 35.19, P < 0.001$), pikele n mber per panicle ($Q_b = 9.70, P < 0.05$), eed e percen age ($Q_b = 35.88, P < 0.001$), and bioma ($Q_b = 12.98, P < 0.01$) (Table 2). Ho e er, empera re repon e in panicle n mber ($Q_b = 0.91, P = 0.738$) and grain eigh ($Q_b = 3.31, P = 0.184$) ere no ignifican l differen among he pe of high empera re rea men. Dra ic red c ion in grain ield and eed e percen age occ rred in he high da (-56.3% and -53.4%, re pec i el), nigh (-31.9% and -18.0%, re pec i el), and hole da (-68.3% and -35.4%, re pec i el) empera re rea men (Fig. 2). Bioma decrea ed nder high nigh empera re, herea an oppo i e repon e a ob er ed nder high hole da empera re and no

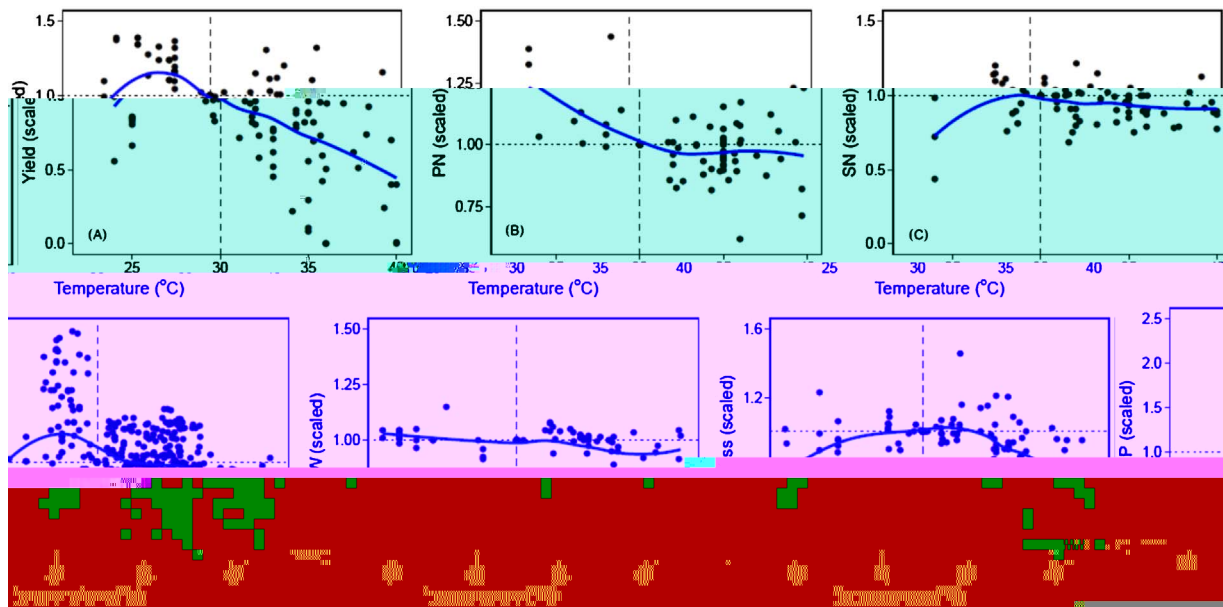


Fig. 3. Do e-re pon e anal i of high da empera re effec on rice field a rib e . General re pon e of (A) grain field (GY), (B) panicle n mber (PN), (C) pikele n mber per panicle (SN), (D) eed e percen age (SSP), (E) grain eigh (GW), and (F) bioma (BM) o high da empera re. The reference al e for empera re i indica ed b do ed line (30, C).

