Variability and relationship between agronomic traits and grain yield in rice (*Oryza sativa* L.) under heat stress conditions

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Abstract A high temperature at the flowering stage of rice, which is the most critical time, causes spikelet fertility to decrease among different rice varieties. Variability and relationship between agronomic characteristics and grain yield in 15 rice varieties were investigated under high-temperature conditions from 40°C to 45°C for 6 hours during the daytime at their reproductive stage. The results showed that high temperature significantly declined seed set and yield per plant of all varieties. Based on the seed set at high temperature, M9962 was the most tolerant, while Sinlek, Khao Dawk Mali 105, Chainat 1, and RD49 were susceptible. The genotypic coefficient of variation (GCV) and phenotypic coefficient of variation (PCV) had analyzed. All traits had lower GCV than that of PCV. The spikelets number per panicle, seed set, and 1,000-grain weight had higher heritability than other traits under high temperatures. Phenotypic correlation coefficients at high temperatures among all traits were estimated. The greatest directly positive affected on yield per plant was seed set following by panicle weight under high temperatures. It indicated that seed set and panicle weight could be applied for selecting high yielding genotypes under high-temperature conditions.

Keywords: Genotypic co-efficient, High temperature, Phenotypic co-efficient, Seed set, Yield

Introduction

The importance of rice to consumers is widespread around the world and can be grown under the proper temperature ranging from 27 to 32°C for normal development (Yin *et al.*, 1996). Presently, the temperature in Thailand increase by 1°C from 1951 to 2017 due to global climate change and the maximum average temperature from March to June was higher than 35°C (Department of Meteorology, 2018). As the temperature increased by 1°C, the yields of rice were assessed to be reduced by 10% (Peng *et al.*, 2004). In China, the yield decreased

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by 10%-20% due to high temperature during flowering stage (Luo *et al.*, 2015; Wang, 2016). A high temperature exceeding 35°C more critically affects the reproductive stage than the vegetative stage (Satake and Yoshida, 1978; Yoshida, 1981; Matsui *et al.*, 2000). Under high temperature, spikelet fertility declined due to anther dehiscence and pollen activity inhibition (Satake and Yoshida, 1978; Coast *et al.*, 2016) and grain filling decreased at the early ripening stages (Wei *et al.*, 2002).

However, high temperature of 40-45°C at flowering stage had a lower seed set than in the booting stage (Cheabu et al., 2018), inhibited anther dehiscence and pollen shed (Yoshida, 1981; Matsui et al., 2000; Prasad et al., 2006; Jagadish et al., 2010), increased sterile spikelets number and reduced the yield of japonica rice (Satake and Yoshida, 1978). Various rice varieties had different effects on seed set under high temperatures (Cheabu et al., 2018; Malumpong et al., 2020). A temperature of 38°C decreased the completed spikelet of sensitive and tolerant variety of rice about 18% and 71%, respectively (Jagadish et al., 2010). While, Madan et al. (2012), a temperature of 38°C reduced the seed set of tolerant and sensitive rice by 4.4% and 9.8%, respectively. High temperature during anthesis adversely affects the fertilization process. Normally, the fertilization of rice completes within five to six hours after pollination, and the kernel appears after two to three days (Krishnan and Dayanandan, 2003). As the fertilization rate declined, the spikelets number per panicle decreased that affected to sink size and yield-producing capacity limitation (Kobayashi et al., 2004; Matsushima, 1995). Furthermore, high temperature affected grain filling stage and decreased grain yield due to a rapid seed growth rate but a short time to seed dry weight (Yoshida and Hara, 1977; Oh-e et al., 2007; Xie et al., 2009).

In Thailand, the high temperature during flowering stage of rice in March-April may lead to the reduction of seed set and seed yield. Each variety of rice differently responds to high temperatures. Thus, variety screening under high temperatures can be identified sensitive and tolerant varieties. The purposes of the research were to investigate the variability of agronomic traits and grain yield under high-temperature stress in 15 rice varieties. In addition, the relationships between agronomic traits and grain yield were analyzed using correlation and path coefficient assessments.

Materials and methods

Rice materials

Fifteen rice varieties were used in this study, including 13 varieties from the Rice Department, Thailand, RD31, RD41, RD47, RD49, RD57, RD61,

RD71, Suphan Buri 60 (SP60), Chainat 1 (CN1), Phitsanulok 2 (PL2), Pathum Thani 1 (PTT1), Khao Dawk Mali 105 (KDML105); two varieties from Kasetsart University, Thailand, Sinlek (sensitive variety) and M9962 (tolerant variety).

Growth conditions

The experiment was performed in the field and a high-temperature greenhouse at the Rice Science Center, Kasetsart University, Kamphaeng Saen campus, Nakhon Pathom, Thailand (14°01'16'' N, 99°58'54'' E) from September to December 2018. A split plot in completely randomized design with 4 replications was applied in the pot experiment. Main plots consisted of two growth conditions in the field (30-35°C) and high-temperature greenhouse (40-45°C) conditions as treatment during the daytime and subplot was 15 rice varieties. All varieties of rice were sown in a plastic tray with soil and the rice seedlings of each variety were transplanted at 30 days after sowing (DAS). Each pot contained one plant in plastic pots (17 cm width, 17 cm length, and 21 cm height) containing sieved sandy loam soil. The water level of 3.0 to 4.0 cm was maintained until the plants attained physiological maturity. Each pot applied urea 46-0-0 of 0.5 and 0.6 g at 45 DAS (the mid-tillering) and 65 DAS (panicle initiation) stages. Pest management was sprayed following the high-yield recommendations.

