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SOYBEAN SCREENING FOR HEAT TOLERANCE AT EARLY GROWTH STAGE FOR SELECTIVE BREEDING

H. BASHIR[1], SAMANHUDI[2*], PARJANTO[2], A. SETYAWATI[2], and H.S.B. MUSTAFA[3]

[1]Department of Agronomy, Faculty of Agriculture, Sebelas Maret University, Surakarta, Indonesia
[2]Department of Agrotechnology, Faculty of Agriculture, Sebelas Maret University, Surakarta, Indonesia
[3]Directorate of Oilseeds, Ayub Agricultural Research Institute, Faisalabad, Pakistan
[*]Corresponding author's email: samanhudi@staff.uns.ac.id
Emails addresses of co-authors: agrihassanba@gmail.com, parjanto@staff.uns.ac.id, andriyanasetyawati@staff.uns.ac.id, hafiz.saad.aari@punjab.gov.pk

SUMMARY

Soybean (*Glycine max* L.) is an important edible-oil crop whose productivity faces threats of rising temperature under climate change, making the identification of heat-tolerant genotypes crucial. This study evaluated 18 soybean genotypes for heat tolerance across five temperatures (25 °C, 30 °C, 35 °C, 40 °C, and 45 °C), focusing on survival rate, shoot and root lengths, and total plant weight. Gepak Kuning, Argomulyo, and Demas 1 showed robust resilience and consistent superiority. The highest broad-sense heritability (H^2 up to 1.00) recorded was for these traits, underscoring their breeding potential. Correlation showed positive associations among root length, shoot length, and leaf area, suggesting these as tolerance indicators. Heat tolerance index (HTI) classified Gepak Kuning, Argomulyo, and Demas 1 as tolerant; Devon 1, Denasa 1, and Derap 1 as moderately tolerant; and Detap 1, Grobogan, and Dering 3 as susceptible. The study identified promising heat-tolerant genotypes and traits for climate-smart soybean breeding.

Keywords: Soybean (*G. max* L.), heat stress, early growth stage, heat tolerance index, thermo-tolerance screening

Key findings: Soybean (*G. max* L.) genotypes Gepak Kuning, Argomulyo, and Demas 1 revealed significant heat tolerance at 45 °C with the highest survival rate and heat tolerance index. Positive correlation between root-shoot traits enables integrated selection strategies to enhance plant vigor under tropical heat stress conditions.

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INTRODUCTION

Soybean (*Glycine max* L.) is a primary oilseed crop valued for its protein, oil, and biofuel potential (Chen, 2025; Gaguan and Nagal, 2025). Although global production has its concentration in the United States, Brazil, and Argentina, Indonesia faces a persistent deficit and imports over two million tons annually, underscoring the need to raise local productivity despite generally favorable growing conditions (Rotundo *et al.*, 2024; Fattah *et al*., 2024; Dewi and Anandari, 2025; Sibuea *et al*., 2024).

Low soybean productivity in Indonesia indicates a link to poor seed quality, suboptimal agronomy, and abiotic stress (Fattah *et al*., 2024; Setiawan *et al*., 2025). Heat stress is especially critical in tropical environments. Soybean performs best near 26 °C, yet temperatures in many Indonesian growing areas frequently surpass 35 °C, disrupting physiology, seed setting, and grain yield (Thenveettil *et al*., 2025; Maucieri *et al*., 2025; Moseley *et al*., 2025).

Long-term records corroborate this trend; mean air temperature across Indonesia has risen by about 0.8 °C–1.0 °C since the 1960s, with a further 0.8 °C–1.4 °C projected by mid-century and more frequent days above 35 °C in the lowland soybean regions of Java and Sulawesi (Maucieri *et al*., 2025). Exposure to high temperatures at the seedling stage can cause lasting morphophysiological damage, with this vulnerability expected to intensify under climate change, making the development of heat-tolerant cultivars increasingly vital (Zhang *et al*., 2025a and b).

Despite this need, few studies have screened soybean genotypes for heat tolerance, and no cultivar has yet been formally identified as heat-resilient in Indonesia (Fattah *et al*., 2024; Setiawan *et al*., 2025; Maucieri *et al*., 2025; Thenveettil *et al*., 2025). The present study therefore evaluated the morphophysiological responses of soybean cultivars to seedling-stage heat stress and identified genotypes with superior tolerance as candidates for future breeding.

MATERIALS AND METHODS

Plant materials and procedure

Eighteen soybean (*G. max* L.) cultivars (Deja 1, Deja 2, Demas 1, Dega 1, Dena 1, Dena 2, Detap 1, Derap 1, Devon 1, Devon 2, Gepak Kuning, Dering 1, Dering 2, Dering 3, Denasa 1, Denasa 2, Grobogan, and Argomulyo) were samples used in this study. These represent local and commercial Indonesian cultivars. The study employed a fully nested experimental design with five temperature levels (25 °C control, 30 °C, 35 °C, 40 °C, and 45 °C) as the main factor, with the cultivars nested within each temperature having three replications. Each replication was one cup of four seedlings, representing one experimental unit (270 units in total: 18 cultivars × 5 temperatures × 3 replications).

