Effectiveness of heat tolerance rice cultivars in preserving grain appearance quality under high temperatures - A meta-analysis

Hitomi Wakatsuki*, Takahiro Takimoto*, Yasushi Ishigooka**, Motoki Nishimori*, Mototaka Sakata***, Naoya Saida***, Kosuke Akagi***, David Makowski****, Toshihiro Hasegawa*

* Institute for Agro-Environmental Sciences, NARO, Tsukuba, 305-8604, Japan

** Hokkaido Agricultural Research Center, NARO, 082-0081, Japan

***Kochi Prefectural Agricultural Research Center, Nankoku, 783-0023, Japan

**** Applied Mathematics and Computer Science (MIA 518), INRAE AgroParisTech, Université Paris-Saclay, 75231, Paris, France

Email addresses

Hitomi Wakatsuki, kawatsuki55@affrc.go.jp
Takahiro Takimoto, t.takimoto@naro.affrc.go.jp
Yasushi Ishigooka, isigo@naro.affrc.go.jp
Motoki Nishimori, mnishi@naro.affrc.go.jp
Mototaka Sakata, mototaka_sakata@ken2.pref.kochi.lg.jp
Naoya Saida, naoya_saida@ken4.pref.kochi.lg.jp
Kosuke Akagi, kousuke_akagi@ken4.pref.kochi.lg.jp
David Makowski, david.makowski@inrae.fr

Corresponding Autor
Toshihiro Hasegawa
Institute for Agro-Environmental Sciences
National Agriculture and Food Research Organization (NARO)
3-1-3 Kannondai, Tsukuba, Ibaraki 305-8604, Japan
Tel: +81 29 838 8204
E-mail: thase@affrc.go.jp

Abstract

Background: Climate change, particularly rising temperatures, negatively affects rice grain quality, increasing chalky grain percentage (CG) and hampering rice grade and price. Heat-tolerant cultivars have been bred and released since the 2000s, but the effectiveness of heat tolerance in reducing the occurrence of CG has yet to be quantified.

Objectives: This study aimed to measure the effectiveness of breeding for better heat tolerance in reducing the negative impact of high temperatures on rice quality.

Methods: Through a systematic literature search, we developed a dataset including 1297 field observations covering 48 cultivars from five different heat tolerant ranks (HTRs) at 44 sites across Japan. A linear mixed-effect model (LME) and a random forest model (RF) were fitted to the data to analyze the effect of HTR and climatic factors such as the cumulative mean air temperature above 26 °C (TaHD), mean solar radiation, and mean relative humidity for 20 days after heading on CG.

Results: The LME model explained 63 % of the variation with a 14% RMSE. The RF partial dependence plot revealed that the logit-transformed CG response to climate factors was linear, supporting the assumption of LME. The statistical analysis showed that CG increased as a function of TaHD ($P < 0.001$), with significant differences among HTRs ($P < 0.001$). The strongest effect of TaHD was obtained for the lowest HTR and was found to decrease with increasing HTR. CG also increased with higher relative humidity ($P < 0.001$) and solar radiation ($P < 0.01$). Based on our modeling, we estimated that as TaHD increased from 20 to 80 °Cd (equivalent to a mean temperature increase from 27 °C to 30 °C), CG increased by 66 points for cultivars with the lowest HTR, 45 points for cultivars with an intermediate HTR, and 19 points for cultivars with the highest HTR. Raising HTR by just one step (from intermediate to moderately tolerant) is projected to increase the proportion of first-grade rice at a grain-filling temperature of 27 °C, but tolerance levels need to be improved further in case of stronger warming.

Conclusions: The effect of high temperatures on CG was highly dependent on the cultivar's HTR. Improvements in HTR effectively reduce the negative impacts of high temperatures on rice grain quality.

Significance: Heat-tolerant cultivars are projected to suppress the prevalence of CG more than threefold compared with heat-sensitive cultivars when grain-filling temperature increases from 27 to 30 °C.

Keywords

Climate change adaptation, Chalky grain, High-temperature, Oryza sativa, Systematic literature search

1. Introduction

Ongoing climate change, particularly rising temperatures, negatively affects rice grain yield and quality (Krishnan et al., 2011). Since rice (*Oryza sativa*) is mostly consumed as whole grain, the quality of rice involves a few unique traits different from other cereals, including milling, eating and cooking properties, grain appearance, and nutritional quality (Neerja and Renu, 2020). Among various quality traits, appearance quality, especially grain chalkiness, has been of primary concern in major rice-production areas in the world because it affects the milling, eating, and cooking properties and is strongly affected by climate change (Cheng et al., 2005; Fitzgerald et al., 2009; Chun et al., 2010; Lanning et al., 2011; Ali et al., 2019). Not only does low quality with CG lower the market price, but milling losses caused by fragile CG also reduce head rice yield and create direct income reduction (Lyman et al., 2013). A few simulation studies estimated increasing economic losses due to the further degradation of grain quality resulting from increased temperatures under climate change by the mid-century in Japan (Masutomi et al., 2019) and in Europe (Cappelli and Bregaglio, 2021).

The chalkiness of grain is due to the presence of an opaque part in the grain endosperm, and is often classified into milky-white, basal-white, and white-back/belly, depending on the locations where opaque parts appear(Nagato and Ebata, 1965). It looks opaque because light reflects irregularly in endosperms with larger air spaces formed by loosely packed starch granules, often caused by insufficient starch accumulation induced by high temperatures during the grain-filling period (Morita, 2008). The occurrence of CG increases as the temperature during the grain-filling period increases. In Japan, as extremely high temperatures have become more frequent since the beginning of the 1990s (Japan Meteorological Agency, 2015), CG has been increasingly reported across the country by the Ministry of Agriculture, Forestry, and Fisheries of Japan (MAFF, 2021). To reduce the heat-induced damage on appearance quality, genetic improvement of heat tolerance is considered effective, and heat-tolerant cultivars have been bred and released since the 2000s(Ishimaru et al., 2016). The cultivation area of heat-tolerant cultivars increased from 2.3 % in 2010 to 11 % in 2020, and it is expected to expand more (MAFF, 2021).

However, tolerance levels differed even among 'heat-tolerant cultivars'. In 2018, MAFF established nine heat tolerance ranks (HTRs) to promote heat tolerance breeding and assigned several check cultivars to each HTR (MAFF, 1998; Kaji et al., 2016; Tamura et al., 2018). Rice breeders determine the HTRs of rice cultivars by comparing their proportions of CG in high-temperature settings (mean temperature for 20 days after heading of around 27 °C). They provide consistent measures of heat tolerance among diverse cultivars, but the effects of introducing different HTRs on the occurrence of CG are yet to be quantified. A lack of quantified effectiveness of different HTRs in response to temperatures limits our ability to develop quantitative breeding targets in specific regions and at specific global warming levels.

Many experimental studies have investigated the effects of high temperatures on grain appearance quality of various cultivars across Japan for different purposes, including variety selection and management improvement (See a list of references in Supplementary Materials). A few studies

105 have quantified the effects of air temperature and solar radiation on the occurrence of CG in specific
106 conditions (Okada et al., 2011; Masutomi et al., 2015; Takimoto et al., 2019). Masutomi et al. (2022)
107 conducted a parameter sensitivity test to demonstrate the importance of CG dependence on
108 temperature in the impacts of climate change on rice grain quality. It remains unclear, however, how
109 much actual cultivars with high HTRs can alleviate the negative impacts of ongoing and projected
110 climate change, which is necessary to develop concrete breeding targets in different regions and
111 global warming levels.

112 Previous modelling studies often used parameters for individual cultivars, referred to as
113 "genetic coefficients" (e.g., Mavromatis et al., 2001), but lack of data availability frequently limits
114 model applicability for a large number of cultivars. An option would be to use the same set of
115 coefficients for all cultivars belonging to the same HTR groups, thus reducing the need for cultivar-
116 specific coefficients. The advantages of deriving HTR-based parameters are twofold. First, the
117 effectiveness of increasing heat tolerance levels can be easily quantified in response to global
118 warming levels, leading to the development of breeding targets for specific areas and temperatures.
119 Second, each parameter can be derived using more observations covering a wide range of
120 environments, improving the robustness of parameters and estimates. To examine the above
121 hypothesis, we need a large dataset covering cultivars with various HTRs obtained from widely
122 different environments. In this study, we conducted a systematic literature and database search to
123 develop a nationwide dataset on rice grain appearance quality of cultivars of different HTRs. We then
124 performed a meta-analysis to model the effects of temperature and other weather conditions on the
125 CG of various HTRs. The results are used to examine the effectiveness of cultivar improvement in
126 reducing the negative impact of temperature on rice quality.

