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Screening of rice genotypes for heat tolerance at reproductive-stage based on growth, biomass, and harvest index under field conditions

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Abstract

Rice (*Oryza sativa* L.) productivity is increasingly threatened by rising temperatures during the reproductive stage, when even brief episodes of heat stress can cause substantial yield loss. Twenty-two rice genotypes, comprising advanced breeding lines (IET series) and released/candidate varieties (CO-51, MTU-1290, MTU-1296 and US-314), were evaluated under naturally occurring heat stress imposed from panicle initiation to maturity using polytunnel structures, alongside an ambient-temperature control, in a field experiment conducted in a split-plot design with three replications during the 2024 kharif season at Pantnagar, Uttarakhand, India. Heat stress significantly reduced plant height (4.27-13.11%; mean 108.29 to 98.91 cm), leaf dry weight (17.54-68.78%) and total dry matter at flowering (13.28-58.51%), shoot dry weight (16.07-50.76%; mean 725.30 to 486.99 g m⁻²) and total biomass at harvest (20.40-55.23%; mean 1232.53 to 766.63 g m⁻²), harvest index (mean 37.13% to 30.99%), and grain yield (25.998–65.05%; mean 460.89 to 238.51 g m⁻²) across genotypes. Grain yield showed a strong positive correlation with total dry matter at harvest ($r = 0.75$) and harvest index ($r = 0.75$) under heat stress, but only a weak correlation with total dry matter at flowering ($r = 0.31$), indicating that yield stability depended more on biomass retention through to harvest and efficient assimilate partitioning than on early vegetative growth. Genotypes IET 29700, US-314, and IET 30660 exhibited the least yield reduction and maintained stable or improved harvest index under stress, identifying them as promising heat-tolerant donors, whereas IET 30505 and CO-51 were the most heat-susceptible. These findings support grain yield, total dry matter at harvest, and harvest index as reliable, field-applicable selection criteria for heat-tolerance breeding in rice.

Keywords: Rice, heat stress, grain yield, harvest index, heat tolerance, genotypic variation

1. Introduction

Rice (*Oryza sativa* L.) is the primary staple food for more than half of the global population and plays a pivotal role in sustaining food and livelihood security, particularly across South and Southeast Asia (Muthayya *et al.*, 2014) [6]. However, the increasing frequency of high-temperature events associated with climate change poses a serious challenge to sustainable rice production. According to recent global climate assessments, the Earth's mean surface temperature has already increased by approximately 1.0 °C above pre-industrial levels, and further warming is projected to intensify both the occurrence and severity of heat waves during crop-growing seasons (IPCC, 2023). Rice is especially vulnerable to elevated temperature during its reproductive phase, particularly from panicle initiation to flowering and grain filling. Exposure to heat stress during this critical developmental period, even for a short duration, can severely reduce grain yield by impairing pollen viability, limiting anther dehiscence, and increasing spikelet sterility (Wu *et al.*, 2021) [13].

The adverse effects of heat stress on rice productivity arise from a complex series of morphological and physiological alterations (Shrestha *et al.*, 2022) [11]. Elevated temperature suppresses vegetative growth by reducing plant height and limiting the accumulation of dry matter in leaves and stems, while simultaneously disrupting the transport of photo assimilates from source tissues to developing sinks (Shi *et al.*, 2017) [10]. These detrimental effects become more pronounced during the reproductive stage, when inefficient assimilate partitioning lowers both

harvest index and grain yield, two of the most important indicators of crop performance under heat stress (Zafar *et al.*, 2022) ^[15]. Importantly, cultivated rice exhibits considerable genetic variability in its response to elevated temperature, with some genotypes maintaining superior growth and productivity under stress. This inherent diversity provides valuable opportunities to identify heat-tolerant germplasm for direct cultivation as well as for use as donor parents in breeding programmes aimed at developing climate-resilient rice varieties (Kumar *et al.*, 2024) ^[5].

Grain yield performance under heat stress is not determined by a single characteristic but results from the combined capacity of a genotype to sustain biomass production (source strength) and efficiently allocate assimilates to developing grains, as reflected by harvest index (Rohila *et al.*, 2026) ^[9]. Therefore, a comprehensive assessment of heat tolerance requires the simultaneous evaluation of growth-related traits, including plant height and leaf and stem dry weight; biomass accumulation parameters such as total dry matter at flowering, shoot dry weight, and total dry matter at harvest; and partitioning efficiency through harvest index. Examining the relationships between these traits and grain yield using correlation analysis provides a more complete understanding of genotype performance under stress conditions. Such a multi-trait approach facilitates the identification of genotypes based not only on the extent of yield reduction but also on the physiological mechanisms responsible for that decline, whether associated with reduced biomass production, inefficient assimilate partitioning, or a combination of both. This information is particularly valuable for designing targeted breeding strategies aimed at improving heat tolerance. In the present study, heat stress screening was conducted under field conditions using polytunnel structures to generate naturally elevated temperatures throughout the growing season. Compared with short-term controlled-environment experiments, this approach more effectively captures the cumulative impact of heat stress under practical agronomic conditions.

