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Phenological and physiological responses of hybrid rice under different high-temperature at seedling stage

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Abstract

Background: The projected increase in global temperature is expected to negatively impact food production in many regions. Rice exposure to heat stress can limit plant growth in different stages, especially at the seedling stage. In this experiment, two Indica parental lines N22 (heat tolerant) and BIM (heat sensitive) along with their F_2 hybrid were elucidated under different high temperatures (28 °C, 35 °C, and 42 °C) at the seedling stage.

Results: The results indicated that the F_2 hybrid inherited the heat tolerance rate from the male heat-tolerant N22 parent. Based on phenological and physiological attributes, the F_2 hybrid exhibited excessive-performance as compared to its BIM parent under different high-temperature conditions. Specifically, absorbing the ample available water through the long-rooted system enabled rice seedlings to carry out high transpirational cooling. Furthermore, there was a strong relationship ($r=0.89$, $p<0.01$) between root length and transpiration rate under 42 °C. The temperature 35–42 °C caused a significant reduction in seedlings' growth, chlorophyll content, and survival rate (18–20%), while the relative heat injury percentage and leaf temperature increased in heat-sensitive BIM parent as compared to F_2 hybrid.

Conclusion: This study suggests that the breeding of heat-tolerant hybrid rice plays an important role in the production of a resilient rice plant through heat-tolerant seedlings at the initial vegetative growth stage.

Keywords: Heat stress, Heat injury, Survival rate, Transpiration rate, Deep rooting system

Background

Rice is a major staple food, consumes by more than half of the world's population providing 20% of calorie ingested worldwide (Chaturvedi et al. 2017), and up to 80% of caloric necessities in Asia (Mahajan et al. 2010). The global rice production growth rate must be increased 1.0–1.2% annually to achieve the requirements of a rapid population growth (Ricepedia 2020). Due to environmental constraints, it is estimated that rice yield will decline by 41% through the end of this century (Shah et al. 2011).

The surface temperature of the earth has increased due to global climate change in recent decades and is expected to rise 5 °C by the end of this century (Tollefson 2020). Heat stress has a destructive influence on rice metabolic processes in all growth stages (Mittler and Blumwald 2010). Critical optimum and high temperatures are 25–30 °C and 35 °C for the response of rice seedlings to temperature, sequentially (Yoshida 1981). Additionally, elevated critical high temperatures can be catastrophic to seed germination and lead rice plants to death at the seedling stage (Satake and Yoshida 1978). The survival

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rate of rice seedlings under 42 °C, 45 °C, and 48 °C for 3 h decreased 33.3%, 75–100%, and lethal temperature, respectively (Hsuan et al. 2019). Heat stress decreases the yield of rice plants by yellowing the leaves (IRRI 2020), and damaging the main apparatus of photosynthesis in the vegetative stage (Wang et al. 2018). Particularly, the increment of a minimum 1 °C high temperature can continuously reduce 10% of yield (Peng et al. 2004). According to Prasad et al. (2017), crop physiological processes such as photosynthesis, respiration, leaf temperature, and plant growth can be drastically affected by heat stress. Heat stress has detrimental effects on the plant root system that provides water uptake, nutrient uptake, and support for other parts of plant (Valdés-López et al. 2016), leading to disruption of root growth and development (Sehgal et al. 2017), as well as shoot and root fresh, and dry weight (Li et al. 2019). The chlorophyll content is the primary key component for photosynthesis which can be represented by SPAD value; this can be drastically affected through high temperature at the vegetative stage (Himono and Shii 2012). Elevated temperature instigated cell membrane injury (Cai et al. 2015; Hasanuzzaman et al. 2019), which can be determined by the releasing of damaged cells' electrolyte leakage (Dias et al. 2010). Also, the production rate of electrolyte leakage has a positive correlation with the increment of high temperature and its duration (Agarie et al. 1995).

The above problems can be solved through effective breeding techniques by producing new heat-tolerant rice varieties (Janni et al. 2020), and screening the available genetic resources to identify resilient rice accessions for different growth stages in various regions. This study is the progress to develop new approaches for rice resiliency under time treatment for late cultivation technique to secure rice plant at the flowering stage, which is rarely reported. Late planting exposes rice seedlings to a high temperature that can bring more problems and damages. Therefore, this study aimed to elucidate the heat-tolerance mechanism and survival rate of hybrid rice produced from heat-tolerant N22 rice variety under different critical high temperatures at the seedling stage.

