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Identification of Heat-Tolerant Rice Genotypes through Phenotypic Selection and Multi-Trait Characterization for Genetic Diversity

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Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

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Abstract

Rice (*Oryza sativa* L.) is highly vulnerable to elevated temperature, particularly during reproductive development, when impaired spikelet fertility and grain filling can substantially reduce yield. This study evaluated heat-stress responses among 49 rice genotypes, including released varieties, advanced breeding

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lines and tolerant and susceptible checks, during kharif 2021 at the Regional Agricultural Research Station, Maruteru. Genotypes were grown under ambient control conditions and in a polyhouse where heat stress was imposed from panicle initiation to maturity. During the stress period, mean maximum and minimum temperatures were 30.3 °C and 25.4 °C under ambient conditions and 35.3 °C and 27.9 °C inside the polyhouse, respectively. Phenological, morpho-physiological and yield-related traits were assessed to identify genotypes with stable performance under heat stress. Heat stress reduced mean chlorophyll a from 3.20 to 2.75 mg g^{-1} FW, chlorophyll b from 1.29 to 0.76 mg g^{-1} FW, cell membrane stability from 55.9% to 47.4%, spikelet fertility from 89.7% to 50.4% and grain yield from 29.4 to 15.9 g $plant^{-1}$. Considerable genotypic variation was observed across traits. N22 maintained the strongest overall performance under stress, with 81.4% membrane stability, 84.0% spikelet fertility and 21.5 g $plant^{-1}$ grain yield. Rasi, L 663, L 672, MTU 1239, CL 448 and CL 452 also showed comparatively stable responses, while Vandana, MTU 1166 and MTU 1001 were susceptible. The tolerant group comprised MTU 1223, MTU 1239, L 663, L 672, L 674, CL 448, CL 452, N22 and Rasi. The findings indicate that chlorophyll retention, membrane thermostability, spikelet fertility and grain-yield stability are useful selection criteria for identifying rice genotypes with improved tolerance to reproductive-stage heat stress.

Keywords: Oryza sativa L.; heat tolerance; heat stress; phenotypic selection; genetic diversity; chlorophyll retention; grain yield.

1. Introduction

Rice (*Oryza sativa* L.) is the second most significant cereal crop globally (El-Okkiah et al., 2022). It is a primary staple food for more than two-thirds of the world's population and is often regarded as synonymous with food. It is cultivated extensively across tropical and subtropical regions and is commonly called the "Global Grain" (Bautista & Counce, 2020). Owing to its relatively small genome, extensive germplasm diversity, abundance of molecular genetic tools and efficient transformation system, rice is considered a model crop in cereal research (Li et al., 2018; Paterson et al., 2005; Wang & Han, 2022). In India, rice is grown on approximately 45 million hectares, with annual production of 178.30 million tonnes and an average yield of 122 million metric tonnes of milled rice (Agriculture Census Division, 2019; Asma et al., 2023; Fahad et al., 2015; Teja et al., 2022).

Rising global temperatures due to climate change led to an increase of approximately 0.5 °C during the 20th century, with projections suggesting a further rise of 1.5 to 4.5 °C within the current century (Hoegh-Guldberg et al., 2019; Peraudeau et al., 2015; Pillai & Tulasi, 2008). The Intergovernmental Panel on Climate Change (IPCC, 2014) predicts that, by 2081-2100, global average surface temperature could increase by 0.3-1.7 °C under minimal greenhouse gas emissions and by 2.6-4.8 °C under high-emission scenarios, relative to the 1986-2005 baseline (Nguyen, 2018). These climatic shifts pose significant threats to crop productivity worldwide. Although plants possess inherent adaptive mechanisms that help them cope with environmental stressors, these responses are often insufficient to sustain optimal yield levels. For example, Matsui et al. (2001) observed that plants can reduce panicle temperature by as much as 10 °C through transpiration cooling, which helps maintain spikelet fertility. In addition, traits such as elongated, upright flag leaves that shield panicles from intense solar radiation have been associated with improved heat tolerance.

Rice is highly susceptible to high temperature and rising global air temperatures are expected to compromise yield by 5-10%, as well as grain quality and nutritional content (Fahad et al., 2016; Fahad et al., 2019; Shrestha et al., 2022). Although elevated atmospheric CO_2 levels can enhance rice productivity because rice is a C3 plant (Shimono et al., 2009; Wang et al., 2020), heat stress often counteracts this positive response (Kadam et al., 2014). High temperatures, particularly during the reproductive and grain-filling phases, adversely affect yield and grain quality (Bahuguna et al., 2015). In tropical and subtropical regions, where rice is predominantly cultivated, elevated daytime temperatures during anthesis and grain filling present a significant challenge. For instance, temperature increases of 3.6 °C to 7.0 °C above the critical threshold between heading and mid-ripening stages resulted in reductions in photosynthetic activity of 11.2% and 35.6%, respectively (Fahad et al., 2016). To address these climate-induced risks, there is an urgent need to strengthen rice resilience through targeted crop improvement in phenological, physiological and molecular traits.

Photosynthetic pigments are important plant physiological traits, primarily because they capture light energy and generate reducing agents such as ATP and NADPH (Seelam & Jespersen, 2025; Simkin et al., 2022).

However, these pigments, particularly chlorophyll ‘a’ and chlorophyll ‘b’, are vulnerable to elevated temperatures. Exposure to heat stress alters the balance among chlorophyll ‘a’, chlorophyll ‘b’ and carotenoids, often resulting in a noticeable reduction in total chlorophyll content (Batool et al., 2019; Farooq et al., 2009; Kumar et al., 2020). High temperatures also stimulate the production of reactive oxygen species (ROS), which act as secondary stressors. These ROS interact with membrane lipids, primarily unsaturated fatty acids, leading to lipid peroxidation and subsequent accumulation of malondialdehyde (Pospíšil, 2016; Shi et al., 2017). Because biological membranes are susceptible to heat, their structural proteins may undergo conformational changes at the tertiary and quaternary levels (Wang et al., 2025). This compromises membrane integrity and increases permeability, as evidenced by greater electrolyte leakage. The resulting rise in electrical conductivity under heat-stress conditions reflects a decline in the membrane thermal stability index (Hemantaranjan et al., 2014; Ifeduba et al., 2024; Taratima et al., 2022; Ministry of Agriculture, Government of India, 2019–2020).

Genetic variability within rice germplasm is fundamental to the success of crop improvement programmes, particularly for enhancing tolerance to high-temperature stress (Mthiyane et al., 2024). This variability is especially important during the reproductive stage, when maintaining high spikelet fertility is critical for yield stability, and these traits can be effectively targeted through direct phenotypic selection. In addition, correlation analysis between yield and its associated traits under heat stress provides insights into trait interdependence (Seelam et al., 2025), enabling effective indirect selection strategies. Identifying such genotypes can help breeders select superior lines with better adaptation to future climate scenarios.

However, information remains limited on the comparative performance of locally relevant released varieties and advanced breeding lines under controlled reproductive-stage heat stress. In particular, the combined use of phenological, physiological and yield-related traits for identifying stable heat-tolerant rice genotypes requires further evaluation. Addressing this gap is essential for selecting donor parents and developing breeding strategies for heat-prone rice-growing environments.

Therefore, this study aimed to assess the phenotypic response and molecular characterisation (Seelam et al., 2025) of rice genotypes under control and heat-stress conditions, with stress imposed in a polyhouse during the reproductive phase.

2. Materials and Methods

2.1 Plant Materials

The study was conducted during kharif 2021 using forty-nine rice genotypes (Supplementary Table 1), comprising released varieties and advanced breeding lines obtained from the Regional Agricultural Research Station (RARS), Maruteru. The experiment was carried out in an artificial polyhouse facility established at RARS. Weather data during the crop growth period were collected from the meteorological observatory at RARS, and polyhouse conditions were continuously monitored using a data logger (RC-4HC) (Fig. 1). During the cropping season, the mean monthly maximum and minimum ambient temperatures were 30.60 °C and 25.84 °C, respectively, while during the stress period from panicle initiation to maturity, the corresponding values were 30.3 °C and 25.4 °C under ambient conditions and 35.3 °C and 27.9 °C inside the polyhouse, representing increases of 5.0 °C and 2.5 °C, respectively (Fig. 2). The genotypes were evaluated in an augmented design with two replications, and observations were recorded on five randomly selected plants from each entry; mean values were computed and used for analysis. Data were collected on various morpho-physiological and yield-related traits under both conditions. At physiological maturity, plants were harvested manually and threshed by hand, and the grains and straw were cleaned and sun-dried to approximately 14% moisture content for further evaluation.

2.2 Chlorophyll Estimation

Total chlorophyll, chlorophyll a (CHLa) and chlorophyll b (CHLb) contents in the leaves were estimated according to the Porra method (Porra et al., 1989; Thompson et al., 2025) using a spectrophotometer. Chlorophyll content was estimated from the flag leaf collected one week after flowering. One gram of fresh leaf tissue was cut into small pieces, placed in a volumetric flask containing 25 mL of 80% acetone and stored in the dark for 1 to 2 days to ensure complete extraction of leaf pigments. The values were expressed as milligrams per

gram fresh weight. Chlorophyll a content, chlorophyll b content and total chlorophyll content were calculated according to Lichtenthaler and Wellburn (1983).