In view of these considerations, the present study was conducted to assess the performance of twenty-two rice genotypes, including advanced breeding lines (IET series) and released/candidate varieties (CO-51, MTU-1290, MTU-1296, and US-314), under naturally occurring heat stress from panicle initiation through crop maturity. The study aimed to: (i) assess the extent of genotypic variation in plant height, leaf and stem dry weight, total dry matter at flowering and harvest, shoot dry weight, harvest index, and grain yield under heat-stress conditions relative to the ambient-temperature control; (ii) determine the relationships between grain yield and key growth, biomass accumulation, and assimilate partitioning traits using correlation analysis; and (iii) identify rice genotypes capable of maintaining biomass production, harvest index, and grain yield under elevated temperature, thereby identifying promising donor parents for the development of heat-tolerant rice cultivars.

2. Materials and Methods

A field experiment was carried out during the 2024 *kharif* season at the Dr. Norman E. Borlaug Crop Research Centre, Govind Ballabh Pant University of Agriculture and Technology, Pantnagar, Uttarakhand, India. The experimental site is situated in the Tarai region at 29°N latitude and 79°29'E longitude, with an altitude of 243.84 m above mean sea level. The region is characterized by a humid subtropical climate, with hot summers that are conducive to evaluating the effects of high-temperature stress on rice. Twenty-two rice genotypes, comprising CO-51, IET 29694, IET 29700, IET 30505, IET 30555, IET 30561, IET

30635, IET 30651, IET 30653, IET 30656, IET 30660, IET 31433, IET 31440, IET 31444, IET 31510, IET 31512, IET 31515, IET 31533, IET 31540, MTU-1290, MTU-1296, and US-314, obtained from ICAR–Indian Institute of Rice Research (ICAR-IIRR), Hyderabad, were used in the study.

Seedlings were transplanted during the first week of July in two adjacent experimental blocks. One block was maintained under ambient field conditions and served as the control, whereas the second block was used to impose heat stress during the reproductive stage. Heat stress was generated by covering the experimental block with a polytunnel constructed using a bamboo framework enclosed with a 100-µm (0.1 mm) UV-transparent PVC film. The structure was designed with open air inlets and outlets to facilitate adequate ventilation, and its height was maintained at approximately 2.0 m to ensure normal crop growth and sufficient air circulation. Heat treatment was imposed from panicle initiation until crop maturity. The experiment was laid out in a split-plot design with three replications. Ambient and heat-stress environments constituted the main plots, while the twenty-two rice genotypes were assigned to the subplots. Daily minimum and maximum temperatures inside the polytunnel were monitored using a maximum–minimum thermometer. During the treatment period, the daytime maximum temperature within the polytunnel remained approximately 10–12°C higher than that of the ambient environment. Plant height, leaf dry weight, and stem dry weight were recorded ten days after the initiation of heat stress at the flowering stage. Total dry matter was measured at both flowering and harvest to assess biomass accumulation throughout crop development. Shoot dry weight, harvest index, and grain yield were determined at physiological maturity following standard agronomic procedures.

2.1 Measurement of Plant Height, Leaf dry weight, Total Dry Matter, Harvest Index and Grain Yield

At the flowering stage, plant height was measured on representative plants using a measuring tape from the soil surface to the tip of the tallest panicle (excluding awns, where present). For the determination of total dry matter (TDM), the entire above-ground biomass of the sampled plants was harvested, oven-dried at 65°C until a constant weight was attained, and subsequently weighed. Leaf dry weight was determined by separating all leaves from the sampled plants before oven drying at 65°C to a constant weight. At physiological maturity, the harvest index (HI) was calculated as the ratio of economic yield (grain yield) to total biological yield using the following equation:

$$\text{Harvest index} = \frac{\text{Economic yield}}{\text{Biological yield}} \times 100$$

At physiological maturity, grain yield was estimated by harvesting plants from a representative sampling area within each experimental plot. The harvested grains were cleaned and dried to a constant moisture content before weighing. Grain yield was then expressed on an area basis as grams per square metre (g m^{-2}), providing a standardized measure for comparing the productivity of different genotypes under ambient and heat-stress conditions.

2.2 Statistical Analysis

The experimental data were subjected to analysis of variance (ANOVA) to evaluate the effects of heat stress, genotype, and their interactions on the measured traits. Statistical analyses were performed using R software (version 4.4.2). Pearson's correlation analysis was carried out to examine the relationships among the studied traits, and graphical representations were generated using

the same software. Treatment means were compared using the critical difference (CD) test at the 5% level of significance ($P \leq 0.05$). The standard error of the mean [S.Em. ($\pm$)] was calculated and presented for all measured parameters.

3. Results

3.1 Effect of Heat Stress on Plant Height

Plant height was significantly affected by heat stress across all rice genotypes (Table 1). Compared with the ambient-temperature control, plant height decreased by 4.27–13.11%, with an average reduction of 8.66%. Among the evaluated genotypes, IET 30505 exhibited the greatest decline in plant height (13.11%), indicating high sensitivity to elevated temperature, whereas IET 29700 showed the smallest reduction (4.27%), demonstrating superior tolerance. The check variety, US-314, also maintained relatively stable growth under heat stress, recording only a 5.07% reduction in plant height. Most of the remaining genotypes experienced greater reductions than the check, suggesting comparatively lower tolerance to high-temperature stress, while IET 29700 and IET 30561 performed similarly to or better than US-314. Across all genotypes, the mean plant height decreased from 108.29 cm under ambient conditions to 98.91 cm under heat stress. Furthermore, the significant genotype $\times$ temperature interaction (CD at 5% = 3.188) indicated substantial variation among genotypes in their response to elevated temperature, highlighting the existence of genetic diversity for heat tolerance with respect to plant height.

