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RESEARCH ARTICLE

Impact of sowing date and irrigation regime on wheat performance under heat and drought stress in the Indo-Gangetic plains of Bihar

T Murugesh, A Mishra & R Kumar*

Department of Agricultural Biotechnology and Molecular Biology, College of Basic Sciences and Humanities, Dr. Rajendra Prasad Central Agricultural University, Samastipur 848 125, Bihar, India

*Correspondence email - rajeev.k@rpcau.ac.in

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Abstract

Wheat (*Triticum aestivum* L.) is a staple crop in the Indo-Gangetic Plains, where rising temperatures and limited water availability threaten productivity. A field experiment was conducted during the 2022–23 rabi season at Dr Rajendra Prasad Central Agricultural University, Pusa, Bihar, to evaluate six wheat genotypes under three contrasting conditions: normal sowing with full irrigation, late sowing to induce terminal heat stress and normal sowing with restricted irrigation (single irrigation at 45 days after sowing). Morphological, phenological and yield traits were assessed, including plant height, spike and peduncle length, days to heading, flowering and maturity and grains per spike. Late sowing markedly accelerated phenology and reduced grains per spike by up to 38 %, whereas restricted irrigation delayed maturity and reduced grains per spike by up to 31 %. Genotypic differences were evident: DH5-167 exhibited strong vegetative resilience but low reproductive performance, while IC-252874 maintained higher grains per spike despite moderate vegetative susceptibility. Multivariate analyses revealed that the first two principal components explained 86.38 % of the total variation. Genotypes were separated primarily according to treatment along these components, indicating a stronger influence of environmental stress on phenotypic expression than genotype. Overall, the results highlight a trade-off between vegetative growth and reproductive stability under abiotic stress and suggest that combining traits conferring reproductive resilience to heat with those prolonging grain filling under drought can enhance yield stability in wheat grown in the Indo-Gangetic Plains.

Keywords: abiotic stress; climate resilience; genotype × environment interaction; principal component analysis; yield stability

Introduction

Wheat (*Triticum aestivum* L.) is a staple crop that feeds over 40 % of the world's population and is the most widely cultivated cereal globally, providing approximately 20 % of daily caloric and protein intake (1–3). In the Indo-Gangetic Plains (IGP) of India, it underpins national food and livelihood security, but climate change–driven increases in temperature and declining water availability threaten sustainable production (4). Terminal heat stress during late reproductive stages accelerates senescence, reduces photosynthetic activity and shortens the grain filling period, while restricted irrigation exacerbates yield losses by limiting assimilate supply (5, 6). The rice-wheat cropping system (RWCS) dominates the IGP, particularly in Bihar, contributing nearly half of India's food grain production and supporting 40 % of its population (7). However, prolonged rice cultivation, heavy post-monsoon rainfall and excess residual soil moisture frequently delay wheat sowing. As a result, crops often face terminal heat stress during reproductive stages, making the IGP increasingly vulnerable to productivity declines (8, 9).

Although heat and drought stress in wheat have received considerable attention, much of the available evidence originates from controlled experiments or idealised irrigation regimes that do not fully represent farmer-managed conditions in the Indo-Gangetic Plains. In practice, water scarcity often forces farmers to adopt a single, one-off irrigation around 45 days after sowing as a means of conserving limited water resources.

Results from recent field experiments indicate that such restricted irrigation can improve water-use efficiency; however, yield responses remain highly variable and are strongly influenced by genotype, particularly when elevated temperatures coincide with reproductive development (6, 10). Additional field studies conducted under irrigated and semi-arid wheat-growing environments have shown that deficit or restricted irrigation alters phenological progression, biomass allocation and grain yield, with outcomes depending on both genotype and the timing of water limitation (11–13). Collectively, these findings emphasize the importance of evaluating wheat performance under realistic field management scenarios.

Field-based assessments further demonstrate that terminal heat stress during reproductive stages substantially reduces grain set and yield stability in wheat grown under rice-wheat systems, where delayed sowing is common (14). Broader analyses across Indian wheat-growing regions similarly identify terminal heat episodes as a major driver of yield losses and increased production risk in the Indo-Gangetic Plains (5). Physiological evidence also suggests that genotypic variation in tolerance to combined heat and water stress is closely linked to differences in phenological adjustment, assimilate partitioning and hormonal regulation during critical growth phases (15). Such relationships provide a strong rationale for using stress indices and multivariate analytical approaches to identify germplasm capable of maintaining stable performance under concurrent stress conditions.

