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Rice yield and quality in response to daytime and nighttime temperature increase – A meta-analysis perspective

Qiong Su [a,*], Jai S. Rohila [b], Shyam Ranganathan [c], R. Karthikeyan [a,*]

[a] Department of Agricultural Sciences, Clemson University, SC 29634, USA
[b] Dale Bumpers National Rice Research Center, United States Department of Agriculture, Agricultural Research Services, Stuttgart, AR 72160, USA
[c] School of Mathematical and Statistical Sciences, Clemson University, SC 29634, USA

A R T I C L E I N F O

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A B S T R A C T

Increased heat stress during cropping season poses significant challenges to rice production, yet the complex stoichiometry between rice grain yield, quality and high daytime, nighttime temperature remains with gaps in current knowledge. We conducted a meta-analysis using a combined dataset of 1105 experiments for daytime temperature and 841 experiments for nighttime temperature from published literature to investigate the effects of high daytime temperature (HDT) and high nighttime temperatures (HNT) on rice yield and its various components (such as panicle number, spikelet number per panicle, seed set rate, grain weight) and grain quality traits (such as milling yield, chalkiness, amylose and protein contents). We established relationships between rice yield, its components, grain quality and the HDT/HNT, and studied phenotypic plasticity of the traits in response to HDT and HNT. Results showed that HNT had a more detrimental impact on rice yield and quality when compared with the HDT. The optimum daytime and nighttime temperatures for best rice yield were approximately 28 °C and 22 °C, respectively. Grain yield showed a decline by 7% and 6% for each 1 °C increase in HNT and HDT, respectively, when exceeded the optimum temperatures. Seed set rate (i.e., percent fertility) was the most sensitive trait to HDT and HNT and accounted for most of the yield losses. Both the HDT and HNT affected grain quality by increasing chalkiness and decreasing head rice percentage, which may affect marketability of the rice produced. Additionally, HNT was found to significantly impact nutritional quality (e.g., protein content) of rice grains. Our findings fill current knowledge gaps on estimations of rice yield losses and possible economic consequences under high temperatures and suggest that impacts on rice quality should also be considered for selection and breeding of high-temperature tolerant rice varieties in response to HDT and HNT.

1. Introduction

Climate change, driven by increasing atmospheric concentrations of greenhouse gases, and associated climatic consequences poses significant challenges to global crop production (Kummu et al., 2021; Singh and Su, 2022a; Singh and Su, 2022b) and food security (FAO, 2015; Hertel, 2016; Singh and Su, 2022c). Rice (*Oryza sativa* L.) is a major staple crop for nearly 45% (>3.5 billion) of the world's population (Wing et al., 2018). However, rice production is vulnerable to heat stress, particularly in tropical and subtropical regions where high temperatures can significantly reduce rice yield (Horie, 2019; Saud et al., 2022; Welch et al., 2010). Furthermore, these regions are projected to experience increased intensity, frequency, and duration of heat stress in a changing climate (IPCC, 2019; Singh and Su, 2022d). For instance, in South Asia, a major rice production region, heat-stressed areas are projected to increase by up to 21% by 2050 compared to the baseline period of 1950–2000 (IPCC, 2019). Therefore, it is crucial to comprehensively assess the adverse effects of high temperatures on rice production and understand the underlying factors influencing yield losses.

A better understanding of the key traits associated with high daytime temperature (HDT) and high nighttime temperature (HNT) may help in speeding up stress biology and breeding programs to sustain rice production under climate change. Process-based crop models have been widely used to evaluate the effects of heat stress on rice yield (Ahmad et al., 2009; Elliott et al., 2014; Zhao et al., 2017). However, these models often lack periodic updates with the latest greenhouse experiments or field trials, leading to inadequate simulations of the effects of high temperatures on rice growth, development, and yield (Boote et al.,

* Corresponding authors.
E-mail addresses: qsu@clemson.edu (Q. Su), rkarthi@clemson.edu (R. Karthikeyan).

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2018; Schauberger et al., 2017). Moreover, existing process-based crop models fail to differentiate the impacts of HDT and HNT (Xiong et al., 2012; Zhang et al., 2014). For instance, response curves and upper-temperature thresholds for phenology, seed set (i.e., spikelet fertility), and other processes that affect yield are typically developed based on mean temperature (Boote et al., 2018). Recent studies have reported a more rapid increase in nighttime temperatures than daytime temperatures in several rice growing regions globally (Mendez et al., 2021; Sreenivasulu, 2018). This asymmetric warming trend is projected to continue in the future (Seneviratne et al., 2021). Moreover, HNT-stress tends to persist for longer durations and affect larger areas compared to HDT-stress (Dunn et al., 2020), highlighting the need for a better understanding of the distinct impacts of HDT and HNT on rice yield.

To date, an increasing amount of data from greenhouse experiments and field trials are becoming available, allowing for the quantitative parameterization of rice growth, development, and yield in response to HDT and HNT (Jagadish et al., 2015; Shi et al., 2017; Wu et al., 2021; Yang et al., 2017). For example, Xiong et al. (2017) conducted a dose-response analysis to illustrate the general response of rice yield to HDT and HNT. However, dose-response analysis alone is insufficient for establishing yield-HDT/HNT response functions, limiting their applications in analyzing the impacts of temperature increase on global rice yield predictions.

Furthermore, current knowledge on the impact of heat stress on rice quality remains limited. Previous studies have indicated that both HDT (Shi et al., 2017) and HNT (Ambardekar et al., 2011; Bahuguna et al., 2017; Chen et al., 2021; Lanning et al., 2011) stress during the grain filling stages have detrimental effects on milling quality, chalkiness, and nutritional value of rice. These factors ultimately lead to a decline in both the quantity and market value of high-quality rice (Lyman et al., 2013; Zhou et al., 2021a). However, the upper-temperature thresholds for milling quality, chalkiness, and nutritional value of rice have not been established in previous studies, and the responses of these factors to HDT and HNT stresses have not been comprehensively analyzed (Xiong et al., 2017).

To address these limitations, we conducted a comprehensive evaluation of the response curves of rice yield, yield components, milling yield, and grain quality traits to HDT and HNT stresses using a meta-analysis approach. Furthermore, we quantitatively parameterized these response curves by testing five models to establish the relationship between rice yield, HDT, and HNT stresses. The differentiation between the impacts of HDT and HNT on rice yield and quality enhanced the accuracy and reliability of future impact assessments related to climate change. The proposed model can be served as a valuable tool for predicting regional and global rice yield production under a changing climate. Additionally, we identified critical temperature thresholds for phenology, seed set, and other processes that affect rice yield and grain quality traits under both the HDT and HNT, enabling the identification of vulnerable stages and processes that could help in establishing targeted mitigation strategies. The objectives of this study were to (1) evaluate the overall responses of rice yield, yield components, milling yield, and grain quality to HDT and HNT, (2) establish a relationship between rice yield and HDT and HNT stresses, and (3) determine the upper-temperature thresholds for phenology, seed set, and other processes that affect yield and grain quality traits.

