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Unveiling the photosynthesis and translocation efficiency in Indian foxtail millet genotypes to dissect tolerance to interactive drought and high temperature stress

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Abstract

Foxtail millet, a C4 cereal, is predominantly grown in the arid and semi-arid regions of Asia. Its yield is significantly reduced due to drought and high-temperature stresses. This yield reduction primarily occurs due to a lack of allocation of assimilates produced during photosynthesis to maturing grain when exposed to abiotic stress. To address this issue, a field study was conducted under a rain-out shelter using 24 genotypes, including four checks to assess the genetic variability in photosynthetic rate, grain filling rate, grain filling duration, dry matter translocation, translocation efficiency and contribution rate when drought and heat stress was imposed from peak vegetative to mid grain filling period. The diverse genotypes were classified as tolerant (Group I) and susceptible (Group II) genotypes using the photosynthetic rate. The genotypes with photosynthetic rates of > 29 µmol m^{-2} sec^{-1} were grouped into a tolerant category. The genotype ISe-15 was identified as tolerant based on higher values recorded for dry matter translocation (5.11 g $plant^{-1}$), translocation efficiency (33.80 g $plant^{-1}$) and contribution rate (27.47 g $plant^{-1}$) under interactive stress. The genotype IC0479711 was identified as susceptible with low photosynthetic rate (24.2 µmol m^{-2} sec^{-1}) coupled with less TE (6.78 g $plant^{-1}$). Thus, the study concluded that foxtail millet genotypes with higher photosynthetic rates coupled with the efficient translocation of assimilates for grain filling under stress can tolerate combined drought and high-temperature stress.

Keywords

drought; dry matter translocation; foxtail millet; high temperature; photosynthetic rate; yield

Introduction

Foxtail millet (*Setaria italica* L.) is an important C4 cereal and one of the oldest cultivated grains, predominantly grown in arid and semi-arid regions of China, some parts of India and Japan (1). The major production sites include India, China, Russia and Africa. It is rich in calcium and phosphorous and micronutrients such as iron, zinc and magnesium. Foxtail millet is remarkably drought-tolerant and resilient to temperature fluctuations, making it an ideal crop for diverse climatic conditions (2). However, despite these advantageous traits, its productivity and photosynthetic efficiency tend to remain low when flowering and grain filling coincide with drought and high-temperature stress (3). The yield of foxtail millet was reduced from 20 to 60% under drought and high-temperature stress (4).

Major production constraints attributed to the lower productivity of foxtail millet are mainly the inherent genetic limitations, limited photosynthetic efficiency, low fertile marginal lands with low input supply and inadequate agricultural practices (5). The photosynthetic rate of foxtail millet tends to be higher than that of many other crops under conditions of high light intensity and elevated temperatures typical of arid and semi -arid regions (4). However, the specific photosynthetic rates can vary among different cultivars and in response to environmental factors such as water availability, temperature and nutrient status. Hence, the photosynthetic rate was taken as a selection criterion for grouping varieties for drought and heat tolerance.

Under drought and high-temperature stress conditions, plants often prioritize the allocation of assimilates towards survival mechanisms. They promote root growth to access deeper soil moisture or synthesis of osmolytes and antioxidants. This can result in reduced allocation of assimilates towards above-ground growth (6), dry matter translocation (DMT), translocation efficiency (TE), grain filling rate (GFR), duration and contribution rates (CR). The increased partitioning of stem reserves under high-temperature stress acts as a true tolerance mechanism as well as a potential strategy to improve yield exhibited by tolerant genotypes (7).

The high air temperature and tissue temperature are interrelated and have a significant impact on plant physiology, growth and productivity of a plant especially under conditions of prolonged or extreme heat stress (8). High air temperatures cause indirect changes in soil moisture availability. Increased atmospheric temperature leads to higher evapotranspiration thereby reducing soil water. Elevated tissue temperatures can directly impact cellular processes, including enzyme activity, protein denaturation, membrane integrity and photosynthesis. They can also increase the risk of heat stress injury, leading to tissue damage, wilting and reduced growth and yield (9). Foxtail millet has many mechanisms to modulate assimilation partitioning under stress conditions. However, the extent of these responses can vary depending on the severity and duration of the stress. High-temperature stress at the grain filling stage could reduce the assimilate supply from shoot to grain, shorten the grain filling duration (GFD) and ultimately reduce grain yield (10). A significant reduction in seed number and grain yield of foxtail millet under drought (11) and high-temperature stress (12) was observed. Considering the lack of research on combined stress in foxtail millet, this study aimed to i) assess the impact of drought and high-temperature stress on the photosynthetic efficiency of foxtail millet genotypes and group them into tolerant and susceptible to drought and high-temperature stress ii) investigate the translocation of the photo-assimilates by quantifying the amount of dry matter production (DMP) at anthesis and maturity iii) calculate the translocation efficiency, contribution rate and grain filling traits in low and high photosynthetic groups under combined stress iv) to correlate the yield under stress with grain filling traits in foxtail millet.

Materials and Methods

Plant materials and stress treatments

A field experiment was conducted in a rain-out shelter (ROS) at the Department of Crop Physiology, Tamil Nadu Agricultural University (TNAU), Coimbatore. Twenty-four foxtail millet genotypes, including four checks sourced from the Indian Institute of Millet Research (IIMR), Hyderabad and Centre of Excellence (CoE) for Millets, Athiyandhal, TNAU (Table 1), were used to study the effects of drought and high temperature on grain filling traits and grain yield. The experiment was laid out in an augmented design with two replications for checks alone. The seeds (2-3 seeds) were sown in ridges and furrows with a spacing of 22.5 cm × 10 cm at a depth of 3 cm. The fertilizer dose of N: P_2O_5 at 44: 22 kg ha^{-1} was applied. The plants were subjected to two treatments *viz.,* control (irrigated) and combined drought and natural high-temperature stress. The stress was imposed from a peak vegetative stage [30 days after sowing (DAS)] to mid grain filling stage (60 DAS). The plants were irrigated normally until the peak vegetative stage. Thereafter, the irrigation was withdrawn for the period of 30 days from 30 DAS to 60 DAS for stressed plants alone. For high-temperature stress, the sowing was taken up in such a way that these 30 days coincide with high air temperature. The air temperature and relative humidity prevailing in the experimental field during the stress period were recorded using Micrometeorological Instruments to measure Near Canopy in Rice, (MINCERs), Japan as this records the data in periodic intervals. This will be highly efficient to monitor the weather conditions in the stressed plots and soil moisture was monitored using a soil moisture meter (Fig. 1a, 1b).