Methods

Plant materials

Three datasets of experiments for the elucidation of F_2 hybrid rice seedlings' physiological responses to heat stress were analyzed in this study, which conducted at the Tokyo University of Agriculture (Setagaya Campus, Tokyo). The first experiment was conducted in 2018 for evaluating the heat tolerance rate of Berenj-I-Mahin (BIM, Afghan rice) and Nagina22 (N22) heat-tolerant rice variety at the flowering stage. Experiment two has been done in 2019 for crossing of BIM with N22 rice variety, for the genetic improvement of heat tolerance rate of Afghan rice variety. The F_1 hybrid seeds were consecutively cultivated in a glasshouse during the winter season for the production of F_2 hybrid seeds. The third experiment was conducted in June 2020, using a growth chamber (CHF-405 Cultivation Chamber, Japan). In this experiment, two parental lines (N22 and BIM), and their F_2 hybrid were exposed to different high temperatures at the seedling stage. Initially, the F_2 seeds were subjected to 60 °C for 3 days to break physiological dormancy due to fresh production, while other varieties' seeds were produced in 2018. Then, rice seeds were put under running water for pre-germination for 2 days and cultivated in plastic cell trays. The trays were fixed into the plastic water tub for holding the require water and placed in a growth chamber for heat stress. The irrigation managed through pipe to ensure the water level constant daily within the plastic tub. Rice seedlings were subjected for 3 weeks under three different temperature conditions; 28 °C (control), 35 °C (optimum high temperature), and 42 °C (severe critical high temperature) with 50% relative humidity as shown in Fig. 1.

Seedlings' growth and physiological parameters

Seedling growth attributes including plant height, number of leaves, and survival rate were recorded at 5 days interval. At the final growth stage of seedlings; the number of tillers, shoot and root length, shoot and root fresh and dry weight, chlorophyll content using SPAD value meter (SPAD-502 Plus; Spectrum Technologies, Aurora, IL), and physiological parameters such as photosynthetic rate, stomatal conductance, transpiration rate, and leave temperature were measured using LCi-SD Portable Photosynthesis System (ADC Bioscientific, Hoddesdon, UK). Rice plant leaf was put into the LCi-SD machine chamber for 1 min to read the parameters.

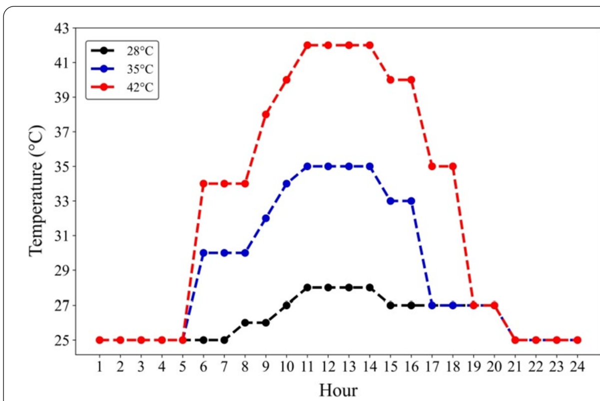

Fig. 1 Temperature settings for heat treatment in the growth chamber

Determination of relative heat injury and malondialdehyde

Relative heat injury percentage determined by cell membrane thermal stability (CMTS, measured by electrolyte leakage) in rice at the seedling stage similar to the method described by Prasad et al. (2006) with some modifications. The samples were dipped in deionized water and kept in a refrigerator at 5 °C for 2 h. Then, 1-cm leaf disks were cut, and a single disk was put in a vial with 2 mL of deionized water. Both the heat-stressed and ambient-treatment vials were divided into two categories: (1) those simply stored at room temperature, and (2) those subjected to heat treatment at 47 °C for 12 h in a water shaking bath. Both categories were then stored in a refrigerator at 5 °C for 12 h. The released electrolytes in the water were then measured by an electrical conductivity meter (LAQUA twin, Horiba, Fukuoka, Japan) at room temperature. For the second measurement of the aqueous phase, all of the vials were autoclaved for 20 min at 100 °C and cooled at room temperature for electrolyte reading (EC) readings. Furthermore, the determination of malondialdehyde (MDA) was done based on the method described by Jiang and Huang (2001) and Prabath Pathirana et al. (2011).