2. Materials and methods

2.1. Data collection

A literature search on the Web of Science (https://www.webofscience.com/wos/woscc/basic-search), Google Scholar (https://scholar.google.com/), and China Integrated Knowledge Resources System (https://oversea.cnki.net/index/) was conducted in August 2022 using the following keywords: 'rice' and 'high temperature', 'rice' and 'elevated temperature', 'rice' and 'increased temperature', 'rice' and 'heat stress', and 'rice' and 'warming'. A total of 40,140 papers were found initially, and 73 papers were selected based on the following criteria: (1) at least two temperature treatments were conducted; (2) rice plants grown under other treatments (e.g., nitrogen supplementation, drought, and CO_2concentration) were excluded; and (3) field trials that could disentangle the effects of HNT and HDT were included. The list of selected papers and experiment settings, including treatment types (HDT or HNT), treatment start and end dates, and experiment types (greenhouse or field), when available, is provided in Table S1 in Appendix A.

The yield components included panicle number, spikelet number per panicle, seed set rate (i.e., percent fertility), grain weight, and biomass. Milling yield parameters include brown rice (i.e., rice after removing the husk of rough rice) percentage, milled rice percentage (i.e., proportion of rice grain that remains after it has gone through the milling process), and head rice percentage (i.e., proportion of whole, intact grains in a sample of milled rice, usually include grains larger than three-quarters of the intact grain size). Grain quality parameters included grain length, width, thickness, chalkiness percentage, amylose content, and protein content. Here, chalkiness percentage refers to the ratio of chalkiness area to total grain area. WebPlot Digitizer 4.6 (https://automeris.io/WebPlotDigitizer/ was used to extract the values shown in figure form.

2.2. Dose-response curves

Dose-response curves (Poorter et al., 2010; Poorter et al., 2012) were constructed to analyze the responses of rice yield, yield components, milling yield, and quality parameters to HDT and HNT stresses. For each experiment, we defined traits measured at 32 °C (daytime temperature) and 22 °C (nighttime temperature) as the reference values. These two values were selected because they were covered in most experiments. If the experiment at the reference temperature was not conducted, the reference value was then obtained by linearly interpolating values at two adjacent temperature levels (Poorter et al., 2010). The rice traits measured at different temperature levels were normalized by dividing the values by the traits observed or calculated at the reference temperature. It is noted that the normalized values do not have a normal distribution, with values ranging from 0 to infinity. Here, local regression (loess), a nonparametric technique, was used to fit the dose-response curves using R 4.2.2 (https://cran.r-project.org). The dose-response curves were used to determine the upper-temperature thresholds for rice yield, yield components, milling yield, and grain quality. The mean change rate (CR) of each trait from daytime or nighttime temperature at T_1 to T_2 (in % per °C) is calculated as

$$\mathrm{CR} = \frac{(Y_{T_2} - Y_{T_1})}{Y_{T_1}(T_2 - T_1)} \times 100 \tag{1}$$

where Y_{T_2} and Y_{T_1} are the normalized values of each trait at daytime or nighttime temperature of T_2 (°C) and T_1 (°C) in the dose-response curves, respectively.

2.3. Regression models

Random regression mixed models (RRMMs) can be used to quantify the population level (i.e., the overall response of rice varieties) and individual level (i.e., single rice variety) of plant phenotypic plasticity in response to environmental (e.g., temperature) change (Arnold et al., 2019; Morrissey and Liefting, 2016). To better evaluate the overall population-level effect of heat stress (HDT or HNT) on rice yield, we tested one linear fixed-effect model (Eq. 2), one quadratic fixed-effect model (Eq. 3), and three quadratic mixed-effect models (Eqs. 4–6).

The basic linear fixed-effect model is:

$$Y_i = \alpha + \beta_1 T_i + e_i \tag{2}$$

where Y_i is the normalized rice yield for observation i; T_i is the mean-centered daytime or nighttime temperature; α and β_1 are the fixed effects of the population level intercept and slope coefficient, respectively; and e_i is the residual.

The basic quadratic fixed-effect model is:

$$Y_i = \alpha + \beta_1 T_i + \beta_2 T_i^2 + e_i \quad (3)$$

where α and β_1 are the fixed effects of the population level intercept and linear slope coefficient of the quadratic function, respectively; β_2 is the fixed effect of the population-level quadratic coefficient that reflects the curvature of the regression.

From Eq. 2, by allowing the intercept coefficient to vary among rice varieties (i.e., f_j) in a random intercepts regression model, we obtained a quadratic fixed-effect model with random intercepts:

$$Y_{ij} = \alpha + \beta_1 T_i + \beta_2 T_i^2 + f_j + e_{ij} \quad (4)$$

If both intercept and slope coefficients (i.e., $g_{1,j}$) were allowed to vary among rice varieties, we obtained a quadratic fixed-effect with a random intercept and a linear random slope random regression model:

$$Y_{ij} = \alpha + \beta_1 T_i + \beta_2 T_i^2 + f_j + g_{1,j} T_i + e_{ij} \quad (5)$$

Allowing the random effect of rice varieties to vary in curvature (i.e., $g_{2,j}$), we obtained a quadratic fixed-effect with a random intercept and a quadratic random effect random regression model:

$$Y_{ij} = \alpha + \beta_1 T_i + \beta_2 T_i^2 + f_j + g_{1,j} T_i + g_{2,j} T_i^2 + e_{ij} \quad (6)$$

where f_j, $g_{1,j}$, and $g_{2,j}$ are the random effects of the intercept, slope, and curvature coefficient of the quadratic function, respectively.

Standard model selection approaches, including the coefficient of determination (R^2) and Akaike Information Criterion (AIC), were used to select the best-fit model. Here, the conditional R^2 function (i.e., R^2C) from the MuMIn package in R (Bartoń, 2018) was used to represent the proportion of variance explained by both the random and fixed effects (Johnson, 2014; Nakagawa and Schielzeth, 2013). AIC values were used to balance the model complexity against the goodness of fit, which was performed using lme4 packages in R (Bates et al., 2015). The model with the lowest AIC value was considered the best fitting model among the alternatives considered (Akaike, 1974; Burnham and Anderson, 2002).