127

2. Material and Methods

2.1. Selection of studies

We conducted a systematic literature search from three different sources to obtain CG data of rice cultivars grown under field conditions (Figure1).

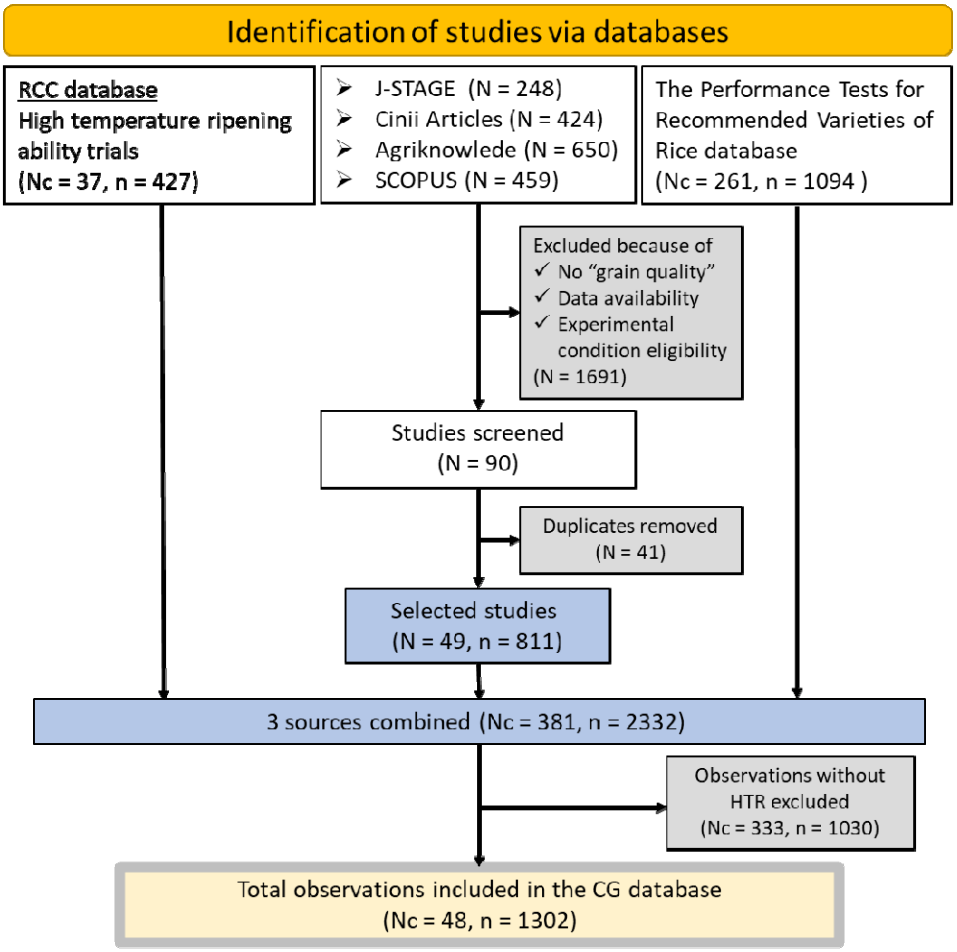

Figure 1. A PRISMA diagram depicting data collection and selection processes. Nc is the number of cultivars, N is the number of studies (articles) found through the literature search, and n is the number of observations.

The first data source is the Rice Cultivar and Characteristics (RCC) database developed by the Institute of Crop Science, NARO (https://ineweb.narcc.affrc.go.jp/), containing breeding progress, morphological and ecological characteristics, and appearance and taste quality characteristics of

142 more than 500 varieties registered by MAFF. In this study, we focused on 63 cultivars： 39 cultivars
143 selected as standard cultivars of different heat tolerance ranks under the Plant Variety Protection
144 and Seed Act (No. 83 of 1998)(MAFF, 1998), and 24 cultivars released as heat-tolerant cultivars
145 (Supplementary Table1). Using 63 cultivars' names as search terms, we searched experimental data
146 in the RCC database and selected relevant data according to the following criteria. i) Experiments
147 were conducted under open field conditions without warming treatments. Pot experiments and
148 glasshouse experiments were excluded. ii) Experimental results should include CG, heading dates,
149 and precise experimental field locations. In this study, we defined CG as the total % of milky-white,
150 basal-white, belly-white, and back-white grains. We identified 427 observations of 32 cultivars to
151 meet our criteria from the database.

152 The second data source consists of four databases containing peer-reviewed scientific papers
153 and bulletins of national and prefectural agricultural research stations in Japan:
154 i) J-STAGE (https://www.jstage.jst.go.jp/browse/-char/en)
155 ii) CiNii Research (https://cir.nii.ac.jp/?lang=en)
156 iii) SCOPUS
157 iv) AgriKnowledge, a database for agricultural science and technology of Japan
158 (https://agriknowledge.affrc.go.jp/).
159 In December 2021, we searched J-STAGE and CiNii Research, using "Kouon-tojuku" in Japanese,
160 meaning "grain filling under high temperatures", as a search term, and obtained 248 and 424 results,
161 respectively. For the SCOPUS search, the following equation was used;
162 **Search equation:** PUBYEAR > 2001 AND (TITLE-ABS((("heat stress tolerance" OR "heat tolerance" OR
163 "heat stress") AND ("genotyp*" OR "cultivar" OR "grain quality" OR "nutrient quality"))) OR
164 AUTHKEY((("heat stress tolerance" OR "heat tolerance" OR "heat stress") AND ("genotyp*" OR
165 "cultivar" OR "grain quality" OR "nutrient quality")))) AND (TITLE-ABS({greenhouse gas} OR {global
166 warming} OR {climate change} OR {climatic change} OR {climate variability} OR {climate warming}) OR

AUTHKEY({greenhouse gas} OR {global warming} OR {climate change} OR {climatic change} OR {climate variability} OR {climate warming})) AND NOT ((TITLE-ABS(MRV) OR AUTHKEY(MRV))) MRV stands for Measurement, Reporting, and Verification, the process for quantifying greenhouse gas emissions, and was used with "NOT" to exclude papers that focused on climate change mitigation. The SCOPUS search resulted in 459 articles. In June 2022, we conducted an additional search in Agriknowledge using the 63 cultivars' names as a search string and collected 650 articles. From a total of 1781 papers obtained from the four databases, we manually selected studies using the same two criteria described earlier. This manual selection screened 1691 papers and returned 90 studies. After removing duplicates, 49 studies (articles) were selected containing 811 field observations of 128 cultivars.

The third data source was the Performance Tests for Recommended Varieties of Rice data of Kochi Prefecture from 2013 to 2020, provided by the Kochi Prefectural Agricultural Research Center, containing 1094 sets of field observations of 261 cultivars. In all three sources combined, the dataset consists of 2332 observations of 381 cultivars collected between 1994 and 2020 in 46 experimental sites covering 33 prefectures (Figure 2).

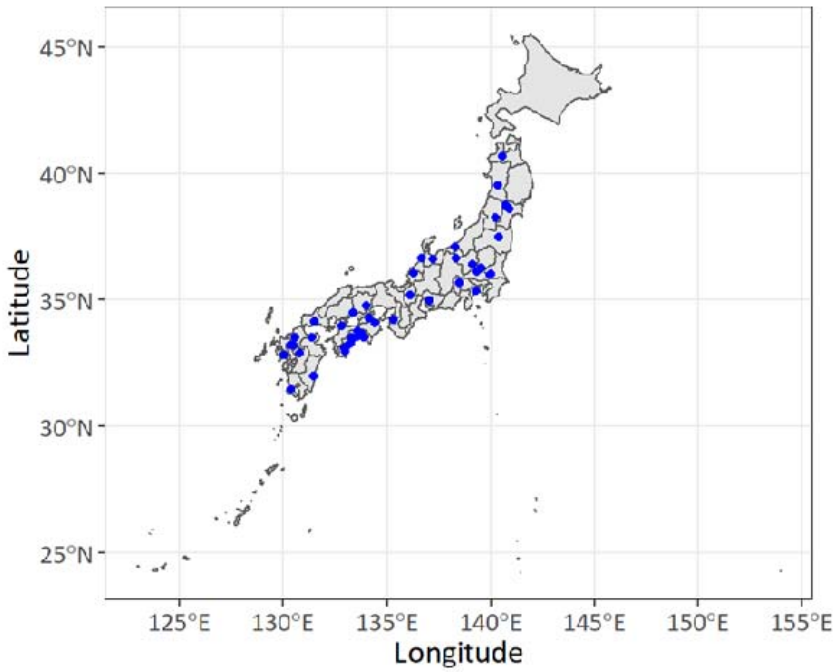

Figure2. Geographical distribution of the 46 experimental sites in the rice quality dataset in Japan