Statistical analysis

The data were analyzed based on the analysis of variance, Spearman's correlation analysis, and principal component analysis (PCA) with Python 3. Differences among means considered using Tukey's test at 0.05% level. Relative heat injury percentage (RI%) was calculated based on CMTS $(\%) = (1 - (T1/T2))/(1 - (C1/C2)) \times 100\%$, where T and C stand for heat-treated and control conductivity, respectively. 1 and 2 represent conductance before and after autoclaving. Based on CMTS, the relative injury degree is measured as RI $(\%) = 100 - \text{CMTS}$.

Results

Tolerance of heat stress of the parental lines

In the first experiment, the heat tolerance rate of parental lines was evaluated based on the fertility rate of spikelets under heat stress conditions at the flowering stage. N22 showed a higher spikelet fertility rate of 71.6% as compared to BIM (42.6%) under heat-stress conditions. This result showed that BIM rice was highly susceptible scored 5 (41–60%) based on the standard issued by IRRI (2002). Additionally, BIM rice produced a high amount of MDA (7.98%) as compared to N22 (6.01%) under heat stress conditions. Therefore, BIM crossed with N22 to improve Afghan rice variety against high temperature conditions.

Seedlings' growth parameters under heat-stress environment

In this experiment, high temperature significantly ($p < 0.05$) suppressed growth of rice seedlings, including the plant height, number of leaves per plant, root and shoot length, root and shoot weight, and seedling biomass as shown in Table 2. BIM had a higher plant height compared to N22 and F_2 under 28 °C. Seedlings height increased under 35 °C and 42 °C compared to 28 °C at 5 days after sowing (DAS) in both parents and their F_2 hybrid, while BIM decreased seedlings' height under 35 °C and 42 °C at 15 DAS. On the contrary, N22 and F_2 were stable under all treatments at 10 and 15 DAS (Fig. 2).

The number of leaves increased in parents and F_2 under 35 °C and 42 °C compared to 27 °C. In accordance to plant height, the number of leaves per plant was also in parallel under different high-temperature conditions. At 15 DAS, N22 and F_2 increased the number of leaves by 19.5% and 27.1%, respectively, while BIM decreased the number of leaves by 0.6% under 42 °C compared to the 27 °C group as shown in Fig. 2.

As the temperature increased from 28 to 35 °C, the root and shoot length enhanced in both parents and their F_2 hybrid, while decreased under 42 °C. The results revealed that there was a significant difference between N22 and F_2 root length compared to BIM under all treatments, while root length was suppressed in both parents and F_2 under 42 °C. The BIM rice variety had a thick root diameter with a short root system, thus the root fresh weight of BIM was higher than N22 variety under 28 °C, while significantly decreased under 35 °C. Shoot fresh weight was in parallel with the increment of temperature from 28 to 35 °C in both parents and F_2 hybrid. The differences of shoot fresh weight were varied among varieties, herein, temperature affected the fresh weight in BIM variety under 35 °C and 42 °C.

Furthermore, optimum high temperatures influenced tiller production in N22, BIM, and F_2 from 1.9, 1.8, and 1.5 to 2.3, 1.2, and 1.6 under 35 °C, and to 2.3, 1.3, and 2.2 under 42 °C, respectively (Table 1). The high number of tillers increased the total biomass production weight (Table 2). The number of tillers increased in N22 and F_2 under different temperature conditions, while BIM was in opposition.