Table 1. List of genotypes and checks used in the study

Genotypes			
S. No	**Genotypes**	**S. No**	**Genotypes**
G1	Sea 12	G11	IC0403440
G2	IC0403470	G12	ISe- 23
G3	ISe- 254	G13	IC0479455
G4	Tenai 2201	G14	ISe- 57/A
G5	Tenai 2202	G15	ISe- 128/1
G6	IC0403487	G16	EC0529793
G7	ISe- 2/3	G17	ISe- 183/1
G8	IC0479711	G18	ISe- 213/1
G9	ISe- 365	G19	IC0479804
G10	ISe- 26	G20	ISe- 15
Checks			
S. No	**Checks**	**S. No**	**Checks**
C 1	SIA 326	C 3	Suryanandi
C 2	Co (Te 7)	C 4	ATL 1

Measurement of photosynthetic rate, leaf and panicle temperature

The photosynthetic rate of the flag leaf was measured using a portable photosynthesis system (CID-340 Handheld Photosynthesis System, USA) between 9.30 and 13.30 hrs on 50 DAS. For each genotype, three readings were taken and the mean was calculated. The flag leaf temperature and panicle temperature were measured using a hand-held infrared radiometer (Apogee, MI -220) on 51 DAS between 10.30 and 12.00 hrs. Three primary panicles and their corresponding flag leaf were used for measuring the tissue temperatures.

Grain filling traits

For assessing grain filling rate, six panicles in total were tagged per genotype during stress imposition. Three panicles at 15 days after flowering (DAF) and the other three panicles at 22 DAF were harvested. The harvested panicles were oven-dried and 1000 seed weight was recorded. Grain filling rate was defined as the ratio of the difference between 1000 seed weight on 22 DAF and

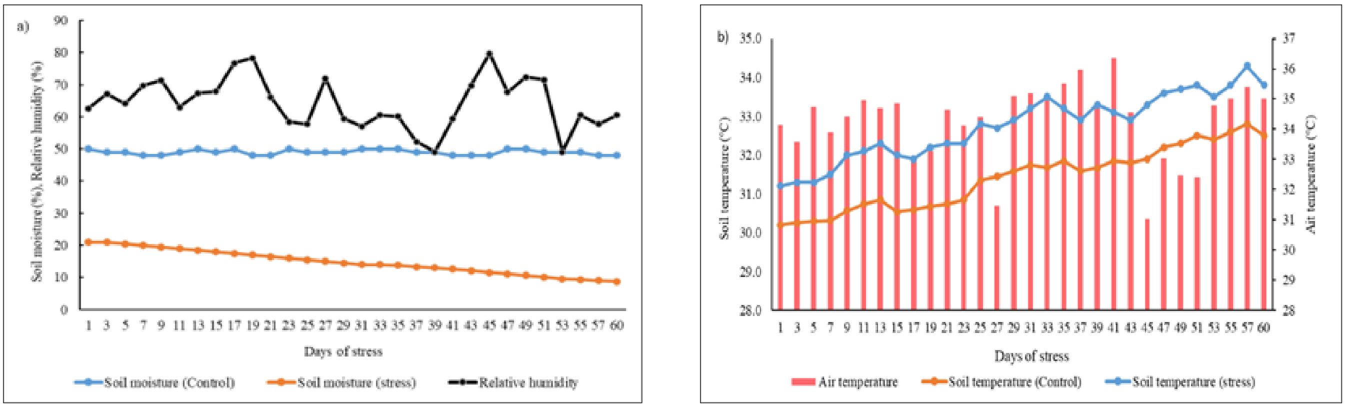


Fig. 1. Weather conditions during the stress period (from peak vegetative to mid-grain filling stage) in the rain-out shelter a) soil moisture and relative humidity, b) soil and air temperature.

15 DAF to the interval between these two days and expressed as g day^{-1} (13). GFD was computed as the number of days from flowering to 95% physiological maturity (14).

Estimation of dry matter partitioning, translocation efficiency and contribution rate

Dry matter translocation was calculated as the difference between above-ground dry matter at harvest and above-ground dry matter at flowering and expressed as g plant^{-1}. Translocation efficiency was calculated as the ratio of DMT to the dry matter of vegetative organs during flowering and expressed as a percentage (%). The contribution rate was estimated as the ratio of DMT to grain yield and expressed as a percentage (15).

Yield and yield components

At physiological maturity, the plants were harvested and three plants per genotype were collected and oven-dried at 70°C for five days to record the yield and yield components. The panicle length was measured using a ruler and expressed as cm panicle^{-1}. The panicle weight was measured and expressed as g panicle^{-1}. The 1000 seed weight was estimated by standard procedure (16) and expressed as g. Grain yield was recorded and expressed as g plant^{-1}. The dry weight of the whole plant was weighed to obtain total dry matter production (TDMP) and expressed as g plant^{-1}.

Statistical analysis

The experiment was laid out in an augmented design in which only checks had two replications. The data were analysed using TNAUSTAT (17). Mean, standard deviation, standard error and critical difference values were calculated and checked for significance levels at 5% ($P < 0.05$) and 1% ($P < 0.01$). The cluster analysis for photosynthetic rate was performed using NTSys software. A Pearson correlation was performed using R software package version R 4.3.1 to correlate the grain yield with grain filling traits. Genotypic coefficient of variation (GCV), phenotypic coefficient of variation (PCV), heritability and genetic advance as % of the mean (GAM) were calculated using error mean sum of squares and test entries mean sum of squares.