Chl a (µg/ml) = 12.25 $A_{663.2}$ – 2.79 $A_{646.8}$

Chl b (µg/ml) = 21.5 $A_{646.8}$ – 5.1 $A_{663.2}$

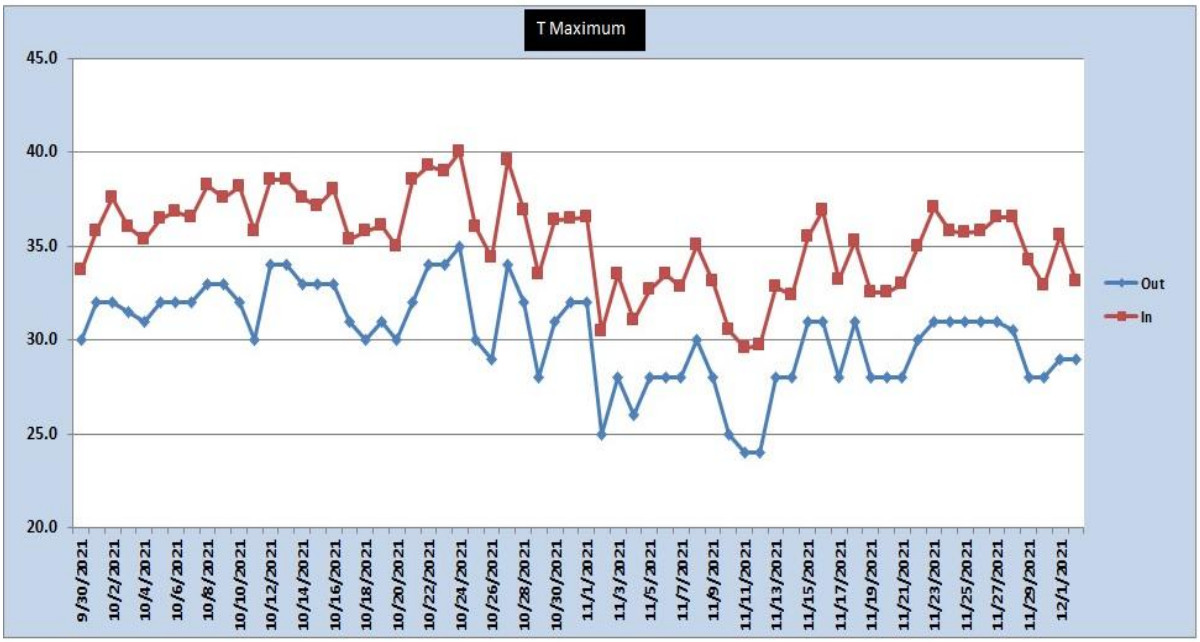
Total chlorophyll (µg/ml) = Chl a + Chl b

Table 1. Effect of high temperature on total chlorophyll content and cell membrane thermostability of rice genotypes

Genotype	Total Chlorophyll (mg g^{-1} FW)			CMS (%)		
	Control	Heat stress	Reduction %	Control	Heat stress	Reduction %
MTU 7029	4.80	3.92	18.2	49.6	43.5	12.4
MTU 2077	5.40	3.94	27.0	41.2	31.1	24.5
MTU 1061	4.58	3.28	28.3	46.7	34.2	26.7
MTU 1064	3.19	2.18	31.5	44.5	33.8	24.0
PLA 1100	4.07	3.15	22.7	43.4	35.1	19.1
MTU 1140	4.81	4.06	15.5	53.9	47.0	12.9
MTU 1172	4.21	3.30	21.6	48.3	40.9	15.4
MTU 1075	4.50	3.38	24.8	39.2	33.6	14.5
MTU 1223	4.84	4.05	16.3	72.9	66.7	8.5
MTU 1155	4.37	3.30	24.4	46.8	42.1	10.1
MTU1224	4.78	3.77	21.0	43.6	38.8	10.9
MTU 1031	4.36	3.51	19.4	57.6	43.4	24.6
MTU 1032	4.57	3.69	19.3	45.4	40.8	10.1
MTU 1190	4.67	3.46	25.9	34.2	29.1	15.0
MTU 1239	4.10	3.45	15.6	76.1	67.3	11.6
MTU 1262	5.64	4.49	20.3	53.9	39.2	27.3
MTU 1184	4.34	3.30	23.8	65.3	55.7	14.7
MTU 1194	4.39	3.24	26.0	59.1	49.2	16.8
MTU 1238	4.53	3.45	23.9	55.8	44.3	20.5
MTU 1253	4.87	3.46	28.9	45.0	38.6	14.2
MTU 1271	3.86	3.02	21.6	57.3	53.5	6.6
MTU 1315	4.96	3.55	28.4	59.6	48.6	18.5
MTU 1318	4.52	3.73	17.5	54.5	37.5	31.3
MTU 1166	4.39	3.58	18.3	49.7	40.8	17.9
MTU 1232	4.39	3.28	25.2	52.8	38.8	26.5
L 648	4.50	3.69	18.0	65.8	54.6	17.1
L 663	4.99	4.30	13.8	75.3	70.4	6.5
L665	3.76	2.38	36.8	55.6	45.0	19.0
L 667	4.66	3.63	22.0	44.2	40.1	9.3
L 668	4.71	3.91	16.9	44.9	39.2	12.6
L 669	4.72	3.38	28.4	60.4	53.6	11.3
L 670	4.59	3.38	26.3	44.5	39.2	11.8
L 672	3.04	2.83	6.9	77.7	70.5	9.3
L 674	3.11	2.89	7.1	68.1	62.4	8.4
L 676	3.25	2.77	14.6	69.2	54.0	22.0
L 677	3.06	2.62	14.1	63.7	45.8	28.1
CL 446	3.45	2.95	14.4	47.9	39.8	16.9
CL 447	3.97	3.52	11.4	42.9	37.4	12.9
CL 448	2.57	2.41	6.0	71.2	61.9	13.0
CL 449	2.55	2.06	19.2	43.3	38.9	10.2
CL 450	3.40	2.61	23.1	60.0	50.2	16.3
CL 451	3.89	3.68	5.4	67.0	58.8	12.2
CL 452	3.11	2.82	9.4	74.0	67.5	8.7

Genotype	Total Chlorophyll (mg g^{-1} FW)			CMS (%)		
	Control	Heat stress	Reduction %	Control	Heat stress	Reduction %
CL 453	2.70	2.39	11.6	68.4	54.9	19.8
CL 454	3.18	2.65	16.5	42.1	38.4	8.9
N22	3.40	3.36	1.3	83.9	81.4	3.0
Vandana	3.60	2.38	33.8	34.1	22.1	35.1
Rasi	2.82	2.61	7.4	82.5	78.9	4.4
MTU 1001	2.98	1.98	33.5	45.8	28.5	37.9
Mean	3.20	2.75		55.9	47.4	
Maximum	3.97	3.68		83.9	81.4	
Minimum	2.41	1.88		34.1	22.1	
CD (5%)	0.096	0.036		1.59	1.10	
CV %	9.18	11.46		8.2	9.3	

Fig. 1. Inner view of heat stress experimental unit consisting of automatic temperature recorder (Data logger)



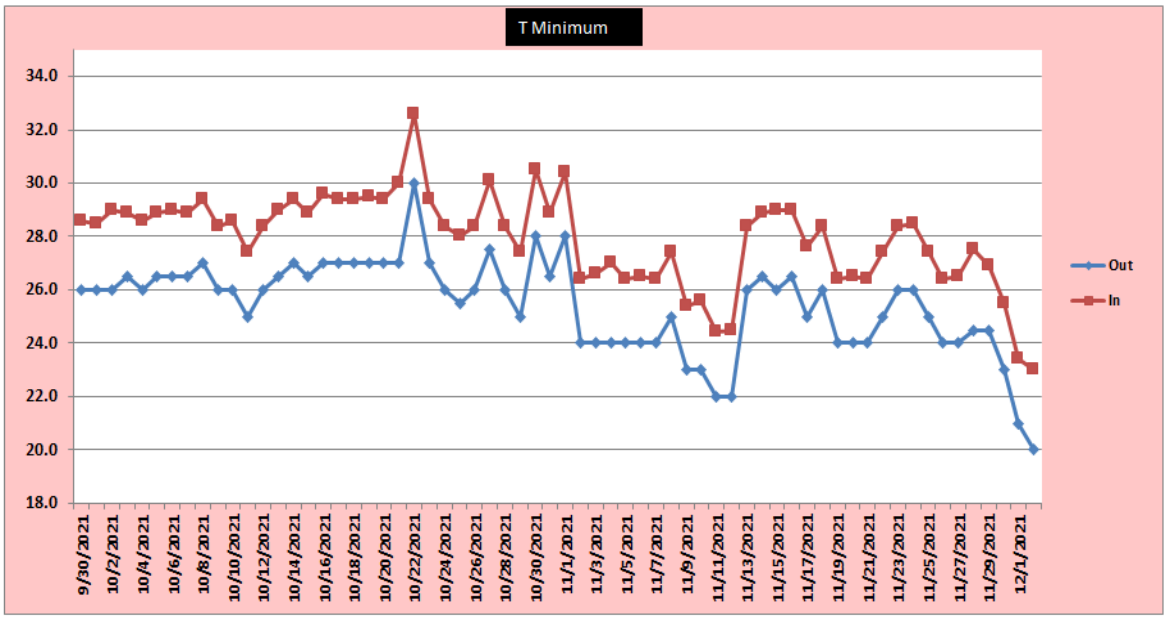


Fig. 2. Maximum and minimum temperature (°C) during the crop growing period inside and outside the polyhouse during *kharif* 2021