After transplanting to the booting stage (R2), rice plants were assessed under field conditions (30-35°C) (Jagadish *et al.*, 2013). Then, rice plants (20 pots per variety) were maintained in the field conditions as a control. The other 20 pots per variety were treated in a high-temperature greenhouse of 40-45°C with 50% relative humidity from 10.00 am until 4.00 pm (6 hours per day) at the booting stage until harvesting. Usually, the temperature was gradually raised beginning at 6.00 am from about 30°C to 40–45°C at 10:00 am. Subsequently, the greenhouse temperature was reduced to 28–30°C at night (18:00 to 6:00). The minimum and maximum temperature, relative humidity, and light intensity were measured five-minute intervals using the WatchDog 1000 Series data logger (Spectrum Technologies, Inc., USA).

Agronomic traits and grain yield

Five rice plants per replication of each variety were used to assess plant height and tillers number per plant. Three panicles of each variety were randomly chose and tagged at the flowering stage (R4). The first three panicles from each rice plant under high and field conditions were sampled after complete maturation (R9). For panicle weight, the first three panicles of rice were harvested and weighed. Each panicle was separated and counted the number of filled and unfilled grains per panicle and weighed filled grains per panicle. The percentage of seed set was calculated between the filled grains number dividing to the total spikelets number per panicle. The seed set percentage was used to classified the heat tolerant level according to IRRI (2013), where, highly susceptible (<11%), susceptible (11-40%), moderately tolerant (41-60%), tolerant (61-80%), and highly tolerant (>80%). The grain yield was calculated to units of "g" per plant at 14% moisture content. After threshing, the grains were weighed to obtain the 1,000-grain weight, and this step was repeated three times. In addition, grain width and length were measured from 20 seeds of each replication.

Statistical analysis

The data were evaluated using analysis of variance (ANOVA) with appropriate transformations in R program version 3.6.1 (R Core Team, 2017). The mean was compared by least significant difference (LSD) at significance levels of 0.01 and 0.05. For parameters showing significant differences among the experiments, values from all experiments were combined to gain the mean and standard error. The agronomic traits and grain yield were analyzed correlation using Microsoft Excel software.

Genotypic and phenotypic variances

The genotypic and phenotypic variances of agronomic traits and grain yield were estimated using the specified formula by Johnson *et al.* (1955).

Genotypic variance,
$$\sigma^2_g = GMS-EMS/r$$

Where GMS = genotypic mean square; EMS = error mean square and r = number of replications.

Phenotypic variance,
$$\sigma_p^2 = \sigma_g^2 + EMS$$

Where σ_{g}^{2} = Genotypic variance

Heritability

Heritability in a broad sense (h_b^2) was computed followed by Johnson *et al.* (1955).

Heritability
$$=\frac{\sigma^2 g}{\sigma^2 p} x100$$

Where h^2 = Heritability in the broad sense was separated into low (< 30%), medium (30-60%), and high (> 60%) according to Johnson *et al.* (1955).

Genotypic coefficient of variation (GCV) and phenotypic coefficient of variation (PCV)

GCV and PCV values were calculated using the formula of Burton and DeVane (1953) and Singh and Chaudhury (1985) followed by

$$GCV = \frac{\sqrt{\sigma^2 g}}{x} x100$$
$$PCV = \frac{\sqrt{\sigma^2 p}}{x} x100$$

Where x = Population mean

GCV and PCV values were classified as low (<10%), moderate (10-20%), and high (>20%) (Sivasubramanian and Madhavamenon, 1973).

Path Coefficient Analysis

Path coefficient was analyzed using the phenotypic correlation coefficients as recommended by Dewey and Lu (1959).

$$r_{ij} = P_{ij} + \sum r_{rk} P_{kj},$$

where r_{ij} = the mutual association between yield-related trait (the independent character *i*) and grain yield (the dependent character *j*) as evaluated by the phenotypic correlation coefficients; P_{ij} = the direct effects of the independent character *i* on the dependent character *j* as determined by the path coefficients; and $\sum r_{rk}P_{kj}$ = the summation of the indirect effects of the independent character *i* on a given dependent character *j* through all other independent characters *k*. the contribution of the remaining unknown characters is captured as the residual followed by

$$\mathbf{P}_{\mathbf{R}} = \sqrt{(1 - \sum P_{ij} r_{ij})}$$

Results

Microclimate data during experimentation

The field experiment spanned the late rainy season from September to December 2018, during which the seasonal daytime temperatures (10:00–16:00) in the field conditions and greenhouse had an average temperature of 28.1°C and 39.9°C and a maximum temperature of 32.8°C and 49.6°C. These values indicated that the average maximum temperature in greenhouse was higher than

in field conditions of 11.8°C. The average relative humidity in the field and greenhouse was 67.4% and 51.2%, while the maximum relative humidity in the field and greenhouse was 87.6% and 71.3%, respectively. The relative humidity in the field was greater than in the greenhouse conditions by 16.2% due to fan ventilation in the greenhouse controlling the relative humidity. The field and greenhouse conditions had an average light intensity of 1,254.1 and 610.0 μ mol m⁻² s⁻¹, respectively. The greatest light intensity in the field and greenhouse conditions was 1,833.3 and 997.7 μ mol m⁻² s⁻¹, respectively, which indicated that the mean of light intensity in the field was greater than greenhouse conditions of 644.1 μ mol m⁻² s⁻¹ due to the plastic sheet in greenhouse (Figure 1).