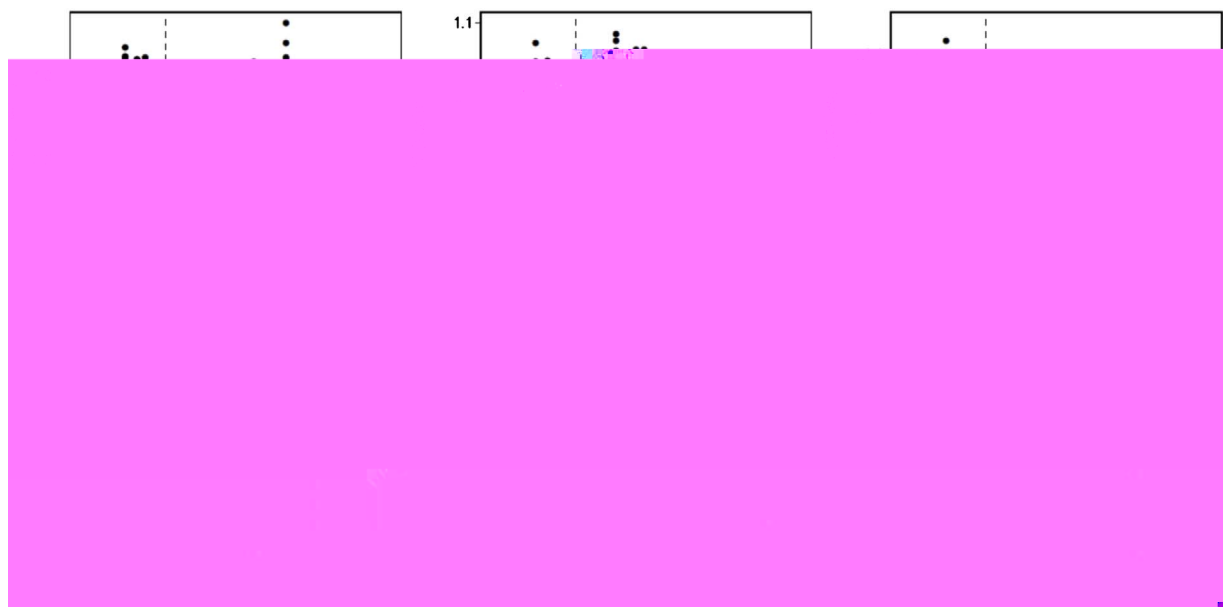


Fig. 4. Do e-re pon e anal i of high nigh empera re effec on rice field a rib e . General re pon e of (A) grain field (GY), (B) panicle n mber (PN), (C) pikele n mber per panicle (SN), (D) eed e percen age (SSP), (E) grain eigh (GW), and (F) bioma (BM) o high nigh empera re. The reference al e for empera re i indica ed b do ed line (24, C).

en i i of eq ipmen ere nlikel o ha e a rong effec on hi d (Fig. S9).

4. Discussion

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

Similar o mo C₃ plan , rice leaf ligh - a ra ed pho o n he i increa e from a ba e empera re o a lo er op im m and hen decline i h increa ing empera re from an pper op im m. O erall, he op im m empera re for pho o n he i a appro ima el 30 C in rice. Ho e er, he op im m empera re co ld be hif ed b he gro h empera re: plan gro n nder rela i el lo empera re ho ed grea er pho o n he ic capaci nder lo er empera re , hich re l ed in a lo er op im m empera re, herea plan gro n

nder rela i el high empera re ho ed grea er capaci for pho o n he i nder higher empera re , hich re l ed in a higher op im m empera re. An increa e in he capaci of pho o n he ic en me ch a R bi co i likel for pho o n he ic acclima ion o lo empera re , herea pho o n he ic acclima ion o high empera re ma in ol e an increa e in he hea abili of he pho o n he ic appara (Sage and K bien, 2007; Yamori e al., 2014, 2010). Here, e fo nd ha he do e-re pon e c re of pho o n he i o empera re a incon i en i h he do e-re pon e c re of bioma o da empera re ; h , he decrea e in bioma nder high da empera re might be primaril ca ed b he decline in pho o n he i . Moreo er, bioma co ld decline beca e of an increa e in pho ore pira ion nder high empera re ; ho e er, pho ore pira ion da a re limi ed e o he echnical limia ion in i mea remen . Dark re pira ion i con sidered he primar fac or ha affec rice bioma and field nder high nigh empera re (Peng e al., 2004). Ba ed on o r re l , dark

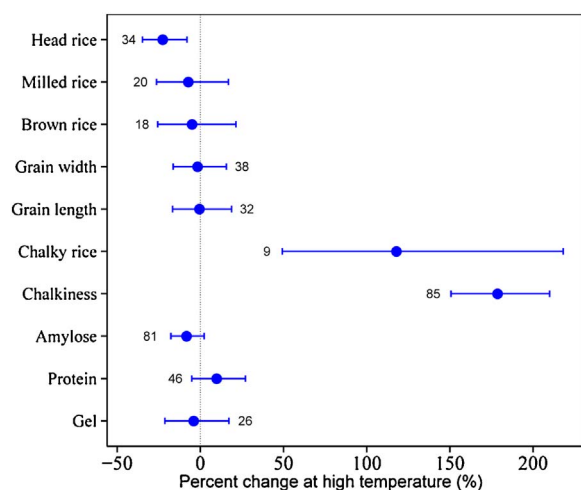


Fig. 5. Effect of high temperature on rice grain quality. Error bars represent 95% confidence interval. The value near the error bar indicates the number of data points for meta-analysis.