2.3 Cell membrane Stability (CMS) Analysis

Cell membrane stability (CMS) was assessed following Haque et al. (2009), with modifications. Leaf samples were washed with deionised water, cut into pieces and placed in test tubes containing 10 mL of deionised water. Two sets of samples were prepared: one maintained at 28 °C (control) and the other incubated at 52 °C for 1 h (heat treatment), with three replications each. After treatment, the tubes were kept at room temperature for 24 h, and initial conductance was recorded using a conductivity meter. Samples were then autoclaved at 121 °C (15 lb) for 20 min to ensure complete electrolyte leakage, and final conductance was measured. MTS was calculated using the formula of Blum and Ebercon (1981):

$$\text{CMS (\%)} = [1 - (T1/T2)] / [1 - (C1/C2)] \times 100,$$

where C1 and C2 represent the initial and final conductance of the control, respectively, and T1 and T2 represent the initial and final conductance of the heat-treated samples, respectively.

Days to 50% flowering: The number of days taken for 50% of plants to flower in each genotype was recorded as days to 50% flowering and expressed in days.

Plant height (cm): Plant height of the tagged plants was recorded by measuring the height from the base of the plant to the tip of the flag leaf or panicle on the main stem and expressed in centimetres (cm).

Ear-bearing tiller number per plant: The number of ear-bearing tillers per plant was counted under both heat-stress and control conditions and expressed as ear-bearing tiller number per plant.

2.4 Spikelet Fertility (%)

Spikelet fertility was calculated using the following formula and expressed as per cent.

$$\text{Spikelet fertility} = \frac{\text{Number of filled grains}}{\text{Total number of grains}} \times 100$$

2.5 Grain Yield (g/plant)

At physiological maturity, panicles from each plant under both stress and non-stress conditions were harvested, sun-dried, threshed and cleaned, and grain weight was recorded and expressed in grams per plant.

2.6 Data Analysis

Analysis of variance for all characters was performed according to the standard statistical procedure for an Augmented Randomised Complete Block Design (Augmented Design II), as described by Federer (1956). The data was analysed using R Studio software.

3 Results and Discussion

3.1 Chlorophyll 'a' and Chlorophyll 'b'

In plants, leaves act as the primary photosynthetic organs, and more than 90% of dry matter yield in crops is attributed to leaf photosynthesis (Makino, 2011). Chlorophyll is the main photosynthetic pigment. A higher chlorophyll concentration is necessary for photosynthesis to continue at a regular rate under heat-stress conditions. In this study, chlorophyll 'a' content varied widely among the 49 genotypes (Supplementary Table 2). Under control conditions, values ranged from 2.41 to 3.97 mg g^{-1} FW (mean 3.20), whereas under heat stress they ranged from 1.88 to 3.68 mg g^{-1} FW (mean 2.75). The highest chlorophyll 'a' levels were recorded in CL 447 (3.97 mg g^{-1} FW), MTU 1262 (3.96) and MTU 2077 (3.93) under control, while CL 451 (3.68), MTU 2077 (3.54) and CL 447 (3.52) were superior under stress. MTU 1064 showed the lowest content under both conditions (2.41 and 1.88 mg g^{-1} FW). Consistent with earlier reports (Lohitha et al., 2019), chlorophyll 'a' declined significantly under heat stress. Combined analysis revealed that N22 (1.3%), CL 451 (5.4%) and CL 448 (6.0%) had the smallest decreases, whereas Vandana (33.8%), MTU 1001 (33.5%) and CL 450 (23.1%) showed the maximum reductions.

Table 2. Effect of high temperature on spikelet fertility and grain yield per plant of rice genotypes

S. No.	Genotypes	Spikelet fertility %			Grain yield (g/plant)		
		Control	Heat stress	Per cent reduction	Control	Heat stress	Per cent reduction
1	MTU 7029	89.9	54.7	39.1	29.7	14.3	51.6
2	MTU 2077	90.6	59.7	34.1	27.7	15.7	43.3
3	MTU 1061	89.4	37.4	58.1	30.0	13.6	54.7
4	MTU 1064	86.7	35.7	58.8	24.7	14.9	39.7
5	PLA 1100	91.1	47.3	48.0	33.3	13.4	59.7
6	MTU 1140	93.3	36.1	61.3	36.7	14.7	60.0
7	MTU 1172	90.2	52.7	41.5	28.0	13.9	50.4
8	MTU 1075	88.1	62.0	29.6	39.3	14.5	63.2
9	MTU 1223	89.6	70.0	21.9	33.7	20.3	39.6
10	MTU 1155	89.1	35.6	60.0	28.0	13.7	51.1
11	MTU1224	89.0	40.7	54.2	25.3	15.2	40.1
12	MTU 1031	86.3	57.0	33.9	23.7	15.7	33.6
13	MTU 1032	93.8	43.6	53.4	34.7	16.3	52.8
14	MTU 1190	83.3	44.0	47.2	35.3	13.7	61.3
15	MTU 1239	88.1	77.2	12.3	25.7	19.7	23.3
16	MTU 1262	81.3	34.0	58.2	29.3	18.3	37.5
17	MTU 1184	94.3	65.1	30.9	23.7	16.3	30.9
18	MTU 1194	89.8	36.9	58.9	30.7	12.3	59.7
19	MTU 1238	89.1	43.7	50.9	27.3	15.3	43.9
20	MTU 1253	94.2	24.3	74.2	36.3	14.3	60.5
21	MTU 1271	94.5	44.8	52.6	33.7	17.0	49.5
22	MTU 1315	93.0	46.6	49.9	35.3	16.0	54.7
23	MTU 1318	90.4	54.4	39.8	37.0	13.0	64.8
24	MTU 1166	96.0	22.5	76.5	28.7	11.7	59.3
25	MTU 1232	84.8	48.0	43.3	25.3	16.7	34.2
26	L648	90.9	66.7	26.6	31.0	13.3	56.9
27	L 663	89.5	73.4	18.0	38.7	21.0	45.6
28	L 665	86.7	44.1	49.0	32.0	14.5	54.6
29	L 667	92.4	41.0	55.6	23.0	13.3	42.1
30	L 668	84.3	33.8	59.9	36.3	14.7	59.6

S. No.	Genotypes	Spikelet fertility %			Grain yield (g/plant)		
		Control	Heat stress	Per cent reduction	Control	Heat stress	Per cent reduction
31	L 669	83.6	44.7	46.5	37.7	16.3	56.6
32	L 670	88.9	48.4	45.6	23.7	16.0	32.3
33	L 672	93.7	70.6	24.6	20.3	19.7	3.2
34	L 674	92.6	70.2	24.1	24.3	18.3	24.6
35	L 676	87.3	36.2	58.4	26.3	18.0	31.6
36	L 677	91.2	66.2	27.3	28.7	20.3	29.0
37	CL 446	89.3	37.9	57.6	32.7	17.0	47.9
38	CL 447	85.4	30.6	64.1	23.7	13.3	43.6
39	CL 448	92.2	73.4	20.4	26.7	20.3	23.7
40	CL 449	94.1	53.3	43.3	29.0	13.0	55.1
41	CL 450	95.1	41.4	56.4	22.7	14.7	35.2
42	CL 451	86.3	66.0	23.5	25.0	15.7	37.3
43	CL 452	91.4	72.0	21.2	29.3	19.9	32.1
44	CL 453	95.6	63.4	33.6	36.3	16.1	55.6
45	CL 454	82.0	29.6	63.9	31.3	13.3	57.4
46	N22	91.7	84.0	8.3	23.5	21.5	8.5
47	Vandana	83.3	26.9	67.7	19.7	10.7	45.7
48	Rasi	93.3	74.4	20.2	26.1	19.6	24.9
49	MTU 1001	93.1	27.4	70.5	37.3	12.3	66.9
	Maximum	96.0	84.0		39.3	21.5	
	Minimum	81.3	22.5		19.7	10.7	
	Mean	89.7	50.4		29.4	15.9	
	CD (5%)	2.667	0.807		1.287	0.778	
	CV %	2.95	10.78		14.07	10.49	

Mean chlorophyll b content was 1.29 mg g^{-1} FW under control and 0.76 mg g^{-1} FW under stress (Table 2). MTU 1061 (1.89), L 670 (1.84) and MTU 1190 (1.81) recorded the highest levels under control, while MTU 1140 (1.36), L 677 (1.34) and Rasi (1.32) were superior under stress. MTU 1064 consistently had the lowest values (0.77 under control and 0.30 under stress). Similar reductions in chlorophyll b under heat stress have also been reported, with Zafar et al. (2017) recording the lowest levels in the heat-sensitive variety Basmati-385. On the final day of stress application, Thussagunpanit et al. (2015) reported that high temperature decreased chlorophyll a by 43.84%, chlorophyll b by 49.53%, total chlorophyll (a + b) by 45.03% and carotenoids by 61.84% compared with non-stressed plants, indicating that heat stress impairs the light-harvesting capacity of chlorophyll pigments (Calatayud & Barreno, 2004; Jin et al., 2016; Zhu et al., 2011). In the present study, combined analysis showed that MTU 1140 (3.6%) had the smallest decline, lower than the tolerant checks N22 (9.2%) and Rasi (8.3%), while MTU 2077 (72.5%), L 665 (66.8%) and MTU 1224 (65.3%) exhibited the greatest reductions.