Results

Clustering of foxtail millet genotypes for drought and high-temperature tolerance/susceptibility based on photosynthetic rates under stress

Grain filling rate, translocation efficiency and TDMP depend on the genotype's ability to produce photo-assimilates. Hence, the photosynthetic rate was used as a key physiological trait and an efficient phenotyping tool to group the foxtail millet genotypes for combined drought and high-temperature stress. There was a significant reduction in photosynthetic rate in foxtail millet genotypes exposed to drought and high-temperature stress compared to the control. Cluster analysis of photosynthetic rate in foxtail millet genotypes exposed to drought and high-temperature stress revealed two major clusters or groups. Nine genotypes *viz.,* IC0403440, ISe- 15, ISe- 57/A, Ise- 213/1, IC0479804, IC0479455, ISe- 128/1, EC0529793 and ISe- 183/1 along with four checks [Suryanandhi, SIA 326, CO (Te 7) and ATL 1] recorded photosynthetic rate of 29.4 to 35.1 µmol m^{-2} sec^{-1}. Genotypes with photosynthetic rate of > 29 were classified as Group I (Tolerant category). The other eleven genotypes *viz.,* Sea 12, ISe- 2/3, ISe- 254, ISe- 23, IC0479711, IC0403470, Tenai 2201, Tenai 2202, IC0403487, ISe- 365 and ISe- 26 recorded lower photosynthetic rate of 22.7 to 27.8 µmol m^{-2} sec^{-1}when exposed to combined stress of drought and high temperature. These genotypes were classified as Group II (Susceptible category) (Fig. 2).

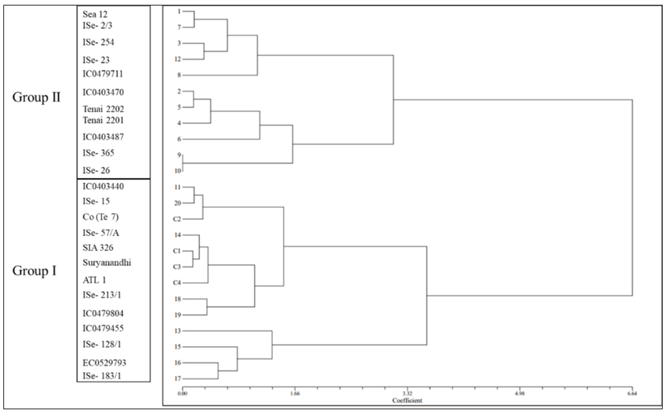
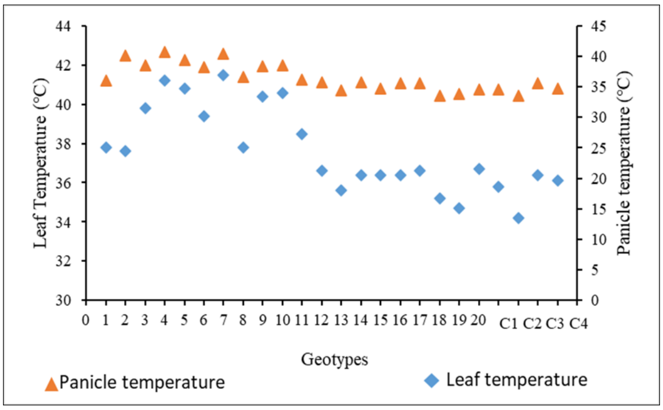


Fig. 2. Clustering of foxtail millet genotypes based on photosynthetic rate under drought and high-temperature stress from peak vegetative to mid-grain filling stage.

Tissue temperature and grain-filling traits

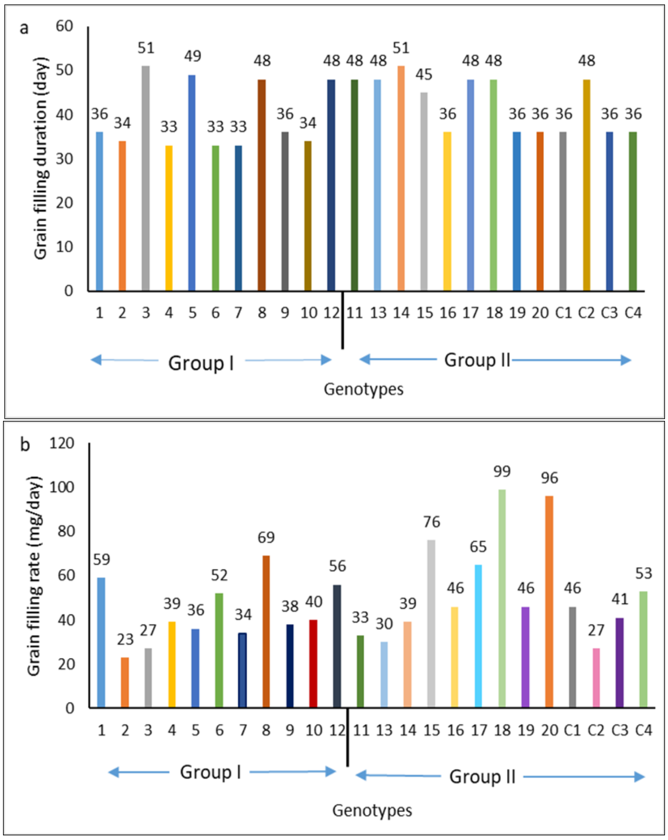
The leaf temperature varied significantly ($P < 0.01$) between checks and genotypes versus Checks, for genotypes ($P < 0.05$) under combined stress conditions. The panicle temperature varied significantly ($P < 0.05$) under control conditions. In addition, it varied significantly for checks and genotypes vs Checks ($P < 0.01$) under combined stress conditions. Tolerant genotypes recorded lesser leaf and panicle temperatures ranging from 33.6 to 35.7 °C and 34.2 to 36.7 °C respectively under combined stress conditions than the susceptible genotypes (Fig. 3). GFD and GFR decreased under combined stress conditions than the control. On average, tolerant genotypes exhibited longer grain filling duration and higher grain



Genotypes from left to right (1- Sea 12; 2- IC0403470; 3- ISe- 254; 4- Tenai 2201; 5- Tenai 2202; 6- IC0403487; 7- ISe- 2/3; 8- IC0479711; 9- ISe- 365; 10- ISe - 26; 11- IC0403440; 12- ISe- 23; 13- IC0479455; 14- ISe- 57/A; 15- ISe- 128/1; 16 - EC0529793; 17- ISe- 183/1; 18- ISe- 213/1; 19- IC0479804; 20- ISe- 15; C1- SIA 326; C2- Co (Te 7); C3- Suryanandi; C4- ATL 1).