repiration increased drastically with increased temperature (Fig. 1), which explained the decrease of biomass under high night temperature. Meta-analysis indicated that biomass increased significantly under high day temperature (Fig. 2C), because the high temperature increased biomass production by 2.1-fold when compared to control temperature (21 °C) (Fig. S10). Additionally, dose-response analysis suggested that the increased temperature might contribute to the biomass when compared to control temperature (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 percentage, and grain weight. In the current study, we found that grain yield decreased significantly (-39.6%) under high temperature (Fig. S2), with the reduction primarily caused by a decrease in seed percentage (-33.3%). Additionally, spikelet number per panicle and grain weight decreased slightly but not significantly under high temperature. The results suggested that reproductive and organ are more sensitive to high temperature than vegetative growth. In fact, a significant effect of high temperature after the heading stage was detected on seed percentage, but not for the high temperature before the heading stage (Fig. S5). The decrease in seed percentage indicated that high temperature was a major factor of the effect of temperature on yield and growth of the ovaries during the pre-anthesis period, in addition to temperature effect on anther dehiscence and production, anther viability, and germination of pollen during anthesis (Iqbal et al., 2009; Jagadi et al., 2007, 2010b; Madan et al., 2012; Rang et al., 2011).

Our analysis also showed that the response of grain yield and seed percentage to high temperature differed significantly with genotype and growth condition (Table 2). The genotype-dependent response of seed percentage to high temperature is observed in many studies (Jagadi et al., 2010a, 2007; Marzama et al., 2013; Zi ka and Ordonez, 1996). The difference in high temperature tolerance among genotypes might be caused by several mechanisms. First, genotype difference occurs in pollination ability, characterized by traits such as pollen number, anther size and shape, and anther dehiscence (Jagadi et al., 2007; Madan et al., 2012). For example, Marzama et al. (2013) found that genotype with larger anthers and more abundant pollen had better pollination ability under high temperature. 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, genotype

with an early-morning flowering trait had less risk of the cooler morning air than a midday (Iqbal et al., 2010). In the present study, we found that the reduction of yield in pot was more serious than in the field (Fig. S3). Meteorologically, creating a large temperature gradient under field condition is more difficult than for pot in the laboratory and greenhouse. Moreover, the extreme high temperature were reached in the field. Additionally, other environmental factors are also difficult to control in the field, such as humidity, and the interaction between high temperature and other environmental factors under field condition may contribute to the difference. Recent studies have more open-field studies are required to confirm the temperature response (Jia and Dingkuhn, 2012; Marzama et al., 2014).

Overall, grain yield decreased under both high day and night temperature. This result is in contrast to the report 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 temperature of different time and ear in their study were close to 30 °C; however, the maximum day temperature in the current study was 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 effect of high day and night temperature on rice yield formation. The reduction of grain yield under high day temperature is primarily caused by the reduction in seed percentage. However, decreased spikelet number per panicle, grain weight, and biomass production in addition to decreased seed percentage contributed to the decline of grain yield under high night temperature (Fig. 2–4; Fig. 2). The decrease in spikelet number per panicle and grain weight, which determines the sink capacity, might be caused by the decline in assimilate supply due to the increase in respiration under high night temperature. In fact, spikelets are likely to compete for assimilable assimilate during panicle formation in wheat (Fischer and Sockman, 1980). During grain filling, carbohydrate are derived from either current photosynthesis or translocated from assimilate accumulated in the leaf sheath and culm before heading. Reduced grain weight under high night temperature 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 effect of high day and night temperature on rice yield formation is novel. However, such a conclusion could be confirmed with different real-time methods between day and night in terms of the environment, timing, and duration of high temperature treatments. In addition to the meta-analysis, the dose-response analysis also confirmed that high day and night temperature had different effects on yield components. Therefore, the intensity of high temperature treatments should not be a confounding factor for the differential effect of high day and night temperature on rice yield formation. Furthermore, the timing and duration of high temperature treatments were randomly variable across all studies (Table S3); however, high day and night temperature treatments did not have any consistent difference in timing and duration of the treatments. We also checked the timing of high temperature treatments for the observation 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 (day or night). It is well known that the reactive oxygen species (ROS) can be generated under the condition including high temperature and plant cell (e.g. membrane) injury by accumulated ROS (Aada, 2006). Recently, Lai et al. (2012) found that ROS-response gene expression is a time-of-day-specific phase of the pre- and diurnal and circadian condition, and the efficiency of ROS scavenging is high during the day. Beeson 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 potential antioxidant which can efficiently scavenge ROS in the plant cell – under high night temperature.