Figure 1. The average air temperature (°C), relative humidity (%), and light intensity (μ mol m⁻² s⁻¹) under field and high temperature conditions about 10 am to 4 pm in August - December 2018 from reproductive stage to harvesting

Effects of high temperature on agronomic characteristics

The main effects of temperature, variety, and their interactions significantly (P < 0.05) affected agronomic traits. The plant height of all varieties under high temperatures was higher than in the field conditions. RD61, PSL2, and M9962 under both of the field and high-temperature conditions did not significantly different in plant height. The temperature did not significantly different in number of tillers per plant. However, the varieties and their interactions were significant (P < 0.05). Under field conditions, RD61 showed a larger number of tillers per plant, but it did not significantly different from RD31 and RD57. While, RD29, RD31, RD49, RD57, RD61, and RD71 under high temperature had declined in the number of tillers per plant by 20.0-40.2% (Figure 2).

The panicle weight in the field (3.13 g) was significantly higher than in high-temperature conditions (2.15 g). Thus, the high temperature decreased the panicle weight by 31.3% compared with the field condition. Among rice varieties, a greater panicle weight was found in RD29 and RD31, although it did not significantly differ from RD41 and RD47 in the field condition. However, high temperature reduced the panicle weight in all varieties by 11.4-55.8% in comparison to the field conditions. The top five varieties were dramatically decreased in panicle weight due to high temperature, including Sinlek (55.8%), followed by RD29, RD31, Chainat 1, and Khao Dawk Mali 105. In contrast, the high temperature did not significantly affect Suphan Buri 60, Pathum Thani 1, RD41, M9962, and Phitsanulok 2 with panicle weight reduction from 11.4-21.2% in comparison to the field conditions (Figure 2).

The high temperature significantly reduced filled grain weight per panicle in all varieties by 22.3-70.6% in comparison to the field conditions. Sinlek had the greatest affected by the high temperature to decrease filled grain weight (70.6%), followed by RD29, Khao, Dawk, Mali 105, Chainat 1, RD31, RD47, RD49, RD57, RD71, RD41, RD61 and Phitsanulok 2, ranging between 60.2 and 30.8% (Figure 3). However, the grain width and grain length during the grainfilling of all varieties between field and high-temperature conditions were not significantly different (Figure 3).

The high temperature did not result in a significantly different grain yield per plant compared with field conditions. Whereas, the varieties and their interactions had significantly different on yield per plant. All varieties was reduced the yield per plant ranging from 4.8-52.4% under high temperature. Under field conditions, RD31 had the highest yield per plant at 23.05 g, while a greater yield per plant under high-temperature conditions was found in RD29 (15.01 g) and RD49 (14.58 g). However, the high temperature largely decreased the yield of Sinlek by 52.4%, followed by RD31 and RD71 by 39.8 and 28.2%, respectively, in comparison to the field condition (Figure 4).



Figure 2. Plant height, number of tillers per plant, and panicle weight of rice grown under field and high temperature conditions in the late rainy season of 2018.



Figure 3. Filled grain weight per panicle, grain width, and grain length of rice grown under field and high temperature conditions in the late rainy season of 2018

A greater seed set percentage was found under field (75.0%) compared to high-temperature (42.9%) conditions. Under field conditions, RD29 (85.2%) had the highest seed set percentage, but no significant effect was observed for other varieties, except for Chainat 1, Pathum Thani 1, Khao Dawk Mali 105, Sinlek, and M9962. However, the high temperature decreased the seed set in all varieties by 18.6 - 63.1%. M9962 under high temperature showed the greatest seed set of 63.1%, indicating that this variety was tolerant to heat stress. High temperature reduced the seed set percentage in Sinlek (18.6%), which had the greatest seed set reduction by 69.6%, followed by Khao Dawk Mali 105, RD29, RD49, Chanat 1, and RD47, respectively (Figure 4). Thus, this study divided rice varieties into three groups according to IRRI (2013) with the seed set at high temperature: tolerant (61 to 80%, 1 variety), moderately tolerant (41% to 60%, 10 varieties), and susceptible (<40%, 4 varieties). RD29, RD47, RD57, RD31, RD71, Suphan Buri 60, RD61, Pathum Thani 1, Phitsanulok 2, and RD41 were identified as moderately tolerant, and Single, Khao Dawk Mali 105, Chainat 1, and RD49 were susceptible to high temperature (Figure 4).



Figure 4. Yield per plant, seed set, and 1,000 seed weight of rice grown under field and high temperature conditions in the late rainy season of 2018

The 1,000 grains weight was significantly lower under high-temperature than field conditions in all varieties. As shown in Figure 4, 1,000 seed weight decreased under high temperature. The interaction between temperature x

cultivar was significantly different for 1,000-seed weight (P < 0.05). The seed weight in Chainat 1 was reduced of 1.7%, Khao Dawk Mali 105, RD57, RD29, Pathum Thani 1, RD31, and M9962 ranging from 2.7% to 7.5%. While, RD47 had the highest reduced in seed weight (13.9%) under high temperature. (Figure 4).