3.2 Effect of Heat Stress on Leaf Dry Weight and Total Biomass Production at Flowering

Heat stress significantly reduced both leaf dry weight and total dry matter (TDM) accumulation across all rice genotypes compared with the ambient-temperature control (Table 2). The reduction in leaf dry weight ranged from 17.54% to 68.78%, with an overall mean decline of 42.36%, whereas TDM decreased by 13.28–58.51%, averaging 35.27% across genotypes. Among the evaluated entries, MTU-1290 exhibited the greatest reduction in leaf dry weight (68.78%), while IET 30505 recorded the largest decline in TDM (58.51%), indicating a pronounced susceptibility to heat stress. In contrast, the check variety US-314 maintained the highest biomass under elevated temperature, showing the smallest reductions in both leaf dry weight (17.54%) and TDM (13.28%). Most of the remaining genotypes experienced considerably greater biomass losses than the check, reflecting their relatively lower tolerance to heat stress. On average, leaf dry weight declined from 241.25 to 138.99 g m⁻², while total dry matter decreased from 844.99 to 546.95 g m⁻² under heat-stress conditions. Moreover, the significant treatment $\times$ genotype interaction (CD at 5% = 10.509 for leaf dry weight and 22.008 for TDM) demonstrated considerable variation among genotypes in their ability to maintain biomass accumulation under elevated temperature, highlighting the presence of differential heat tolerance for these traits.

3.3 Effect of Heat Stress on Shoot Dry Weight and Total Dry Matter at Harvest

Heat stress caused a significant reduction in shoot dry weight across all evaluated rice genotypes compared with the ambient-temperature control (Table 3). The decline ranged from 16.07% to 50.76%, with an average reduction of 32.86%. Among the tested genotypes, IET 30505 exhibited the greatest decrease in

shoot dry weight (50.76%), followed closely by IET 31510 (50.17%), indicating a high level of susceptibility to elevated temperature. In contrast, the check variety US-314 recorded the smallest reduction (16.07%), demonstrating a superior capacity to maintain above-ground biomass under heat-stress conditions. Most of the remaining genotypes experienced substantially greater reductions than the check, reflecting comparatively lower tolerance to heat stress. Overall, the mean shoot dry weight decreased from 725.30 to 486.99 g m⁻² under heat stress. Furthermore, the significant treatment $\times$ genotype interaction (CD at 5% = 61.724) indicated considerable genotypic variation in shoot biomass retention under elevated temperature.

Similarly, total biomass at harvest was significantly affected by heat stress in all rice genotypes (Figure 1). Compared with the ambient environment, total biomass decreased by 20.40–55.23%, with a mean reduction of 36.63%. The greatest decline was observed in IET 30505 (55.23%), whereas the check variety US-314 showed the smallest reduction (20.40%), highlighting its superior ability to sustain biomass production under high-temperature conditions. Most of the evaluated genotypes recorded markedly greater biomass losses than the check, indicating increased sensitivity to heat stress. Across all genotypes, the mean total biomass at harvest declined from 1232.53 to 766.63 g m⁻². The significant treatment $\times$ genotype interaction (CD at 5% = 74.956) further demonstrated substantial differences among genotypes in their capacity to maintain biomass accumulation under heat stress, emphasizing the existence of genetic variability for this important productivity-related trait.

Table 1: Effect of heat stress on plant height of rice genotypes at flowering ($\pm$ indicates standard error of mean). ($\downarrow$) show per cent decrease, respectively, under heat stress as compared to control

Genotype	Plant Height (cm)		
	Ambient temperature	Heat stress	% change
CO-51	110.00 $\pm$ 1.15	103.00 $\pm$ 2.08	6.36($\downarrow$)
IET 29694	111.00 $\pm$ 0.88	101.67 $\pm$ 1.76	8.41($\downarrow$)
IET 29700	109.33 $\pm$ 0.67	104.67 $\pm$ 1.45	4.27($\downarrow$)
IET 30561	108.33 $\pm$ 0.67	101.67 $\pm$ 2.03	6.15($\downarrow$)
IET 30555	106.67 $\pm$ 0.67	98.33 $\pm$ 1.76	7.81($\downarrow$)
IET 30505	109.33 $\pm$ 0.67	95.00 $\pm$ 1.73	13.11($\downarrow$)
IET 30635	112.00 $\pm$ 1.53	101.33 $\pm$ 2.33	9.52($\downarrow$)
IET 30651	106.67 $\pm$ 0.88	98.67 $\pm$ 2.40	7.50($\downarrow$)
IET 30653	108.00 $\pm$ 1.15	100.67 $\pm$ 0.67	6.79($\downarrow$)
IET 30656	104.67 $\pm$ 0.88	92.00 $\pm$ 1.15	12.10($\downarrow$)
IET 30660	107.67 $\pm$ 1.45	95.67 $\pm$ 2.03	11.15($\downarrow$)
IET 31433	117.33 $\pm$ 1.45	107.67 $\pm$ 1.45	8.24($\downarrow$)
IET 31440	113.00 $\pm$ 2.08	100.67 $\pm$ 0.67	10.91($\downarrow$)
IET 31444	107.00 $\pm$ 1.00	97.00 $\pm$ 1.73	9.35($\downarrow$)
IET 31510	102.33 $\pm$ 2.33	94.00 $\pm$ 2.31	8.14($\downarrow$)
IET 31512	109.67 $\pm$ 0.88	99.00 $\pm$ 1.00	9.73($\downarrow$)
IET 31515	108.00 $\pm$ 1.53	99.00 $\pm$ 1.00	8.33($\downarrow$)
IET 31533	109.33 $\pm$ 0.88	101.33 $\pm$ 1.20	7.32($\downarrow$)
IET 31540	106.67 $\pm$ 1.67	98.33 $\pm$ 1.67	7.81($\downarrow$)
MTU-1290	98.00 $\pm$ 1.15	86.33 $\pm$ 3.18	11.90($\downarrow$)
MTU-1296	99.00 $\pm$ 2.65	87.67 $\pm$ 1.45	11.45($\downarrow$)
US-314	118.33 $\pm$ 1.20	112.33 $\pm$ 1.45	5.07($\downarrow$)
Mean A	108.288	98.909	
	Treatment	Genotype (G)	T$\times$G
S.Em $\pm$	0.249	1.131	1.583
CD at 5%	1.633	3.188	N/A