3.2 Total Chlorophyll Content

Heat stress causes the production of reactive oxygen radicals in plants because of an imbalance between photosynthesis and respiration, which damages chloroplast membranes and oxidises chlorophyll pigments (Sharkey, 2005; Sun & Guo, 2016; Wang et al., 2018). The ability to synthesise more chlorophyll under high-temperature stress is an important criterion for stress tolerance (Zhou et al., 2018). In this study, total chlorophyll ranged from 3.19 to 5.64 mg g^{-1} FW under control and from 2.18 to 4.54 mg g^{-1} FW under stress (Table 1; Fig. 3). MTU 1262 (5.64), MTU 2077 (5.40) and CL 451 (5.27) had the highest content under control, while N22 (4.54) and MTU 1262 (4.49) were superior under stress. MTU 1064 consistently showed the lowest values (3.19 and 2.18). Minimal reductions were observed in N22 (3.5%), Rasi (7.7%) and CL 448 (10.2%), while Vandana (42.2%), L 665 (36.8%), MTU 1001 (36.3%) and MTU 1064 (31.5%) showed the greatest losses (Table 1). Previous studies also reported similar reductions, with N22 maintaining higher stability than sensitive checks (Veronica et al., 2018; Lohitha et al., 2019).

3.3 Cell Membrane Thermostability (CMS)

Under heat stress, uninterrupted functioning of cellular membranes is essential for photosynthesis and respiration to proceed accurately (Allakhverdiev et al., 2008; Niu & Xiang, 2018). Consequently, membrane

thermostability has been recognised as a key determinant of heat tolerance. In this study, membrane thermostability was assessed by measuring relative electrolyte leakage caused by stress injury. The genotypes N22, Rasi and L 672 recorded the highest membrane stability under both control and heat-stress conditions. N22 maintained 83.9% under control and 81.4% under stress, while Rasi showed 82.5% and 78.9%, and L 672 displayed 77.7% and 70.5%, respectively. In contrast, Vandana exhibited the lowest membrane thermostability, with only 34.1% under control and 22.1% under stress. When reductions between treatments were compared, N22 had the smallest decline (3.0%), whereas Vandana showed the greatest reduction (35.1%) (Table 1; Fig. 4).

These findings are consistent with previous reports showing that heat stress alters the lipid composition of membranes, thereby influencing their stability. For example, creeping bentgrass exposed to 35 °C exhibited higher lipid saturation (Liu & Huang, 2004), while tall fescue showed increased unsaturation under 40/35 °C conditions (Hu et al., 2018) and wheat displayed the opposite trend, with reduced unsaturation (Narayanan et al., 2016). Such changes often involve an increase in saturated fatty acids or a decrease in unsaturated fatty acids (Mondal et al., 2024; Narayanan et al., 2016). Importantly, Hu et al. (2018) suggested that greater unsaturation enhances photosynthetic membrane stability and may contribute to improved heat tolerance. The superior performance of genotypes such as N22, Rasi and L 672 in maintaining higher membrane thermostability in this study could therefore be attributed to similar lipid adjustments, enabling them to preserve cellular integrity and function under heat stress.

3.4 Days to 50% Flowering

Days to 50% flowering varied widely among genotypes, ranging from 87 to 129 days under control conditions and from 87 to 127 days under heat stress (Supplementary Table 3). Under control conditions, N22 (87 days), Vandana (89 days), Rasi (92 days), CL 454 (101 days) and MTU 1001 (106 days) recorded the earliest flowering. Under stress, Vandana (86 days) and N22 (87 days) maintained early flowering, followed by Rasi (90 days), CL 454 (101 days) and MTU 1001 (104 days). The late-maturing genotypes MTU 1262 and MTU 1166 required 129 days to flower under control, while MTU 1262 and MTU 1318 showed delayed flowering (127 days each) under stress.

Notably, ten genotypes showed no difference in flowering duration, while MTU 1223 recorded the greatest reduction (seven days). These findings align with Sailaja et al. (2015), who reported reduced flowering duration across genotypes under heat stress, and Masuduzzaman et al. (2016), who observed significant variation for this trait among 1,217 screened lines. Early flowering under stress, as observed in Vandana and N22, may represent an adaptive escape mechanism that enables plants to complete reproductive stages before severe stress occurs.

3.5 Plant Height

Plant height showed clear reductions under heat stress (Supplementary Table 3). Under control, height ranged from 100 cm (Rasi) to 163 cm (MTU 1184), with a mean of 135.9 cm, while under stress the range was 100 cm (Vandana) to 152 cm (MTU 1184), with a reduced mean of 129.7 cm. Shorter genotypes across conditions included Rasi (101 cm), Vandana (103 cm), CL 452 (110 cm) and N22 (115 cm), while MTU 1184 consistently recorded the greatest height (157 cm mean). The reduction in plant height under elevated temperatures is consistent with earlier reports (Prasad et al., 2006; Sailaja et al., 2015), which attributed shorter stature to suppressed stem elongation and ROS-induced cellular damage. Shorter plants under stress may indicate impaired vegetative growth, which can negatively influence biomass partitioning and yield potential (Fageria, 2007; Fu et al., 2016; Wu et al., 2022).

3.6 Ear-Bearing Tillers per Plant

Ear-bearing tiller number declined significantly under heat stress, highlighting its sensitivity during panicle initiation. The average number of productive tillers decreased from 12 under control to 10 under stress (Supplementary Table 3). Rasi produced the maximum number of tillers (21 under control and 16 under stress), while N22 consistently showed the fewest (10 under control and 7 under stress). MTU 7029, a popular mega-variety, also showed reductions (16 under control and 12 under stress). Similar declines in tiller number under high temperature have been reported by Samol et al. (2015) and Oh-e et al. (2007), who observed reduced tillering and fewer productive culms under elevated temperature regimes. Given its role in determining sink capacity, tiller number under stress serves as a key trait for selecting heat-tolerant genotypes (Vishnu Prasanth et al., 2017). Genotypes such as Rasi, which sustain relatively higher tiller numbers under stress, may hold promise for breeding programmes targeting resilience.

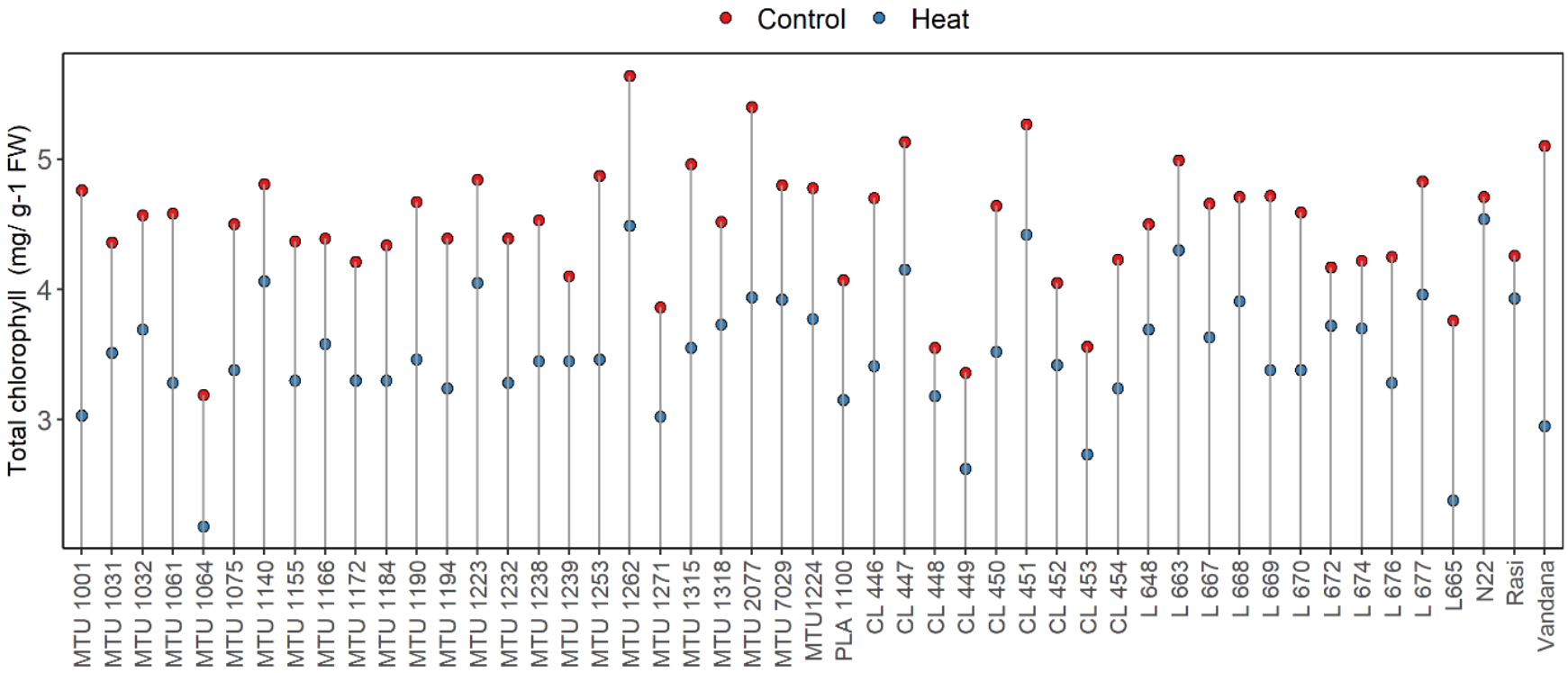


Fig. 3. Effect of high temperature on total chlorophyll content of rice genotypes