2.2 Data extraction

Table1. List of variables obtained from the systematic literature search

Variables	Unit	Definition
Prefecture		Prefecture of experimental site
Municipality		Municipality of experimental site
Institution/Station		Name of institution and or experimental station
Latitude	°N	Latitude of experimental site
Longitude	°E	Longitude of experimental site
Altitude	m	Altitude of experimental site
Year		Year of experiment
Cultivar		Name of cultivar
Heading DOY		Heading day of year
HTR		Heat Tolerance Rank (HTR) from 3 (susceptible) to 7 (tolerant)
Tave	℃	Average temperature of 20 days after heading
TaHD	℃ d	Cumulative mean air temperature above 26 ℃ for 20 days after heading
SR	$MJ\ m^{-2}\ d^{-1}$	Average solar radiation for 20 days after heading
RH	%	Average relative humidity for 20 days after heading
CG	%	% of chalky grains
Reference		Source of the data records

We extracted attributes such as prefecture, location of experimental sites, latitude and longitude (when available), cultivar name, heading date, and grain quality for 2332 observations (Table 1). In addition to the variables listed in Table 1, the dataset contains sieve size for grain screening and CG measurement methods, such as “manual visual inspection” and “mechanical grain discriminator”. The standard errors and numbers of replicates were not available in the selected studies and could thus not be extracted. Of the 321 cultivars in our dataset, 48 have been classified in one of the existing heat tolerance ranks, while the rest have not been classified. Of the 48 cultivars with known HTRs (Table 2), 33 were listed in the MAFF guideline, ten were rated in reference to the standard cultivars, and their HTRs were reported in the RCC database. HTRs of the other five cultivars were obtained from the literature (Wada et al., 2010; NARO, 2011; Mizobuchi et al., 2018; NARO, 2018) (Table 2). A total of 1302 observations of the 48 classified cultivars were registered in our dataset. However, data in the zero nitrogen fertilizer plots (n = 5) were excluded from the following statistical analysis because nitrogen deficiency was reported to increase CG substantially (Wakamatsu et al., 2008) and hinders cultivar comparisons. The 48 cultivars registered in our dataset belonged to HTRs ranging from 3 (susceptible) to 7 (tolerant) (Table 2). Currently, cultivars with HTRs higher than 7 or lower than 3 have not been registered.

Weather data were extracted from the gridded daily meteorological dataset with a 1-km resolution developed by NARO (Ishigooka et al., 2017). We averaged daily mean temperature, solar radiation (SR), and relative humidity (RH) for 20 days after heading, a critical period affecting the occurrence of CG (Morita, 2008). Where shading treatments were imposed, the incident SR was corrected using the shading ratio reported in each study. We derived TaHD as a heat stress index for rice quality, defined as the cumulative mean air temperature above the threshold temperature (T_b) for 20 days after heading, following earlier research (Usui et al., 2016; Ishigooka et al., 2017; Nishimori et al., 2020) as follows;

TaHD = $\sum_{i=1}^{20} \max\ (Ta_i - Tb, 0)$

Ta_i is the daily mean temperature on the *i*-th day from the heading date (Table 1). Tb was set at 26 °C in our study based on a preliminary test that showed that 26 °C was appropriate across different HTRs (Supplementary Figure 1), in agreement with previous studies (Usui et al., 2016; Ishigooka et al., 2017; Nishimori et al., 2020).

Table 2. Number of observations (n) and names of cultivars for each heat tolerance rank (HTR) group

HTR	n	Cultivars
3	296	Akanezora[1)], Akisayaka, Aoinokaze, Hinohikari, Hatsuboshi, Matsuribare, Sainokagayaki, Satojiman
4	83	Kinuhikari, Koganebare, Koisomeshi[3)], Sinrei, Tachiharuka, **Yumiazusa**[2)]
5	540	Akitakomachi, **Chihominori**, **Emidawara**, Haenuki, Harumoni[4)], Hitomebore, **Inahokkori**, **Kankinokaze**, Koshihikari, Mutsuhomare, Nikomaru, Nipponbare
6	159	**Akiharuka**, Akisakari, Fukei227, Hanaechizen,Koganemasari, **Koinoyokan,** Kokoromachi, Mineharuka, **Nijinokirameki**, , Nishihikari, Shifukunominori, Tochiginohoshi, **Tsukiakari,** Tsuyahime, **Tsuyakirari**
7	224	Eminokizuna, Fusaotome, Genkitsukushi[5)], Natsuhikari[6)], Natsuhonoka, Otentosodachi, Yosakoibijin[6)]
Total	1302	

1) Cultivars in plain text are standard cultivars designated to each HTR in the MAFF guideline (MAFF, 1998).
2) Cultivars in bold text are recently released cultivars registered in the RCC database with their HTR classified following the MAFF guideline.
3) HTR based on NARO (2018)
4) HTR based on NARO (2011)
5) HTR based on Wada et al. (2010).
6) HTR based on Mizobuchi et al. (2018)

2.3 Statistical analysis

All analyses were conducted using R (R Core Team, 2022). We used a parametric linear mixed effects (LME) model and a non-parametric machine learning model (random forest, RF) to quantify the effects of weather variables (TaHD, mean RH, and SR) and HTR on CG. The following logit transformation was applied to stabilize the variance of CG proportion data (Yandell, 1997), logit (CG)

= ln (CG/(100-CG)). The variables TaHD, mean RH, and SR were treated as numerical variables and HTR as a factor. The use of two very different types of models (LME and RF) allowed us to test the robustness of the results to the model assumptions.

The following LME model was applied to examine the effects of HTRs and environmental factors on CG;

$$logit(CG_{ijk}) = \beta_1(HTR_j) + \beta_2(HTR_j) \times TaHD_i + \beta_3 SR_i + \beta_4 RH_i + u_i + \varepsilon_{ijk} \quad (1)$$

where *i*, *j*, and *k* are the indices of the reference-site (i.e., unique combination of article reference and site name), cultivar, and sub-treatment number for each site-cultivar, $\beta_1, \ldots, \beta_4$ are fixed parameters, u_i is a random reference-site effect, ε_{ijk} is a random residual term. The sub-treatment includes different nitrogen applications, planting patterns, or previous crops. Only TaHD × HTR interaction was included in this model because our preliminary tests indicated interactions between other environmental variables and HTR were not significant. The model was fitted using the lme4 R package (Bates et al., 2015). The significance of the effects of explanatory variables was tested using ANOVA, and differences among HTRs were tested using the marginal means of CG estimated using the emmeans package (Lenth, 2022). We also used the metafor package (Viechtbauer, 2010) to illustrate CG responses to climatic factors with 95 % confidence intervals computed using bootstrapping.

We also used an RF model to determine the effects of HTR and climatic factors on CG without making a linear assumption and without the need to select any specific interaction (all interactions are taken into account in RF). This model was implemented using the randomForest package with the following settings (mtry = 2, ntree = 500) (Liaw and Wiener, 2001). CG was also logit-transformed before training RF. The importance of variables in the RF model was evaluated with the mean increase in mean square error (MSE) (computed by random permutation of the model input values), and the partial dependence plot function was used as an analysis tool to detect influential explanatory variables and then show how the average RF model responses are influenced by each predictor.

Both LME and RF models were fitted/trained with 80% of the total observations selected randomly while keeping the same proportions of HTR categories as in the entire dataset using the "sample" function in R. The fitted/trained models were then evaluated by computing the root mean square error (RMSE) with the test data, which accounted for 20% of all observations.