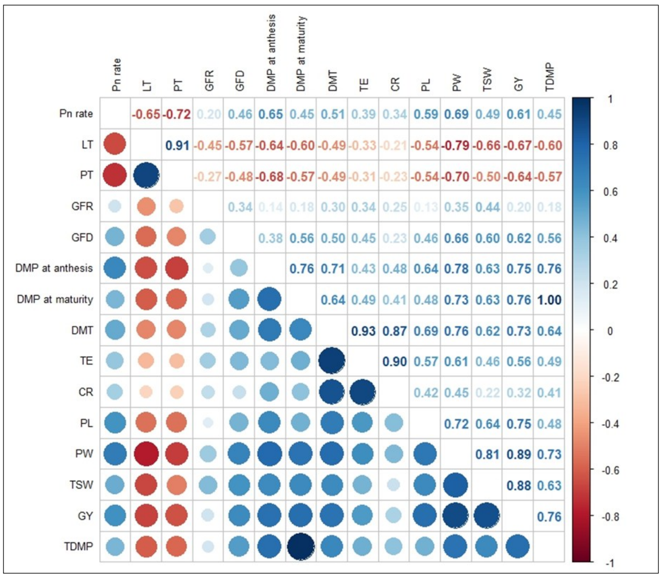
Fig. 3. Leaf and panicle temperature of foxtail millet genotypes exposed to drought and high-temperature stress from peak vegetative to mid-grain filling stage.

filling rate than the susceptible genotypes (Fig. 4a, 4b). Leaf temperature and panicle temperature showed a negative correlation with all other physiological, grain filling and yield traits studied. The correlation coefficient of leaf temperature ranged from -0.21 to -0.79 and panicle temperature from -0.23 to -0.70 (Fig. 5).



Genotypes from left to right (1- Sea 12; 2-IC0403470; 3- ISe- 254; 4-Tenai 2201; 5- Tenai 2202; 6- IC0403487; 7- ISe- 2/3; 8-IC0479711; 9- ISe- 365; 10- Ise-26; 11 - IC0403440; 12-ISe- 23; 13- IC0479455; 14-ISe- 57/A; 15- ISe- 128/1; 16- EC0529793; 17- Ise- 183/1; 18- ISe- 213/1; 19- IC0479804; 20- ISe- 15; C1- SIA 326; C2- Co (Te 7); C3- Suryanandi; C4- ATL 1).

Fig. 4. Grain filling traits in foxtail millet genotypes under drought and high-temperature stress from peak vegetative to mid grain filling stage a) Grain filling duration, b) Grain filling rate.



Pn rate- Photosynthetic rate; LT - Leaf temperature; PT - Panicle temperature; GFR- grain filling rate; GFD- Grain filling duration; DMP- Dry matter production; DMT- Dry matter translocation; TE- Translocation efficiency; CR- Contribution rate; PL - Panicle length; PW - Panicle weight; TSW - 1000 seed weight; GY - Grain Yield; TDMP - Total dry matter production

Fig. 5. Correlation of grain yield with physiological and grain filling traits of foxtail millet genotypes exposed to drought and high-temperature stress from peak vegetative to mid-grain filling stage.

Dry matter production at anthesis and harvest

DMP at anthesis varied significantly ($P < 0.01$) for genotypes vs checks under control and combined stress conditions. In the tolerant group, DMP at anthesis ranged from 17.56 - 25.43 g plant^{-1} which was higher than the susceptible group (13.54 to 16.81 g plant^{-1}). DMP at harvest varied significantly for genotypes under normal conditions ($P < 0.05$) and stressed conditions ($P < 0.01$). Similarly, DMP at harvest was found to be higher in the tolerant group (19.98 to 29.70 g plant^{-1}) than in the susceptible group (Table 2). The check ATL 1 recorded the highest (29.70 g plant^{-1}) DMP at harvest. Comparable with the checks, the genotype EC0529793 recorded a higher DMP at harvest and DMP at anthesis of 27.52 g plant^{-1} and 22.21 g plant^{-1} respectively.

Dry matter translocation, TE and CR

Dry matter translocation varied significantly ($P < 0.01$) for genotypes vs checks under control and combined stress conditions. The tolerant group showed a higher DMT ranging from 2.12 to 5.11 g plant^{-1} than the susceptible group under combined stress conditions. TE and CR varied significantly ($P < 0.01$) for genotypes, checks and genotypes vs checks both under control and combined stress conditions. The tolerant group recorded comparatively higher TE and CR ranging from 11.68 to 33.80% and 10.42 to 27.47% respectively under combined drought and high-temperature stress than the susceptible group (Table 3). The check (ATL 1) recorded a higher DMT, TE and CR of 5.04 g plant^{-1}, 24.91% and 21.43% respectively. The genotype ISe-15 recorded the highest DMT, TE and CR of 5.11 g plant^{-1}, 33.8% and 27.47% respectively which was more than the check, followed by ISe-183/1. A lower value of DMT, TE and CR was observed in IC0479711. The DMT and TE had a strong positive correlation with grain yield. Similarly, CR was also positively correlated with grain yield (Fig. 5). Results indicate that both TE and CR act as driving forces for improving grain yield by enhancing grain filling.

Table 2. Variation in dry matter production at anthesis and maturity in foxtail millet genotypes under combined drought and high-temperature stress