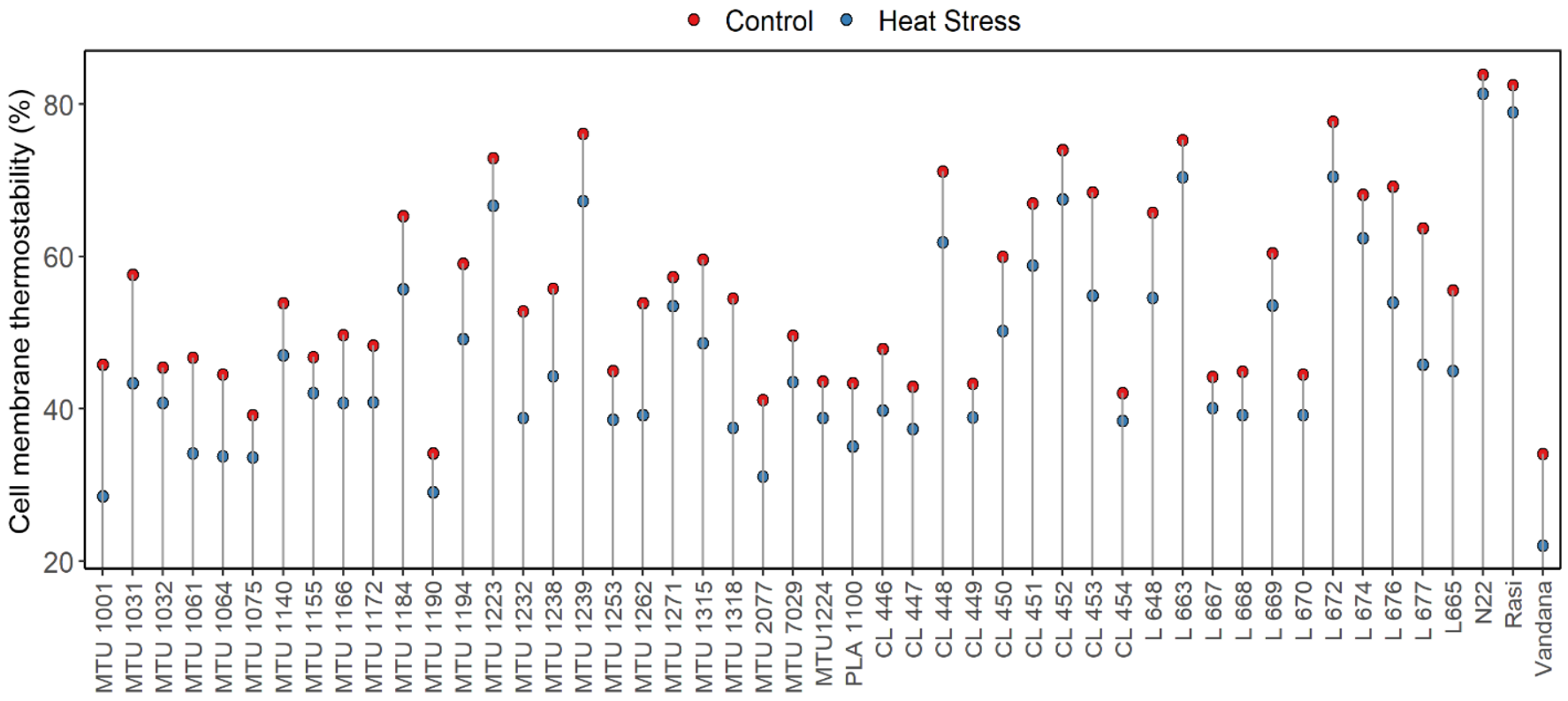


Fig. 4. Effect of high temperature on membrane thermostability (%) of rice genotypes

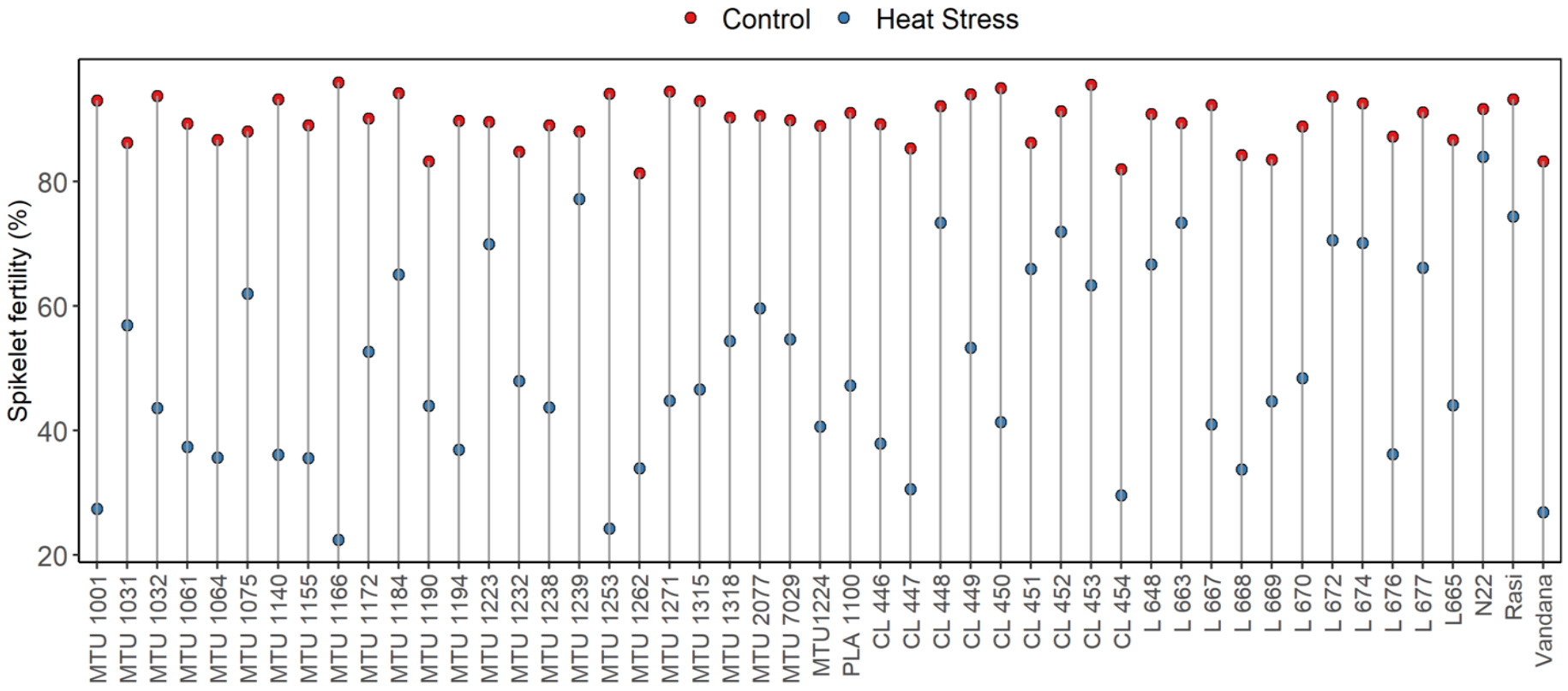
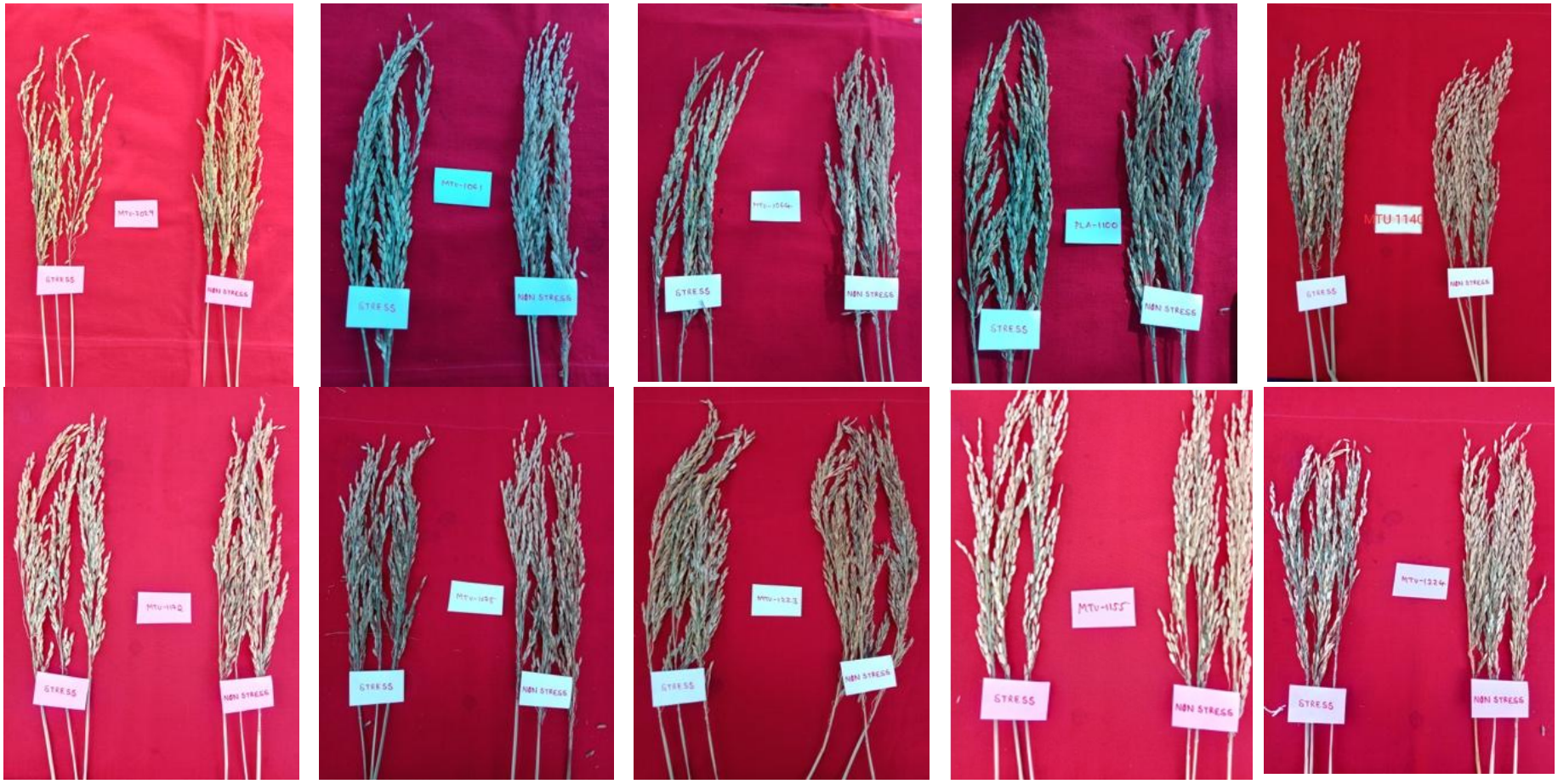