3. Results

3.1 Grain quality observed in rice cultivars with different heat tolerance

The dataset used in our analysis contained 1297 CG observations for 48 cultivars of five different HTRs, obtained at 44 sites (196 site × year combinations) across Japan. HTR5 (intermediate tolerance level) recorded the most observations, accounting for 41% of the dataset, followed by HTR3 (susceptible, 23%) (Table 2). HTR4 (moderately susceptible) had the fewest observations but still had over 80 observations. CG spanned from 0 to 100 % (Supplementary Figure 2a), with a skewed distribution to the right. The overall mean CG was 20.7 %, 5.4 points greater than the median (15.3 %) (Table 3). Logit-transformed CG data, however, showed a bell-shaped symmetric distribution (Supplementary Figure 2b). The average values of CG obtained for each HTR class ranged from 12 to 29%, and declined as HTR increased (Table 3).

Air temperature, relative humidity (RH), and solar radiation (SR) averaged over 20 days after heading varied greatly among 196 site-years. The mean air temperature ranged from 20.8 °C to 30 °C with a median of 26.5 °C, implying that more than half of the observations were exposed to temperatures above the threshold temperature of 26°C (Supplementary Figure 2c). Mean SR and RH ranged from 7.4 to 23.8 MJ m^{-2} d^{-1} and from 64.2 % to 94.7 %, respectively (Supplementary Figures 2d and 2e). Weather conditions were similar among HTRs (Table 3, Supplementary Figure 2c-e). CG increased almost linearly with TaHD in all HTRs, but the increase in CG values was greater in low HTR levels than in high HTR levels (Figure 3).

Table3. Mean measured CG (%), mean and standard error and weather conditions (averaged over 20 days after heading) for each HTR

HTR	Mean CG (%) +SE			Median CG (%)	Mean Temperature (°C)	TaHD(°C d)	Mean SR (MJ m^2 d^{-1})	Mean RH (%)
3	29.4	±	6.4	24.5	26.5	24.1	16.1	78.1
4	26.4	±	6.1	22.4	26.9	28.9	16.7	76.3
5	20.6	±	5.2	16.5	26.3	21.5	16.7	80.2
6	14.6	±	4.2	11.8	26.5	23.3	16.2	80.0
7	11.8	±	3.7	8.2	26.0	18.9	16.0	82.2
Total	20.7	±	4.2	15.6	26.3	21.2	16.6	80.6

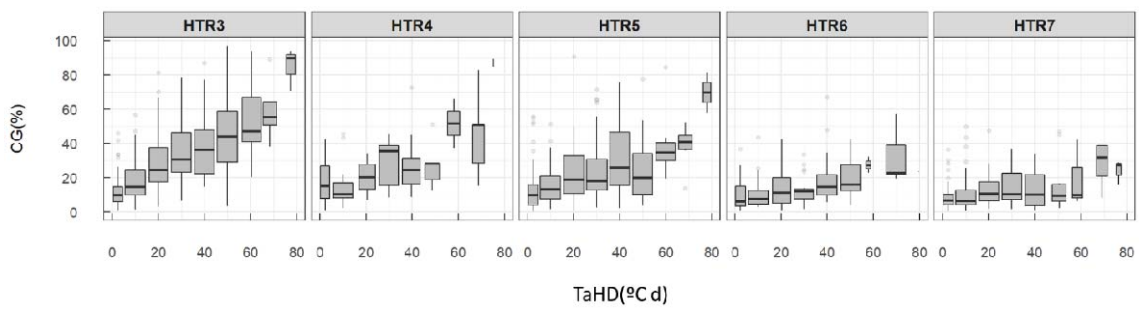

Figure3. Boxplot of measured CG (%) in relationship to TaHD (°C d, representing the sum of temperature above 26°C, 20 days after heading) for each HTR category. Each box indicates the interquartile range (IQR) and the middle line in the box represents the median. The upper- and lower-end of whiskers are median 1.5×IQR±median. Open circles are values outside the 1.5×IQR.

3.2 Model comparison

We first applied the LME model (Eq.1) to test if the effect of temperature on CG differed among HTRs and if other environmental factors had a significant effect on CG. Overall, the model explained 63% of the CG when accounting for the reference-site effects, and 33% without (i.e., based on climate- and HTR-related inputs only). The RMSE of LME with the test data set was about 15% without accounting for reference-site effects (Figure 4).

303 The LME results revealed a strong effect of TaHD on CG (Table 4, $P < 0.001$), and a significant
304 interaction between TaHD and HTRs ($P < 0.001$). The TaHD effect (i.e. coefficient) was greatest in
305 HTR3 and decreased progressively as HTRs increased. Intercepts also differed significantly among
306 HTRs, being smaller in HTR5, 6, and 7 than in HTR3 ($P < 0.001$). The effects of SR and RH were both
307 significantly positive ($P < 0.005$ and $P < 0.001$, respectively), with RH having a larger influence than SR
308 (Table 4). The marginal mean CG values revealed that increasing HTRs from 4 to 5 could significantly
309 reduce CG by 7.7 points and that increasing HTRs from 5 to 6 would decrease CG even further, by 5.0
310 points, when the other environmental factors (SR and RH) were set to their mean values.
311 We also tested the RF model using the same explanatory variables and found that it
312 explained 49% of the CG variation of the train data set. The RMSE with the test data set was about
313 14%, comparable to that of LME (Figure 4). The variable importance analysis of the RF model showed
314 that TaHD was the most influential variable, followed by HTR, RH, and SR, in close agreement with
315 the LME model (Table 4, Supplementary figure 3).
316
317
318 **Table 4**. ANOVA results of the rice LME model, estimated parameters, and estimated marginal means
319 for each HTR.

	Variables	Mean Square	DFn(1)	DFd(2)	F value	*P*(3)
ANOVA	TaHD	105.6	1	1117	176.1	0.000***
	HTR	15.06	4	1257	24.99	0.000***
	SR	4.534	1	811	7.558	0.006**
	RH	25.70	1	1137	42.85	0.000***
	TaHD x HTR	4.325	4	1236	7.209	0.000***
	HTR	Estimate4)	SE	df	t value	*P*
Intercepts						
	HTR3	-7.314	0.855	987	-8.557	0.000***
	HTR4-HTR3	0.025	0.193	1282	0.127	0.899
	HTR5-HTR3	-0.501	0.102	1270	-4.922	0.000***
	HTR6-HTR3	-0.906	0.131	1248	-6.891	0.000***
	HTR7-HTR3	-1.020	0.114	1242	-8.933	0.000***
Coefficients for covariates						
TaHD	HTR3	0.046	0.003	1245	13.56	0.000***
	HTR4-HTR3	-0.012	0.005	1242	-2.204	0.028*
	HTR5-HTR3	-0.011	0.003	1245	-3.351	0.001**

	HTR6-HTR3	-0.014	0.004	1228	-3.352	0.001**
	HTR7-HTR3	-0.020	0.004	1227	-5.156	0.000***
SR		0.042	0.015	811	2.749	0.006**
RH		0.057	0.009	1137	6.546	0.000***

	Estimated marginal mean CG (%)[5)]	Confidence limits (%)	
		Lower	Upper
HTR 3	26.5 a	22.8	30.8
HTR 4	22.3 a	17.8	27.3
HTR 5	14.6 b	12.3	17.2
HTR 6	9.6 c	7.9	11.7
HTR 7	7.7 d	6.2	9.3

1) Degree of freedom for the numerator

2) Degree of freedom fo the denominator estimated using the Kenward-Roger method in the lme4 R package (Bates et al., 2015).

3) ***, P< 0.001; **, P < 0.01; and * , P<0.05 .

4) Estimated parameters in Eq. (1) based on the logit-transformed CG.

5) Estimated marginal means based on the untransformed CG. Values followed by the same alphabetic letters are not statistically different at P=0.05 using Tukey's method. Note that the difference between HTR6 and 7 was found significant, whereas that between HTR 3 and 4 was not, despite it being greater in the latter comparison. This was because the pairwise comparison was made using the logit-transformed data; the difference was greater in the HTR6-7 comparison than in the HTR3-4.