Cocopeat served as the growing medium for its water-retention properties. Soybean genotype seeds (8 per cup, 14 cm × 9 cm) entailed sowing and maintenance under regulated laboratory conditions with a photoperiod (12:12 h light: dark). Before the imposition of heat stress, raising all seedlings was under a uniform baseline environment maintained at 25 °C, 60%–70% relative humidity, and a photosynthetic photon flux density of approximately 300 μmol m^{-2} s^{-1} supplied by the chamber lighting. Seed germination completion occurred within five to seven days after sowing. After germination, the emerged seedlings in each cup received thinning to retain four uniform plants per cup. Heat stress imposition was at the two fully developed trifoliate leaves (V2 stage, reached at a comparable physiological age across cultivars). This comprised exposing seedlings to target temperatures for four hours daily over four consecutive days in an intelligent growth chamber (relative humidity held at 60%–70% throughout the treatment period), followed by a one-week recovery period before measurements.

Traits measurement and analysis

Data recorded on morphophysiological parameters included survival rate, root and shoot lengths, root-to-shoot ratio, fresh and dry plant weights (oven-dried at 70 °C for 48 h), relative water content (RWC; Barrs and Weatherley, 1962), SPAD chlorophyll, leaf area, and membrane stability index (Premchandra *et al*., 1990). Heat tolerance index (HTI) calculation for each trait followed Fernandez (1992). The HTI = $(Y_s \times Y_p) / (\bar{Y}_p)^2$, where Y_s is the trait value of a given genotype under heat stress, Y_p is its value under the control (25 °C) condition, and $\bar{Y}_p$ is the mean control value across all genotypes. Based on the resulting HTI values, genotypes' classification consisted of tolerant (HTI ≥ 1.0), moderately tolerant (0.5 ≤ HTI < 1.0), or susceptible (HTI < 0.5). All data analysis used a nested analysis of variance (ANOVA), correlation, principal component analysis (PCA), and regression in R (version 4.4.1) at $P < 0.05$. Where the ANOVA detected significant effects, mean separation continued using Tukey's honestly significant difference (HSD) test at $P < 0.05$. Genotypic and phenotypic variance components reached estimation from the ANOVA mean squares, where genotypic variance is $\sigma^2_g = (MS_g - MS_e) / r$, and phenotypic variance is $\sigma^2_p = \sigma^2_g + (MS_e / r)$. The MS_g is the mean square of genotypes, MS_e is the error mean square, and r is the number of replications. Broad-sense heritability computation was as $H^2 = \sigma^2_g / \sigma^2_p$ and expressed on a 0–1 scale. Figures generated engaged R software, and their editing used Inkscape software.

RESULTS

Survival rate

Soybean (*G. max* L.) genotype survival progressively declined with increasing temperature. The analysis of variance confirmed a highly significant effect of temperature treatment (F = 121.06, $P < 0.01$) and a significant genotype × treatment interaction (F = 1.25), whereas the main effect of genotype was non-significant (Table 1). It indicates seedling survival was under primary control of the temperature level and its interaction with genotype rather than by genotype alone. All cultivars showed 100% survival under control (25 °C). Survival remained high at 30 °C (lowest in Grobogan, 66%), then declined to 50%–75% at 35 °C–40 °C. Under extreme stress (45 °C), only Demas 1, Gepak Kuning, and Argomulyo survived (25%–50%), while the remaining 15 cultivars showed complete mortality.

Genetic variability and genetic parameters

Heat stress significantly affected genotypes for root length, shoot length, leaf area, and total plant weight (Table 2a–b). The ANOVA confirmed highly significant effects of treatment, genotype, and their interaction for these traits ($P < 0.01$ in all cases, Table 1), the treatment effect being the strongest source of variation (e.g., F = 2398.74 for root length and F = 5443.46 for shoot length). Root and shoot lengths exhibited a slight enhancement at 30 °C. But they declined sharply under severe stress, with shoot length falling to 9.07 ± 0.28 cm at 45 °C. The coefficient of variation reached 29.59% for root length and 21.09% for leaf area (35 °C). Broad-sense heritability estimated from the variance components was moderate to high, ranging from $H^2 = 0.61$ (relative water content, 25 °C) to 1.00 (meristem node, leaf area, and total plant weight). It stayed high ($H^2 > 0.84$) for primary growth traits across treatments, indicating a predominantly genetic control, though meristem node, shoot length, and total plant weight declined at 45 °C as the environmental component increased.

Morphophysiological traits

Heat stress reduced all morphophysiological traits (Figure 1a–i). Most cultivars showed normal growth under control and some stimulation at 30 °C, then progressively declined at higher temperatures. At 45 °C, only Demas 1, Gepak Kuning, and Argomulyo

Table 1. Summary of the nested analysis of variance (F- and p-values) for survival and morphophysiological traits of 18 soybean genotypes evaluated across five temperature levels.