Fig. 5. Effect of high temperature on spikelet fertility (%) of rice genotypes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NON STRESS
PLA-1100
MTU 1140
MTV-1155


STRESS
NON STRESS


MTU-1318
STRESS
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MTU-1166
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NON STRESS
MTU-1232
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MTU-1001
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Fig. 6. Phenotyping of spikelets under Control and Heat Stress Conditions

Table 3. Classification of 49 rice genotypes for thermotolerance

S. No.	Score	Genotypes
1	Tolerant (>65 % spikelet fertility, > 19 grams of grain yield, > 65 % MTS)	MTU 1223, MTU 1239, L 663, L 672, L 674, CL 448, CL 452, N22, Rasi.
2	Moderately tolerant (30-65 %spikelet fertility, 12-19 grams of grain yield, 30- 65 % MTS)	MTU 7029, MTU 2077, MTU 1061, MTU 1064, PLA 1100, MTU 1140, MTU 1172, MTU 1075, MTU 1155, MTU 1224, MTU 1031, MTU 1032, MTU 1190, MTU 1262, MTU 1184, MTU 1194, MTU 1238, MTU 1271, MTU 1315, MTU 1318, MTU 1232, L 648, L 665, L 667, L 668, L 669, L 670, L 676, L 677, CL 446, CL 447, CL 449, CL 450, CL 451, CL 453, CL 454
4	Susceptible (<30 % spikelet fertility, <12 grams of grain yield, <30 % MTS)	MTU 1253, MTU 1166, Vandana, MTU 1001

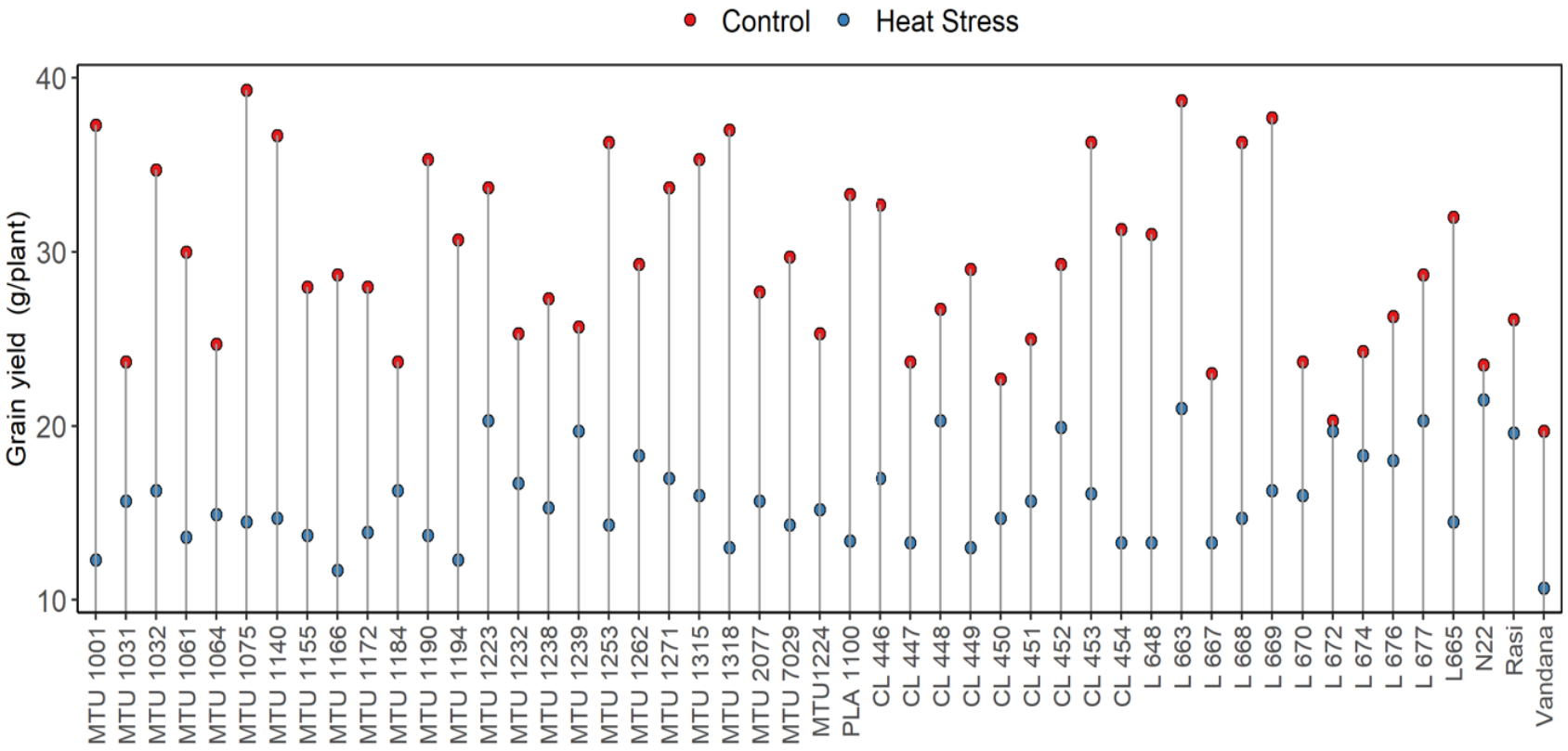

Fig. 7. Effect of high temperature on grain yield (g/plant) of rice genotypes

3.7 Spikelet Fertility (%)

Reduced spikelet fertility in panicles is a major consequence of heat stress during the reproductive stage. Spikelet fertility was highly sensitive to elevated temperature stress (Table 2). Under control conditions, fertility ranged from 81.3% to 96.0%, with a mean of 89.7%. In contrast, under heat stress, values declined markedly, ranging from 22.5% to 84.0%, with a mean of 50.4%. Under non-stress conditions, MTU 1166 recorded the highest spikelet fertility (96.0%), comparable to the tolerant check N22 (91.7%). However, under stress, N22 (84.0%), MTU 1239 (77.2%) and Rasi (74.4%) maintained the highest fertility levels. By contrast, MTU 1166 (22.5%) and MTU 1253 (24.3%) showed the lowest spikelet fertility under stress, confirming their susceptibility. Combined analysis revealed that N22 (8.3%), MTU 1239 (12.3%), L 663 (18.0%), Rasi (20.2%) and CL 448 (20.4%) sustained minimal fertility loss and can be considered heat tolerant. In contrast, MTU 1166 (76.5%) and MTU 1253 (74.2%) exhibited the largest declines, reflecting high vulnerability to stress (Fig. 5). For phenotyping this trait, spikelets from plots under heat stress and control were harvested separately and compared (Fig. 6).