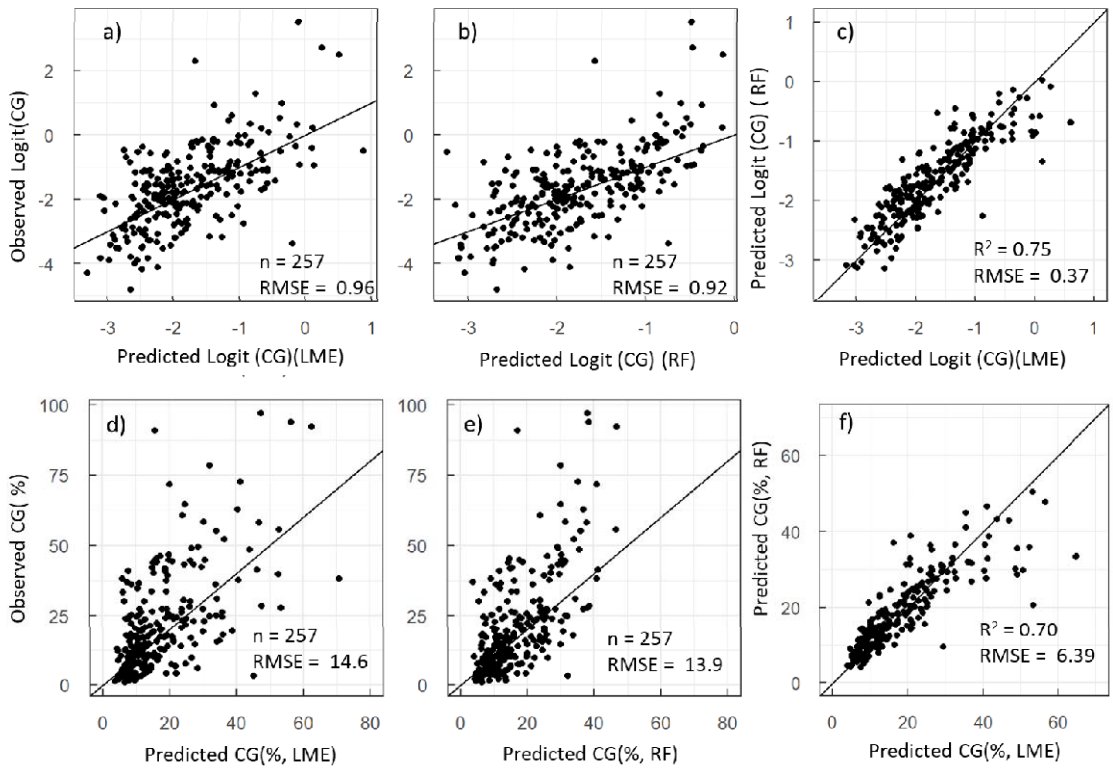

Figure 4. Relationships between observed and predicted values from the LME (a in logit scale, d in %) and the RF model (b in logit scale, e in %), and between the predicted values of the two models (c in logit scale, f in %).

3.3 Responses of CG to temperature, solar radiation, and humidity

Both models predicted similar responses of Logit (CG) to TaHD, SR, and RH (Supplementary Figure 3). The partial dependence plots of the RF model indicated that Logit(CG) responded almost linearly to all climatic variables studied, confirming that the linear assumption of the model LME was plausible. Since the RF and LME models showed similar goodness of fit (Section 3.2) and responses to climatic factors, we chose the LME model to describe the responses of CG to TaHD, RH, and SR for the different HTRs, due to its simplicity and interpretability.

CG increased as a function of TaHD for all HTRs, but the response was much weaker for high HTRs than for low HTRs (Figure 5). When SR and RH were fixed to their mean observed values, increasing TaHD from 20 to 80 °C d was projected to increase CG by 66 points for HTR3, 45 points for HTR5, and 19 points for HTR7, confirming the effectiveness of heat-tolerant cultivars in reducing the

negative impacts of high temperatures. The projected responses also showed that CG increased with both increasing RH and SR (Figure 5) to a greater extent for low HTRs than for high HTRs. When TaHD and SR were held constant, increasing RH from 70 to 90% was projected to increase CG by 22 points for HTR3, 14 points for HTR5, and 8 points for HTR7. The effect of HTR was smaller for SR; increasing SR from 10 to 22 MJ m^{-2} was estimated to raise CG by 9.8 points for HTR3, 6 points for HTR5, and only 4 points for HTR7 (Figure 5)

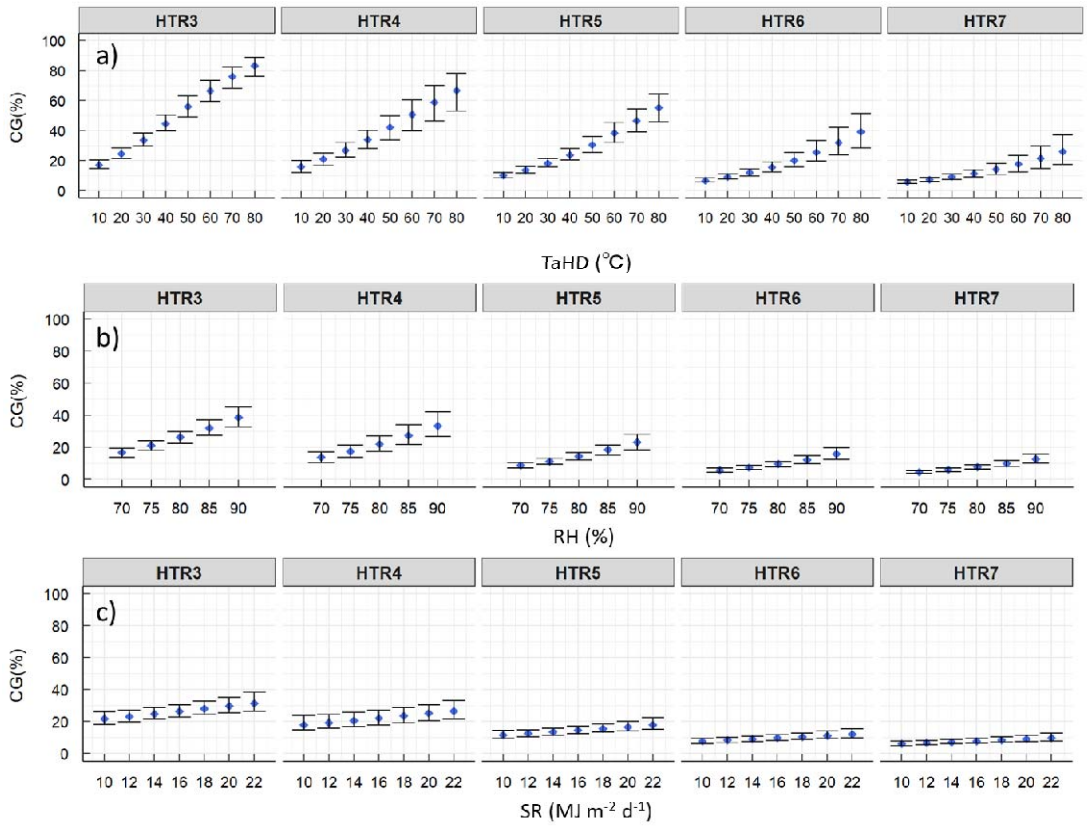

Figure 5. Response of CG (%) to TaHD (a), RH (b), and SR (c) estimated with the LME model for each heat tolerance rank (HTR). Error bars show 95% confidence intervals. Response to each weather variable was drawn by fixing other two environmental variables at their average values in the dataset: SR = 16 MJ m^{-2} d^{-1}, RH = 80%, and TaHD = 22 °C d.

4. Discussion

Using a systematic literature search strategy, we collected 2,332 field trials of 321 cultivars conducted at 46 experimental stations across Japan. The dataset covers all regions except Hokkaido, where temperatures are low and heat damage has yet to be reported. The dataset contains standard cultivars with contrasting levels of heat tolerance. All the data were obtained in open fields, without additional warming, in conditions close to real farms. The dataset also includes key climatic variables and geographical information for each observation, facilitating the analysis of quality-climate relationships. We aimed to quantify the effects of improving cultivars' heat tolerances to alleviate heat damage on rice grain quality. To that end, we used recently established national-level standardized cultivars' heat tolerance ranks in Japan (HTR) to develop a quantitative effectiveness measure against heat damage on rice quality.

We tested two different models; a parametric model based on mixed-effect regression (LME) and a non-parametric model based on the random forest (RF) algorithm. The LME model assumes a linear relationship between the response and explanatory variables, while the RF model makes no linear assumption but is more difficult to interpret (Xie et al., 2021). Our results demonstrated that the two models agreed on their capacity to predict the CG variation in the test data (RMSE = 14 or 15 %), the importance of explanatory variables (TaHD > HTR > RH > SR), and the linear responses of CG to weather-related variables. Both models were able to detect the negative effect of high temperature on quality, which was found to be highly dependent on cultivars' HTR. Each HTR group includes 6–15 cultivars (Table 2), bred in different locations and years from various backgrounds. They were selected as reference cultivars for each HTR based on their performance under high grain-filling temperatures (mean temperatures for 20 days after heading are typically around 27–28 °C). (Kaji et al., 2016; Tamura et al., 2018). The proposed models demonstrated that increasing HTR could reduce the occurrence of CG at high temperatures (>26 °C), and we found that a shift of HTR by one rank could decrease CG by more than 5%.