Genetic parameters for quantitative traits under high temperature

Plant height, filled grains number per panicle, seed set, panicle weight, 1,000-grain weight and grain yield per plant gave a highly significant (P < 0.01) among the genotypes, environment, and interaction of genotype by environment. While panicle per plant had not significantly difference among rice varieties (Table 1).

Traits	Genotypes	Environment	G×E	Error	CV
11410	(G)	(E)	5 E	Liitti	(%)
Plant height (cm)	5877.36**	1700.15**	133.01**	39.78	5.06
Panicle per plant	19.53	56.02	13.96	1.47	15.35
Panicle length (cm)	36.98**	0.67	11.23**	1.82	5.59
Panicle weight(g)	5.72**	154.36**	2.26**	0.32	17.85
Number of spikelets per panicle	1269.82**	465	3831**	112	24.06
Number of filled grains per panicle	5006.31**	16884.12**	4335.21**	441.02	28.62
Number of unfilled grains per panicle	6701**	19010.44**	2992.23	342.01	30.19
Seed set (%)	2233.54**	93186.78**	896.74**	58	13.88
Grain length (mm)	0.07**	0.03	0.01	0.001	3.16
1,000-grain weight (g)	0.74**	4.22**	0.07**	0.005	2.71
Grain yield per plant (g)	4.01**	174.89**	3.15**	0.27	26.76

Table 1. Mean squares of agronomic traits, yield, and yield components of 15 rice varieties

**highly significant at $P \le 0.01$, C.V; coefficient of variation

All traits gave higher PCV than the corresponding GCV. The greatest PCV was observed in unfilled grains number per panicle (38.62%), grain yield per plant (29.59%) and filled grains number per panicle (27.85%). Higher GCV was presented for unfilled grains number per panicle (28.73%) and seed set (19.24%). The quantitative traits had heritability ranging from low (13.4%) to high (98.68%). Grain length showed the highest heritability of 98.68% followed by plant height (97.74%) (Table 2). It indicated that the high heritability in each traits was less influenced by the environment. Whereas, the lower heritability of

the filled grains number per panicle (13.40%) and grain yield per plant (21.45%) gave highly affected by the environment of high temperature.

Characters	Phenotypic	Genotypic	PCV	GCV	Heritability
	variance	variance	(%)	(%)	(%)
	(δ ² p)	(δ ² g)			
Plant height (cm)	489.75	478.67	17.97	17.76	97.74
Panicle per plant	1.63	0.46	16.16	8.59	28.52
Panicle length (cm)	3.08	2.15	7.28	6.09	69.63
Panicle weight (g)	0.48	0.29	22.62	17.58	60.49
Number of spikelets per panicle	1058.17	738.92	23.49	19.63	69.83
Number of filled grains per panicle	417.17	55.92	27.85	10.20	13.40
Number of unfilled grains per panicle	558.42	309.08	38.62	28.73	55.35
Seed set (%)	186.09	111.42	24.87	19.24	59.87
Grain length (mm)	0.01	0.01	9.63	9.63	98.68
1,000-grain weight (g)	0.06	0.06	9.40	9.40	89.50
Grain yield per plant (g)	0.33	0.07	29.59	13.63	21.45

Table 2. Estimation of phenotypic and genetic variances of agronomic traits related to the yield of 15 rice varieties under high temperature

Correlation and path coefficient analysis

In field condition, grain yield per plant were highly significant and positive relation with panicle weight (0.95^{**}) , number of filled grains per panicle (0.89^{**}) , a total of spikelets per panicle (0.83^{**}) , primary branch (0.76^{**}) , plant height (0.60^{**}) and day of heading (0.80) (Figure 5A). However, the correlation results in the high-temperature stress were highly significant and positive relation of grain yield per plant with panicle weight (0.89^{**}) , seed set (0.84^{**}) , and the number of filled grains per panicle (0.69^{**}) ; while 1,000-grain weight (-0.53^{**}) , grain length (-0.70^{**}) and unfilled grains number per panicle (-0.65^{**}) were negatively correlated to grain yield per plant under high-temperature (Figure 5B).



Figure 5. Correlation coefficients for (A) field condition and (B) high temperature stress related each traits. GY: grain yield per plant (g); GW: 1,000-grain weight (g); GL: grain length (mm); PW: panicle weight (g); SS: seed set (%); FGP: filled grains number per panicle; UFGP: unfilled grain number per panicle; SP: a total of spikelet per panicle; PB: primary branch; PL: panicle length (cm); FL: flag leaf length (cm); PH: plant height (cm); PP: panicle per plant; DH: day of heading

Path coefficient was analyzed for all other traits of grain yield per plant (Figure 6). At the field condition, it showed that the directly affected of the filled grains number per panicle was positive and high (0.581) and its indirectly affected via a total of spikelets per panicle (0.934) was positive. While, in the high-temperature, all characters excepting 1,000-grain weight, filled grains number per panicle, and unfilled grains number per panicle had negatively direct effects on grain yield. Seed set showed the greatest positive directly affected on yield per plant of 0.575, meaning a higher seed set lead to increase grain yield. The phenotypic correlation between seed set and grain yield ($r^2 = 0.84$; P < 0.01) and panicle weight had yielded the next highest and directly affected on grain yield (0.439). The phenotypic correlation between the traits was positive and statistically significant ($r^2 = 0.89$; P < 0.01). It indicates that a reliable criteria for high-yielding genotypes was seed set and panicle weight in heat stress environments.