3. Results

The means of the daytime and nighttime temperatures of all experiments were 33.5 and 26.3 °C, respectively (Table 1). The histogram of daytime and nighttime temperatures used in this study is shown in Fig. S1. Approximately 90% of the daytime temperature ranged from 27 to 40 °C, and 95% of the nighttime temperatures ranged from 20 to 36 °C. It is noted that the sample sizes from experiments conducted at low temperature (e.g., HDT <27 and HNT <20 °C) were relatively small. Therefore, the 95% confidence intervals for the fitted curves were provided to estimate the uncertainty in the results.

3.1. Rice yield and yield components

High daytime temperatures significantly reduced rice yield at approximately 6% per °C when exceeding the optimum daytime temperature (28 °C), mainly due to the decreased seed set rate (3% per °C, 28–37 °C; 12% per °C, 37–42 °C) (Fig. 1). The slightly reduced spikelet number per panicle (2% per °C, 26–37 °C), biomass (1% per °C, 27–37 °C), and grain weight (1% per °C, 27–37 °C) contributed to the yield loss from 28 to 37 °C, but these effects were not significant when the daytime temperature was higher than 37 °C. For example, spikelet number per panicle, grain weight, and biomass remained stable when the temperature increased from 37 to 40 °C. Of all the studied yield components, panicle number was least affected by HDT, consistent with the meta-analysis study by Xiong et al. (2017). Xiong et al. (2017) also found that rice yield increased with daytime temperature when the temperature was lower than the optimum daytime temperature of 28 °C. However, we found considerable uncertainties existed when the temperature was lower than 28 °C (Fig. 1a), due to limited available experimental data in this range (Fig. S1). Therefore, the response of rice yield to daytime temperatures below 28 °C was difficult to estimate based on the current dataset.

Our results showed that the seed set rate was the most sensitive to HDT (Fig. 1d), consistent with previous studies (Jagadish et al., 2007; Satake and Yoshida, 1978). The result suggest that seed set rate can be used as the main phenotypic trait in selecting heat-tolerant germplasm. We further analyzed the seed set rate (in percentage) in response to HDT to provide a more accurate evaluation of the HDT impact (Fig. S2a). Overall, HDT negatively affected the seed set rate when the temperature exceeded the optimum daytime temperature of 29–33 °C. The average seed set rate of all rice varieties was maintained above 75% when the daytime temperature varied from 25 to 35 °C. However, it decreased rapidly from 75% at 35 °C to approximately 30% at 42 °C. Hence, 35 °C can be used to identify heat-susceptible varieties (Satake and Yoshida, 1978). Considerable differences were observed among rice genotypes/varieties. For example, T226 did not show a decrease in seed set rate even up to 39 °C (Cao et al., 2009; Tang et al., 2005). The most heat-tolerant varieties (i.e., N22 and NL-44) were reported to have seed set rates of 85% at 42.2 °C daytime temperature conditions (Bahuguna et al., 2015).

The optimum nighttime temperature for rice yield was found to be approximately 22 °C (Fig. 2a). High nighttime temperatures showed more profound negative impacts on rice yield than HDT, with approximately 7% per °C (4% per °C, 22–30 °C; 10% per °C, 30–35 °C) when exceeding the optimum daytime temperature. These detrimental effects are mainly due to reduced seed set rate (4% per °C, 22–30 °C; 6% per °C, 30–35 °C) and grain weight (2% per °C, 22–30 °C; 5% per °C, 30–35 °C) (Fig. 2b-f). When the nighttime temperatures were lower than 22 °C, rice yield increased with nighttime temperatures, which was possibly due to the increased spikelet per panicle and biomass (Fig. 2c and f). It is noted that experiments at relatively lower nighttime temperatures (e.g., <22 °C) are few, and therefore, the role of seed set rate played in this temperature range was uncertain. Overall, panicle number and spikelet per panicle had limited impacts on rice yield under HNT (>22 °C). The biomass yield response to HNT was nonlinear, with biomass yield decreasing at approximately 2% per °C from 22 to 30 °C and increasing at approximately 2% from 30 to 35 °C. Similar to HDT, HNT had a limited impact on panicle number (Fig. 2b).

High nighttime temperatures negatively impacted the seed set rate when exceeding the optimum daytime temperature of 24–25 °C (Fig. S2b). The average seed set rate of all rice varieties in the study remained above 75% when the nighttime temperature varied from 21 to 28 °C, but it dropped to 50% at 32 °C and 30% at 35 °C. The results suggest that it is likely that a nighttime temperature of 28 °C can be used to identify heat-susceptible varieties using seed set rate as a trait of choice. Current studies were mainly conducted at HNTs ranging from 29 to 35 °C under controlled environmental conditions or field-based temperature-controlled chambers (Bahuguna et al., 2017; Cheng et al., 2009; Shi et al., 2013). As illustrated in Fig. 2a, HNT negatively affected rice yield at approximately 22 °C, which was also demonstrated in previous studies in natural field conditions (Nagarajan et al., 2010; Peng

Table 1
Temperature range and means of daytime and nighttime temperature from experiments of 73 papers used in this study.

Heat stress type	No. of experiments	Control range (°C)	Heat stress range (°C)	Mean temperature (°C)
Daytime	1105	18–38	23–42	33.5 ± 4.4
Nighttime	841	14–29	16–36	26.3 ± 4.4