386 Earlier, Nishimori et al. (2020) showed that, from a nationwide survey in Japan, the
387 percentage of first-grade rice sharply dropped by 3-4 points each point rise in CG when CG exceeded
388 5 %. When CG exceeded 25 %, the first-grade rice % was nearly zero and was replaced by second or
389 third-grade rice. Reducing CG by raising HTR can help to maintain appearance quality (Table 4) and,
390 thus, quality grade in hotter climates. For instance, at a mean grain-filling temperature of 27 °C
391 (0.6 °C higher than the average of the entire dataset, Table 3, equivalent to TaHD = 20 °C d), CG was
392 estimated to be 24.5 % (95% CI ranging from 21.2 to 27.75%) for HTR3 (susceptible) (Figure 5),
393 implying that it is already difficult for HRT3 cultivars to produce first-grade rice. At the same grain-
394 filling temperature, CG was calculated to be 13.6 % (95% CI, 11.4 ~ 15.9 %) with HTR5 (intermediate)
395 and 9.0 % (7.5~10.9) with HTR6 (moderately tolerant) (Figure 5), indicating that raising HTR by just
396 one step could substantially contribute to attaining first-grade rice. When the air temperature
397 further rises, however, the adaptation limit is reached, even with HTR6 or 7. For instance, at a grain-
398 filling temperature of 28.5 °C (TaHD = 50 °C d), CG was projected to reach 20% (16.2~25.4) for HTR6
399 and 14% (11.1~18.1) for HTR7, indicating that the reduction of first-grade rice is inevitable, calling for
400 further improvement in heat tolerance.

401 Our results confirmed that grain-filling temperature is the dominant climatic factor affecting
402 CG. The variable TaHD (cumulative temperature above the threshold value 26°C) was found to be a
403 key factor, as reported elsewhere (Nishimori et al., 2020). Some researchers used a different base
404 temperature for different genotypes, assuming that heat tolerance would raise the threshold
405 temperature (Takimoto et al., 2019; Masutomi et al., 2022). We also examined this possibility by
406 varying the base temperature for each HTR, but found that the best model fit was obtained with a
407 base temperature of about 26 °C regardless of HTRs (Supplementary Figure 1). We, therefore, fixed
408 the base temperature at 26 °C for all HTRs. It is possible that the intercepts of the LME model, which
409 also differed significantly among HTRs, accounted for the CG variation near the threshold
410 temperature.

411 Two other climatic factors, RH and SR, were also found to have significant effects on CG
412 according to the LME model. CG increased with both RH and SR, but the effect of RH was stronger,
413 with the F value being 43 for RH and 7.6 for SR (Table 4). To our knowledge, only a few have studies
414 reported the effects of RH on CG; one of them used a growth chamber to impose RH treatments, and
415 the other statistically analyzed climatic factors on CG of field-grown rice in wet and dry seasons
416 (Wakamatsu et al., 2009; Zhao and Fitzgerald, 2013), both demonstrating that CG increased with RH
417 in line with the current findings. The effect of SR on CG has been frequently reported (Deng et al.,
418 2018; Ishimaru et al., 2018), with evidence that a specific type of chalk, milky-white grains, which
419 depends on assimilate supply (Kobata et al., 2004; Tsukaguchi and Iida, 2008), increased under low
420 SR (Ishimaru et al., 2018). Some modelling studies have already considered the effects of SR (Okada
421 et al., 2011; Yoshida et al., 2016; Takimoto et al., 2019), accounting for the rise in CG when solar
422 radiation is limited. Our analysis showed, however, that high SR had a positive impact on CG although
423 the effect of SR was much smaller than that of TaHD or RH (Table 4, Figure 5). This difference in
424 importance could be explained in part by the fact that our response variable was the overall
425 occurrence of different types of chalk. The occurrences of chalky grains, such as basal-, belly-, or
426 back-white grains, were reportedly insensitive to solar radiation (Morita et al., 2016). An important
427 mechanism by which SR increases CG despite its positive effects on assimilate supply is greater
428 incident radiation, which raises panicle temperatures. High RH could also raise panicle temperatures
429 by reducing transpirational cooling (Yoshimoto et al., 2022). The fact that both RH and SR increased
430 CG suggests that the indirect impacts of these climatic factors on CG via panicle temperatures
431 override a beneficial effect of SR through increased assimilate supply, which could reduce the
432 occurrence of milky-white grains. It is important to note that increases in CG with rising RH and SR
433 decreased with higher HTRs, implying that the effects of RH and SR were heat-mediated (Figure 5).

434 Our models can play at least two roles in genetic improvements in heat tolerance. First,
435 when combined with climate scenarios, the model can be used to backcast quantitative breeding
436 targets that are temporally and spatially explicit. Breeding targets can also be defined based on

437 global warming levels. Because the lead time in breeding is often long, the breeding target—heat
438 tolerance level in the current context—must be developed well before variety release. Current
439 temperatures during the grain-filling period vary across regions. For instance, our dataset showed
440 grain-filling temperatures averaged for each prefecture in the recent decade, ranged from below
441 25 °C to above 28 °C. They are projected to rise over time as global warming proceeds, strongly
442 suggesting that the breeding target for HTR needs to be tailored for each region and time. The
443 current models can estimate CG from major climatic factors for different tolerance levels and can
444 help design locally specific targets. The models are built on the Japanese rice dataset but might be
445 applied to other countries/regions where standard cultivars are already established. Second, the
446 models may be used to derive objective and quantitative heat tolerance ranks for new cultivars
447 based on field trials and their environmental conditions. Heat tolerance ranks of new cultivars are
448 currently determined based on relative cultivar performances, established comparing candidate lines
449 with standard cultivars. The proposed models may potentially assist expert judgment by providing
450 quantitative tolerance levels from multiple field data sets, although further testing of the model is
451 needed for this purpose.

452 Another modeling approach is needed to design future heat-tolerant cultivars. Recently,
453 several genes and QTLs have been identified that reduce specific types of chalk under high
454 temperatures (Wada et al., 2015; Miyahara et al., 2017). Some attempts at pyramiding these QTLs
455 and genes are already occurring. It is yet to be determined, however, the effectiveness of these
456 genes in reducing CG as temperatures rise. A bottom-up modeling strategy that accounts for the
457 effects of these genes under different warming levels is necessary for this purpose.

458 In principle, the proposed models could be used to estimate the effects of weather- and
459 cultivar-related inputs, but many other factors are involved in the CG variation. The LME model
460 explained 63 % of the variations when accounting for the reference-site effects. Other factors may
461 include some management factors such as nitrogen application (Wakamatsu et al., 2008; Tanaka et

al., 2010), planting density (Morita et al., 2012), and water management (Chiba et al., 2017). To improve the model's accuracy, more covariates related to soil or management practices are necessary. Because the model is empirical, it cannot be extrapolated. The maximum TaHD in the dataset was 80 °C d, which is equivalent to the average grain-filling temperature of 30 °C. According to the climate projections based on various greenhouse gas emissions, the mean air temperature in Japan may rise by 0.6 ~ 3.0 °C and by 1.1 ~ 6.7 °C from the 1981-2000 period by mid- and late-century, respectively (Ishigooka et al., 2017), suggesting that grain-filling temperatures could exceed 30 °C, particularly in currently warm regions. In addition, the current model does not account for atmospheric CO_2 concentration or wind speed. Notably, the effect of CO_2 is relevant in the context of climate change because elevated CO_2 exacerbates the heat-induced degradation of rice appearance quality (Yang et al., 2007; Usui et al., 2016), which could dramatically influence the projected impacts of climate change on grain appearance quality (Ishigooka et al., 2021). There are a few reports that show heat-tolerant cultivars effectively sustain appearance quality under elevated CO_2 levels (Usui et al., 2014; Hasegawa et al., 2019), but this needs to be examined more extensively. Further expansion of the rice CG dataset and model improvement will be needed.