Figure 6. Comparison of genotypic path coefficient diagram between (A) field condition and(B) high-temperature stress of effective relationships between yield component traits and grain yield (GW: 1,000 grain weight; GL: grain length; PW: panicle weight; SS: seed set; FGP: Number of filled grains per panicle; UFGP; Number of unfilled grains per panicle; SP: a total of spikelets per panicle)

Discussion

Global warming causes air temperature increase and has an impact on rice production. A high temperature exceeding 35°C induces floret sterility and decreases rice yield (Afuakwa *et al.*, 1984; Matsui *et al.*, 1997; Nakagawa *et al.*, 2003). An average temperature of 39.9°C in the greenhouse was conducted during 10.00 am to 4.00 pm. This temperature was higher than the typical field condition of 11.8°C. The relative humidity had no difference in both the field and high-temperature greenhouse conditions. While the greenhouse had light intensity lower (644.1 µmol m⁻² s⁻¹) than field conditions due to a plastic sheet was used to cover the greenhouse similar to Jagadish *et al.* (2007), who observed a light intensity of 650 µmol m⁻² s⁻¹ in the greenhouse. Additionally, Murchie *et al.* (1999) reported an optimum light intensity for growth and photosynthesis in rice with a saturation of less than 1,000 µmol m⁻² s⁻¹. It was confirmed that the rice plants had been directly affected by extremely high temperatures, while the relative humidity and light intensity did not affect growth.

The plant height, tillers number per plant, yield components, and grain yield had affected by high temperatures in all 15 varieties. However, the degree to which each characteristic was affected differed depending on the genotypic variation (Matsui *et al.*, 2001). The plant height in all varieties herein was higher under high temperatures when compared to field conditions. This was supported by Oh-e *et al.* (2007), who found that the plant height under high temperatures steeper increase than field conditions. Among rice varieties showed variation of tillers number per plant and tillers number per plant of most varieties decreased under high temperatures. Therefore, tillers number per plant in ambient conditions had greater than high temperatures at the maturity stage.

High temperatures reduce yield by causing spikelet sterility at the flowering and grain filling stage (Cheabu *et al.*, 2019; Malumpong *et al.*, 2019; Malumpong *et al.*, 2020). High temperatures also decreased grain weight by inhibiting photosynthesis and starch biosynthesis enzymes (Long *et al.*, 2015; Wang *et al.*, 2012). The reduction of the rate of photosynthesis by high temperature decreased sucrose accumulation in the leaf and its translocation to the phloem. The starch biosynthesis enzyme is sensitive to high temperatures and has a reduced yield via the inhibition of starch synthesis and grain filling (Fu *et al.*, 2016). In this study, the seed set of all varieties decreased under high temperatures. The decreased seed set was associated with a high temperature-induced decrease in pollen production and shedding during flowering. Spikelet sterility is greatly increased at a temperature above 35 °C (Nakagawa *et al.*, 2003; Jagadish *et al.*, 2007). Contradicting results were observed for a heat-tolerant accession, M9962, with better anther dehiscence, higher pollen germination, and higher spikelet fertility (Cheabu *et al.*, 2019; Malumpong *et al.*, 2019). The

genetic variation of rice showed a different of floret sterility under high temperature stress (Sheehy *et al.*, 2005; Malumpong *et al.*, 2020).

High temperature largely affected 15 rice varieties in terms of yield reduction. During the flowering and grain filling stage, high temperature negatively affected yield due to the reduction of sterile spikelets and the short duration of grain filling (Oh-e *et al.*, 2007; Tian *et al.*, 2007; Xie *et al.*, 2009). In addition, high daytime temperature reduced pollen viability and number of germinated pollens that affected to fail in fertilization process (Prasad *et al.*, 2006). At the ripening stage, the high temperature decreased yield due to the respiration of seed (Tanaka *et al.*, 1995).

The size of grain was affected by high temperature (Cao *et al.*, 2008, Chaturvedi *et al.*, 2017). The grain width and length in all varieties had no significant difference in both high-temperature and field conditions. The opposite results showed that high temperatures during early seed development decreased the seed size in rice (Begcy *et al.*, 2018). The 1,000-grain weight of all varieties slightly decreased under high temperatures. This result indicated that high temperature negatively affects the early seed development stage and then decreases starch accumulation. High temperature inhibits the translocation of starches from source to sink and affects accumulation in the seed and grain (Brown *et al.*, 1996; Jeng *et al.*, 2003; Folsom *et al.*, 2014). Zhang *et al.* (2018) found that heat-susceptible rice cultivars had a lower grain weight under heat stress. The decreasing grain weight affected by high temperature due to limitation of sucrose allocation into the grains. It indicated that the kernel weight in plants was regulated by sugar metabolism as treated by heat stress (Wang *et al.*, 2008; Ruan, 2014).

Genotypic and phenotypic variance analysis found that all traits had GCV lower than PCV, indicating that the environment influenced the traits. In this study, high GCV was presented for unfilled grains number per panicle. It is a possibility to improve yield through this trait selection (Bitew, 2016) The filled grains number per panicle and grain yield showed low heritability combined with a low genetic advance that might not be recommended for selection. However, the spikelets number per panicle, seed set, and 1,000-grain weight belonging to higher heritability indicated that it might be recommended as an effective selection for these traits under high temperature conditions (Hossain *et al.*, 2021).