Traits	Genotype (V)		Treatment (T)		V × T	
	F	p	F	p	F	p
d.f.	17	—	4	—	68	—
Survival rate	1.27 ns	0.220	121.06 **	<0.001	1.25 ns	0.136
Meristem node	530.66 **	<0.001	1704.30 **	<0.001	25.54 **	<0.001
Root length	806.80 **	<0.001	2398.74 **	<0.001	26.08 **	<0.001
Shoot length	366.39 **	<0.001	5443.46 **	<0.001	17.54 **	<0.001
Total plant weight	700.36 **	<0.001	9107.72 **	<0.001	9.90 **	<0.001
Root-to-shoot ratio	83.33 **	<0.001	147.53 **	<0.001	4.55 **	<0.001
Relative water content	19.31 **	<0.001	717.44 **	<0.001	6.47 **	<0.001
Leaf area	635.96 **	<0.001	4596.96 **	<0.001	21.72 **	<0.001
SPAD	223.08 **	<0.001	930.30 **	<0.001	4.19 **	<0.001
Membrane stability index	378.38 **	<0.001	383.90 **	<0.001	14.35 **	<0.001

Note: F = F-value; *P* = probability value. ** Significant at $P < 0.01$; * Significant at $P < 0.05$; ns = nonsignificant. V × T = genotype × temperature interaction. Error d.f. = 150.

Table 2a. Estimates of variability and genetic parameters of soybean genotypes under control (25 °C), mild (30 °C), and moderate (35 °C) temperature conditions.

Treat-ments	Traits	Means	S.E.	Ranges	S.D.	Variance	Genotypic Variance	Phenotypic Variance	CV	Herita-bility
25 °C	Meristem Node	2.11	0.08	1-3	0.57	0.33	0.34	0.34	27.09	1.00
	Root Length	11.05	0.31	6.99 - 16.07	2.27	5.14	4.93	5.06	20.52	0.97
	Shoot Length	16.85	0.24	14 - 20	1.74	3.03	2.88	2.97	10.34	0.97
	RWC	83.37	0.05	82.39 - 83.96	0.33	0.11	0.04	0.06	0.40	0.61
	Total Plant Weight	1.52	0.03	1.08 - 1.89	0.21	0.04	0.04	0.04	13.51	1.00
	Root: Shoot Ratio	0.75	0.01	0.6 - 0.88	0.07	0.00	0.00	0.00	9.26	0.92
	Leaf Area	240.54	5.93	133.7 - 310.3	43.55	1896.42	1970.66	1970.70	18.10	1.00
	SPAD	35.96	0.40	28 - 41	2.91	8.45	8.28	8.44	8.08	0.98
	MSI	39.04	0.95	27 - 58	6.95	48.30	46.77	47.87	17.80	0.98
30 °C	Meristem Node	2.89	0.10	2-4	0.74	0.55	0.58	0.58	25.75	1.00
	Root Length	13.86	0.53	7.74 - 22.56	3.93	15.45	16.03	16.04	28.36	1.00
	Shoot Length	20.57	0.43	15.7 - 30.3	3.19	10.17	10.50	10.52	15.50	1.00
	RWC	86.78	0.08	86 - 87.88	0.55	0.30	0.16	0.21	0.64	0.76
	Total Plant Weight	1.71	0.03	1.2 - 2.16	0.24	0.06	0.06	0.06	14.30	1.00
	Root: Shoot Ratio	0.77	0.02	0.53 - 0.92	0.12	0.01	0.01	0.01	15.27	0.99
	Leaf Area	281.67	6.57	156.7 - 366.3	48.30	2332.97	2423.62	2423.89	17.15	1.00
	SPAD	37.17	0.37	30 - 42	2.72	7.42	7.37	7.48	7.33	0.99
	MSI	38.74	0.96	29 - 60	7.03	49.40	48.70	49.55	18.14	0.98
35 °C	Meristem Node	2.72	0.12	1-4	0.88	0.77	0.80	0.80	32.24	1.00
	Root Length	12.06	0.49	5.03 - 19.16	3.57	12.74	13.21	13.21	29.59	1.00
	Shoot Length	18.25	0.38	12.8 - 23.8	2.76	7.64	7.88	7.89	15.14	1.00
	RWC	83.70	0.25	77.21 - 84.95	1.86	3.48	3.51	3.55	2.23	0.99
	Total Plant Weight	1.52	0.03	1.08 - 1.89	0.21	0.04	0.04	0.04	13.54	1.00
	Root: Shoot Ratio	0.72	0.01	0.53 - 0.86	0.10	0.01	0.01	0.01	14.29	0.95
	Leaf Area	251.62	7.22	111.7 - 327.4	53.07	2816.38	2805.51	2844.42	21.09	0.99
	SPAD	36.56	0.38	29 - 41	2.80	7.84	7.55	7.74	7.66	0.98
	MSI	40.19	1.00	29 - 63	7.35	54.08	54.79	55.24	18.30	0.99

Table 2b. Estimates of variability and genetic parameters of soybean genotypes under severe (40 °C) and extreme (45 °C) temperature treatments.