Conclusions

We aimed to quantify the effects of improving cultivars' heat tolerance ranks (HTRs) to alleviate heat damage on rice grain quality using recently established national-level standardized cultivar heat tolerance ranks in Japan. A linear mixed effect model and a random forest model were developed and tested with a dataset containing 1,297 field trials of 48 cultivars from 44 experimental stations across Japan, covering all regions where high temperatures are a source of concerns. The two models agreed on their capacity to predict the variation in chalky grain percentage (CG) in test data (RMSE = 14 or 15%), the importance of explanatory variables, and linear responses to climatic variables. The proposed models demonstrated that increasing HTR could reduce the occurrence of CG, especially

under high temperature conditions. Increasing the HTR by a single step (from intermediate to moderately tolerant) can significantly increase the chances of obtaining first-grade quality rice under grain filling temperatures of up to 27°C, but tolerance levels must be improved if more extreme temperatures are expected. The proposed models can be used to backcast quantitative, temporally, and spatially explicit breeding targets under climate change.

Acknowledgements

This study was performed by the Environment Research and Technology Development Fund (JPMEERF20S11820) of the Environmental Restoration and Conservation Agency of Japan and in part by the Joint linkage call supported by NARO and INRAE, and by the project CLIMAE of INRAE.

References

Ali, F., Waters, D.L.E., Ovenden, B., Bundock, P., Raymond, C.A., Rose, T.J., 2019. Heat stress during grain fill reduces head rice yield through genotype dependant increased husk biomass and grain breakage. Journal of Cereal Science 90. doi:10.1016/j.jcs.2019.102820

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models Usinglme4. Journal of Statistical Software 67. doi:10.18637/jss.v067.i01

Cappelli, G.A., Bregaglio, S., 2021. Model‐based evaluation of climate change impacts on rice grain quality in the main European rice district. Food and Energy Security 10. doi:10.1002/fes3.307

Cheng, F.M., Zhong, L.J., Wang, F., Zhang, G.P., 2005. Differences in cooking and eating properties between chalky and translucent parts in rice grains. Food Chemistry 90, 39-46. doi:10.1016/j.foodchem.2004.03.018

Chiba, M., Terao, T., Watanabe, H., Matsumura, O., Takahashi, Y., 2017. Improvement in Rice Grain Quality by Deep-flood Irrigation and its Underlying Mechanisms. Japan Agricultural Research Quarterly: JARQ 51, 107-116. doi:10.6090/jarq.51.107

Chun, A., Song, J., Kim, K.-J., Lee, H.-J., 2010. Quality of head and chalky rice and deterioration of eating quality by chalky rice. Journal of Crop Science and Biotechnology 12, 239-244. doi:10.1007/s12892-009-0142-4

Deng, F., Wang, L., Pu, S.-L., Mei, X.-F., Li, S.-X., Li, Q.-P., Ren, W.-J., 2018. Shading stress increases chalkiness by postponing caryopsis development and disturbing starch characteristics of rice grains. Agricultural and Forest Meteorology 263, 49-58. doi:10.1016/j.agrformet.2018.08.006

Fitzgerald, M.A., McCouch, S.R., Hall, R.D., 2009. Not just a grain of rice: the quest for quality. Trends in Plant Science 14, 133-139. doi:10.1016/j.tplants.2008.12.004

Hasegawa, T., Sakai, H., Tokida, T., Usui, Y., Nakamura, H., Wakatsuki, H., Chen, C.P., Ikawa, H., Zhang, G., Nakano, H., Matsushima, M.Y., Hayashi, K., 2019. A High-Yielding Rice Cultivar "Takanari" Shows No N Constraints on CO2 Fertilization. Front Plant Sci 10, 361. doi:10.3389/fpls.2019.00361

Ishigooka, Y., Fukui, S., Hasegawa, T., Kuwagata, T., Nishimori, M., Kondo, M., 2017. Large-scale evaluation of the effects of adaptation to climate change by shifting transplanting date on rice production and quality in Japan. Journal of Agricultural Meteorology 73, 156-173. doi:10.2480/agrmet.D-16-00024

Ishigooka, Y., Hasegawa, T., Kuwagata, T., Nishimori, M., Wakatsuki, H., 2021. Revision of estimates of climate change impacts on rice yield and quality in Japan by considering the combined effects of temperature and CO2 concentration. Journal of Agricultural Meteorology 77, 139-149. doi:10.2480/agrmet.D-20-00038

Ishimaru, T., Hirabayashi, H., Sasaki, K., Ye, C., Kobayashi, A., 2016. Breeding efforts to mitigate damage by heat stress to spikelet sterility and grain quality. Plant Production Science 19, 12-21. doi:10.1080/1343943X.2015.1128113

Ishimaru, T., Nakayama, Y., Aoki, N., Ohsumi, A., Suzuki, K., Umemoto, T., Yoshinaga, S., Kondo, M., 2018. High temperature and low solar radiation during ripening differentially affect the composition of milky-white grains in rice (Oryza sativa L.). Plant Production Science 21, 370-379. doi:10.1080/1343943X.2018.1520047

Japan Meteorological Agency, 2015. Climate Change Monitoring Report 2014. Japan Meteorological Agency, , Tokyo, Japan

Kaji, R., Ohta, H., Fukushima, A., Tsuda, N., Moriyama, S., Kon, C., Endo, T., Nakagomi, Y., Sato, H., Kawamoto, T., Kato, K., Goto, H., Abe, Y., Sasaki, S., Yoshida, N., Otera, M., 2016. Selection of Standard Rice Varieties for Evaluating Grain Quality under High Temperature during Ripening Stage for Tohoku Region. Bulletin of TOHOKU Agricultural Research Center 118, 49-55. doi:10.24514/00001292

Kobata, T., Uemuki, N., Inamura, T., Kagata, H., 2004. Shortage of Assimilate Supply to Grain Increases the Proportion of Milky White Rice Kernels under High Temperatures. Japanese Journal of Crop Science 73, 315-322. doi:10.1626/jcs.73.315

Krishnan, P., Ramakrishnan, B., Reddy, K.R., Reddy, V.R., 2011. Chapter three - High-Temperature Effects on Rice Growth, Yield, and Grain Quality. In: Sparks, D.L. (Ed.), Advances in Agronomy. Academic Press, pp. 87-206.

Lanning, S.B., Siebenmorgen, T.J., Counce, P.A., Ambardekara, A.A., Mauromoustakos, A., 2011. Extreme nighttime air temperatures in 2010 impact rice chalkiness and milling quality. Field Crop Res 124, 132-136. doi:10.1016/j.fcr.2011.06.012

Lenth, R.V., 2022. emmeans: Estimated Marginal Means, aka Least-Squares Means.

Liaw, A., Wiener, M., 2001. Classification and Regression by RandomForest. Forest 23.

Lyman, N.B., Jagadish, K.S., Nalley, L.L., Dixon, B.L., Siebenmorgen, T., 2013. Neglecting rice milling yield and quality underestimates economic losses from high-temperature stress. PLoS One 8, e72157. doi:10.1371/journal.pone.0072157

MAFF, 1998. The guideline for variety registration, "Rice". In: MAFF (Ed.), The plant variety protection and seed act

MAFF, 2021. Climate change impacts report 2020. Ministry of Agriculture, Forestry and Fisheries (MAFF), .

Masutomi, Y., Arakawa, M., Minoda, T., Yonekura, T., Shimada, T., 2015. Critical air temperature and sensitivity of the incidence of chalky rice kernels for the rice cultivar “Sai-no-kagayaki”. Agricultural and Forest Meteorology 203, 11-16. doi:10.1016/j.agrformet.2014.11.016

Masutomi, Y., Takimoto, T., Manabe, T., Imai, Y., Tamura, M., Kobayashi, K., 2022. Breeding targets for heat-tolerant rice varieties in Japan in a warming climate. Mitigation and Adaptation Strategies for Global Change 28, 2. doi:10.1007/s11027-022-10027-4

Masutomi, Y., Takimoto, T., Shimamura, M., Manabe, T., Arakawa, M., Shibota, N., Ooto, A., Azuma, S., Imai, Y., Tamura, M., 2019. Rice grain quality degradation and economic loss due to global warming in Japan. Environmental Research Communications 1. doi:10.1088/2515-7620/ab52e7

Mavromatis, T., Boote, K.J., Jones, J.W., Irmak, A., Shinde, D., Hoogenboom, G., 2001. Developing Genetic Coefficients for Crop Simulation Models with Data from Crop Performance Trials. Crop Science 41, 40-51. doi:10.2135/cropsci2001.41140x

Miyahara, K., Wada, T., Sonoda, J.-y., Tsukaguchi, T., Miyazaki, M., Tsubone, M., Yamaguchi, O., Ishibashi, M., Iwasawa, N., Umemoto, T., Kondo, M., 2017. Detection and validation of QTLs for milky-white grains caused by high temperature during the ripening period in Japonica rice. Breeding Science 67, 333-339. doi:10.1270/jsbbs.16203

Mizobuchi, M., Takata, S., Sakata, M., Kameshima, M., Yoshida, Y., 2018. "Kouiku 76 gou", A new extremerly early rice line with superior eating quality and grain appearance under high temperatures during ripening. Bulletin of Kochi Agricultural Research Center 27, 55-64.