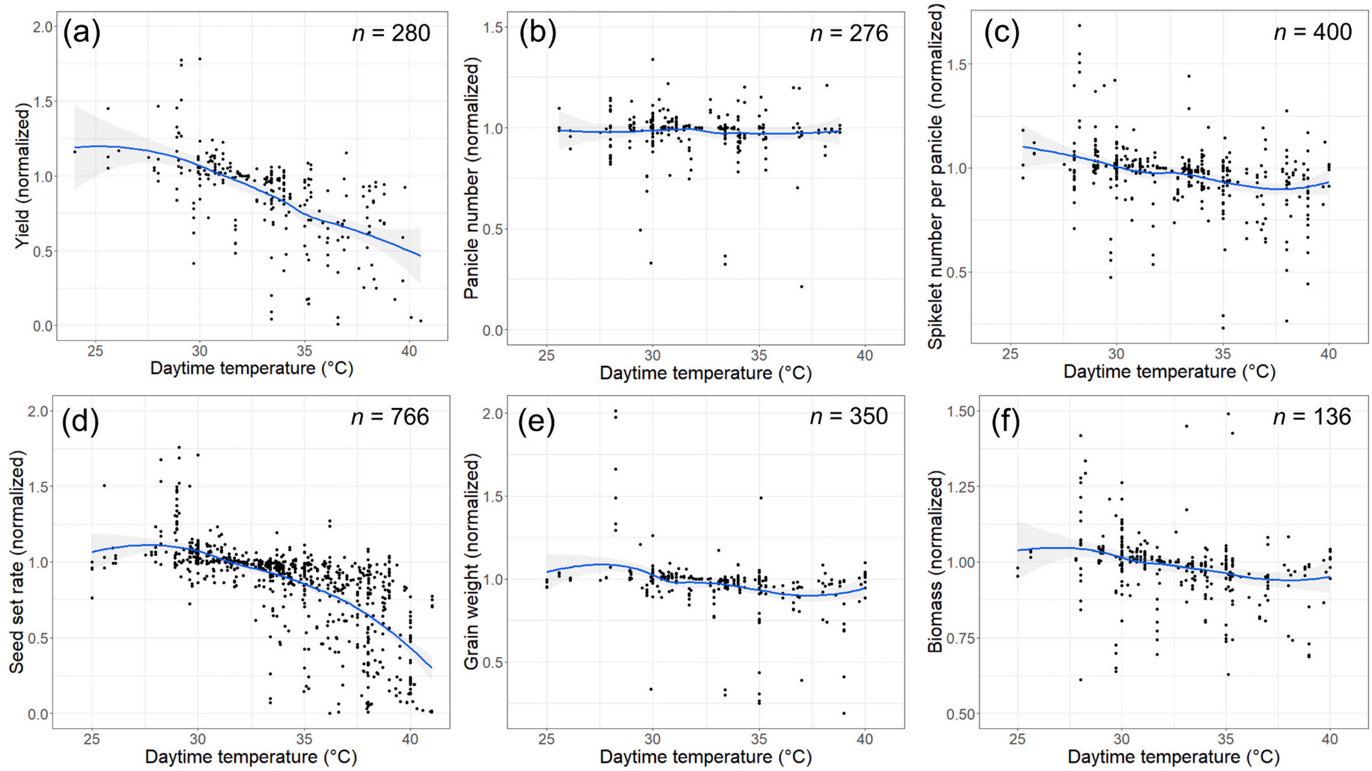

Fig. 1. Normalized rice yield, yield component, and biomass in response to high daytime temperature change (n = 2208 from 41 studies). (a) Yield, (b) panicle number, (c) spikelet number per panicle, (d) seed set rate, (e) grain weight, and (f) biomass. The values are normalized based on the reference temperature (32 °C). Shaded area indicates the 95% confidence interval for the fitted curves.

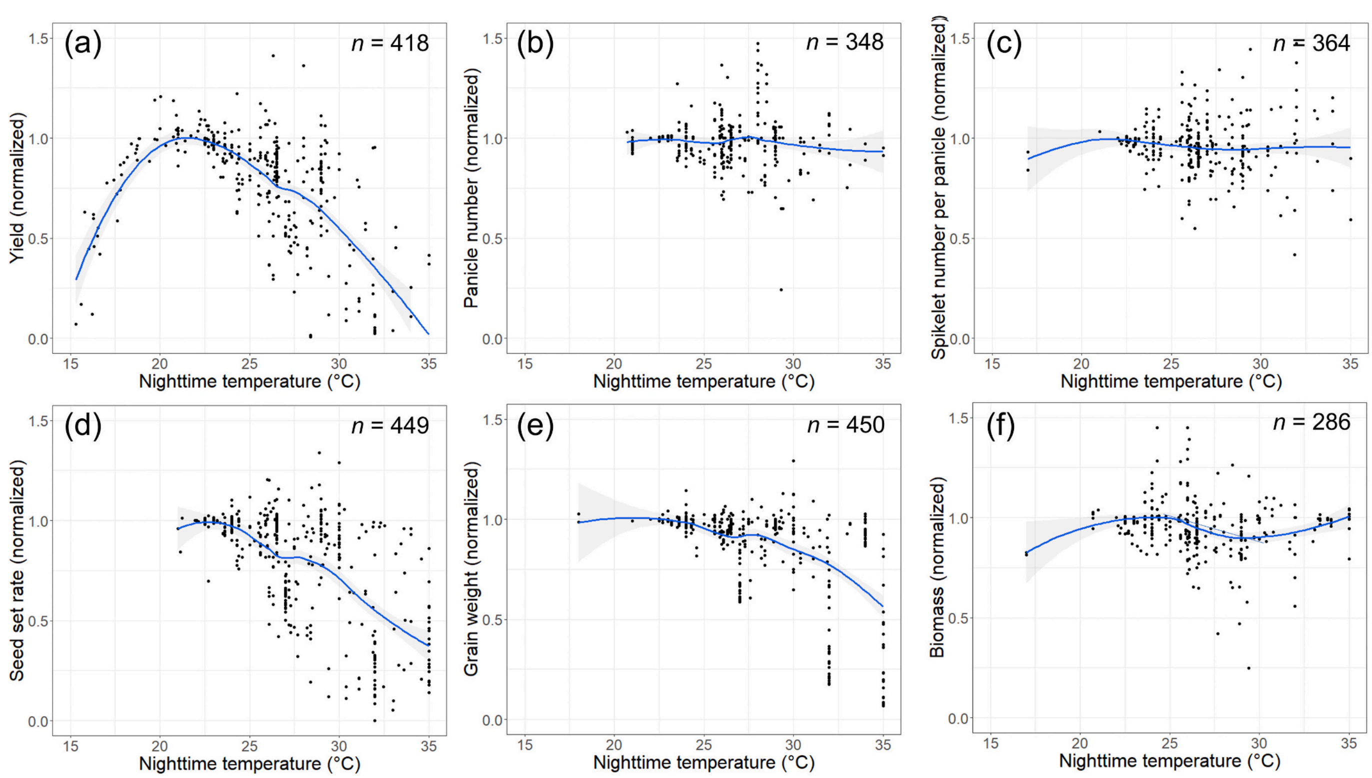

Fig. 2. Normalized rice yield, yield component, and biomass in response to high nighttime temperature change (n = 2315 from 37studies). (a) Yield, (b) panicle number, (c) spikelet number per panicle, (d) seed set rate, (e) grain weight, and (f) biomass. The values are normalized based on the reference temperature (22 °C). Shaded area indicates the 95% confidence interval for the fitted curves.

et al., 2004).