Equally important is identifying germplasm capable of maintaining productivity under these constraints. To address this need, six contrasting wheat genotypes were selected to represent both practical cultivation relevance and breeding potential. IC-252874 is a known heat-tolerant germplasm line; HD 2967 and PBW 723 are widely cultivated, high-yielding varieties commonly grown in the Indo-Gangetic Plains; GIZA 168 represents an internationally adapted cultivar; and DH5-167 and DH5-164 are doubled haploid lines derived from a heat-tolerant × elite cultivar cross. Evaluating these contrasting genetic backgrounds under terminal heat and restricted irrigation provides an opportunity to identify adaptive traits critical for developing climate-resilient wheat in the IGP. Therefore, the experiment was conducted at Dr Rajendra Prasad Central Agricultural University, Bihar, under three contrasting conditions: (i) normal sowing with full irrigation, (ii) late sowing with full irrigation (terminal heat stress) and (iii) normal sowing with restricted irrigation (single irrigation at 45 DAS). It was hypothesized that genetic variation among these genotypes would result in distinct morphological, phenological and yield responses under stress, providing insights for breeding climate-resilient wheat in the IGP.

Materials and Methods

Experimental site and climate

A field experiment was conducted during the rabi season of 2022–2023 at the research farm of Dr. Rajendra Prasad Central Agricultural University (RPCAU), Pusa, Bihar (25°57′08″ N, 85°40′ 13″ E), located in the eastern Indo-Gangetic Plains. The site experiences a subtropical climate characterized by cool winters and moderate relative humidity, typical of major wheat-growing environments in the Indo-Gangetic Plains. The experimental soil is calcareous alluvial in nature, with a neutral to slightly alkaline pH and is representative of the dominant alluvial soils of the region. Daily environmental data, including maximum and minimum temperatures, maximum and minimum relative humidity and rainfall, were recorded throughout the crop growth period. Weekly patterns of temperature, relative humidity and rainfall during the experimental season are presented in Fig. 1A-1B.

Plant material

Six wheat (*Triticum aestivum* L.) genotypes were evaluated. IC-252874 is a heat-tolerant germplasm line. HD 2967 and PBW 723 are high-yielding, widely cultivated varieties in South Asia.