Genotypes/ checks	DMP at anthesis (g plant^{-1})		DMP at harvest (g plant^{-1})	
	Control	Stress	Control	Stress
Tolerant group - Group I				
IC0403440	27.08 ± 0.62	21.51 ± 0.48	29.49 ± 0.57	23.63 ± 0.44
IC0479455	23.69 ± 0.55	17.56 ± 0.28	27.70 ± 0.64	19.98 ± 0.25
ISe- 57/A	24.22 ± 0.37	17.78 ± 0.81	28.77 ± 0.91	19.94 ± 0.79
ISe- 128/1	25.68 ± 0.21	18.33 ± 0.96	29.74 ± 0.37	20.15 ± 0.89
EC0529793	24.97 ± 0.50	22.21 ± 0.65	29.88 ± 0.79	27.52 ± 0.53
ISe- 183/1	23.75 ± 0.64	18.47 ± 1.12	29.38 ± 0.89	23.01 ± 1.04
ISe- 213/1	24.52 ± 0.91	22.02 ± 0.55	28.64 ± 0.48	25.98 ± 0.25
IC0479804	22.98 ± 0.53	18.01 ± 0.90	27.25 ± 0.33	20.28 ± 0.93
ISe- 15	23.13 ± 0.59	18.49 ± 0.13	28.87 ± 0.85	23.61 ± 0.60
SIA 326 (Check 1)	27.65 ± 0.44	25.43 ± 0.38	31.75 ± 0.61	28.95 ± 0.87
Co (Te 7) (Check 2)	27.19 ± 0.45	22.47 ± 0.53	32.65 ± 0.48	27.02 ± 0.29
Suryanandi (Check 3)	27.04 ± 0.48	23.24 ± 0.44	32.52 ± 0.58	28.13 ± 0.38
ATL 1 (Check 4)	28.70 ± 0.54	24.66 ± 0.78	34.48 ± 0.57	29.70 ± 0.76
Susceptible group - Group II				
Sea 12	20.25 ± 1.19	15.38 ± 0.71	21.93 ± 0.86	16.64 ± 0.37
IC0403470	18.86 ± 0.70	15.35 ± 0.30	20.73 ± 0.75	16.87 ± 0.44
ISe- 254	15.78 ± 0.86	13.54 ± 0.72	17.38 ± 0.94	14.83 ± 0.27
Tenai 2201	18.91 ± 0.40	15.81 ± 0.39	21.00 ± 0.54	17.56 ± 0.57
Tenai 2202	20.30 ± 0.71	16.19 ± 0.83	22.49 ± 0.57	17.19 ± 0.86
IC0403487	20.42 ± 0.90	14.31 ± 0.58	23.93 ± 0.41	15.67 ± 0.91
ISe- 2/3	20.20 ± 0.54	15.67 ± 0.78	22.95 ± 0.39	17.54 ± 0.63
IC0479711	18.37 ± 0.32	14.88 ± 1.28	19.40 ± 0.39	15.70 ± 1.23
ISe- 365	18.68 ± 0.70	15.98 ± 0.59	21.22 ± 0.87	17.54 ± 0.65
ISe- 26	20.05 ± 0.57	14.00 ± 0.56	23.57 ± 0.91	16.01 ± 0.26
ISe- 23	17.05 ± 0.81	15.13 ± 0.52	25.78 ± 0.84	17.09 ± 0.41
	CD	**CD**	**CD**	**CD**
Genotypes	4.12*	NS	5.35*	3.40**
Checks	NS	NS	NS	NS
Genotypes vs Checks	3.57**	4.58**	4.63**	2.94**

Values are mean ± SE (standard error) of three samples. Significant changes are highlighted by an asterisk (*). *P ≤ 0.05; ** P ≤ 0.01; NS - non significant. S. Ed - Standard error of difference; CD - Critical difference.

Table 3. Variation in dry matter translocation and translocation efficiency in foxtail millet genotypes exposed to drought and high-temperature stress

Genotypes/ checks	DMT (g plant^{-1})		TE (%)		CR (%)	
	Control	Stress	Control	Stress	Control	Stress
Tolerant group – Group I						
IC0403440	2.40 ± 0.27	2.12 ± 0.07	10.69 ± 1.32	11.68 ± 0.66	11.79 ± 1.46	20.15 ± 1.29
IC0479455	4.01 ± 1.17	2.42 ± 0.03	22.26 ± 6.97	16.95 ± 0.67	15.71 ± 4.65	12.88 ± 0.27
ISe- 57/A	4.55 ± 1.03	2.16 ± 0.35	23.62 ± 5.52	15.35 ± 2.87	18.47 ± 4.51	11.81 ± 2.24
ISe- 128/1	4.06 ± 0.58	2.15 ± 1.31	19.02 ± 3.14	12.33 ± 1.48	16.87 ± 2.74	10.42 ± 0.77
EC0529793	4.91 ± 0.39	2.31 ± 0.13	24.99 ± 1.85	12.80 ± 1.13	19.16 ± 1.41	13.04 ± 1.20
ISe- 183/1	5.63 ± 0.89	3.80 ± 0.86	30.78 ± 5.30	30.58 ± 2.76	23.47 ± 3.24	24.54 ± 1.25
ISe- 213/1	4.12 ± 0.44	3.96 ± 0.32	21.38 ± 3.24	22.72 ± 2.40	16.07 ± 1.26	21.60 ± 1.80
IC0479804	4.27 ± 0.84	3.45 ± 1.82	23.35 ± 5.22	15.59 ± 0.63	17.09 ± 3.64	12.23 ± 0.36
ISe- 15	5.74 ± 0.42	5.11 ± 0.65	31.15 ± 2.21	33.80 ± 4.43	22.48 ± 2.12	27.47 ± 3.90
SIA 326 (Check 1)	4.10 ± 0.25	3.51 ± 0.59	18.26 ± 0.94	16.30 ± 2.56	16.02 ± 1.35	15.88 ± 3.02
Co (Te 7) (Check 2)	5.46 ± 0.18	4.56 ± 0.65	25.53 ± 1.10	23.96 ± 3.98	21.27 ± 1.04	20.41 ± 3.17
Suryanandi (Check 3)	5.46 ± 0.18	4.88 ± 0.59	25.17 ± 0.85	25.31 ± 3.45	22.06 ± 1.14	21.45 ± 2.31
ATL 1 (Check 4)	5.77 ± 0.06	5.04 ± 0.32	25.50 ± 0.47	24.91 ± 2.00	22.01 ± 0.51	21.43 ± 1.68
Susceptible group - Group II						
Sea 12	1.68 ± 0.33	1.26 ± 0.46	10.20 ± 2.62	10.55 ± 4.40	08.70 ± 1.92	11.45 ± 4.43
IC0403470	1.87 ± 0.06	1.51 ± 0.67	12.22 ± 0.33	12.42 ± 5.73	09.87 ± 0.26	13.41 ± 5.76
ISe- 254	1.60 ± 0.39	1.29 ± 0.51	11.98 ± 3.10	11.64 ± 5.34	07.96 ± 2.09	11.42 ± 4.77
Tenai 2201	2.09 ± 0.20	1.75 ± 0.95	13.43 ± 1.06	12.58 ± 7.78	10.65 ± 1.22	13.81 ± 5.53
Tenai 2202	2.18 ± 0.49	1.00 ± 0.28	13.37 ± 3.38	07.51 ± 2.19	10.10 ± 2.06	07.74 ± 2.53
IC0403487	3.51 ± 0.63	1.36 ± 0.36	20.81 ± 4.82	10.77 ± 2.30	17.21 ± 3.16	09.40 ± 2.20
ISe- 2/3	2.75 ± 0.93	1.86 ± 0.18	16.95 ± 6.25	15.08 ± 2.13	13.62 ± 4.94	12.03 ± 1.72
IC0479711	1.02 ± 0.71	0.82 ± 0.19	07.15 ± 5.07	06.78 ± 1.69	05.73 ± 4.02	06.62 ± 1.51
ISe- 365	2.54 ± 0.34	1.56 ± 0.58	16.28 ± 2.01	11.59 ± 4.37	12.53 ± 2.10	10.28 ± 4.06
ISe- 26	3.51 ± 0.35	2.02 ± 0.39	21.24 ± 1.61	16.45 ± 4.10	18.86 ± 1.95	17.62 ± 2.28
ISe- 23	4.73 ± 0.82	1.96 ± 0.47	28.10 ± 5.86	16.37 ± 4.68	20.98 ± 3.89	11.02 ± 2.30
	CD	**CD**	**CD**	**CD**	**CD**	**CD**
Genotypes	NS	NS	4.19**	4.46**	3.06**	4.50**
Checks	NS	NS	2.96**	3.15**	2.16**	3.18*
Genotypes vs Checks	2.45**	1.71**	3.63**	3.86**	2.65**	3.90**