Therefore, the efficiency of ROS scavenging during the high temperature of rice production is more efficient in the high temperature. In addition, the high temperature and accumulation of heat shock protein (HSP) and cold shock protein (CSP) also regulate plant responses in heat tolerance, however, mechanisms are still unclear (Grover et al., 2013; King and Macrae, 2015). Further studies will be necessary to reveal the mechanism of rice yield response to a climatic warming.

4.3. High temperature effects on grain quality

Among grain quality traits, chalkiness, chalkiness, and head rice percentage showed significant responses to high temperature treatments, whereas the effects of high temperature on other grain quality traits were not significant. High temperature increased chalkiness and chalkiness, reduced head rice percentage. The effects of high temperature treatments on chalkiness are greater under high temperature than under high temperature and high temperature alone. Chalkiness is one of the key factors in determining rice quality and commercial price and decreases from grain appearance and therefore decreases market acceptance. Head rice percentage is a decisive factor for milling rice quality. Previous studies reported that grain quality traits such as chalkiness and head rice percentage are more efficient in high temperature (Cooper et al., 2008; Fitzgerald and Reirreccion, 2009; Madan et al., 2012; Sreeniwasula et al., 2015). The high temperature reduces the filling rate, increases non-uniform filling and impurities in orange brown color, which leads to chalk formation. The gaps formed due to abraded arch granule formation are highly susceptible to making chalk grain more brittle and for forming fissures along the grain (Sreeniwasula et al., 2015). As a result, chalk grain cracks during grain processing, which declines head rice percentage as a consequence of the increased amount of broken grain (Sreeniwasula et al., 2015).

5. Conclusions

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

Funding sources

This study was supported by the Major International Joint Research Project of China National Science Foundation (No. 31361140368), Program of Introducing Talents of Discipline to Universities in China (the 111 Project no. B14032), and the Special Fund for Agro-scientific Research in the Public Interest of China from the Ministry of Agriculture (No. 201203096).

Acknowledgments

The authors thank Mr. Cheng Sun, Xiaochun Ma, and Mi Wencheng Wang for their valuable comments on the draft. Dongliang Xiong thanks the China Scholarship Council (CSC) for his funding of his Ph.D. study abroad.

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.jep.2017.06.007>.

References

Ainsworth, E.A., Dale, P.A., Bernacchi, C.J., Dermod, O.C., Heath, E.A., Moore, D.J., Morgan, P.B., Naidu, S.L., Ra, H.S.Y., Zhang, X.G., Cousins, P.S., Long, S.P., 2002. A meta-analysis of elevated [CO₂] effects on wheat (Triticum aestivum) phenology, growth and yield. *Global Change Biol.* 8, 695–709.

Ainsworth, E.A., 2008. Rice production in a changing climate: a meta-analysis of responses to elevated carbon dioxide and elevated ozone concentration. *Glob. Change Biol.* 14, 1642–1650.

Adachi, K., 2006. Production and scavenging of reactive oxygen species in chloroplasts and their functions. *Plant Physiol.* 141, 391–396.

Beech, Y., Back, K., 2014. Melatonin in rice seedling in vitro enhanced a high temperature and under dark condition dependent increase in N-acetylserine and N-acetylserine methyltransferase activity. *J. Pineal Res.* 56, 189.

Cleland, W.S., DeLinn, S.J., Grover, E., 1988. Regression biophysical modeling, proper use, and computational algorithm. *J. Econom.* 37, 87–114.

Coates, O., Elli, R.H., Murdoch, A.J., Quinone, C., Jagadish, K.S.V., 2015. High temperature induced carbon sequestration for pikele fertility, pikele yield, and flowering characteristics and grain quality in rice. *Func. Plan Biol.* 42, 149–161.

Cooper, N.T.W., Siebenmorgen, T.J., Conner, P.A., 2008. Effects of high temperature during kernel development on rice phytochemical properties. *Cereal Chem.* 85, 276–282.