Grain weight is highly associated with grain dimensions, including length, width, and thickness (Xie et al., 2015). The normalized grain dimensions in response to HDT and HNT are detailed in Fig. S3. Elevated temperatures negatively affected grain weight/dimensions, with HNT having more profound impacts than HDT (Fig. 1e and Fig. 2e), consistent with earlier reports (Morita et al., 2005). Under HDT conditions, grain length (>34 °C) and width (>35 °C) were reduced, but grain thickness increased, which slightly compensated for the weight loss due to reduced length and width (Fig. S3a-c). Therefore, grain weight under HDT was not affected significantly (Fig. 1e). Overall, HNT had a more pronounced effect on grain width than on length and thickness (Fig. S3d-e). Reduced grain width under HNT conditions has been reported in many studies (Counce et al., 2005; Fahad et al., 2016; Morita et al., 2005; Shi et al., 2016b), which was possibly induced by endosperm cell size reduction due to reduced source availability under higher dark respiration under HNT conditions (Morita et al., 2005).

3.2. Milling yield and quality

In addition to yield impacts, HDT and HNT were found to have adverse effects on milling quality and rice grain quality, with more pronounced impacts under HNT conditions (Figs. 3 and 4). Under HDT conditions, the milled yield percentage was reduced at 1% per °C from 25 to 30 °C, stayed stable at 30–35 °C, and then was reduced at 1% per °C from 35 to 40 °C (Fig. 3a). A similar trend was also observed for head rice percentage under HDT higher than 35 °C (1% per °C from 35 to 40 °C, Fig. 3b) and brown rice percentage under HDT higher than 28 °C (<1% per °C from 28 to 40 °C, Fig. 3c).

Chalkiness is formed due to insufficient and loosely packed starch accumulations during grain-filling stages (Ambardekar et al., 2011; Dong et al., 2014; Hakata et al., 2012; Impa et al., 2021), which significantly increases the proportion of broken kernels and reduces milling quality (Fitzgerald and Resurreccion, 2009; Lyman et al., 2013). Under HDT conditions, the chalkiness almost linearly increased with elevated daytime temperature (6% per °C, > 25 °C, Fig. 3d).

We also observed a nonlinear effect of HDT stress exposure on the nutritional value of rice (Fig. 3e and f), with a slightly decreasing trend for amylose content and an increasing trend for protein content under HDT from 25 to 32 °C and relatively stable values for amylose and slightly decreased for protein contents from 32 to 40 °C. The amylose content is linked with water absorption and volume expansion during cooking, directly affecting cooking and eating quality (Ahmed et al., 2015; Han and Hamaker, 2001). Under HDT conditions, the activity of enzymes involved in starch synthesis was reduced, leading to a decreased starch accumulation in grain (Ahmed et al., 2015; Yamakawa et al., 2007; Zhang et al., 2021). A relatively stable trend of amylose content from 32 to 40 °C was probably due to the limited experimental data in this study.

High nighttime temperature significantly affected milling yield and quality, with reduced percentages of milled, head, and brown rice, increased chalkiness, and reduced amylose content, and protein content under HNT conditions (Fig. 4). The effect of HNT stress exposure on the milling yield and quality was nonlinear. At a relatively low night temperatures (18–23 °C), the milled rice and head rice percentages slightly decreased (2% per °C) with increasing nighttime temperature. The effects of HNT on milled rice and head rice percentages were stable from 23 to 26 °C. At relatively higher HNT (>26 °C), milled rice and head rice percentages were decreased at 5% and 3% per °C, respectively. The brown rice percentage decreased by <1% per °C from 18 to 23 °C and by 2% from 23 to 26 °C. Kernal chalkiness increased under HNT at a rate of 3% per °C from 18 to 30 °C, with relatively stable chalkiness under HNT from 23 to 26 °C. High nighttime temperature also negatively affected the nutritional value of rice (Fig. 4e and f), with amylose content and protein content decreasing at 1% (22–35 °C) and 3% (22–32 °C) per °C, respectively.