Table 2: Effect of elevated temperature on leaf dry weight (g/m²) and total dry matter (g/m²) at flowering in 22 rice genotypes. $\pm$ indicates standard error of mean. (↓) show percent decrease under heat stress as compared to control

Genotype	Leaf dry weight (g/m ²)			TDM(g/m ²)		
	Ambient temperature	Heat stress	% change	Ambient temperature	Heat stress	% change
CO-51	211.00 $\pm$ 3.61	153.50 $\pm$ 2.73	27.25(↓)	893.38 $\pm$ 6.68	631.67 $\pm$ 3.23	29.295(↓)
IET 29694	232.67 $\pm$ 4.80	122.67 $\pm$ 2.29	47.28(↓)	980.67 $\pm$ 3.59	576.67 $\pm$ 11.45	41.1965(↓)
IET 29700	224.67 $\pm$ 1.76	182.50 $\pm$ 2.29	18.77(↓)	735.17 $\pm$ 1.73	599.00 $\pm$ 5.08	18.5219(↓)
IET 30561	228.00 $\pm$ 3.61	124.17 $\pm$ 3.18	45.54(↓)	927.33 $\pm$ 10.84	600.17 $\pm$ 4.42	35.2804(↓)
IET 30555	275.83 $\pm$ 2.40	130.00 $\pm$ 1.32	52.87(↓)	956.50 $\pm$ 7.69	578.50 $\pm$ 5.06	39.5191(↓)
IET 30505	181.33 $\pm$ 4.93	76.83 $\pm$ 1.59	57.63(↓)	968.00 $\pm$ 8.07	401.67 $\pm$ 13.26	58.5055(↓)
IET 30635	377.83 $\pm$ 4.04	186.00 $\pm$ 3.35	50.77(↓)	1134.83 $\pm$ 7.56	740.33 $\pm$ 9.09	34.7628(↓)
IET 30651	216.67 $\pm$ 2.40	137.33 $\pm$ 1.59	36.62(↓)	740.33 $\pm$ 9.49	486.00 $\pm$ 3.46	34.3539(↓)
IET 30653	227.83 $\pm$ 2.60	122.00 $\pm$ 3.21	46.45(↓)	715.83 $\pm$ 2.09	499.00 $\pm$ 6.46	30.291(↓)
IET 30656	266.00 $\pm$ 1.15	132.17 $\pm$ 1.76	50.31(↓)	720.00 $\pm$ 6.30	442.67 $\pm$ 1.97	38.5185(↓)
IET 30660	169.00 $\pm$ 0.29	126.50 $\pm$ 1.44	25.15(↓)	810.33 $\pm$ 9.76	525.50 $\pm$ 2.89	35.1501(↓)
IET 31433	210.00 $\pm$ 2.46	134.17 $\pm$ 1.04	36.11(↓)	718.50 $\pm$ 6.50	456.67 $\pm$ 8.90	36.4417(↓)
IET 31440	231.17 $\pm$ 2.93	162.17 $\pm$ 1.30	29.85(↓)	992.67 $\pm$ 10.10	719.50 $\pm$ 9.35	27.5185(↓)
IET 31444	178.00 $\pm$ 8.35	138.33 $\pm$ 2.47	22.28(↓)	651.17 $\pm$ 9.88	451.50 $\pm$ 4.16	30.6629(↓)
IET 31510	176.50 $\pm$ 4.52	116.33 $\pm$ 1.20	34.09(↓)	655.50 $\pm$ 9.31	430.50 $\pm$ 6.05	34.3249(↓)
IET 31512	219.67 $\pm$ 3.43	121.00 $\pm$ 3.61	44.92(↓)	910.33 $\pm$ 2.31	579.67 $\pm$ 3.32	36.3237(↓)
IET 31515	270.83 $\pm$ 4.41	143.17 $\pm$ 4.64	47.14(↓)	921.17 $\pm$ 7.04	603.33 $\pm$ 7.58	34.5033(↓)
IET 31533	342.50 $\pm$ 2.08	186.83 $\pm$ 7.36	45.45(↓)	1132.83 $\pm$ 9.38	769.67 $\pm$ 10.75	32.0583(↓)
IET 31540	147.83 $\pm$ 1.76	116.00 $\pm$ 1.73	21.53(↓)	516.83 $\pm$ 7.53	388.67 $\pm$ 4.32	24.7985(↓)
MTU-1290	339.00 $\pm$ 8.18	105.83 $\pm$ 3.35	68.78(↓)	798.33 $\pm$ 9.14	459.83 $\pm$ 4.77	42.4008(↓)
MTU-1296	410.17 $\pm$ 3.49	199.17 $\pm$ 4.73	51.44(↓)	1041.00 $\pm$ 3.61	512.17 $\pm$ 4.41	50.8005(↓)
US-314	171.00 $\pm$ 5.63	141.00 $\pm$ 3.61	17.54(↓)	669.00 $\pm$ 7.75	580.17 $\pm$ 4.93	13.2785(↓)
Mean A	241.25	138.985		844.987	546.947	
	Treatment	Genotype (G)	T×G	Treatment	Genotype (G)	T×G
S.Em $\pm$	0.454	2.625	3.655	1.612	5.185	7.343
CD at 5%	2.976	7.396	10.509	10.558	14.607	22.008