The investigation entitled correlation and path coefficient analysis for agronomic traits of rice at the field and high temperatures was carried out. It was found that the greatest directly positive affected on yield per plant was seed set and panicle weight under high temperatures. This experiment was consistent with Prasanth *et al.* (2017) and Oladosu *et al.* (2018) resulted that the major traits for high yield per plant under high temperature was filled grain number and spikelet

fertility percentage. In addition, Poudel *et al.* (2021) reported that panicle weight exhibited a positive correlation and highly positive direct effect on grain yield in wheat. Kande *et al.* (2018) found that grain yield had highly positive direct effect to kernel weight and the number of kernel ears. Whereas, Aman *et al.* (2020) found that ear height gave the highest directly affected on protein quality in maize.

In the current study, there are differently sensitive and tolerant heat-stress rice varieties. M9962 was confirmed as a heat-tolerant variety, while RD29, RD47, RD57, RD31, RD71, Suphan Buri 60, RD61, Pathum Thani 1, Phitsanulok 2, and RD41 were moderately tolerant, and Sinlek, Khao Dawk Mali 105, Chainat 1 and RD49 were susceptible to high temperature. For the variability and relationship of agronomic traits and grain yield, the PCV was greater than that of the GCV for all traits. The spikelets number per panicle, seed set, and 1,000-grain weight had higher heritability than other traits under high temperatures. Phenotypic correlation coefficients at high temperatures among all traits were estimated. The results presented that yield per plant gave the highest directly positive affected by seed set followed by panicle weight under high temperature. It indicates that a reliable criteria for screening high-yielding genotypes in high-temperature conditions was seed set and panicle weight.

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References

- Afuakwa, J. J., Crookston, R. K. and Jones, R. J. (1984). Effect of temperature and sucrose availability on kernel black layer development in maize. Crop Science, 24:285-288.
- Aman, J., Bantte, K., Alamerew, S. and Sbhatu, D. B. (2020). Correlation and path coefficient analysis of yield and yield components of quality protein maize (*Zea mays L.*) hybrids at Jimma, Western Ethiopia. International Journal of Agronomy, Article ID 9651537.
- Begcy, K., Sandhu, J. and Walia, H. (2018). Transient heat stress during early seed development primes germination and seedling establishment in rice. Frontiers in Plant Science, 9:1768. Doi: 10.3389/fpls.2018.01768.
- Bitew, J. M. (2016). Estimation of genetic parameters, heritability and genetic advance for yield related traits in upland rice (*Oryza sativa* L. and *Oryza glaberrima* Steud.) genotypes in northwestern Ethiopia. World Scientific News, 47:340-350.
- Brown, R. C., Lemmon, B. E. and Olsen, O. A. (1996). Development of the endosperm in rice *Oryza* sativa L.: Cellularization. Journal of Plant Research, 109:301-313.
- Burton, G. W. and DeVane, E. H. (1953). Estimating heritability in tall fescue (*Festuca arundinacea*) from replicated clonal material. Agronomy Journal, 45:478-481.

- Cao, Y. Y., Duan, H., Yang, L. N., Wang, Z. Q., Zhou, S. C. and Yang, J. C. (2008). Effect of heat stress during meiosis on grain yield of rice cultivars differing in heat tolerance and its physiological mechanism. Acta Agronomica Sinica, 34:2134-2142.
- Chaturvedi, A. K., Bahuguna, R. N., Shah, D., Pal, M. and Jagadish, S. V. K. (2017). High temperature stress during flowering and grain filling offsets beneficial impact of elevated CO₂ on assimilate partitioning and sink strength in rice. Scientific Reports, 7:8227.
- Cheabu, S., Moung-ngam, P., Arikit, A., Vanavichit, A. and Malumpong, C. (2018). Effects of heat stress at vegetative and reproductive stages on spikelet fertility. Rice Science, 25:218-226.
- Cheabu, S., Panichawong, N., Rattanametta, P., Wasuri, B., Kasemsap, P., Arikit, S., Vanavichit, A. and Malumpong, C. (2019). Screening for spikelet fertility and validation of heat tolerance in a large rice (*Oryza sativa* L.) mutant population. Rice Science, 26:229-238.
- Coast, O., Murdoch, A. J., Ellis, R. H., Hay, F. R. and Jagadish, K. S. V. (2016). Resilience of rice (*Oryza* spp.) pollen germination and tube growth to temperature stress. Plant Cell Environment, 39:26-37.
- Department of Meterology. (2018). Knowledge of Meterology. Retrieved from https://www.tmd.go.th/info/info.php?FileID=20.
- Dewey, D. R and Lu, K. H. (1959). A correlation and path-coefficient analysis of components of crested wheatgrass seed production. Agronomy Journal, 51:515-518.
- Folsom, J. J., Begcy, K., Hao, X., Wang, D. and Walia, H. (2014). Rice fertilization-independent endosperm regulates seed size under heat stress by controlling early endosperm development. Plant Physiology, 165:238-248.
- Fu, G., Feng, B., Zhang, C., Yang, Y., Yang, X., Chen, T., Zhao, X., Zhang, X., Jin, Q. and Tao, L. (2016). Heat stress is more damaging to superior spikelets than inferiors of rice (*Oryza sativa* L.) due to their different organ temperatures. Frontiers in Plant Science, 7:1637.
- Hossain, M., Azad, A. K., Alam, S. and Eaton, T. E. (2021). Estimation of variability, heritability and genetic advance for phenological, physiological and yield contributing attributes in wheat genotypes under heat stress condition. American Journal of Plant Sciences, 12:586-602.
- IRRI. (2013). Standard evaluation system for rice. 5th edition. International Rice Research Institute, Phillippins.
- Jagadish, K. S. V., Craufurd, P., Shi, W. and Oane, R. (2013). A phenotypic marker for quantifying heat stress impact during microsporogenesis in rice (*Oryza sativa* L.). Functional Plant Biology, 41:48-55.
- Jagadish, S. V. K., Craufurd, P. Q. and Wheeler, T. (2007). High temperature stress and spikelet fertility in rice (*Oryza sativa*. L.). Journal of Experimental Botany, 5:1627-1635.
- Jagadish, S. V. K., Mathurajan, R., Oane, R., Wheeler, T. R., Heuer, S., Bennett, J. and Carufurd, P. Q. (2010). Physiological and proteomic approaches to address heat tolerance during anthesis in rice (*Oryza sativa* L.). Journal of Experimental Botany, 61:143-156.
- Jeng, T. L., Tseng, T. H., Wang, C. S., Chen, C. L. and Sung, J. M. (2003). Starch biosynthesizing enzymes in developing grains of rice cultivar Tainung 67 and its sodium azide-induced rice mutant. Field Crops Research, 84:261-269.
- Johnson, H. W., Robinson, H. X. and Comstock, R. E. (1955). Estimates of genetic and environmental variability in soybeans. Journal of Agronomy, 47:314-318.
- Kande, M., Ghimire, S. K., Ojha, B. R. and Shrestha, J. (2018). Correlation and path coefficient analysis for grain yield and its attributing traits of maize inbred lines (*Zea mays L.*) under heat stress condition. International Journal of Agriculture Environment and Food Sciences, 2:124-130.
- Kobayashi, S., Fukuta, Y., Yagi, T., Sato, T., Osaki, M. and Khush, G. S. (2004). Identification and characterization of quantitative trait loci affecting spikelet number per panicle in rice (*Oryza* sativa L.). Field Crop Research, 89:253-262.
- Krishnan, S. and Dayanandan, P. (2003). Structural and histochemical studies on grain filling in the caryopsis of rice (*Oryza sativa* L.). Journal of Bioscience, 28:455-469.