These findings are consistent with earlier studies showing that high temperatures during flowering impair reproductive success. Hu et al. (2021) and Zhang et al. (2018) reported that reduced pollen germination and poor anther dehiscence under heat stress lead to spikelet sterility. Hurkman et al. (2009) further demonstrated that exposure to >33 °C at heading significantly decreased spikelet fertility and increased seed sterility. Similarly, Sailaja et al. (2015) reported declines in fertility and grain yield across multiple rice genotypes under high temperature. Poor development of rice spikelets, especially inferior spikelets, caused by heat stress reduced rice grain yield.

3.8 Grain Yield (g/plant)

Heat stress significantly decreases rice yield because it hinders grain filling, pollen viability, growth and photosynthesis (Fahad et al., 2019). Heat stress also affects the reproductive stage of rice, thereby reducing production. Grain yield per plant showed a marked decline under elevated temperature stress (Table 2). Under control conditions, yield ranged from 19.7 g to 39.3 g, with a mean of 29.4 g plant^{-1}, while under stress it declined to 10.7-21.5 g, with a mean of 15.9 g plant^{-1}. Under non-stress conditions, MTU 1075 recorded the highest yield (39.3 g), followed by L 663 (38.7 g), L 669 (37.7 g) and MTU 1001 (37.3 g). However, under heat stress, N22 (21.5 g) sustained the highest yield, closely followed by L 663 (21.0 g), L 677 (20.3 g) and MTU 1223 (20.3 g). Notably, L 663 performed on par with N22, indicating its strong potential as a tolerant genotype. In contrast, Vandana (19.7 g) showed the lowest yield under control conditions, while under heat stress Vandana (10.7 g), MTU 1166 (11.7 g) and MTU 1001 (12.3 g) recorded the poorest performance, confirming their susceptibility. The marked reduction in yield under stress is primarily due to impaired translocation of soluble sugars to spikelets and reduced starch synthase activity during grain development (Fu et al., 2016). Percentage reduction analysis revealed that L 672 (3.2%), N22 (8.5%) and MTU 1239 (23.3%) had the smallest losses, while MTU 1001 showed the maximum decline (66.9%) (Fig. 7). Genotypes with lower yield reduction therefore represent stable performers under stress conditions.

These findings are consistent with earlier reports. Su et al. (2023) and Peng et al. (2004) demonstrated that yield decreases by approximately 10% for every 1 °C rise in mean temperature. Ma et al. (2009) reported such losses due to inhibition of grain filling, while Cao et al. (2008) and Mohammed and Tarpley (2014) observed severe declines, up to 90%, when rice was continuously exposed to high temperatures during the reproductive and grain-filling stages. Poli et al. (2013) further reported significant yield reductions in N22 and its mutant under heat stress. Overall, the present study highlights that genotypes MTU 1223, MTU 1239, L 663, L 672, L 674, CL 448 and CL 452 maintained yield stability comparable to the tolerant checks N22 and Rasi, making them promising candidates for breeding programmes aimed at enhancing heat tolerance (Table 3).

4. Limitations of the Study

This study was conducted at a single research location, the Regional Agricultural Research Station, Maruteru, during one cropping season; therefore, genotype performance may vary under different environments, seasons and management conditions. The heat-stress treatment was imposed in a polyhouse from panicle initiation to maturity, which enabled controlled temperature elevation but may not fully represent the complexity of field heat events, including fluctuations in radiation, humidity and soil moisture. The evaluation focused mainly on

phenological, morpho-physiological and yield-related traits, while molecular validation was not included in the present experiment. Although previously reported SSR-based work provides complementary evidence on genetic diversity for thermotolerance, the present results require further confirmation using multi-location trials, larger genotype panels and integrated physiological and molecular analyses. Additional assessment across flowering and grain-filling stages under natural field heat stress would help refine the selection of stable donor parents for breeding programmes in diverse rice-growing agroecological regions and seasons.

5. Conclusion

The present study identified clear genotypic variation in rice responses to elevated temperature during the reproductive stage. Heat stress imposed from panicle initiation to maturity reduced chlorophyll content, membrane stability, spikelet fertility and grain yield across the tested material, but the magnitude of reduction differed among genotypes. N22 showed the most consistent heat-tolerant response, maintaining high membrane thermostability, spikelet fertility and grain yield under stress. Rasi, L 663, L 672, MTU 1239, CL 448 and CL 452 also expressed comparatively stable performance and may be useful sources of tolerance in breeding programmes. In contrast, Vandana, MTU 1166, MTU 1253 and MTU 1001 showed pronounced reductions in fertility and yield, indicating susceptibility to reproductive-stage heat stress. The tolerant genotypes identified in this study were characterised by better chlorophyll retention, higher membrane stability, sustained spikelet fertility and lower grain-yield reduction. These traits can support phenotypic selection for heat tolerance when breeding rice cultivars for warmer production environments. The results also indicate that combining physiological screening with yield-based selection can improve the identification of donor parents for thermotolerance. Further validation of the selected genotypes under multi-location and multi-season field conditions will strengthen their use in rice improvement programmes targeting future climate resilience efforts.

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Competing Interests

Authors have declared that they have no known competing financial interests or non-financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary Data

Supplementary Table 1. List of rice genotypes studied in the present investigation

S.No.	Genotype	Designation	Parentage
1	MTU 7029	-	Vasista/Mahsuri
2	MTU 2077	-	Sowbhagya/ARC 5984
3	MTU 1061	-	PLA 1100/MTU 1010
4	MTU 1064	-	PLA1100/MTU 1010
5	PLA 1100	-	Mahsuri/Vijaya
6	MTU 1140	-	MTU 5249/PLA 8572
7	MTU 1172	-	MTU 7029/MTU 1064
8	MTU 1075	-	MTU 2716/MTU 1010
9	MTU 1223	-	MTU 1081/MTU1064
10	MTU 1155	-	MTU 1001/Annada
11	MTU1224	-	[(JGL 3844/NLR 34449)/BPT 5204
12	MTU 1031	-	MTU 2077/CR 316-639
13	MTU 1032	-	MTU 2077/CR 316-639
14	MTU 1190	-	MTU 1081/Swarnasub1
15	MTU 1239	-	MTU 1075/BM 71
16	MTU 1262	-	(BPT 5204/NLR 34449)/MTU 1075
17	MTU 1184	MTU 20601-1-1-1	PLA 1100/BM 71
18	MTU 1194	MTU 2035-18-1-1	MTU 1081/MTU 1064
19	MTU 1238	MTU 2284-103-1-9	MTU 5249/IR 72
20	MTU 1253	MTU 2087-9-1-1	BPT 5204/OR 2309-19
21	MTU 1271	MTU 2347-87-1-1-1	MTU 1075/MTU 1081
22	MTU 1315	MTU 2091-14-2-1-1	MTU 2077/NBR 11
23	MTU 1318	RM 67-60-1-1-1	MTU 1064/MTU 7029
24	MTU 1166	MTU II 193-22-1-4-2	BPT 5204/MTU 1071
25	MTU 1232	MTU 2336-70-46-25-44	MTU 1075*3/Swarnasub1
26	MTU 1001	Susceptible Check	Vajram(MTU 5249)/MTU 7014
27	L 648	MTU 2293-8-2-1	RGL 11414/WGL 3962
28	L 663	MTU 2651-24-1-1	MTU 7029/MTU 1121
29	L 665	MTU 2137-1-2-6-1	MTU 1075/ MTU 1001
30	L 667	MTU 2263-7-2-1-2-1	MTU 2077/NLR 3042
31	L 668	MTU 2263-7-4-2	MTU 2077/NLR 3042
32	L 669	MTU 2299-53-2-1-2-1	MTU 2077/WGL 3962
33	L 670	MTU 2659-72-1-1	MTU 1121/MTU 3626
34	L 672	MTU 2299-51-1-1-3	MTU 2077/ WGL 3962
35	L 674	MTU 2404-94-1-2-1	MTU 1064/MTU 1075
36	L 676	MTU 2277-25-1-2	MTU 1001/OR 2329-20
37	L 677	ST 5	MTU 7029/ RG 28 L
38	CL 446	MTU 2531-63-1-1-2	PLA 1100/ MTU 1001
39	CL 447	MTU 2535-6-1-1-3	(MTU 7029/MTU 2716)/JGL 17004
40	CL 448	MTU 2625-3-1-4	MTU 1064/JGL 11118
41	CL 449	MTU 2625-13-1-1	MTU 1064/JGL 11118
42	CL 450	MTU 2625-13-1-1	MTU 1064/JGL 11118
43	CL 451	MTU 2632-53-1-2	MTU 1166/BPT 5204
44	CL 452	MTU 409-5-2-1-1	MTU 1229/RP BIO 226
45	CL 453	RM 412-48-1-1-1-1	MTU 1229/BM 71
46	CL 454	-	(MTU 1121/IRBB 50)/MTU 1121/IRBB 58
47	Vandana	Susceptible Check	C-22/Kalakeri
48	Nagina22	Tolerant Check	A selection from Rajbhog
49	Rasi	Tolerant Check	T(N)1/Co.29