Morita, K., Matsushima, T., Yamaguchi, T., Saito, A., Furuhata, M., 2012. Evaluation of the Dense Planting in Late Transplanting Aimed to Avoid High Temperatures During the Ripening Period in Rice Cultivar Koshihikari. Japanese Journal of Crop Science 81, 349-356. doi:10.1626/jcs.81.349

Morita, S., 2008. Prospect for Developing Measures to Prevent High-Temperature Damage to Rice Grain Ripening. Japanese Journal of Crop Science 77, 1-12. doi:10.1626/jcs.77.1

Morita, S., Wada, H., Matsue, Y., 2016. Countermeasures for heat damage in rice grain quality under climate change. Plant Production Science 19, 1-11. doi:10.1080/1343943X.2015.1128114

Nagato, K., Ebata, M., 1965. Effects of High Temperature during Ripening Period on the Development and the Quality of Rice Kernels. Japanese journal of crop science 34, 59-66. doi:10.1626/jcs.34.59

NARO, 2011. A new rice cultivar "Harumoni". Press relsease.

NARO, 2018. A new rice cultivar "Koisomeshi". Press release.

Neerja, S., Renu, K., 2020. Rice Grain Quality: Current Developments and Future Prospects. In: Farooq, S. (Ed.), Recent Advances in Grain Crops Research.

Nishimori, M., Ishigooka, Y., Wakatsuki, H., Kuwagata, T., Hasegawa, T., Yoshida, H., Takimoto, T., Kondo, M., 2020. Rice quality analysis using the Crop Survey database of Japan for climate impact assessment. Climate in Biosphere 20, 1-8. doi:10.2480/cib.J-20-054

Okada, M., Iizumi, T., Hayashi, Y., Yokozawa, M., 2011. Modeling the multiple effects of temperature and radiation on rice quality. Environmental Research Letters 6, 034031. doi:10.1088/1748-9326/6/3/034031

R Core Team, 2022. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Takimoto, T., Masutomi, Y., Tamura, M., Nitta, Y., Tanaka, K., 2019. The effect of air temperature and solar radiation on the occurrence of chalky rice grains in rice cultivars "Koshihikari" and "Akitakomachi". Journal of Agricultural Meteorology 75, 203-210. doi:10.2480/agrmet.D-18-00039

Tamura, K., Kataoka, T., Nakanishi, A., Sato, H., Tamura, Y., Sakai, M., Yamaguchi, O., Wada, T., Tsubone, M., Tatara, I., Tokuda, S., Yoshida, K., Koga, J., Nakayama, M., Fujii, Y., Mitsukawa, M., Shimizu, Y., Hasegawa, W., Shiraishi, M., Nagayoshi, Y., Matsuura, S., Wakamatsu, K.-i., Sato, M., Sonoda, J., Takeuchi, Y., 2018. Standard Rice Varieties with High Temperature Tolerance at the Ripening Stage in the Warm Region of Japan. Japanese Journal of Crop Science 87, 209-214. doi:10.1626/jcs.87.209

Tanaka, K., Miyazaki, M., Uchikawa, O., Araki, M., 2010. Effects of the Nitrogen Nutrient Condition and Nitrogen Application on Kernel Quality of Rice. Japanese Journal of Crop Science 79, 450-459. doi:10.1626/jcs.79.450

Tsukaguchi, T., Iida, Y., 2008. Effects of Assimilate Supply and High Temperature during Grain-Filling Period on the Occurrence of Various Types of Chalky Kernels in Rice Plants (Oryza sativa L.). Plant Production Science 11, 203-210. doi:10.1626/pps.11.203

Usui, Y., Sakai, H., Tokida, T., Nakamura, H., Nakagawa, H., Hasegawa, T., 2014. Heat-tolerant rice cultivars retain grain appearance quality under free-air CO2 enrichment. Rice (N Y) 7, 6. doi:10.1186/s12284-014-0006-5

Usui, Y., Sakai, H., Tokida, T., Nakamura, H., Nakagawa, H., Hasegawa, T., 2016. Rice grain yield and quality responses to free-air CO2 enrichment combined with soil and water warming. Global Change Biology 22, 1256-1270. doi:10.1111/gcb.13128

Viechtbauer, W., 2010. Conducting Meta-Analyses in R with the metafor Package. Journal of Statistical Software 36, 1 - 48. doi:10.18637/jss.v036.i03

Wada, T., Miyahara, K., Sonoda, J.Y., Tsukaguchi, T., Miyazaki, M., Tsubone, M., Ando, T., Ebana, K., Yamamoto, T., Iwasawa, N., Umemoto, T., Kondo, M., Yano, M., 2015. Detection of QTLs for white-back and basal-white grains caused by high temperature during ripening period in japonica rice. Breeding Science 65, 216-225. doi:10.1270/jsbbs.65.216

Wada, T., Tsubone, M., Inoue, T., Ogata, T., Hamachi, Y., Matsue, Y., Oosato, K.F., Yasunaga, T., Kawamura, Y., Ishizuka, A., 2010. "Genkitsukushi", a new rice cultivar with tolerance to high temperature during maturing period and high eating quality. Bulletin of Fukuoka Agricultural Research Center 29, 1-9.

Wakamatsu, K.-i., Sasaki, O., Tanaka, A., 2009. Effects of the Amount of Insolation and Humidity during the Ripening Period on the Grain Quality of Brown Rice in Warm Regions of Japan. Japanese Journal of Crop Science 78, 476-482. doi:10.1626/jcs.78.476

Wakamatsu, K.-i., Sasaki, O., Uezono, I., Tanaka, A., 2008. Effect of the Amount of Nitrogen Application on Occurrence of White-back Kernels during Ripening of Rice under High-temperature Conditions. Japanese Journal of Crop Science 77, 424-433. doi:10.1626/jcs.77.424

Xie, X., Wu, T., Zhu, M., Jiang, G., Xu, Y., Wang, X., Pu, L., 2021. Comparison of random forest and multiple linear regression models for estimation of soil extracellular enzyme activities in agricultural reclaimed coastal saline land. Ecological Indicators 120, 106925. doi:10.1016/j.ecolind.2020.106925

Yandell, B.S., 1997. Practical Data Analysis for Designed Experiments. Chapman and Hall/CRC, FL, USA.

Yang, L., Wang, Y., Dong, G., Gu, H., Huang, J., Zhu, J., Yang, H., Liu, G., Han, Y., 2007. The impact of free-air CO2 enrichment (FACE) and nitrogen supply on grain quality of rice. Field Crop Res 102, 128-140. doi:10.1016/j.fcr.2007.03.006

Yoshida, H., Takehisa, K., Kojima, T., Ohno, H., Sasaki, K., Nakagawa, H., 2016. Modeling the effects of N application on growth, yield and plant properties associated with the occurrence of chalky grains of rice. Plant Production Science 19, 30-42. doi:10.1080/1343943X.2015.1128111

Yoshimoto, M., Fukuoka, M., Tsujimoto, Y., Matsui, T., Kobayasi, K., Saito, K., van Oort, P.A.J., Inusah, B.I.Y., Vijayalakshmi, C., Vijayalakshmi, D., Weerakoon, W.M.W., Silva, L.C., Myint, T.T., Phyo, Z.C., Tian, X., Lur, H.-S., Yang, C.-M., Tarpley, L., Manigbas, N.L., Hasegawa, T., 2022. Monitoring canopy micrometeorology in diverse climates to improve the prediction of heat-induced spikelet sterility in rice under climate change. Agricultural and Forest Meteorology 316, 108860. doi:10.1016/j.agrformet.2022.108860

Zhao, X., Fitzgerald, M., 2013. Climate Change: Implications for the Yield of Edible Rice. PLOS ONE 8, e66218. doi:10.1371/journal.pone.0066218