- Long, S. P., Marshall-Colon, A. and Zhu, X. G. (2015). Meeting the global food demand of the future by engineering crop photosynthesis and yield potential. Cell, 161:56-66.
- Luo, Y., Wu, X. L., Zhou, J. P., Yu, K., Jiang, C. and Wang, C. H. (2015). Effects analysis of extreme high-temperature in 2013 on the single cropping rice in Hefei. Chinese Agricultural Science Bulletin, 31:244-248.
- Madan, P., Jagadish, S. V. K., Craufurd, P. Q., Fitzgerald, M., Lafage, T. and Wheeler, T. R. (2012). Effect of elevated CO₂ and high temperature on seed set and grain quality of rice. Journal of Experimental Botany, 63:3843-3852.
- Malumpong, C., Cheabu, S., Mongkolsiriwatana, C., Detpittayanan, W. and Vanavichit, A. (2019). Spikelet fertility and heat shock transcription factor (Hsf) gene responses to heat stress in tolerant and susceptible rice (*Oryza sativa* L.) genotypes. The Journal of Agricultural Science, 157:283-299.
- Malumpong, C., Siriya, N., Pompech, D., Itthisoponkul, T., Arikit, S., Romkaew, J. and Cheabu, S. (2020). Variation in spikelet fertility and grain quality under heat stress during reproductive stage in Thai non-photosensitive rice (*Oryza sativa* L.) cultivars. International Journal of Agricultural Technology, 16:1425-1444.
- Matsui, T., Namuco, O. S., Ziska, L. H. and Horie, T. (1997). Effects of high temperature and CO₂ concentration on spikelet sterility in indica rice. Field Crops Research, 51:213-219.
- Matsui, T., Omasa, K. and Horie, T. (2000). High temperatures at flowering inhibit swelling of pollen grains, a driving force for thecae dehiscence in rice (*Oryza sativa* L.). Plant Production Science, 3:430-434.
- Matsui, T., Omasa, K. and Horie, T. (2001). The difference in sterility due to high temperature during the flowering period among japonica-rice varieties. Plant Production Science, 4:90-93.
- Matsushima, S. (1995). Physiology of high-yielding rice plants from the viewpoint of yield components. In: Matsuo T, Kumazawa K, Ishii R, Ishihara K, Hirata H. eds., Science of the Rice Plant vol. 2, Physiology, Food and Agriculture Policy Research Center, Tokyo, pp.737-766.
- Murchie, E. H., Chen, Y. Z., Hubbart, S., Peng, S. and Horton, P. (1999). Interactions between senescence and leaf orientation determine in situ patterns of photosynthesis and photoinhibition in field grown rice. Plant Physiology, 119:553-563.
- Nakagawa, H., Horie, T. and Matsui, T. (2003). Effects of climate change on rice production and adaptive technologies. In: Mew TW, Brar DS, Peng S, Dawe D, Hardy B, eds., Rice Science: Innovations and Impact for livelihood. International Rice Research Institute, Phillippins, pp.635-658.
- Oh-e, I., Saitoh, K. and Kuroda, T. (2007). Effects of high temperature on growth, yield and drymatter production of rice grown in the paddy field. Plant Production Science, 10:412-422.
- Oladosu, Y., Rafii, M. Y., Magaji, U., Abdullah, N., Miah, G., Chukwu, S. C., Hussin, G., Ramli, A. and Kareem, I. (2018). Genotypic and phenotypic relationship among yield components in rice under tropical conditions. BioMed Research International, Article ID 8936767, https://doi.org/10.1155/2018/8936767.
- Peng, S., Huang, J., Sheehy, J. E., Laza, R. C., Visperas, R. M., Zhong, X., Khush, G. S. and Cassmon, K. G. (2004). Rice yield decline with higher night temperature from global warming. Proceedings of the National Academy of Sciences of the United States of America, 101:9971-9975.
- Poudel, M. R., Poudel, P. B., Puri, R. R. and Paudel, H. K. (2021). Variability, correlation and path coefficient analysis for agro-morphological traits in wheat genotypes (*Triticum aestivum* L.) under normal and heat stress conditions. International Journal of Applied Sciences and Biotechnology, 9:65-74.
- Prasad, P. V. V., Boote, K. J. and Allen, J. L. H. (2006). Adverse high temperature effects on pollen viability seed-set, seed yield and harvest index of grain-sorghum [Sorghum bicolor (L.)