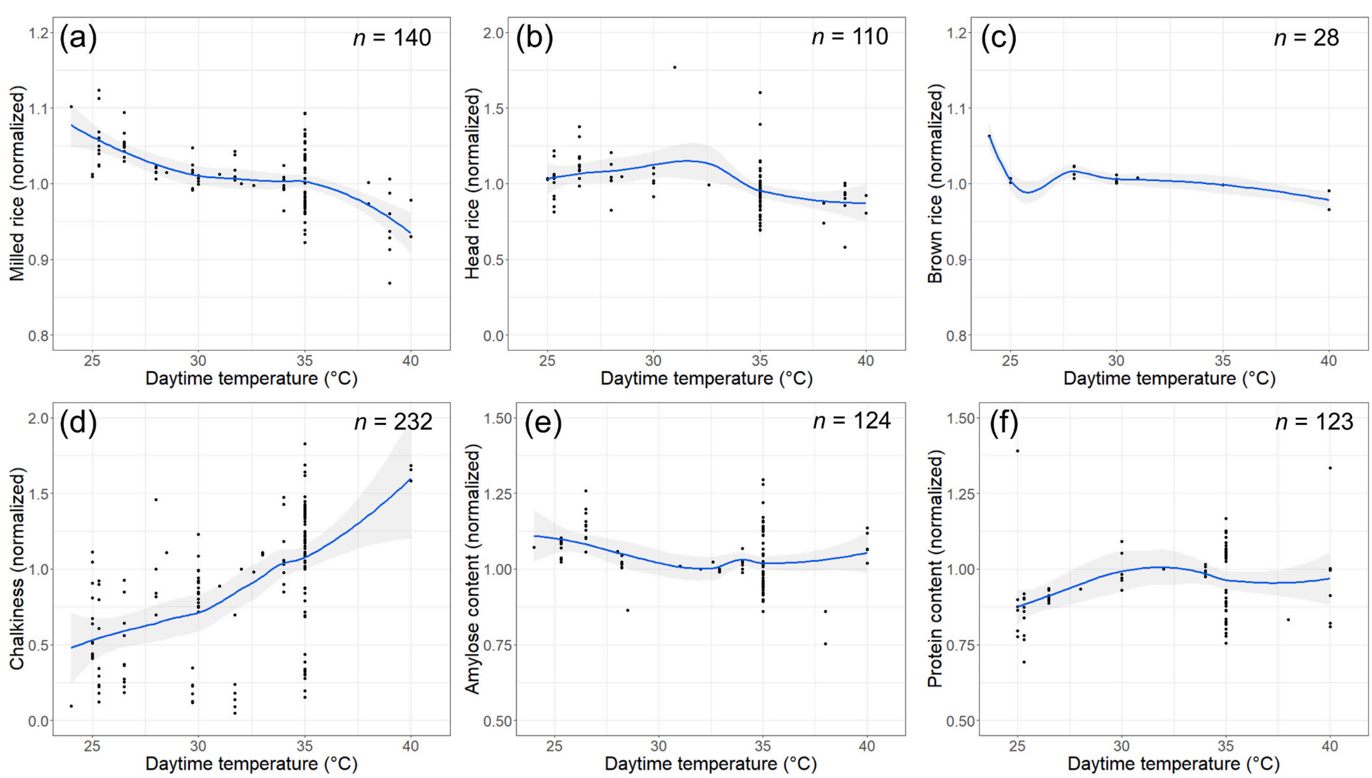

Fig. 3. Normalized milling yield and grain quality in response to high daytime temperature change ($n = 758$ from 18 studies). (a) Milled rice percentage, (b) head rice percentage, (c) brown rice percentage, (d) chalkiness, (e) amylose content, and (f) protein content. The values are normalized based on the reference temperature (32 °C). Shaded area indicates the 95% confidence interval for the fitted curves.

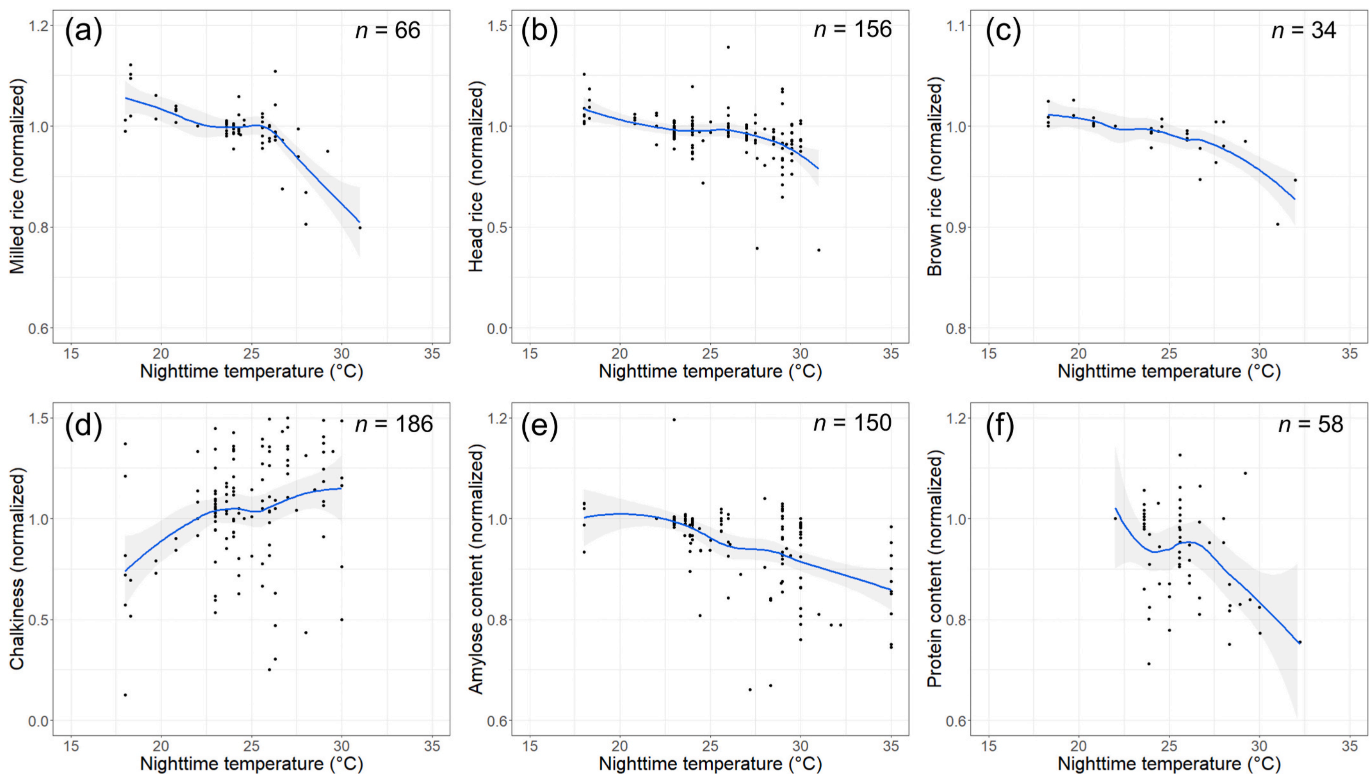

Fig. 4. Normalized milling yield and grain quality in response to high nighttime temperature change ($n = 650$ from 17 studies). (a) Milled rice percentage, (b) head rice percentage, (c) brown rice percentage, (d) chalkiness, (e) amylose content, and (f) protein content. The values are normalized based on the reference temperature (22 °C). Shaded area indicates the 95% confidence interval for the fitted curves.

3.3. Relationship between rice yield and temperature

The optimal models for simulating rice yield in response to HDT and HNT are shown in Fig. 5, with detailed comparisons with other models provided in Tables S2 and S3. The quadratic fixed-effect with a linear effect random regression model (i.e., Eq. 5) produced the best fit for HDT conditions, with an R^2C value of 0.52 and the lowest AIC value of 11.5. It should be noted that limited experimental data ($n = 12$) were available for HDT conditions lower than 28 °C and the trend (slope) for yield in response to daytime temperatures between 24 and 28 °C was not statistically significant ($P = 0.49$) based on the Student's test. Consequently, we assumed a constant normalized yield for daytime temperatures within this range. For HNT conditions, the quadratic fixed-effect with a quadratic effect random regression model (i.e., Eq. 6) was the best fit, with an R^2C value of 0.71 and the lowest AIC value of −166.8. Our analysis indicated that including a random effect that allowed rice varieties to vary in the intercept term (Eq. 4) did not significantly improve the model performance for either HDT or HNT. However, allowing the slopes of rice varieties to vary in addition to the intercepts (Eq. 5) produced the best fit for HDT conditions, suggesting that grain yield might exhibit similar trends at lower HDT and much more significant variations as daytime temperature increases toward extremes. Our analysis also showed that grain yield displayed more complex variations among different varieties under HNT conditions, as indicated by the best-fit model with the random effect due to rice varieties varying in intercept, slope, and curvature (Eq. 6). These results