Supplementary Table 2. Effect of high temperature on chlorophyll 'a', chlorophyll 'b' and total chlorophyll content of rice genotypes

S. No	Genotype	Chlorophyll 'a'			Chlorophyll 'b'		
		Control	Heat stress	Reduction (%)	Control	Heat stress	Reduction (%)
1	MTU 7029	3.41	2.88	15.5	1.39	1.04	25.1
2	MTU 2077	3.93	3.54	9.9	1.47	0.40	72.5
3	MTU 1061	2.69	2.24	16.7	1.89	1.04	44.9
4	MTU 1064	2.41	1.88	22.0	0.77	0.30	61.3
5	PLA 1100	2.89	2.51	13.1	1.18	0.63	46.2
6	MTU 1140	3.39	2.70	20.5	1.41	1.36	3.6
7	MTU 1172	3.21	2.79	13.2	1.00	0.52	48.4
8	MTU 1075	3.45	2.87	16.7	1.05	0.51	51.4
9	MTU 1223	3.64	3.25	10.7	1.20	0.80	33.2
10	MTU 1155	3.35	2.76	17.7	1.01	0.54	46.7
11	MTU1224	3.66	3.38	7.4	1.12	0.39	65.3
12	MTU 1031	3.49	3.09	11.4	0.87	0.42	51.6
13	MTU 1032	3.50	2.93	16.3	1.07	0.76	28.9
14	MTU 1190	2.85	2.59	9.0	1.81	0.87	52.3
15	MTU 1239	2.95	2.70	8.2	1.15	0.75	34.7
16	MTU 1262	3.96	3.35	15.3	1.68	1.14	32.0
17	MTU 1184	3.26	2.55	21.5	1.08	0.75	30.7
18	MTU 1194	2.66	2.48	6.8	1.73	0.77	55.6
19	MTU 1238	3.43	2.87	16.1	1.11	0.58	47.8
20	MTU 1253	3.42	2.83	17.3	1.45	0.63	56.2
21	MTU 1271	2.74	2.34	14.6	1.12	0.69	38.7
22	MTU 1315	3.41	2.94	13.7	1.55	0.61	60.6
23	MTU 1318	3.29	2.83	13.9	1.23	0.90	27.1
24	MTU 1166	3.20	2.92	8.7	1.18	0.66	44.4
25	MTU 1232	2.81	2.42	13.8	1.58	0.86	45.6
26	L 648	3.27	2.83	13.5	1.23	0.87	29.9
27	L 663	3.36	3.11	7.4	1.64	1.20	26.9
28	L665	2.42	1.93	20.2	1.34	0.44	66.8
29	L 667	3.37	2.76	18.1	1.28	0.87	32.3
30	L 668	3.03	2.79	8.0	1.67	1.12	33.0
31	L 669	2.94	2.46	16.1	1.79	0.92	48.5
32	L 670	2.75	2.57	6.6	1.84	0.81	55.8
33	L 672	3.04	2.83	6.9	1.13	0.89	20.9
34	L 674	3.11	2.89	7.1	1.10	0.81	26.2
35	L 676	3.25	2.77	14.6	1.00	0.51	49.0
36	L 677	3.06	2.62	14.1	1.77	1.34	24.4
37	CL 446	3.45	2.95	14.4	1.25	0.46	63.2
38	CL 447	3.97	3.52	11.4	1.15	0.63	45.0
39	CL 448	2.57	2.41	6.0	0.98	0.77	21.1
40	CL 449	2.55	2.06	19.2	0.81	0.56	30.5
41	CL 450	3.40	2.61	23.1	1.24	0.91	27.0
42	CL 451	3.89	3.68	5.4	1.38	0.74	46.3
43	CL 452	3.11	2.82	9.4	0.94	0.60	36.2
44	CL 453	2.70	2.39	11.6	0.86	0.34	60.4
45	CL 454	3.18	2.65	16.5	1.05	0.58	44.5
46	N22	3.40	3.36	1.3	1.31	1.19	9.2
47	Vandana	3.60	2.38	33.8	1.50	0.57	62.3
48	Rasi	2.82	2.61	7.4	1.44	1.32	8.3
49	MTU 1001	2.98	1.98	33.5	1.78	1.05	40.9
	Mean	3.20	2.75		1.29	0.76	

S. No	Genotype	Chlorophyll 'a'			Chlorophyll 'b'		
		Control	Heat stress	Reduction (%)	Control	Heat stress	Reduction (%)
	Maximum	3.97	3.68		1.89	1.36	
	Minimum	2.41	1.88		0.77	0.30	
	CD (5%)	0.096	0.036		0.102	0.021	

Supplementary Table 3. Effect of high temperature on days to 50% flowering, plant height (cm) and ear bearing tillers number/plant of rice genotypes

S. No.	Genotypes	Days to 50% flowering			Plant height (cm)			Ear bearing tillers number/plant		
		Control	Heat stress	Mean	Control	Heat stress	Mean	Control	Heat Stress	Mean
1	MTU 7029	107	107	107	124	121	123	16	12	14
2	MTU 2077	113	113	113	120	118	119	12	10	11
3	MTU 1061	122	121	121	123	128	125	11	10	11
4	MTU 1064	119	119	119	126	124	125	12	11	11
5	PLA 1100	121	120	121	133	122	128	11	9	10
6	MTU 1140	119	118	119	135	119	127	13	11	12
7	MTU 1172	119	119	119	128	130	129	12	10	11
8	MTU 1075	113	110	112	144	137	141	14	12	13
9	MTU 1223	127	120	124	139	132	136	13	10	12
10	MTU 1155	110	109	110	147	137	142	11	10	11
11	MTU1224	109	108	109	125	114	120	11	10	11
12	MTU 1031	127	121	124	123	108	116	12	10	11
13	MTU 1032	112	108	110	142	131	137	11	10	10
14	MTU 1190	108	107	108	145	139	142	13	11	12
15	MTU 1239	115	111	113	136	129	132	12	8	10
16	MTU 1262	129	127	128	132	121	126	13	10	11
17	MTU 1184	128	124	126	163	152	157	12	11	12
18	MTU 1194	122	121	122	137	138	138	11	10	10
19	MTU 1238	112	112	112	146	133	140	12	10	11
20	MTU 1253	115	113	114	147	138	142	13	11	12
21	MTU 1271	118	114	116	142	133	138	12	10	11
22	MTU 1315	121	118	120	139	132	135	12	9	11
23	MTU 1318	127	127	127	128	122	125	11	9	10
24	MTU 1166	129	127	128	151	144	148	12	11	12
25	MTU 1232	121	115	118	122	118	120	10	9	10
26	L648	129	127	128	142	135	139	10	9	10
27	L 663	112	112	112	149	152	150	12	11	12
28	L 665	118	116	117	140	138	139	13	11	12
29	L 667	124	120	122	152	143	148	14	10	12
30	L 668	124	122	123	151	145	148	12	11	12
31	L 669	122	121	122	151	144	148	13	10	12
32	L 670	120	120	120	145	143	144	12	10	11
33	L 672	121	120	121	146	140	143	10	9	10
34	L 674	117	116	117	149	142	146	10	9	10
35	L 676	112	111	112	143	131	137	10	9	10
36	L 677	112	111	112	140	126	133	12	10	11
37	CL 446	115	109	112	130	126	128	11	8	10
38	CL 447	110	108	109	150	132	141	10	10	10
39	CL 448	117	117	117	115	118	117	11	10	10
40	CL 449	114	112	113	154	144	149	11	10	11
41	CL 450	114	112	113	144	139	142	11	10	11
42	CL 451	122	121	122	130	121	126	12	10	11
43	CL 452	122	117	120	107	113	110	12	10	11

S. No.	Genotypes	Days to 50% flowering			Plant height (cm)			Ear bearing tillers number/plant		
		Control	Heat stress	Mean	Control	Heat stress	Mean	Control	Heat Stress	Mean
44	CL 453	117	115	116	134	121	127	16	11	14
45	CL 454	101	101	101	137	140	138	14	11	12
46	N22	87	87	87	115	114	115	10	7	9
47	Vandana	89	86	89	106	100	103	18	11	14
48	Rasi	92	90	86	100	103	101	21	16	18
49	MTU 1001	106	104	105	131	121	126	15	10	12
	Mean	116.0	114.0		135.9	129.7		12.0	10.0	
	Maximum	129.0	127.0		163.0	152.0		21.0	16.0	
	Minimum	87.0	86.0		100.0	100.0		10.0	7.0	
	CD (5%)	2.065	1.381		3.169	1.172		1.143	0.844	
	CV %	9.04	7.40		4.26	4.91		15.88	14.18	

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