Treat-ments	Traits	Means	S.E.	Ranges	S.D.	Variance	Genotypic Variance	Phenotypic Variance	CV	Herita-bility
40 °C	Meristem Node	1.78	0.09	1-3	0.63	0.40	0.42	0.42	35.69	1.00
	Root Length	8.10	0.32	2.37 - 11.85	2.38	5.68	5.87	5.88	29.41	1.00
	Shoot Length	12.97	0.32	8-17	2.37	5.63	5.76	5.79	18.29	1.00
	RWC	68.00	0.80	60 - 74.6	5.86	34.33	23.58	27.46	8.62	0.86
	Total Plant Weight	0.95	0.02	0.6 - 1.22	0.14	0.02	0.02	0.02	14.79	0.99
	Root: Shoot Ratio	0.66	0.01	0.53 - 0.81	0.08	0.01	0.01	0.01	12.18	0.95
	Leaf Area	154.74	4.25	72.4 - 203.9	31.22	974.53	1004.78	1007.33	20.17	1.00
	SPAD	31.15	0.45	22 - 36	3.31	10.96	11.06	11.17	10.63	0.99
	MSI	46.93	1.65	27 - 79	12.16	147.77	152.33	152.73	25.90	1.00
45 °C	Meristem Node	1.89	0.20	1-3	0.60	0.36	0.19	0.26	31.81	0.71
	Root Length	11.22	0.22	10.4 - 12.4	0.65	0.42	0.44	0.47	5.81	0.93
	Shoot Length	9.07	0.28	8 - 10.2	0.85	0.72	0.58	0.67	9.33	0.86
	RWC	56.91	4.78	34.43 - 76.47	14.34	205.54	193.44	213.59	25.19	0.91
	Total Plant Weight	0.95	0.04	0.81 - 1.2	0.12	0.01	0.01	0.01	12.65	0.84
	Root: Shoot Ratio	0.69	0.02	0.6 - 0.77	0.05	0.00	0.00	0.00	7.90	0.93
	Leaf Area	178.70	3.58	165.1 - 192.9	10.75	115.48	149.98	150.98	6.01	0.99
	SPAD	30.44	0.50	29 - 33	1.51	2.28	2.89	2.93	4.96	0.99
	MSI	42.00	0.90	39 - 46	2.69	7.25	9.22	9.33	6.41	0.99

Note: All treatments' application was at constant chamber temperatures (25 °C, 30 °C, 35 °C, 40 °C, and 45 °C). SE = Standard Error; SD = Standard Deviation; CV = Coefficient of Variation

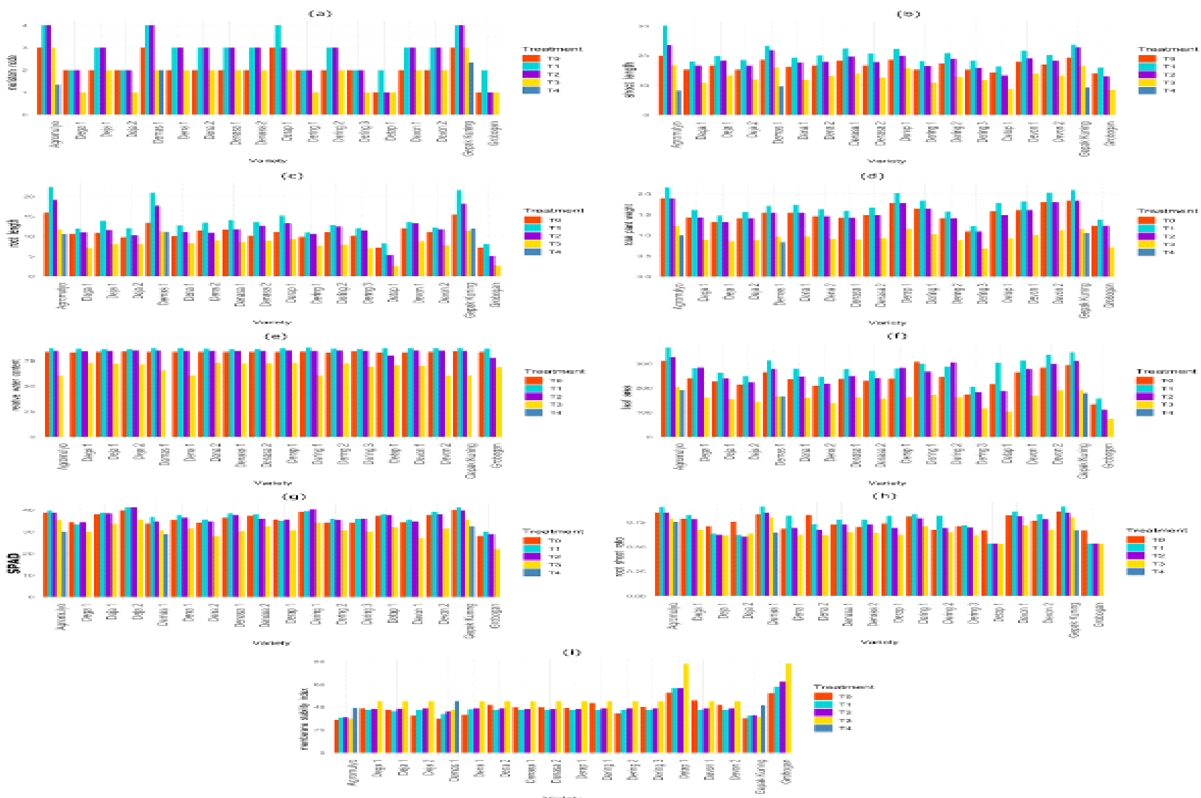

Figure 1(a-i). Effect of different temperature treatments on morphological and physiological traits of soybean genotypes. Average variability of (a) meristem nodes, (b) shoot length, (c) root length, (d) total plant weight, (e) relative water content, (f) leaf area, (g) SPAD value, (h) root: shoot, and (i) membrane stability index.