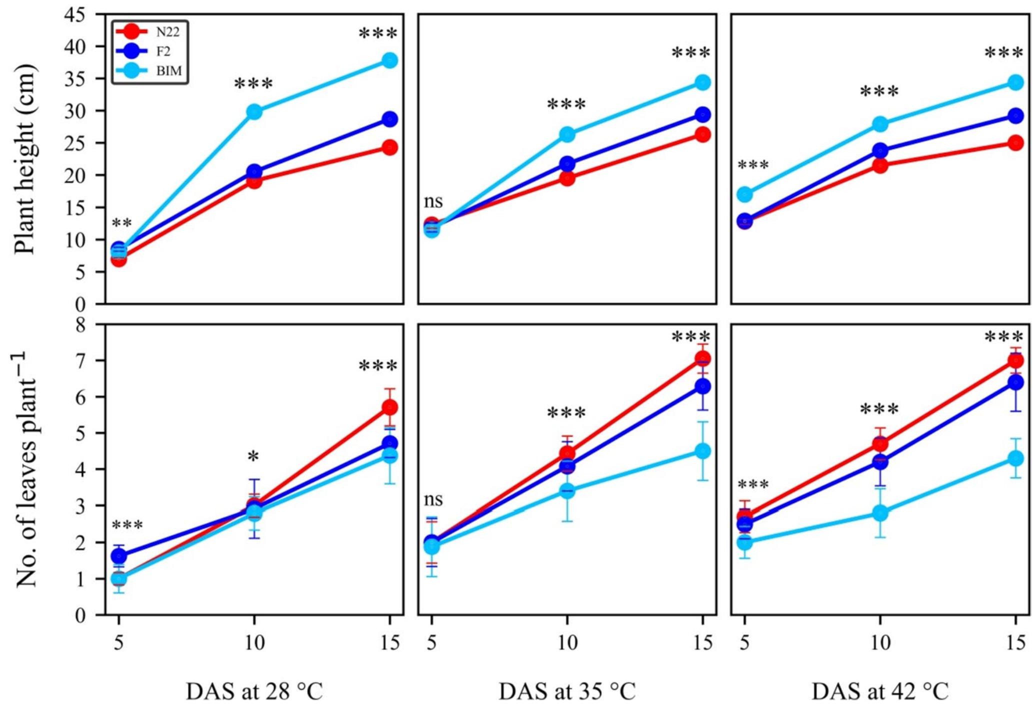

Fig. 2 Differences in seedlings' plant height and the number of leaves per plant ($n = 20$) under different temperature conditions at 5, 10, and 15 DAS

Table 1 Effects of different temperatures on tiller production of N22, BIM, and their F_2 hybrid

Treatment (°C)	Variety		
	N22	BIM	F_2
28	1.92 ± 0.06	1.83 ± 0.08	1.54 ± 0.10
35	2.32 ± 0.18	1.20 ± 0.09	1.63 ± 0.13
42	2.36 ± 0.17	1.35 ± 0.11	2.23 ± 0.16

The data represented as mean ($n = 20$) and followed by standard deviation

Effects of high temperature on chlorophyll content at the seedling stage

Different high temperatures significantly ($p < 0.05$) affected a wide range of chlorophyll content in leaves of rice plants at seedling stage. The highest SPAD value was observed in all leaves of rice seedlings under the 28 °C group compared to 35 °C and 42 °C. SPAD value in BIM variety was higher compared to N22 and F_2 under 28 °C, while BIM was substantially affected by high temperatures compared to N22 and F_2 at 35 °C and 42 °C by 20% and 32%, respectively (Fig. 3).

Effects of high temperature on physiological attributes of rice seedlings

Physiological parameters such as the photosynthetic rate, stomatal conductance, transpiration rate, and leaf temperature are substantially affected by the high temperature in parents and F_2 hybrid as well. The rate of photosynthesis was higher in the 28 °C group compared to other treatments. Heat tolerant N22 had the highest photosynthetic rate under all treatments compared to F_2 and BIM (Table 3). The BIM rice variety substantially decreased the photosynthetic rate under the 42 °C treatment, while F_2 had stable photosynthesis under all treatments. The stomatal conductance rate was significantly different ($p < 0.05$) among the parents and their F_2 under all treatments. There was stability for N22 and F_2 plants' stomatal conductance under 42 °C. In the contrast, stomatal conductance rate of BIM variety significantly affected by high temperatures under 42 °C as shown in Table 3.