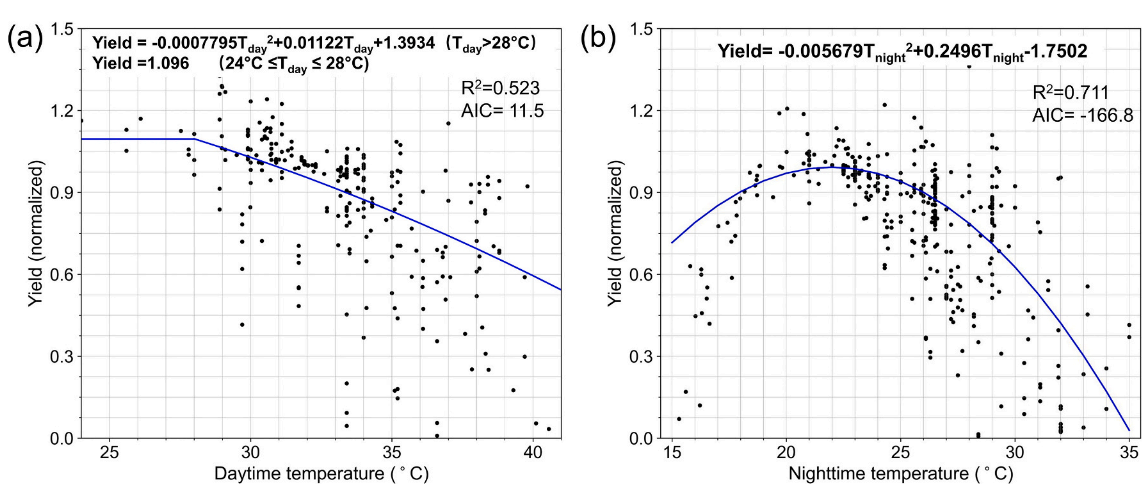

Fig. 5. Projected yield change in response to high (a) daytime and (b) nighttime temperature changes.

indicate that rice varieties exhibit different phenotypic plasticity in response to HDT and HNT, highlighting the importance of evaluating variations between different rice varieties when selecting heat stress-tolerant ones.

The derived HDT/HNT-yield relationship can be directly used to evaluate heat stresses on global and regional rice yields. Our results separated the impacts of HDT and HNT on rice yield, revealing that HNT plays a more important role than HDT in determining rice productivity. As discussed in Section 3.2, data suggest that high temperatures, especially HNT, significantly reduce milling yield and impact grain quality. Neglecting these effects may underestimate the economic implications of market loss under high temperatures. However, due to the limited available data, we did not provide a milling yield/quality-yield relationship. Further research is required to gain a better understanding of HDT/HNT impacts on milling yield and grain quality.

4. Discussion

Heat stress is a critical issue facing rice production in rice growing areas, as warming temperatures due to climate change are expected to negatively impact rice yield and quality. Here, we analyzed the overall responses of rice varieties at population level to HDT and HNT, as well as the upper-temperature thresholds (or temperature range) for seed set, yield traits, and quality traits, as shown in Fig. 6. We also analyzed the impacts of HDT and HNT stress on milling yield and quality, as well as the nutritional quality of rice. Our findings can help in making informed strategies to mitigate the adverse effects of heat stress on rice productivity, and quality, evaluate heat-tolerant germplasm, and provide valuable insights into the potential impacts of climate change on rice production system.

The derived HDT/HNT-yield relationship allows for the separate analysis of the effects of HDT and HNT on rice productivity, which can serve as a valuable tool for evaluating the impact of heat stresses on rice yield, both globally and regionally. Collectively, our results showed that HNT has a more significant negative impact on rice yield than HDT, which is in agreement with previous field studies (Peng et al., 2004; Welch et al., 2010). Since the mean nighttime increase was approximately three times the increase in daytime temperature (Peng et al., 2004), we concluded that rice yield declined by approximately 13% (*i.e.*, $1.5^{\circ}C \times 7\%/^{\circ}C + 0.5^{\circ}C \times 6\%/^{\circ}C = 13\%$) for a 1 °C increase in mean temperature. This yield reduction rate was comparable to the field study conducted by Peng et al. (2004) from 1979 to 2003, in which 10% and 15% yield losses were estimated for a 1 °C increase in nighttime and mean temperature, respectively. As expected, this yield reduction rate was much higher than that in studies using meta-analysis to illustrate rice production in response to mean temperature increases. For example, using a meta-analysis, Zhou et al. (2021b) showed that rice yield in a rice-wheat rotation system in China was significantly decreased by 7.1% under a mean temperature increase of 0.4–1.4 °C. Challinor et al. (2014) carried out a meta-analysis to illustrate rice production in response to mean temperature increases of 1–5 °C in both temperate (decreased by 2–20%) and tropical regions (decreased by 0–5%).

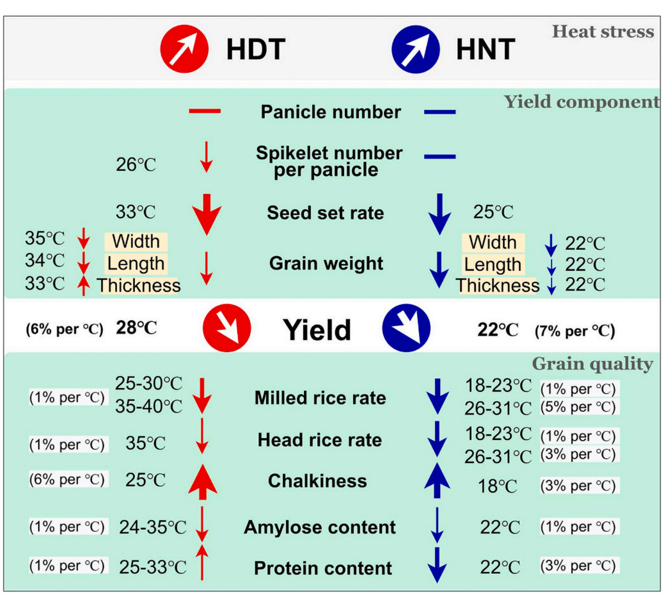

Fig. 6. Rice yield and grain quality responses to high daytime (HDT) and nighttime (HNT) temperature changes. The temperature or temperature range indicates the upper-temperature thresholds or range for each trait. The width of the arrows denotes the intensity of the effect by HDT and HNT on respective trait.