Crispien, P.S., Wang, X., 1998. A meta-analysis of elevated CO₂ effects on food production, form, and phenology. *Oecologia* 113, 299–

2012. *CIRCADIAN CLOCK-ASSOCIATED 1* regulates ROS homeostasis and oxidative stress response. *Proc. Natl. Acad. Sci. U. S. A.* 109, 17129–17134.
- Li le, A.J., Mar in, M., Fitzgerald, M.A., 2000. Chalk and bran in rice grain differ in starch composition and rice yield and cooking properties. *Cereal Chem.* 77, 627–632.
- Lobell, D.B., Auer, G.P., 2003. Climate and management with rice production trends in U.S. agricultural yield. *Science* 299 1032–1032.
- Maclean, J.L., Datta, D.C., Hardy, B., Heil, G.P., 2002. Rice Almanac. IRRI, Los Banos, Philippines, pp. 110.
- Madan, P., Jagadhi, S.V.K., Crawford, P.Q., Fitzgerald, M., Lafarge, T., Wheeler, T.R., 2012. Effect of elevated CO₂ and high temperature on yield and grain quality of rice. *J. E. p. Bo.* 63, 3843–3852.
- Maruama, A., Weerakoon, W.M.W., Wakiyama, Y., Ohba, K., 2013. Effect of increasing temperature on pikelet fertility in different rice cultivars based on temperature gradient chamber experiment. *J. Agron. Crop Sci.* 199, 416–423.
- Masui, T., Kobayashi, K., Nakagawa, H., Yoshimoto, M., Hasegawa, T., Reinke, R., Ang, J., 2014. Lower-han-epedoflore fertility of rice under remel-ho condition in a flood-irrigated field in Northeast India. *Plan. Prod. Sci.* 17, 245–252.
- McGrath, J.M., Lobell, D.B., 2013. Reduction of nitrogen fertilizer allocation on rice and nitrogen decline of crop growth in elevated CO₂ concentration. *Plan. Cell En. Iron.* 36, 697–705.
- Meehl, G.A., Coe, C., Deloria, T., Laif, M., McAnane, B., Mitchell, J.F.B., Soffer, R.J., Taylor, K.E., 2007. The WCRP CMIP3 multi-model data analysis: an overview. *J. Geophys. Res.* 112, 1383–1394.
- Mohammed, A.R., Tarple, L., 2009. High night temperature affects rice productivity through altered pollen germination and pikelet fertility. *Agr. For. Meteorol.* 149, 999–1008.
- Mohammed, A.R., Tarple, L., 2011. Effect of night temperature: pikelet position and allelic acid on yield and yield-related parameters of rice (*Oryza sativa* L.) plants. *J. Agron. Crop Sci.* 197, 40–49.
- Morgan, P.B., Ainsworth, E.A., Long, S.P., 2003. How does elevated CO₂ impact on bean? A meta-analysis of photosynthesis, growth and yield. *Plan. Cell En. Iron.* 26, 1317–1328.
- Peng, S.B., Huang, J.L., Sheehy, J.E., Laing, R.C., Vignani, R.M., Zhong, X.H., Cullen, G.S., Khush, G.S., Casman, K.G., 2004. Rice yield decline in high night temperature from global warming. *Proc. Natl. Acad. Sci. U. S. A.* 101, 9971–9975.
- Peng, S.S., Piao, S.L., Ciais, P., Munnich, R.B., Chen, A.P., Chevallier, F., Dolman, A.J., Janissen, I.A., Penland, J., Zhang, G.X., Vicca, S., Wan, S.Q., Wang, S.P., Zeng, H., 2013. A massive effect of daytime and nighttime warming on Northern Hemisphere vegetation. *Nature* 501, 88–92.
- Poorer, H., Niineme, U., Walther, A., Fiorani, F., Schurr, U., 2010. A method to compare the response of a wide range of environmental factors and plant traits to mean of a meta-analysis of phenological data. *J. E. p. Bo.* 61, 2043–2055.
- Poorer, H., Nikla, K.J., Reich, P.B., Oleksyn, J., Poo, P., Mommer, L., 2012. Biomass allocation to leaves, stem and root: a meta-analysis of temperate forest species and environmental control. *New Phytol.* 193, 30–50.
- Praad, P.V.V., Boore, K.J., Allen, L.H., Sheehy, J.E., Thoma, J.M.G., 2006. Species, ecotype and cultivar differences in pikelet fertility and harvest index of rice in response to high temperature. *Field Crop Res.* 95, 398–411.