The transpiration rate increased in N22, BIM, and F_2 by 60%, 2.4%, and 50% under 35 °C, and 57%, 43%, and 80% under 42 °C compared to the 28 °C group, respectively. Leaf temperature was in opposition to the transpiration rate under all treatments. The increment of transpiration rate caused to reduce leaf temperature in N22 and F_2 under 35 °C and 42 °C. While BIM

Table 2 Effects of different temperatures on plant length, fresh weight, and dry weight of N22, BIM, and their F_2 hybrid

Treatment (°C)	Variety	Length (cm)			Fresh weight (mg)			Dry weight (mg)		
		Shoot	Root	Shoot + Root	Shoot	Root	Shoot + Root	Shoot	Root	Shoot + Root
28	N22	25.0 b	11.4 a	36.5 b	356.8 b	305.0 b	671.9 b	83.6 b	32.9 c	116.5 c
	BIM	39.1 a	8.7 b	47.6 a	451.7 a	555.6 a	1007.3 a	109.9 a	53.7 b	163.6 b
	F_2	25.7 b	12.5 a	38.2 b	424.7 a	605.5 a	1030.2 a	118.2 a	76.1 a	194.3 a
		***	***	***	**	***	***	***	***	***
35	N22	27.9 b	17.0 a	45.0 a	656.7 a	577.9 a	1234.6 a	151.0 a	72.4 a	223.4 a
	BIM	34.3 a	11.3 b	45.7 a	446.2 b	369.4 b	815.6 b	110.4 b	39.6 b	150.0 b
	F_2	26.9 b	18.5 a	45.4 a	587.8 ab	484.7 ab	1072.5 ab	142.6 ab	53.4 b	196.0ab
		*	***	Ns	**	**	**	*	***	**
42	N22	24.2 c	15.8 a	40.0 a	586.1 ab	595.4 a	1181.5 ab	150.3 a	74.1 a	220.1 a
	BIM	34.9 a	10.0 b	44.9 a	471.2 b	475.6 a	946.9 b	124.3 a	53.8 a	178.5 b
	F_2	28.5 b	15.0 a	43.6 a	630.1 a	619.8 a	1250.0 a	153.1 a	66.5 a	219.6 a
		***	***	ns	*	ns	*	ns	ns	**

The data represented as mean ($n = 20$). Significant differences are shown by letters across three temperature within each treatment of two varieties and their F_2 hybrid

***$p < 0.001$, **$p < 0.01$, *$p < 0.05$, and ns: not significant

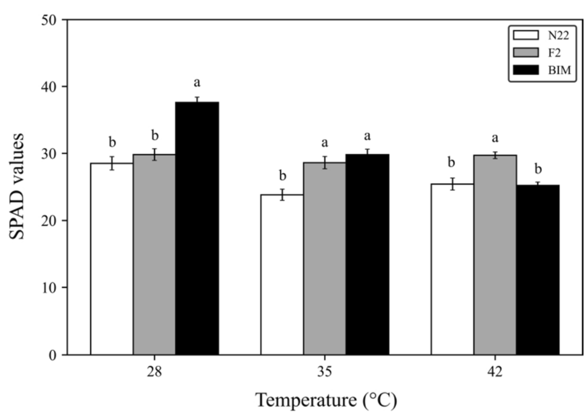

Fig. 3 Effects of different high temperatures on chlorophyll content of N22, BIM, and their F_2 hybrid seedlings at 14 DAS under heat stress ($n = 20$). Different letters denoted statistical signficance differene between varieties and their F_2 hybrid

had a lower transpiration rate, which caused high leaf temperature (Table 3). There was strong relationship ($r = 0.89$, $p < 0.01$) of root length with transpiration rate in F_2 hybrid under 42 °C. Based on PCA, N22 showed a high photosynthetic rate under all treatments, while F_2 hybrid had a similar response to N22 compared to BIM rice variety as shown in Fig. 4. The increment of temperature showed clear effects on the physiological attributes according to PCA in parental lines and their F_2 hybrid.

Relative heat injury

The degree of relative injury differed by heat stress under different high temperatures. Seedlings' relative heat injury percentage under 35 °C was considered as mild heat injury, while under 42 °C treatment there was a severe heat-injury rate as shown in Fig. 5. There was a significant difference ($p < 0.05$) for N22 variety's relative heat injury percentage compared to other rice varieties under all treatments. Based on relative injury percentage, BIM showed high susceptibility under 35 °C and 42 °C treatments compared to 28 °C treatment. F_2 hybrid was similar to N22 variety under 35 °C and did not show a high tolerance rate under 42 °C, but compared to BIM variety had less relative heat injury percentage.