Rice yield is determined by the productive panicle number, spikelet number per panicle, seed set rate, and grain weight. Our meta-analysis suggested that the decreased seed set rate under heat stress was the primary driver of rice yield loss under both HDT and HNT conditions. Therefore, selecting heat stress-tolerant varieties with a high seed set rate under HDT/HNT conditions is a promising strategy to ensure rice productivity in a warming climate. It is worth noting that previous studies have shown a negative relationship between panicle number and spikelet number per panicle due to competition for photosynthetic assimilates (Fageria, 2007). Our finding, however, revealed that panicle number had limited impacts on rice yield at the population level under HDT/HNT. Instead, the reduced spikelet number per panicle accounted for the yield loss under HDT, mainly due to decreased photosynthesis assimilates. We also observed that HNT has more severe impacts on grain weight, with no significant impacts under HDT conditions. However, this may vary at the individual variety level. For example, Shi et al. (2017) reported that HDT has more severe impacts on grain weight than HNT, and the impact of HNT on grain weight was compensated by the rate and duration of grain filling. Overall, our study highlights the importance of considering multiple factors that affect rice yield and the need for targeted breeding effects to develop heat stress-tolerant rice varieties that can maintain high yields under HDT and HNT conditions.

Despite the critical importance of milling yield and quality in the global rice trade, the impacts of HDT/HNT on these parameters have been largely neglected in current studies of temperature stresses on regional and global rice yields. Here, we summarized the upper-temperature thresholds and changing rates with specific temperature ranges of major milling yield and quality parameters (Fig. 6). Our meta-analysis showed that both HDT and HNT reduced the percentages of brown rice, milled rice, and head rice in rough rice, but the impacts of HNT was more significant. Although the mechanisms underlying these negative impacts require further investigation, our findings offer crucial information for improving historical and future projections of heat stress impacts on rice production. The economic implications of yield loss due to high temperatures are likely to be underestimated without adequately accounting for the impacts on rice quality. We also found that HDT and HNT heat stress could substantially alter the nutritional quality of rice, with HNT having a more significant impact. This alternation in rice nutritional quality may pose a significant health risk, especially in regions where rice is a primary food source (Ahmed et al., 2015). Our results underscore the need for further research on the effects of high temperature stress on rice traits such as milling yield, quality, and nutritional value, including effect on essential elements that are important for rice marketability as well as human nutrition point of view.

Previous studies suggest that the highest ambient temperature during day and night is important, but the duration of heat stress can also play a critical role in determining the tolerance or susceptibility of rice germplasm to heat stress (Shi et al., 2016a; Zhen et al., 2020a; Zhen et al., 2020b). Therefore, heat degree-hours (HDH), defined as the cumulative heat-hours that a rice plant is exposed during daytime and nighttime above a certain threshold temperature, could be an effective indicator to assess the impacts of HDT and HNT on rice yield and quality. The calculation of HDH is illustrated in Eqs. (7)–(9):

$$HDH = \sum_{i=1}^{n} HDH_i \tag{7}$$

$$HDH_i = \sum_{j=1}^{24} HHD_j \tag{8}$$

$$HHD_j = \begin{cases} \left(\frac{T_{max} + T_{min}}{2}\right)_j - T_c, & \left(\frac{T_{max} + T_{min}}{2}\right)_j > T_c \\ 0, & \left(\frac{T_{max} + T_{min}}{2}\right)_j \leq T_c \end{cases} \quad (j = 1, 2, \ldots 24) \tag{9}$$

where HDH is the sum of daily heat degree-hours (HDH_i) during n days period, °C·hour; HHD_j is the hourly data of HDH, °C·hour; T_{max} and T_{min} are the maximum and minimum temperature at hourly intervals. T_c is the threshold temperature, which could be set as 28 °C for HDH during daytime and 22 °C for HDH during nighttime based on our analysis. Here, nighttime duration is suggested from 2000 h (8:00 p.m.) to 0600 h (6:00 a.m.) (Counce et al., 2009; Mendez et al., 2021).

The duration of temperature treatment varied widely across the selected studies (Table S1). Most studies applied heat stress throughout the growing season, from transplanting to maturity (Bahuguna et al., 2017; Chakrabarti et al., 2010; Desai et al., 2021), while others applied heat stress only during specific stages of growth, such as vegetative (Glaubitz et al., 2014), flowering (Ishimaru et al., 2010; Jagadish et al., 2007), or grain filling stages (Cooper et al., 2008; Song et al., 2013). Therefore, considering the duration of heat stress at specific growth and developmental stages could be useful to improve our current analysis of the tolerance or susceptibility of rice germplasm to heat stress. Nevertheless, detailed temperature data from heat stress experiments are required to calculate HDH, particularly those conducted in the field or field-based temperature-controlled chambers. Unfortunately, such detailed data are usually unavailable in current published studies. Further research is necessary to collect, share, and analyze these data to enhance our understanding of the effects of heat stress on rice, which, ultimately, allows us to better predict the impact on heat stress on rice production under a changing climate. Such efforts could inform the development of more effective strategies and traits for mitigating the impact of heat stress on rice crops.

5. Conclusions

We have developed relationships between rice yield and high daytime and nighttime temperatures (HDT and HNT) using data from greenhouse experiments and field trials of 73 studies. The results confirmed that HNT had a more pronounced negative impact on yield than HDT. We found that rice yield decreased by 7% and 6% for every 1 °C increase in HNT and HDT, respectively, when exceeded the optimum daytime temperature of 22 and 28 °C. Additionally, we examined the yield components to identify the driving factors of yield loss in response to HNT and HDT. Our meta-analysis showed that a decreased seed set rate under heat stress was the primary cause of rice yield loss under both HDT and HNT conditions, suggesting that the selection of heat stress-tolerant varieties with high seed set rates at HDT/HNT is the most effective strategy to mitigate the negative impacts of high temperatures on rice yield. Additionally, our study found that both HDT and HNT negatively affected grain quality by increasing chalkiness and decreasing milling yield, and HNT had a significant impact on nutritional quality in rice. These findings imply that current estimations of the economic impacts of yield loss under high temperatures could be underestimated without considering additional impacts on grain quality. Overall, our study provides valuable insights for understanding the effects of temperature on rice yield and quality and for developing strategies to mitigate the negative impacts of high temperatures on rice production.

CRediT authorship contribution statement

Qiong Su: Conceptualization, Data curation, Formal analysis, Methodology, Writing – original draft. **Jai S. Rohila:** Methodology, Writing – review & editing. **Shyam Ranganathan:** Methodology, Writing – review & editing. **R. Karthikeyan:** Conceptualization, Supervision, Project administration, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data used in this study can be freely downloaded at: https://bit.ly/rice-heat-stress-dataset. The code used in this study will be made available from the corresponding author(s) upon request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2023.165256.

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