Values are mean ± SE (standard error) of three samples. Significant changes are highlighted by an asterisk (*). *P ≤ 0.05; ** P ≤ 0.01; NS - non significant. S. Ed - Standard error of difference; CD - Critical difference.

Yield and yield components

The 1000 seed weight differed significantly ($P < 0.05$) for genotypes vs checks under control and combined stress conditions. Grain yield differed significantly ($P < 0.05$) for genotypes under both control and combined stress conditions. The 1000 seed weight was higher in Group I range from 2.4 to 3.2 g. In group II, the 1000 seed weight ranged from 1.6 to 2.7 g. A similar trend was observed in grain yield. Group I recorded higher values (17.48 to 23.58 g plant^{-1}) compared to group II (10.61 to 15.73 g plant^{-1}). TDMP showed a significant difference ($P < 0.01$) for genotypes vs checks and genotypes varied significantly ($P < 0.05$) under both control and combined stress conditions. TDMP in group I ranged from 19.98 to 29.71 g plant^{-1} which was higher than group II (Table 4). Among the checks, ATL 1 recorded the highest 1000 seed weight and grain yield of 3.2 g and 23.58 g plant^{-1} respectively. Comparable with checks, the genotype ISe-213/1 recorded a higher 1000 seed weight of 3 g and the genotype IC0479455 recorded a higher grain yield of 18.76 g plant^{-1}. The IC0403470 recorded a lower 1000 seed weight however, grain yield was poor in ISe-23. The 1000 seed weight had a positive correlation with GFD, panicle weight and DMT. Similarly, grain yield had a significant positive correlation with GFD, DMT, panicle weight and 1000 seed weight (Fig. 5). Panicle length and panicle weight of the genotypes and checks under combined stress are presented in Fig. 6.

Genetic parameters for grain filling and yield traits

PCV was found higher or almost equal to GCV for all the traits studied. This indicates that the environmental influence was lesser. Minimum or no difference between GCV and PCV was observed for GFR, GFD and TE. Heritability and GAM were higher for almost all the parameters like photosynthetic rate (86.24 and

Genotypes from left to right in (a) [ISe- 15 (21.7 cm, 9.5 g), ISe- 128/1 (21.2 cm, 9.2 g), IC0479455 (21 cm, 8.3 g), ISe- 213/1 (20.7 cm, 9.5 g), ISe- 183/1 (20.5 cm, 9.3 g), EC0529793 (20.3 cm, 9.1 g), ISe- 23 (20 cm, 8.2 g), ISe- 254 (20 cm, 6.5 g), IC0479711 (19.5 cm, 6.8 g), Tenai 2202 (19 cm, 6.9 g), ISe- 57/A (18 cm, 8.6 g), ISe- 26 (17 cm, 6.7 g), IC0479804 (15.2 cm, 9.3 g), ISe- 365 (14 cm, 7.8 g), IC0403487 (13.5 cm, 7.5 g), ISe- 2/3 (13 cm, 7.5 g), Tenai 2201(9 cm, 5.8 g), Sea 12 (8.8 cm, 6.8 g), IC0403440 (9 cm, 5.8 g), IC0403470 (8.5 cm, 5.7 g)]. Checks from left to right in (b) [SIA 326 (21.5 cm, 8.9 g), CO (Te 7) (20.2 cm, 8.9g), Suryanandhi (22.8 cm, 9.1 g), ATL 1 (22.5 cm, 9.3 g)].

Fig. 6. Genetic variation for panicle length and weight in foxtail millet genotypes subjected to drought and high-temperature stress from peak vegetative to mid-grain filling stage. a) I- Group I (Tolerant genotypes), II- Group II (Susceptible genotypes), b) Checks.

Table 4. Effect of combined stresses on yield and yield components in foxtail millet genotypes