Seedlings' survival responses to high temperature

The survival rate of seedlings under 35 °C in N22 and BIM was affected by 8% and 17%, respectively, while survival decreasing percentage under 42 °C was in N22 (8%), BIM (20%), and F_2 (8%) (Fig. 6). However, these results revealed that the heat tolerance rate of the F_2 hybrid was improved as compared to its BIM parent.

Discussion

Previous studies identified the N22 rice variety being as heat tolerant, especially in the flowering stage (Jagadish et al. 2010), therefore, we have crossed the Afghan BIM rice variety with N22 to improve the BIM rice variety's tolerance rate against high-temperature conditions. However, the major focus of these studies was stress imposed by different high temperatures at the seedling stage. In the current study, we focused on the elucidation of growth parameters and physiological characteristics of the parental lines (N22 and BIM) and their F_2 hybrid at the seedling stage.

Table 3 Comparison of physiological attributes of N22, BIM, and their F_2 rice under 28 °C, 35 °C, and 42 °C conditions

Treatment (°C)	Variety	Photosynthetic rate (μmol CO_2 m^{-2} s^{-1})	Stomatal conductance (mol CO_2 m^{-2} s^{-1})	Transpiration rate (μmol m^{-2} s^{-1})	Leaf temperature (°C)
28	N22	1.03 a	0.05 b	0.9 a	28.0 a
	BIM	1.46 a	0.07 a	0.8 a	28.3 a
	F_2	0.43 a	0.02 c	0.4 b	28.2 a
		ns	**	**	***
35	N22	0.59 a	0.08 a	1.3 a	29.3 c
	BIM	0.45 a	0.03 b	0.8 b	30.6 a
	F_2	0.54 a	0.04 b	0.8 b	29.9 b
		ns	**	**	***
42	N22	0.44 a	0.1 a	2.1 a	27.9 c
	BIM	0.21 a	0.09 b	1.4 b	29.6 a
	F_2	0.42 a	0.1 a	2.1 a	28.8 b
		ns	**	*	***

The data represented as mean ($n = 20$). Significant differences are shown by letters across three temperature within each treatment of two varieties and their F_2 hybrid