Table 3: Effect of elevated temperature on shoot dry weight (g/m²) at harvest in 22 rice genotypes. $\pm$ indicates standard error of mean. (↓) show percent decrease under heat stress as compared to control

Genotype	Shoot weight (g/m ²)		
	Ambient temperature	Heat stress	% change
CO-51	666.50 $\pm$ 30.20	497.67 $\pm$ 9.07	25.3313(↓)
IET 29694	917.33 $\pm$ 14.89	710.75 $\pm$ 6.57	22.52(↓)
IET 29700	805.17 $\pm$ 22.43	659.25 $\pm$ 85.39	18.1225(↓)
IET 30561	677.83 $\pm$ 18.92	498.17 $\pm$ 23.99	26.506(↓)
IET 30555	630.17 $\pm$ 8.99	431.17 $\pm$ 16.98	31.5789(↓)
IET 30505	736.83 $\pm$ 14.46	362.83 $\pm$ 12.55	50.7577(↓)
IET 30635	719.00 $\pm$ 24.05	484.17 $\pm$ 20.90	32.6611(↓)
IET 30651	591.83 $\pm$ 16.65	437.50 $\pm$ 16.87	26.0772(↓)
IET 30653	636.83 $\pm$ 11.43	343.67 $\pm$ 3.45	46.0351(↓)
IET 30656	744.83 $\pm$ 25.99	493.00 $\pm$ 12.57	33.8107(↓)
IET 30660	699.33 $\pm$ 3.79	568.33 $\pm$ 32.92	18.7321(↓)
IET 31433	793.67 $\pm$ 17.03	429.33 $\pm$ 18.16	45.9051(↓)
IET 31440	760.03 $\pm$ 12.57	545.75 $\pm$ 17.50	28.1933(↓)
IET 31444	827.67 $\pm$ 15.49	518.83 $\pm$ 15.39	37.3137(↓)
IET 31510	722.50 $\pm$ 14.80	360.00 $\pm$ 10.30	50.173(↓)
IET 31512	630.50 $\pm$ 34.28	394.67 $\pm$ 7.69	37.4042(↓)
IET 31515	868.00 $\pm$ 25.30	549.83 $\pm$ 16.08	36.6551(↓)
IET 31533	739.67 $\pm$ 23.67	532.83 $\pm$ 6.67	27.963(↓)
IET 31540	720.83 $\pm$ 11.99	437.75 $\pm$ 2.48	39.2717(↓)
MTU-1290	596.00 $\pm$ 5.92	460.33 $\pm$ 6.71	22.7629(↓)
MTU-1296	797.33 $\pm$ 9.73	431.50 $\pm$ 11.53	45.8821(↓)
US-314	674.75 $\pm$ 12.65	566.33 $\pm$ 15.90	16.0677(↓)
Mean A	725.3	486.985	
	Treatment	Genotype (G)	T×G
S.Em $\pm$	3.626	15.03	21.082
CD at 5%	23.754	42.347	61.724