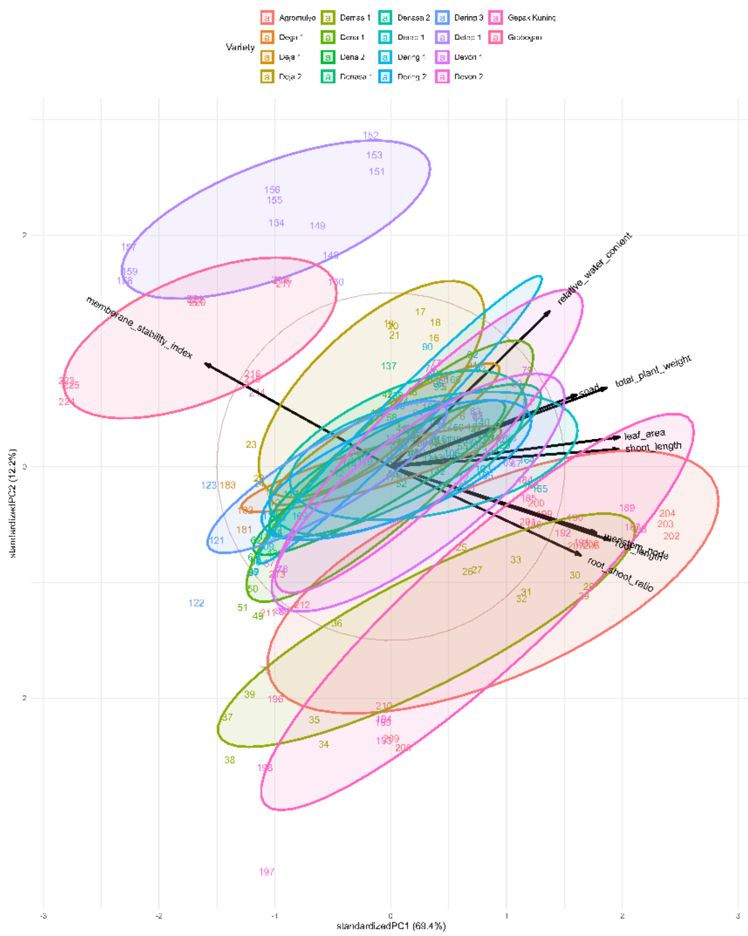

Figure 2. Principal component analysis of morphophysiological traits of soybean genotypes evaluated under varied heat stress conditions.

maintained measurable growth, while other cultivars showed complete inhibition. RWC exceeded 83% under control and declined markedly at 45 °C, where Argomulyo retained the highest value (73.12%). SPAD and MSI followed similar trends, and the root-to-shoot ratio stayed comparatively stable in tolerant genotypes but declined sharply in susceptible ones.

Principal component analysis

The first two principal components explained 82.19% of the total variation (Figure 2). PC1 (70.75%) showed a positive association with all growth traits, particularly root length, shoot length, leaf area, and plant weight, representing overall plant vigor. Meanwhile, PC2 (11.44%) contrasted water-related traits (RWC and MSI) with structural growth traits, indicating a separation between biomass accumulation and physiological stability under heat stress.

Correlation analysis

Pearson correlation revealed significant positive associations among growth traits (Figure 3). Shoot length correlated with plant weight at 35 °C–40 °C ($r = 0.66$) and leaf area with shoot and root lengths ($r = 0.80$). RWC disclosed a positive connection with growth traits under moderate stress but inconsistent under extreme heat, while MSI correlated negatively with root ($r = -0.95$) and shoot length ($r = -0.83$) at 40 °C.