***$p < 0.001$, **$p < 0.01$, *$p < 0.05$ and ns: not significant

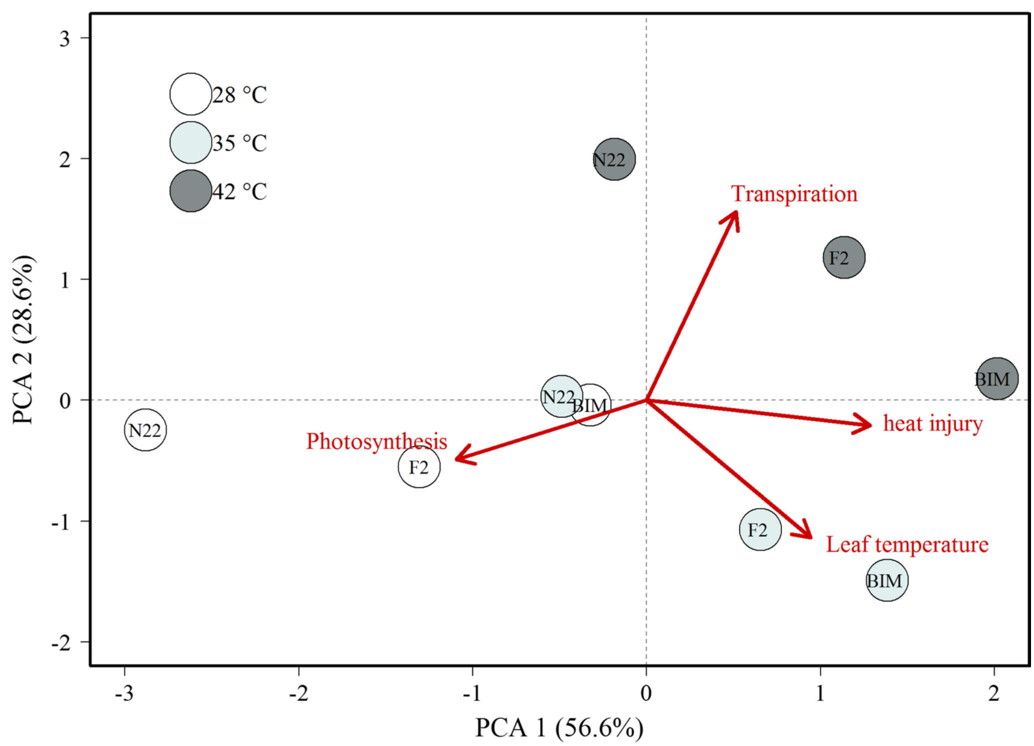

Fig. 4 PCA of photosynthesis, transpiration rate, relative heat injury percentage, and leaf temperature of N22, BIM, and F_2 rice hybrid exposed under 28 °C, 35 °C, and 42 °C high-temperature conditions

Rice plants can still maintain their normal growth at temperatures ranging from 27 to 32 °C without significant negative effects, while temperatures above 32 °C negatively affect all stages of rice plant growth and development (Aghamolki et al. 2014). Similarly, in this experiment, seedling height and number of leaves per plant were significantly ($p < 0.05$) suppressed at > 35 °C, while variation has been seen among varieties. BIM rice

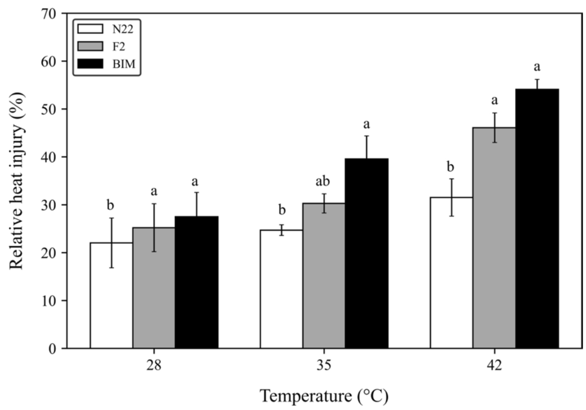

Fig. 5 Effects of different high-temperature conditions on cell membrane thermal stability which is shown in terms of relative heat injury percentage ($n = 5$). Different letters denoted statistical signficance differene between varieties and their F_2 hybrid

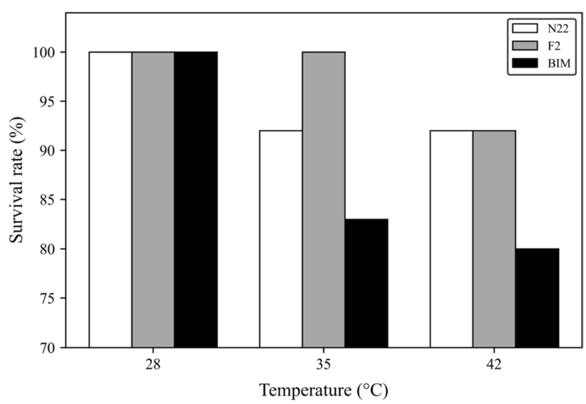

Fig. 6 Effects of different high-temperature conditions on rice seedlings survival percentage of N22, BIM, and their F_2 hybrid ($n = 20$)

variety was highly affected by 42 °C, but N22 and F_2 hybrid showed tolerance under 35 °C and 42 °C (Fig. 2). According to Kilasi et al. (2018), the N22 and IR64 rice varieties had differential responses in both shoot and root growth under heat stress conditions. This experiment also revealed that there were significant differences among parents and their F_2 hybrid in root length and weight under 35 °C and 42 °C conditions. Furthermore, the dry weight of root and shoot significantly decreased in BIM rice variety under high temperature, while N22 and F_2 hybrid did not change the dry weight under 35 °C and 42 °C as shown in Table 2. The root length of F_2 significantly improved as compared to BIM parent under all treatments.