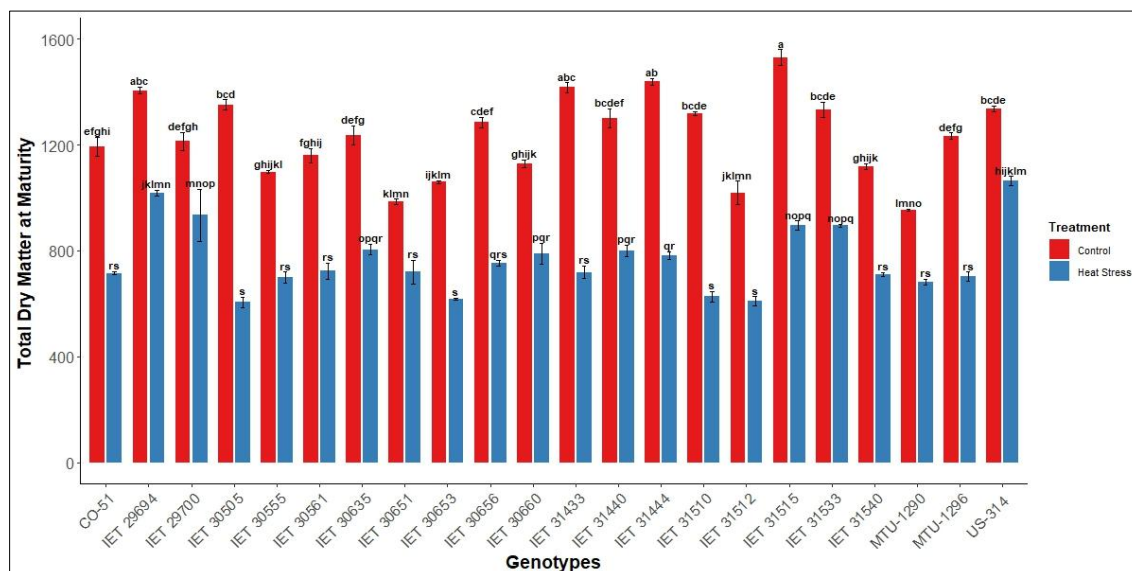


Fig 1: Effect of heat stress on total dr matter at harvesting of 22 rice genotypes

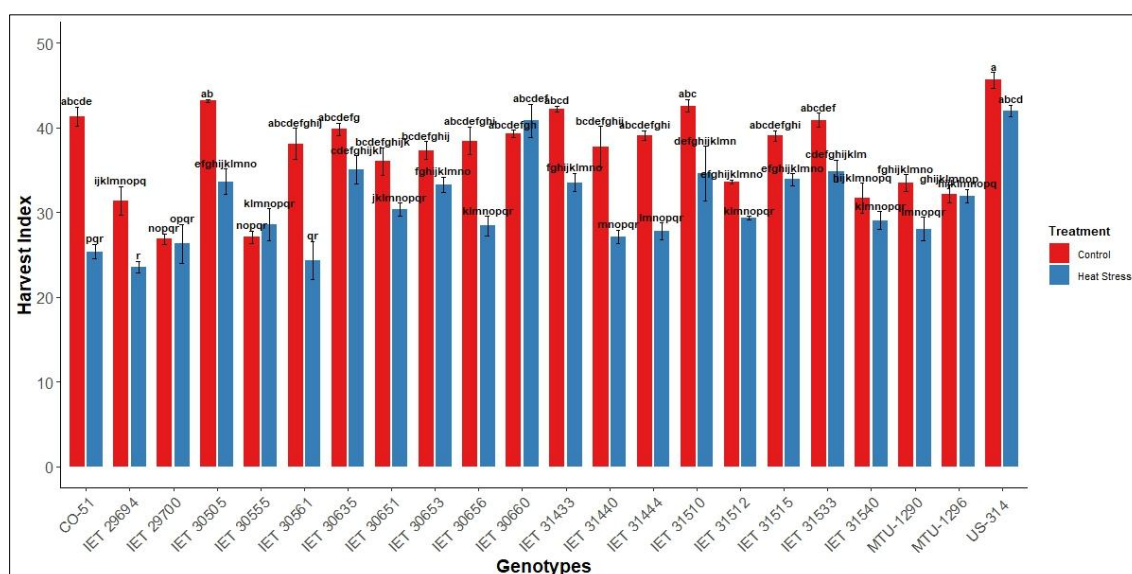


Fig 2: Effect of heat stress on harvest index (%) at harvesting of 22 rice genotypes

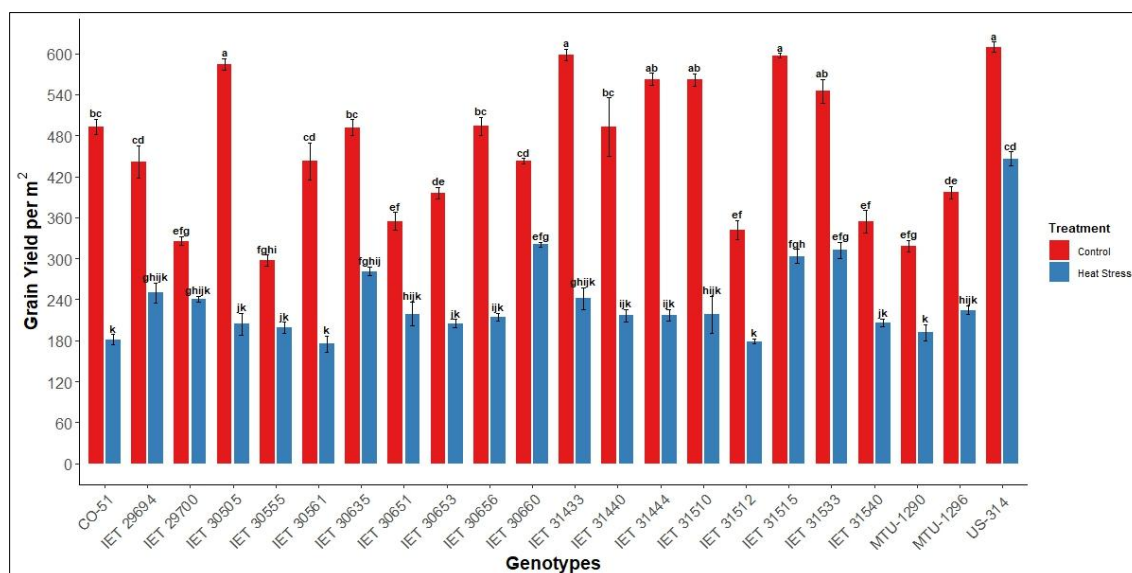


Fig 3: Effect of heat stress on grain yield/m² at harvesting of 22 rice genotypes