Genotype	1000 seed weight (g)		Grain yield (g plant^{-1})		TDMP (g plant^{-1})	
	Control	Stress	Control	Stress	Control	Stress
Tolerant group – Group I						
IC0403440	3.0 ± 0.23	2.6 ± 0.20	22.64 ± 0.42	17.53 ± 0.52	29.49 ± 0.57	23.63 ± 0.44
IC0479455	2.8 ± 0.16	2.5 ± 0.14	25.73 ± 0.73	18.76 ± 0.19	27.70 ± 0.64	19.98 ± 0.25
ISe- 57/A	3.1 ± 0.33	2.4 ± 0.26	24.86 ± 0.96	18.43 ± 0.41	25.43 ± 0.91	27.27 ± 0.79
ISe- 128/1	3.2 ± 0.12	2.5 ± 0.09	24.19 ± 0.52	17.48 ± 0.54	29.74 ± 0.37	20.15 ± 0.86
EC0529793	3.5 ± 0.24	2.6 ± 0.17	25.61 ± 0.60	17.84 ± 0.71	29.88 ± 0.79	27.52 ± 0.53
ISe- 183/1	3.6 ± 0.22	2.8 ± 0.17	23.84 ± 0.61	18.54 ± 0.43	29.38 ± 0.89	23.01 ± 1.04
ISe- 213/1	3.1 ± 0.31	3.0 ± 0.30	25.49 ± 0.70	18.34 ± 0.34	28.64 ± 0.48	25.98 ± 0.25
IC0479804	3.1 ± 0.32	2.5 ± 0.26	25.19 ± 0.49	18.53 ± 0.58	27.25 ± 0.33	20.28 ± 0.93
ISe- 15	3.4 ± 0.23	2.6 ± 0.15	25.64 ± 0.71	18.73 ± 0.60	28.87 ± 0.85	23.61 ± 0.60
SIA 326, Prasad (Check 1)	3.6 ± 0.22	2.8 ± 0.30	25.64 ± 0.52	22.34 ± 0.86	31.75 ± 0.61	28.95 ± 0.87
Co (Te 7) (Check 2)	3.2 ± 0.32	2.7 ± 0.10	25.72 ± 0.39	22.46 ± 0.40	32.65 ± 0.48	27.02 ± 0.29
Suryanandi (Check 3)	3.8 ± 0.39	3.0 ± 0.20	24.83 ± 0.56	22.76 ± 0.99	32.52 ± 0.58	28.13 ± 0.38
ATL 1 (Check 4)	3.7 ± 0.22	3.2 ± 0.20	26.27 ± 0.67	23.58 ± 0.43	34.49 ± 0.57	29.71 ± 0.76
Susceptible group - Group II						
Sea 12	2.5 ± 0.14	2.2 ± 0.13	19.48 ± 0.42	11.27 ± 0.67	21.93 ± 0.86	16.64 ± 0.37
IC0403470	2.2 ± 0.23	1.6 ± 0.17	18.94 ± 0.35	11.23 ± 0.46	20.73 ± 0.75	16.87 ± 0.44
ISe- 254	2.5 ± 0.09	1.9 ± 0.07	20.24 ± 0.55	11.37 ± 0.44	17.38 ± 0.94	14.83 ± 0.27
Tenai 2201	2.3 ± 0.15	1.8 ± 0.12	19.67 ± 0.34	12.67 ± 0.87	21.00 ± 0.54	20.48 ± 0.57
Tenai 2202	2.6 ± 0.16	2.2 ± 0.13	21.46 ± 0.73	13.27 ± 0.83	22.49 ± 0.57	17.19 ± 0.86
IC0403487	2.9 ± 0.29	2.4 ± 0.24	20.43 ± 0.86	14.36 ± 0.67	23.93 ± 0.41	15.67 ± 0.91
ISe- 2/3	2.6 ± 0.27	2.3 ± 0.23	20.61 ± 0.62	15.73 ± 0.93	22.95 ± 0.39	17.54 ± 0.63
IC0479711	2.6 ± 0.16	2.2 ± 0.08	18.43 ± 0.48	12.43 ± 0.55	19.40 ± 0.39	15.70 ± 1.23
ISe- 365	3.1 ± 0.23	2.7 ± 0.18	20.43 ± 0.71	15.23 ± 0.59	21.22 ± 0.87	17.54 ± 0.65
ISe- 26	2.6 ± 0.17	2.1 ± 0.13	18.64 ± 0.44	11.27 ± 0.77	23.57 ± 0.91	16.01 ± 0.26
ISe- 23	2.2 ± 0.08	1.8 ± 0.18	20.43 ± 0.83	10.61 ± 0.66	19.58 ± 0.84	32.42 ± 0.41
	CD	**CD**	**CD**	**CD**	**CD**	**CD**
Genotypes	NS	NS	3.12*	4.70*	4.90*	5.09*
Checks	NS	NS	NS	NS	NS	NS
Genotypes vs Checks	1.56*	1.63*	2.70**	4.07**	4.25**	4.41**

Values are mean ± SE (standard error) of three samples. Significant changes are highlighted by an asterisk (*). *$P \le 0.05$; ** $P \le 0.01$; NS - non significant. S. Ed - Standard error of difference; CD - Critical difference.

43.24%), GFR (100 and 92.12%), GFD (100 and 35.65%), DMP at anthesis (72.56 and 22.51%), DMP at harvest (96.82 and 47%), DMT (81.59 and 87.76%), TE (97.56 and 91.88%), CR (96.76 and 86.61%), PW (94.08 and 27.73%), TSW (73.28 and 23.40%), GY (85.39 and 36.29%) and TDMP (92.88 and 45.08%). Thus, the results clearly showed that selection based on these traits will be effective for dissecting the stress-tolerant/susceptible genotypes to be used in future breeding programs. Among the studied traits lesser difference between GCV and PCV coupled with higher heritability and GAM was observed for GFR, GFD and TE (Table 5).

Discussion

Studying plant adaptations to stressful environments provides insights into the mechanism of tolerance and susceptibility. Revealing these mechanisms helps in breeding tolerant varieties to combat unfavourable conditions. A rain-out shelter experiment with twenty-four foxtail millet genotypes identified the negative impacts of combined heat and drought on grain-filling traits. Similar control environment studies have quantified the ill effects of high temperature on grain filling traits in rice (13, 18). Significant genotypic differences were observed in the photosynthesizing capacities of foxtail millet genotypes under combined stress. Hence, the photosynthetic rate measured at 50 DAS was used as a criterion to cluster the genotypes into tolerant (Group I) and susceptible (Group II) groups. Since, the chloroplast, the site of photosynthesis, is affected by several abiotic stresses like drought, high temperature and salinity, photosynthetic rate has been recognized as a sensitive trait under abiotic stress (19). This can ultimately lead to a reduction in the yield of the crop. Compared to control, the photosynthetic rates declined from 9.2 to 34.2% when exposed to interactive drought and high temperatures. In line with the above findings, a decrease in photosynthetic rate under drought (20) and high temperature (12) was observed in foxtail millet. The performance of each genotype towards tolerance to combined stress was examined based on DMT, TE and CR, in line with the previous studies (13, 21). Group I genotypes, including checks, recorded a higher DMP both at anthesis and harvest. Nearly 30-57% 35-70% increase in DMP at anthesis and harvest were recorded in group I as against group II genotypes. This might be the reason for higher DMT (2.12- 5.11 g plant^{-1}) in group I as against DMT values of 0.82 - 2.02 g plant^{-1} in group II genotypes. So, the results clearly showed that the dry matter production as well as translocation to the grains was greatly hindered in susceptible (Group II) genotypes by the combined stress. In addition, group II genotypes showed decreased values of TE and CR when exposed to interactive stress treatments.

Though the translocation efficiency was generally high in group I genotypes, few of the group II genotypes also exhibited equal translocation efficiency as group I genotypes. The lesser TE and CR in most of the susceptible genotypes might have been due to the lack of remobilization of stored reserves present in the stem and the leaf to the grains (13, 22). Decreased DMT may be due to less non-structural carbohydrates. Reduction in DMT from stems to growing grains decreases TE and ultimately decreases CR (13). Hence, DMT, TE and CR are critical for assessing drought and high-temperature stress tolerance. Concomitant with the above results, a significant positive correlation of DMT, TE and CR was observed with grain yield under combined stress (21).