Moench] are more severe at elevated carbon dioxide due to higher tissue temperatures. Agricultural and Forest Meteorology, 139:237-251.

- Prasanth, V. V., Babu, M. S., Basava, R. K., Tripura Venkata, V. G. N., Mangrauthia, S. K., Voleti, S. R. and Neelamraju, S. (2017). Trait and marker associations in *Oryza nivara* and *O. rufipogon* derived rice lines under two different heat stress conditions. Frontiers in Plant Science, 8:1819. Doi: 10.3389/fpls.2017.01819.
- R Core Team (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ruan, Y. L. (2014). Sucrose metabolism: gateway to diverse carbon use and sugar signaling. Annual Review of Plant Biology, 65:33-67.
- Satake, T. and Yoshida, S. (1978). High temperature induces sterility in *indica* rice at flowering. Japanese Journal of Crop Science, 47:6-17.
- Sheehy, J. E., Elmido, A., Centeno, G. and Pablico, P. (2005). Searching for new plants for climate change. Journal of Agricultural Meteorology, 60:463-468.
- Singh, R. K. and Chaudhury, B. D. (1985). Biometrical method in quantitative genetic analysis. Kalyani Publishers. Ludhiana, New Delhi, India.
- Sivasubramanian, S. and Madhavamenon, P. (1973). Genotypic and phenotypic variability in rice. Madras Agricultural Journal, 60:1093-1096.
- Tanaka, K., Kasai, Z. and Ogawa, M. (1995). Physiology of ripening. In: Matsuo T, Kumazawa K, Ishii KI, Hirata H, eds., Science of the Rice Plant vol. 2. Physiology, Food and Agriculture Policy Research Center, Tokyo, pp.7-118.
- Tian, X. H., Matsui, T., Li, S. H. and Lin, J. C. (2007). High temperature stress on rice anthesis: Research progress and prospects. Chinese Journal of Applied Ecology, 18:2632-2636.
- Wang, D., Heckathorn, S. A., Wang, X. Z. and Philpott, S. M. (2012). A meta-analysis of plant physiological and growth responses to temperature and elevated CO₂. Oecologia, 169:1-13. Doi.10.1007/s00442-011-2172-0.
- Wang, E. T., Wang, J. J., Zhu, X. D., Hao, W., Wang, L. Y., Li, Q., Zhang, L. X., He, W., Lu, B. R., Lin, H. X., Ma, H., Zhang, G. Q. and He, Z. H. (2008). Control of rice grain-filling and yield by a gene with a potential signature of domestication. Nature Genetics, 40:1370-1374.
- Wang, H. Y. (2016). Investigation and prevention-and-control countermeasures for rice high temperature damage: A case of Ma'anshan City in 2013. Journal of Anhui Agricultural Sciences, 44:50-52.
- Wei, M., Wang, G. M., Chen, G. H., Zhu, Z. Z. and Yang, Z. J. (2002). Effect of high temperature at full flowering stage on seed setting percentage of two-line hybrid rice Liangyoupeijiu. Hybrid Rice, 17:51-53.
- Xie, X. J., Li, B. B., Li, Y. X. and Shen, S. H. (2009). High temperature harm at flowering in Yangtze River basin in recent 55 years. Jiangsu Journal of Agricultural Sciences, 25:28-32.
- Yin, X., Kropff, M. J. and Goudriaan, J. (1996). Differential effects of day and night temperature on development to flowering in rice. Annals of Botany, 77:203-213.
- Yoshida, S. (1981). Fundamental of Rice Crop Science. International Rice Research Institute, Los Banos, Philippines.
- Yoshida, S. and Hara, T. (1977). Effect of air temperature and light on grain filling of an indica and japonica rice (*Oryza sativa* L.) under controlled environmental conditions. Soil Science and Plant Nutrition, 23:93-107.
- Zhang, C. X., Feng, B. H., Chen, T. T., Fu, W. M., Li, H. B., Li, G. Y., Jin, Q. Y., Tao, L. X. and Fu, G. F. (2018). Heat stress-reduced kernel weight in rice at anthesis is associated with impaired source-sink relationship and sugars allocation. Environmental and Experimental Botany, 155:718-733.

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