Table 4: Pearson correlation coefficients (r) of grain yield with growth, biomass, and harvest index traits in rice genotypes under ambient and heat stress conditions (n = 22)

Trait pair	r	p-value	Significance
Under Heat Stress			
Grain yield vs. Plant height	0.47	0.027	*
Grain yield vs. Leaf dry weight	0.28	0.207	ns
Grain yield vs. TDM at flowering	0.31	0.160	ns
Grain yield vs. Shoot dry weight	0.44	0.040	*
Grain yield vs. TDM at harvest	0.75	<0.001	**
Grain yield vs. Harvest index	0.75	<0.001	**
Under Ambient Conditions			
Grain yield vs. TDM at flowering	0.04	0.860	ns
Grain yield vs. TDM at harvest	0.83	<0.001	**
Grain yield vs. Harvest index	0.86	<0.001	**
Percentage Reduction (Heat vs. Ambient)			
Yield% reduction vs. TDM-flowering% reduction	0.37	0.090	ns
Yield% reduction vs. TDM-harvest% reduction	0.83	<0.001	**
Yield% reduction vs. HI% reduction	0.80	<0.001	**

3.4 Effect of Heat Stress on Harvest Index and Grain Yield

Harvest index and grain yield were both significantly influenced by heat stress, although the response of harvest index varied among genotypes, whereas grain yield declined consistently across all evaluated entries (Tables 5 and 6). Harvest index exhibited changes ranging from a 2.17% reduction to a 5.47% increase, with the overall mean decreasing from 37.13% under ambient conditions to 30.99% under heat stress. Among the tested genotypes, CO-51 recorded the greatest reduction in harvest index (38.60%), while IET 29700 showed the smallest decline (2.17%). Notably, IET 30660 and IET 30555 exhibited slight increases in harvest index of 4.01% and 5.47%, respectively, indicating their ability to maintain or even improve assimilate partitioning under elevated temperature.

Heat stress caused a pronounced decline in grain yield across all rice genotypes, with reductions ranging from 25.998% to 65.05%. The mean grain yield decreased markedly from 460.89 to 238.51 g m⁻² under heat-stress conditions. IET 30505 was the most adversely affected genotype, recording the greatest yield reduction (65.05%), whereas the check variety US-314 exhibited the smallest decline in grain yield (26.75%) together with a relatively low reduction in harvest index (8.00%). These results indicate the superior capacity of US-314 to sustain assimilate partitioning and reproductive performance under elevated temperature. Most of the evaluated genotypes experienced greater reductions in both harvest index and grain yield than the check, reflecting comparatively higher sensitivity to heat stress during the reproductive stage. In contrast, IET 29700, IET 30660, and IET 30555 maintained stable or improved harvest index under stress, while IET 29700 also displayed grain yield stability comparable to that of US-314. Furthermore, the significant treatment × genotype interactions for harvest index (CD at 5% = 3.768) and grain yield (CD at 5% = 39.354) demonstrated substantial genetic variation in reproductive-stage heat tolerance, identifying IET 30505 and CO-51 as the most heat-sensitive genotypes and US-314 together with IET 29700 as the most heat-tolerant based on reproductive performance.

4. Discussion

High temperature during vegetative and reproductive development in rice disrupts the physiological and biochemical processes governing growth, biomass accumulation, and assimilate partitioning, ultimately limiting grain yield (Shrestha *et al.*, 2022; Zafar *et al.*, 2022) [11, 15]. In the present study, heat stress was imposed as a season-long, whole-canopy exposure

using a polyethylene-sheet tunnel over one field block, with an adjacent open-field block serving as the ambient control a passive warming design that elevates day and night temperature continuously through the crop cycle, distinct from short-duration heat-shock or growth-chamber studies. This distinction matters for interpreting the results: the reductions reported here reflect cumulative, season-long thermal load rather than the effect of a brief high-temperature event at a single developmental stage, and comparisons with the literature are framed accordingly.

Plant height

The reduction in plant height (4.27-13.11%) is consistent with impaired internode elongation, a process in rice that depends on gibberellin (GA) driven cell division at the intercalary meristem followed by cell elongation (Nagai & Ashikari, 2023) [7]. Heat-stressed rice seedlings have independently been shown to exhibit reduced height alongside declining biomass and chlorophyll content under sustained elevated temperature (Taratima *et al.*, 2022) [12], supporting the interpretation that season-long canopy warming suppressed height through cumulative disruption of this growth pathway. This explains why IET 30505 and IET 30656 showed the sharpest reductions, pointing to weaker capacity to sustain meristematic activity under prolonged thermal load, while US-314 and IET 29700 appear better able to maintain this process across the season.

Leaf dry weight and biomass

The decline in leaf dry weight (17.54-68.78%) and total biomass (13.28-58.51%) is consistent with heat accelerated leaf senescence compounding over the growing season. Premature senescence under sustained heat is driven mainly by accelerated chlorophyll breakdown, and heat stress independently impairs photosynthetic capacity by damaging chloroplast components, both reducing biomass accumulation cumulatively (Guan *et al.*, 2025) [1]. Since leaf tissue senescences first, larger proportional losses in leaf dry weight than in whole plant TDM would be expected over an extended stress period a pattern confirmed in the present data. The comparatively small reduction in US-314 and IET 29700 suggests a genuine delay in senescence onset sustained across the season, consistent with reports that indica genotypes differ substantially in their capacity to maintain dry matter accumulation under prolonged field-based warming (Yang *et al.*, 2017) [14].