- Rang, Z.W., Jagadhi, S.V.K., Zhou, Q.M., Crawford, P.Q., Heiser, S., 2011. Effect of high temperature and water stress on pollen germination and pikelet fertility in rice. *Environ. E. p. Bo.* 70, 58–65.
- Roenthal, R., 1979. The file drawer problem and tolerance for null results. *Psychol. Bull.* 86, 638.
- Schnepf, B., Ramirez, A., Porter, J.R., 2014. Temperature and the growth and development of maize and rice: a review. *Glob. Change Biol.* 20, 408–417.
- Sage, R.F., Kubien, D.S., 2007. The temperature response of C₃ and C₄ photosynthesis. *Plan. Cell En. Iron.* 30, 1086–1106.
- Saake, T., Yoshida, S., 1978. High temperature induced fertility in indica rice at flowering. *Jpn. J. Crop Sci.* 47, 6–17.
- Schneider, S.H., 2001. What is 'dangerous' climate change? *Nature* 411, 17–19.
- Shakun, J.D., Clark, P.U., He, F., Marco, S.A., Miller, A.C., Li, Z.Y., O'Brien, B., Schimner, A., Bard, E., 2012. Global warming preceded by increasing carbon dioxide concentration during the last deglaciation. *Nature* 484, 49–54.
- Shi, W.J., Mishra, R., Rahman, H., Selam, J., Peng, S.B., Zhou, Y.B., Jagadhi, K.S.V., 2013. Soil carbon dynamics and proteomic reprogramming under elevated night temperature and their impact on rice yield and grain quality. *New Phytol.* 197, 825–837.
- Shi, W.J., Yin, X.Y., Srik, P.C., Xie, F.M., Schmid, R.C., Jagadhi, K.S.V., 2016. Grain yield and quality response of tropical hybrid rice to high nighttime temperature. *Field Crop Res.* 190, 18–25.
- Sreeniwas, N., Barido, V.M., Mirra, G., Cea, R.P., Anacleto, R., Kishor, P.B.K., 2015. Designing climate-resilient rice high yield grain quality index for high-temperature. *J. E. p. Bo.* 66, 1737–1748.
- van Groenigen, K.J., Oenbergh, C.W., Hungate, B.A., 2011. Increased soil emission of CO₂ under increased atmospheric CO₂. *Nature* 475, 214–216.
- Welch, J.R., Vincen, J.R., Atkinson, M., Moore, P.F., Dobermann, A., Datta, D., 2010. Rice yield in tropical and subtropical Asia is highly sensitive to minimum and maximum temperature. *Proc. Natl. Acad. Sci. U. S. A.* 107, 14562–14567.
- Xiong, D.L., Yu, T.T., Ling, X.X., Fahad, S., Peng, S.B., Li, Y., Huang, J.L., 2015. Sufficient leaf nitrogen and non-structural carbohydrate are beneficial for high-temperature tolerance in three rice (*Oryza sativa*) cultivars and nitrogen response. *Plant Biol.* 42, 347–356.
- Yamada, H., Haka, M., 2010. A study of rice grain filling-related metabolites under high temperature: joint analysis of metabolome and transcriptome demonstrated inhibition of starch accumulation and induction of amino acid accumulation. *Plan. Cell Biol.* 51, 795–809.
- Yamada, H., Hiroe, T., Kuroda, M., Yamaguchi, T., 2007. Comprehensive pre- and post-planting of rice grain filling-related genes under high temperature using DNA microarray. *Plan. Ph. Biol.* 144, 258–277.
- Yamori, W., Noguchi, K., Hikoaka, K., Terahima, I., 2010. Phenotypic plasticity in photosynthesis temperature acclimation among crop species with different cold tolerance. *Plan. Ph. Biol.* 152, 388–399.
- Yamori, W., Hikoaka, K., Wang, D.A., 2014. Temperature response of photosynthesis in C₃, C₄, and CAM plants: temperature acclimation and temperature adaptation. *Photosynth. Res.* 119, 101–117.
- Zika, L.H., Ordóñez, R.A., 1996. Intraspecific variation in the response of rice (*Oryza sativa* L.) to increased CO₂ and temperature: growth and yield response of 17 cultivars. *J. E. p. Bo.* 47, 1353–1359.