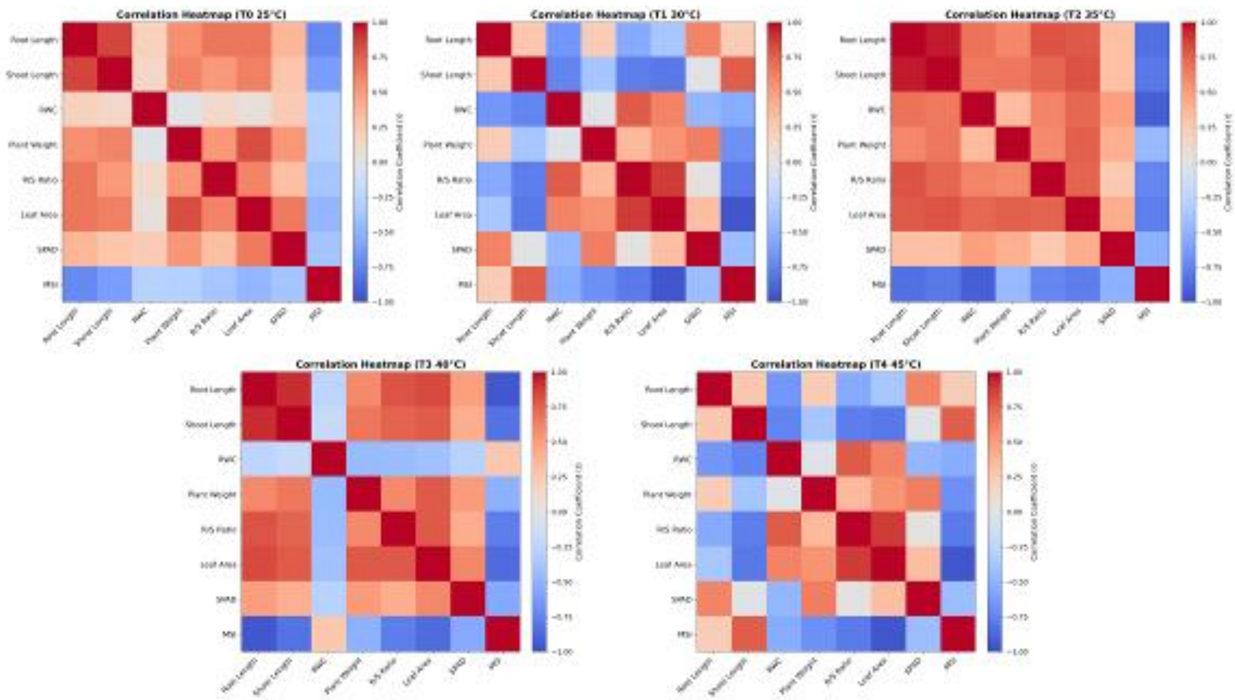

Figure 3. Correlation coefficients among the quantitative traits of soybean genotypes treated with different temperatures (30 °C, 35 °C, 40 °C, and 45 °C) and control (25 °C).

Regression analysis

A mixed-effects regression assessed the effect of temperature (30 °C–45 °C) on HTI with cultivar as a random effect (Figure 4). The model attributed a variance of 0.04323 to cultivars against a residual of 0.2619, indicating meaningful genotypic variation. The fixed effects of 30 °C–40 °C were negligible (t = 0.000), and the 45 °C effect, though slightly positive (0.0052), was nonsignificant (t = 0.165). This apparent contrast with the marked survival differences at 45 °C arises because the computation of HTI regression was only on the three surviving genotypes, among which the index was already uniformly high. Capturing the strong genotypic discrimination at 45 °C is therefore from survival and genotype classification rather than the within-survivor slope; hence, the analyses are complementary rather than contradictory.

Heat tolerance index

Based on HTI, cultivars gained differentiation into tolerant, moderately tolerant, and susceptible groups (Table 3). At 30 °C, Deja 1, Gepak Kuning, and Argomulyo showed the highest HTI, receiving a tolerant classification; at 35 °C, Devon 1 and Grobogan performed best, while Denasa 1 and Denasa 2 were moderately tolerant. At 40 °C, restricted tolerance largely occurred with Gepak Kuning and Argomulyo, and at 45 °C, only Demas 1, Gepak Kuning, and Argomulyo survived, demonstrating extreme tolerance, while the rest were susceptible.