Harvest index and grain yield

Grain yield decline in the susceptible genotypes could be attributed to a combination of reduced total dry matter (TDM) accumulation and reduced harvest index (HI). Correlation analysis (Table 4) supports this interpretation. Under heat stress, grain yield was strongly correlated with TDM at harvest ($r = 0.75$, $p < 0.001$) and harvest index ($r = 0.75$, $p < 0.001$), moderately with plant height ($r = 0.47$) and shoot dry weight ($r = 0.44$), but only weakly and non-significantly with leaf dry weight ($r = 0.28$) and TDM at flowering ($r = 0.31$). This gradient indicates that yield under heat stress was determined mainly by biomass retained through to harvest and by partitioning efficiency, rather than by early vegetative growth consistent with the progressive, season-long senescence driving biomass turnover in this study. The same pattern held, and was stronger, under ambient conditions (TDM at flowering: $r = 0.04$; TDM at harvest: $r = 0.83$; HI: $r = 0.86$), confirming this is a general feature of yield determination in rice rather than a heat-specific artefact, though the decline in the TDM-at-harvest and HI correlations from ambient to heat stress suggests heat introduces additional genotype-specific variability in how these traits translate into yield. This was corroborated at the level of genotypic sensitivity: the percentage reduction in yield correlated strongly with the percentage reduction in TDM at harvest ($r = 0.83$, $p < 0.001$) and HI ($r = 0.80$, $p < 0.001$), but weakly with the percentage reduction in TDM at flowering ($r = 0.37$, ns), confirming that genotypes losing the most harvest-stage biomass and partitioning efficiency were also those losing the most yield.

In IET 30505 and IET 31510, both TDM and HI declined sharply, indicating that yield loss resulted from impairment of both source capacity and partitioning efficiency. In CO-51, the reduction in HI (38.60%) was proportionally greater than the reduction in biomass, suggesting that impaired assimilate partitioning to grain was the primary cause of yield loss, consistent with earlier reports that heat stress during flowering disrupts spikelet fertility and grain-filling more severely than it suppresses vegetative biomass (Prasad *et al.*, 2006) [8], a process mechanistically linked to heat-induced disruption of auxin homeostasis in the pollinated pistil and consequent inhibition of pollen tube elongation (Zhang *et al.*, 2018) [16]. Similarly, IET 30561 and IET 31440 showed disproportionately large reductions in HI relative to biomass loss, whereas IET 31515, IET 30653, and IET 31512 lost more biomass than harvest index, pointing to source limitation rather than partitioning failure as the dominant constraint in these genotypes. In contrast, tolerant genotypes such as IET 29700 and US-314 maintained yield by limiting losses in both TDM and HI simultaneously, reflecting a more balanced physiological response to heat stress, while IET 30555 and IET 30660 recorded an actual increase in HI under heat stress, suggesting improved reproductive-stage partitioning efficiency that helped offset losses in vegetative biomass. This finding, underscoring the joint importance of biomass maintenance and efficient partitioning for yield stability under heat stress, is supported by earlier studies (Jasmin & Rajendran, 2026) [4].

The magnitude of yield loss observed here (25.998-65.05%) sits at the higher end of, but is broadly consistent with, previously reported field-based heat-stress yield reductions of roughly 27-48% across diverse cultivar panels and up to 78% under season-long all-day canopy warming in some genotype-year combinations (Yang *et al.*, 2017) [14]. The wider range and higher maximum loss in the present data likely reflect the combined, compounding effect of season-long source impairment (senescence-driven biomass loss) and anthesis-stage sink impairment (spikelet sterility) occurring within the same stress

event, rather than the two being isolated as in shorter or staged experiments. The decline in total biomass observed across genotypes was largely driven by the sharp reduction in leaf dry weight at flowering, likely resulting from heat-induced acceleration of leaf senescence, a response reported previously in rice under high-temperature stress (Zhao *et al.*, 2026; Guan *et al.*, 2025) [17, 1].

Limitation

As this evaluation was conducted over a single growing season, the genotypic rankings for heat tolerance reported here should be interpreted as preliminary; multi-season or multi-location confirmation is recommended before these genotypes are advanced as heat-tolerance donors, consistent with standard practice in field-based heat-stress screening studies.

5. Conclusion

Prolonged heat stress from panicle initiation to maturity significantly reduced plant growth, biomass accumulation, harvest index, and grain yield in all rice genotypes, although the magnitude of these reductions varied considerably among genotypes. Grain yield under heat stress was closely associated with total dry matter at harvest and harvest index, indicating that the ability to maintain biomass accumulation until maturity and efficiently partition assimilates to the grain are the major determinants of heat tolerance.

Among the evaluated genotypes, IET 29700 consistently exhibited superior performance by maintaining biomass, harvest index, and grain yield under heat stress, while the check variety US-314 also showed stable performance. In contrast, IET 30505 and CO-51 were identified as the most heat-sensitive genotypes. These findings demonstrate that grain yield, total dry matter at harvest, and harvest index are reliable selection criteria for identifying heat-tolerant rice genotypes under field conditions and highlight IET 29700 as a promising donor for future rice heat-tolerance breeding programmes.

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