The decrease in chlorophyll content under heat stress, which is one of the main chloroplast compartments has been considered a typical sign of photo-oxidation and chlorophyll degradation (Chutia and Borah 2012). The photosynthesis processes are interrupted through the reduction of rice leaf chlorophyll content under drought conditions (Awal and Ikeda 2002), and the degradation of chlorophyll pigment due to heat stress induced metabolic imbalance (Sheela and Alexander 1995). These results also showed that BIM rice variety highly decreased chlorophyll content under high temperature, while in N22 and F_2 hybrid the decreasing rate was not significantly different ($p > 0.05$) as shown in Fig. 3.

Heat stress has a marked influence on rice growth and physiological parameters. However, the impact of heat stress on photosynthetic activity and stomatal conductance was greatly variable in different varieties, while depending on the plant tolerance rate, heat-stress duration, and temperature rate. Heat stress can significantly affect the activation of enzyme RuBisCo in rice (Xu and Zhou 2007), which is the limiting factor of photosynthetic rate (Yin et al. 2010), and almost 60% of the assimilation of the required nutrients during grain filling occurs by photosynthesis processes (Liu et al. 2013). Also, the photosynthetic rate is directly correlated with the activity of the root system in which decreases as the plant transitions to maturity stage (Oh-e et al. 2007). In this study, the photosynthetic and stomatal conductance rate decreased under heat-stress conditions in all rice genotypes (Table 3). Kilasi et al. (2018) stated that high temperature is detrimental to most physiological processes including stomatal opening, photosynthesis, and growth rate, which is similar to the results of this experiment.

By changing the temperature in the environment, plant's water content is the main driver of stabilizing their cells' water status through available ample water. However, high temperatures in absence of water instigate high leaf temperature, which is causing catastrophic heat injury (Fahad et al. 2017). The temperature in the range of 35–40 °C drastically decreased the rice plant's transpiration rate (Sánchez-Reinoso et al. 2014). Similarly, in these results, the transpiration rate increased under 42 °C in all three varieties, while N22 and F_2 had a higher transpiration rate as compared to BIM (Fig. 4). Due to low transpiration in the BIM variety, the leaf temperature greatly increased which caused to high relative injury percentage as shown in Fig. 4. Leaf temperature increased in N22, BIM, and F_2 hybrid as temperature increased from 28 to 35 °C, and 42 °C, which the relative heat injury percentage increased as well. N22 was tolerant under all treatments due to low leaf temperature compared to BIM variety. Similar to N22, the F_2 hybrid had low leaf temperature that caused less heat injury in the cells.

Conclusions

Better physiological and morphological responses to heat stress at the seedling stage can help rice plant to healthy growth and high yield. Among the physiological characteristics, the ability of high rate of transpiration caused to lower leaf temperature which keeps seedlings' canopy cool and consequence to less relative heat injury, and seedling's death. Herein, this research recognized that the F_2 hybrid was tolerant against heat stress conditions compared to BIM at the seedling stage due to the capability of high transpirational cooling. The N22 variety bequeathed the long root system traits to F_2 hybrid which can absorb ample water for decreasing leaf temperature by transpirational cooling. This study proposes the elucidation of root relationship with leaf temperature and transpirational cooling, as well as the rice seedlings' responses to high-temperature conditions at the seedling stage. Also, through rice breeding, the production of new heat-tolerant rice cultivars will increase rice production globally.

Abbreviations

BIM: Berenj-I-Mahin; CMTS: Cell membrane thermal stability; DAS: Days after sowing; N22: Nagina22; PCA: Principal component analysis; RI: Relative injury; SPAD: Soil plant analysis and development.

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Authors' contributions

All the authors have made great contribution in this study. Concept: SA, GG, NH, KK, MIS, TZ, and RAR. Research conduction: SA, GG, TZ, and NH. Data collection and monitoring: SA, KK, MIS, and NH. Data analysis: SA, GG, RAR, and TZ. Draft writing of manuscript: SA, KK, NH, and GG. Review and editing of manuscript: SA, MIS, RAR, and TZ. Data visualization: SA, GG, NH, and TZ. All authors have read and approved the final manuscript.

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Availability of data and materials

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Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing of interest

There is no conflict of interest in this study.

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