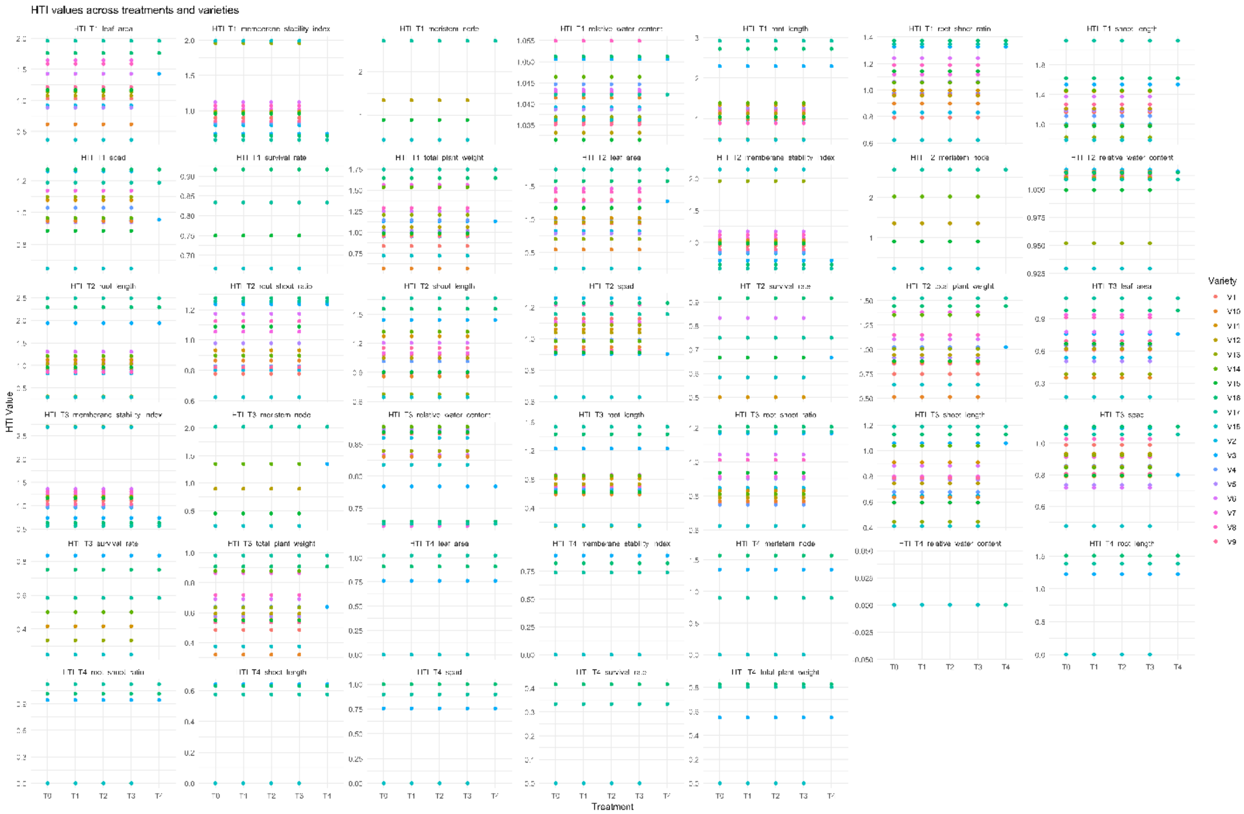

Figure 4. Regression analysis of cultivars across four heat stress treatments.

Table 3. Heat tolerance index (HTI) of soybean cultivars across four heat stress treatments.

Cultivars	30 °C								35 °C							
	X1	X2	X3	X4	X5	X6	X7	X8	X1	X2	X3	X4	X5	X6	X7	X8
Deja 1	1.23	1.16	1.04	0.84	0.79	1.03	1.14	0.90	1.03	1.08	1.01	0.75	0.78	0.94	1.13	0.95
Dering 3	1.00	0.99	1.04	0.57	0.90	0.62	0.95	0.99	0.95	0.86	1.02	0.51	0.87	0.55	0.95	1.03
Denasa 1	1.34	1.45	1.03	0.97	1.00	1.15	1.08	0.98	1.12	1.27	1.01	0.87	0.93	1.02	1.06	1.01
Denasa 2	1.13	1.21	1.03	1.06	0.96	1.08	1.10	0.98	1.04	1.05	1.01	0.95	0.90	0.96	1.04	1.01
Detap 1	0.48	0.83	1.04	1.21	0.62	1.14	1.10	1.96	0.31	0.67	0.95	1.01	0.62	0.71	1.09	1.96
Derap 1	1.38	1.46	1.05	1.54	1.06	1.16	0.97	0.96	1.21	1.32	1.01	1.35	0.90	1.17	0.98	0.99
Dega 1	1.04	0.98	1.03	0.99	1.14	1.17	0.88	0.96	0.96	0.90	1.00	0.88	1.09	1.17	0.91	0.98
Gepak Kuning	2.72	1.62	1.05	1.64	1.37	1.76	1.27	0.64	2.29	1.55	1.02	1.45	1.28	1.58	1.23	0.65
Argomulyo	2.92	2.12	1.04	1.74	1.35	1.96	1.19	0.58	2.49	1.66	1.01	1.53	1.26	1.75	1.16	0.59
Grobogan	0.47	0.79	1.04	0.72	0.62	0.36	0.65	1.99	0.30	0.64	0.93	0.64	0.62	0.26	0.63	2.14
Deja 2	0.97	1.00	1.04	0.95	0.83	0.92	1.26	0.79	0.82	0.90	1.02	0.86	0.80	0.83	1.26	0.83
Demas 1	2.30	1.53	1.05	1.13	1.33	1.43	0.95	0.67	1.94	1.44	1.02	1.02	1.24	1.27	0.90	0.72
Dena 1	1.04	1.11	1.04	1.14	0.98	1.14	1.03	0.82	0.91	1.01	1.01	1.02	0.83	1.01	0.99	0.84
Dena 2	1.26	1.18	1.04	1.02	1.06	0.88	0.94	1.02	1.02	1.05	1.01	0.92	0.98	0.79	0.91	1.07
Devon 1	1.33	1.37	1.04	1.25	1.24	1.43	0.95	1.12	1.30	1.20	1.01	1.10	1.17	1.28	0.92	1.17
Devon 2	1.12	1.21	1.04	1.56	1.12	1.65	1.14	1.02	1.08	1.10	1.01	1.38	1.06	1.46	1.11	1.07
Dering 1	0.89	0.98	1.05	1.29	1.19	1.59	1.19	1.07	0.85	0.89	1.01	1.15	1.13	1.41	1.22	1.12
Dering 2	1.16	1.27	1.04	0.96	0.97	1.21	0.95	0.85	1.13	1.15	1.01	0.86	0.82	1.29	0.93	0.89

Table 3. (cont'd.)