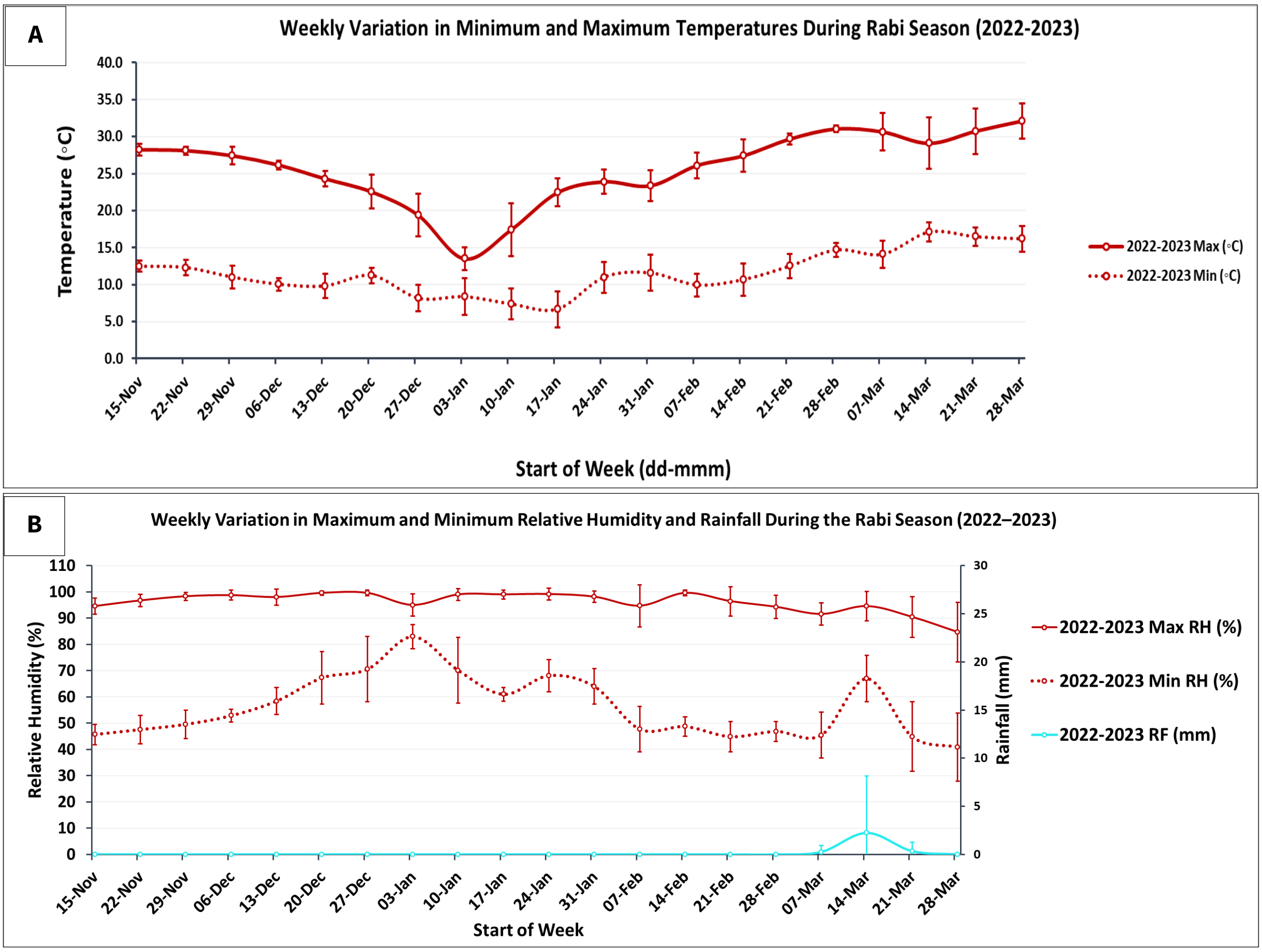


Fig. 1. Weekly weather variation during the Rabi season (2022–2023). **A.** Weekly variation in minimum and maximum temperatures, **B.** Weekly relative humidity (RH) and rainfall (RF); maximum and minimum RH are based on morning and evening observations. Data were recorded daily and averaged weekly (7 days means ± SD). Each point represents the mean for the week starting on the indicated date.

GIZA 168 is an Egyptian variety and DH5-167 and DH5-164 are doubled haploid lines developed from the cross PBW 343 × IC-252874.

Experimental design and treatments

The experiment was conducted in a randomised block design (RBD) with three replications, accommodating all genotypes within each block. Each plot consisted of four rows, each 2 m in length, with an inter-row spacing of 20 cm and an intra-row spacing of approximately 3.5 cm. A 50 cm gap was maintained between adjacent plots to minimize border effects. Three treatments were imposed to simulate abiotic stress conditions. Normal sown (NS) consisted of timely sowing on 15 November with five irrigations scheduled at critical growth stages: crown root initiation, tillering, jointing, booting and grain filling. Late sown (LS) to induce heat stress involved sowing on 15 December with the same irrigation schedule as NS, thereby exposing the crop to elevated temperatures during the reproductive phase. Restricted irrigation (RI) to simulate drought stress involved timely sowing on 15 November with only a single irrigation applied at 45 days after sowing (DAS). No significant rainfall (<5 mm) occurred during the active crop period; a late-March event occurred post-harvest and thus did not influence measured parameters.

Trait measurement

Seven traits were recorded: plant height (PH, cm), spike length (SL, cm), peduncle length (PL, cm), days to 50 % heading (DTH), days to 50 % flowering (DTF), days to maturity (DTM) and grain number per main spike (GPS). Plant height was measured from the soil surface to the tip of the spike, excluding awns; spike length from the base of the spike to the tip, excluding awns and peduncle length from the uppermost node to the base of the main spike. Morphological traits (PH, SL, PL) and the yield trait (GPS) on the main spike were measured from the main spike of five randomly selected plants per replication (15 plants per genotype per treatment). Phenological traits (DTH, DTF, DTM) were recorded at the plot level based on visual observations following the Zadoks growth scale. Days to heading and days to flowering were noted when approximately 50 % of plants in a plot reached the respective developmental stage. Days to maturity were recorded at physiological maturity, determined by grain hardening and complete loss of green colour from the spikes.