The tissue temperatures such as leaf and panicle temperature were higher under combined stress conditions than the control. However, the tolerant genotypes maintained lesser leaf and panicle temperatures than the susceptible genotypes. Similar results of lesser leaf temperature in tolerant genotypes under drought stress conditions were observed in foxtail millet (23). The cooler canopy in tolerant genotypes may be due to better water uptake (23).

The grain filling rate which was captured by taking the difference in 1000 seed weight between 21 DAF and 15 DAF was greatly affected due to combined drought and high temperature. In addition, grain filling duration also decreased under drought and high-temperature stress. Under optimum temperature, decreased grain filling rate is compensated by increased grain filling duration. However, under high-temperature stress, this compensation does not happen resulting in decreased grain weight (24). Every 1 °C increase in high-temperature results in a

Table 5. Genetic parameters of foxtail millet under combined stresses

Trait	Variance			GCV (%)	PCV (%)	Heritability (%)	GAM (%)
	Vg	Vp	Ve				
Pn rate	14.55	16.87	2.32	13.49	14.52	86.24	43.24
LT	1.68	3.60	1.92	3.59	5.26	46.64	5.06
PT	2.59	4.28	1.68	4.31	5.53	60.64	6.91
GFR	0.0005	0.0005	0.00	44.72	44.72	100	92.12
GFD	51.73	51.73	0.00	17.31	17.31	100	35.65
DMP @ anthesis	4.80	6.61	1.81	12.82	15.05	72.56	22.51
DMP @ harvest	22.85	23.60	0.75	23.19	23.56	96.82	47.00
DMT	1.13	1.38	0.25	47.16	52.21	81.59	87.76
TE	51.49	52.78	1.29	45.16	45.72	97.56	91.88
CR	39.31	40.63	1.32	42.74	43.45	96.76	86.61
PL	2.91	5.14	2.23	10.20	13.55	56.63	15.81
PW	1.43	1.52	0.09	13.88	14.31	94.08	27.73
TSW	0.10	0.13	0.04	13.27	15.50	73.28	23.40
GY	8.38	9.81	1.43	19.07	20.63	85.39	36.29
TDMP	21.92	23.60	1.68	22.71	23.56	92.88	45.08

Vg- Genotypic variance; Vp- Phenotypic variance; Ve- Environmental variance; GCV- Genotypic coefficient of variance; PCV- Phenotypic coefficient of variance; GAM- Genetic advance as percent of mean.

decrease in GFD by about 2 to 8 days (13). Similarly, in the present study decreased grain filling rate and duration resulted in decreased grain weight and yield. In addition, translocation of stored reserves in terms of DMT and TE was also found to be decreased under stress conditions, resulting in decreased grain filling rate as reviewed by a previous study (7). When plants were exposed to high-temperature stress during the grain-filling stage, excess biomass accumulated in stems rather than grains. This might have been due to the decreased translocation efficiency, where the photosynthates did not reach the growing grains. Similar results were previously reported in rice by Blum et al. (22). Photosynthates get remobilized to grains after stress was relieved (15). The tolerant genotypes had comparatively longer grain filling duration which was positively correlated with higher panicle weight. This is consistent with the results of the previous study (25), which reported heavier panicles with longer grain filling duration.

Drought and high-temperature stress caused a negative impact on grain yield. Significant reductions in yield components such as panicle length, panicle weight, 1000 seed weight, grain yield and TDMP were observed. Panicle length and panicle weight in group II genotypes were severely reduced leading to shorter and thinner panicles. Similar results were reported in maize hybrids exposed to the combined stress of drought and high temperature (26). Reduced translocation of assimilates resulted in decreased GFR. When the assimilate supply rate couldn't meet the demand for grain growth, grain yield decreased (10). The 1000 seed weight did not show a significant reduction among the tolerant and susceptible groups. However, the checks maintained higher seed weight when exposed to combined stress. Similarly, 1000 seed weight was reduced in finger millet (27) and pearl millet (28) grown under high-temperature conditions.

A highly significant reduction in grain yield under stress was observed in foxtail millet genotypes compared to the control. Similarly, a reduction in grain yield and the number of grains under drought and high-temperature stress was observed in foxtail millet (12, 20). All four checks taken for the study showed a non-significant reduction when exposed to drought and high temperature compared to the control. TDMP also recorded a similar trend as grain yield. TDMP was lower in susceptible groups, this might be due to lower photosynthetic rate, DMT, TE and CR. Similarly, reduced TDMP due to reduced TE, CR and DMT was observed in susceptible rice varieties under high-temperature stress (13). The maintenance of a higher photosynthetic rate by group I genotypes might have contributed to higher grain yield and TDMP. In corroboration with the above findings, a strong positive correlation of grain yield with photosynthetic rate was observed in wheat (29) and in maize hybrids (26). This relationship was confirmed by correlation analysis of grain filling and yield traits in all the foxtail millet genotypes. The results concluded that maintenance of a higher photosynthetic rate followed by longer GFD and better GFR under stress is one of the tolerance mechanisms in foxtail millet to fight heat and drought scenarios.

Conclusion

This study identified key physiological responses influencing grain-filling traits and yield reduction in foxtail millet under combined heat and drought stress. Among the genotypes studied, ISe-15 exhibited the highest tolerance to drought and heat stresses at the reproductive stage. This tolerance was due to higher DMT, TE and CR along with a high photosynthetic rate under combined drought and high-temperature stress. Higher translocation of stored reserves to grain filling along with higher photosynthesis under stress resulted in improved grain weight and yield. These findings suggest that the use of the tolerant genotype ISe-15 is a valuable resource for use in breeding programs aimed at developing heat and drought-tolerant foxtail millet varieties.

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Authors' contributions

GS conducted the experiment, formally analysed and investigated the data, visualized the data and prepared the original draft of the manuscript. VD conceptualized the experiment, reviewed and edited the manuscript. VA reviewed and edited the manuscript. SS reviewed and edited the manuscript. SR reviewed and edited the manuscript. IK reviewed and edited the manuscript. KE reviewed and edited the manuscript. SU reviewed and edited the manuscript. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interests to declare.

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