Cultivars	40 °C								45 °C							
	X1	X2	X3	X4	X5	X6	X7	X8	X1	X2	X3	X4	X5	X6	X7	X8
Deja 1	0.72	0.79	0.87	0.48	0.77	0.61	0.99	1.11								
Dering 3	0.59	0.63	0.83	0.32	0.77	0.35	0.79	1.20								
Denasa 1	0.81	0.91	0.87	0.55	0.83	0.66	0.85	1.19								
Denasa 2	0.73	0.75	0.87	0.59	0.79	0.62	0.93	1.19								
Detap 1	0.15	0.44	0.84	0.63	0.62	0.39	0.92	2.70								
Derap 1	0.85	1.04	0.88	0.88	0.81	0.67	0.85	1.17								
Dega 1	0.62	0.60	0.87	0.55	0.94	0.67	0.80	1.16								
Gepak Kuning	1.43	1.13	0.73	0.91	1.20	0.98	1.10	0.63	1.51	0.63		0.83	1.01	0.91	1.00	0.82
Argomulyo	1.53	1.19	0.73	0.98	1.18	1.09	1.06	0.56	1.38	0.58		0.80	1.12	1.02	0.90	0.74
Grobogan	0.16	0.41	0.82	0.37	0.62	0.17	0.48	2.69								
Deja 2	0.65	0.65	0.86	0.54	0.85	0.53	1.09	0.96								
Demas 1	1.23	1.06	0.78	0.64	1.17	0.76	0.80	0.73	1.22	0.64		0.55	0.94	0.76	0.75	0.89
Dena 1	0.68	0.68	0.73	0.64	0.75	0.65	0.86	0.98								
Dena 2	0.84	0.77	0.87	0.57	0.90	0.50	0.74	1.24								
Devon 1	0.86	0.88	0.83	0.69	1.04	0.78	0.72	1.36								
Devon 2	0.70	0.80	0.72	0.87	0.91	0.93	0.91	1.24								
Dering 1	0.62	0.59	0.73	0.72	1.01	0.91	1.03	1.30								
Dering 2	0.72	0.79	0.87	0.54	0.77	0.69	0.81	1.03								

Note: X1 = Root Length, X2 = Shoot Length, X3 = RWC, X4 = Total Plant Weight, X5 = Root/Shoot Ratio, X6 = Leaf Area, X7 = SPAD, and X8 = MSI.

DISCUSSION

At 45 °C, most cultivars did not survive, except Gepak Kuning, Argomulyo, and Demas 1, revealing pronounced genotypic differences in extreme-heat tolerance (Hammond *et al*., 2025). The survival of only a small tolerant fraction establishes survival rate as an effective early criterion for screening heat-tolerant cultivars (Sana *et al*., 2025; Zhang *et al*., 2025a, b).

High heritability indicates robust genetic control and reliable transmission to the next generation, marking such traits as selection targets (Mejaya *et al*., 2025; Mundhe, 2025). Shoot length, root length, total plant weight, and leaf area showed the highest genotypic variance, indicating that selection under heat stress could yield more resilient cultivars (Hammond *et al*., 2025; Maucieri *et al*., 2025). In this germplasm, the consistently high heritability for leaf area, total plant weight, and meristem node (H^2 approaching 1.00 under moderate stress) implies that the additive genetic component dominated phenotypic expression, thus early-generation selection under controlled heat would be effective. The decline for shoot length and meristem node at 45 °C reflects an enlarged environmental variance and cautions that selection for these traits is most reliable within the moderate 30 °C–40 °C range.

PCA gave a holistic view of trait associations under heat stress (Bogati *et al*., 2025; Tamang *et al*., 2025). The control of PC1 was mainly by shoot length, root length, and total plant weight, identifying these as primary indicators of plant vigor and main selection targets (Hammond *et al*., 2025; Hasan *et al*., 2024; Zhang *et al*., 2025a and b).

Positive correlations among root length, shoot length, and leaf area suggest that improvement in one trait may drive gains in others, consistent with root-shoot dynamics under abiotic stress, wherein a deeper root system supports water uptake and shoot growth (Gowdra *et al*., 2025; Al-Dossary *et al*., 2025). In contrast, the membrane stability index correlated negatively with root and shoot lengths, indicating that cultivars with higher membrane stability sustain less cellular damage but may trade off growth (Pavithra *et al*., 2025; Hasan *et al*., 2024).

Based on HTI, Gepak Kuning, Argomulyo, and Demas 1 consistently scored highest, attaining classification as tolerant, whereas Deja 2 and Devon 1 showed low HTI and were susceptible, consistent with prior use of HTI to rank genotypes in stress (Hammond *et al*., 2025). From a breeding standpoint, the convergence of high survival, high HTI, and high trait heritability in Gepak Kuning, Argomulyo, and Demas 1 makes them suitable parents for recombination and recurrent selection. Conversely, the moderately tolerant group offers complementary alleles for traits, such as relative water content, with these lines already being advanced as crossing parents in our ongoing heat-tolerance breeding program.

Overall, heat tolerance in soybean has the governance of coordinated morphological and physiological traits under strong genetic control, and selection should prioritize high-heritability traits and root-shoot balance to enhance resilience under projected warming.

CONCLUSIONS

The study identified soybean (*G. max* L.) genotypes and key traits for heat tolerance. Gepak Kuning, Argomulyo, and Demas 1 showed superior performance under high-temperature stress, and the high heritability of the key traits marks them as reliable selection targets. These tolerant genotypes require incorporation into breeding programs to develop cultivars resilient to climate-induced heat stress.

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