Data analysis

Data were analysed using R version 4.5.1 (Windows) with the doebioresearch package (version 0.1.0). A two-factor analysis of variance (ANOVA) was performed under the randomised block design framework, considering genotype and treatment as fixed effects. Both main effects and the genotype × treatment interaction were tested to assess differential responses to stress. Means were separated using the least significant difference (LSD) test at $p < 0.05$. Heat Susceptibility Index (HSI) and Drought Susceptibility Index (DSI) were calculated for each trait following the method described in Equation 1 (16).

$$SI = 1 - (Y_s/Y_p) / 1 - (\bar{y}_s/\bar{y}_p) \qquad \text{(Eqn. 1)}$$

Where Y_s and Y_p are the mean values of a genotype under stress (late sown for heat, restricted irrigation for drought) and normal sown (control) conditions, respectively, while $\bar{y}_s$ and $\bar{y}_p$ denote the corresponding means across all genotypes. Genotypes were classified as tolerant ($SI < 0.5$), moderately tolerant (0.5–1.0), or susceptible ($SI > 1.0$) based on their HSI and DSI values.

Pairwise correlations and trait distributions were visualised using the GGally package (version 2.3.0) in R, employing the *ggpairs* function. Scatterplots, density distributions and Pearson correlation coefficients were generated for all phenotypic traits under normal sown (NS), late sown (LS) and restricted irrigation (RI) conditions. Correlation coefficients were computed separately for each treatment as well as across the overall dataset. Replication-level data were used rather than trait means, thereby capturing within-treatment variability in both correlations and trait distributions.

Principal component analysis (PCA) was conducted using the FactoMineR package (version 2.12) in R to explore the multivariate structure and trait contributions across treatments. The dataset comprised 18 observations from six genotypes under three treatments (NS, LS, RI), using the mean values of seven traits (PH, SL, PL, DTH, DTF, DTM, GPS) per genotype-treatment combination. All traits were centred and scaled using the formula (value - mean) / standard deviation to ensure equal contribution regardless of original scale. The factoextra package (version 1.0.7) was used to generate biplots, visualize genotype-treatment associations and display eigenvalue distributions and variable contributions. Principal components with eigenvalues greater than one were retained based on the Kaiser criterion.

To explore trait variation patterns across genotypes and treatments, a heatmap was generated using standardised mean values of seven traits for each genotype–treatment combination. Values were scaled by centring and dividing by the standard deviation to ensure comparability across traits. Hierarchical clustering was applied to both traits and genotype–treatment combinations using Euclidean distance and complete linkage. This enabled identification of co-varying traits and similarities among genotype–treatment responses. The heatmap was constructed using the pheatmap package (version 1.0.13) in R (version 4.5.0) within the RStudio environment, using a purple-red-yellow gradient representing relative trait performance.

Results and Discussion

G × E interactions

A combined analysis of variance (ANOVA) revealed significant effects of genotypes, treatments and genotype × treatment interactions for most traits across environments (Table 1), indicating differential responses of wheat genotypes to terminal heat and restricted irrigation. Genotypic effects were strongest for phenological traits (DTH, DTF, DTM, GPS), while treatment effects were highly significant for all traits, highlighting the dominant influence of environmental conditions on trait expression under stress. The robustness of the model was supported by high coefficients of determination ($R^2 = 0.862–0.993$), non-significant replication effects, low residual variance and acceptable coefficients of variation, confirming the reliability of the experimental data. Such strong environmental control over trait expression is characteristic of wheat grown under combined heat and water stress conditions (15, 17, 18).

To further explore the basis of the ANOVA results, genotype-specific responses across treatments were examined (Table 2). Significant genotype × treatment interactions were detected for all traits except PL, which showed no meaningful interaction. Although PL values are presented to illustrate treatment-induced variation in peduncle elongation, the absence of a significant interaction indicates that these differences primarily reflect a common treatment effect

Table 1. ANOVA summary for six traits showing mean sum of squares (MSS) values

Source of Variation	DF	PH	SL	PL	DTH	DTF	DTM	GPS
Replication	2	20.15^{ns}	1.389^{ns}	8.15^{ns}	0.06^{ns}	2.46^{ns}	1.19^{ns}	18.45^{ns}
Genotype (G)	5	90.46^{**}	2.377^{*}	21.74^{ns}	33.60^{***}	38.91^{***}	35.54^{***}	412.10^{***}
Treatment (T)	2	1089.63^{***}	67.60^{***}	1813.56^{***}	792.17^{***}	962.24^{***}	1609.24^{***}	1077.72^{***}
G × T	10	98.21^{***}	3.206^{**}	7.71^{ns}	19.77^{***}	18.69^{***}	8.93^{***}	70.78^{***}
Error	34	17.02	0.855	10.82	0.64	1.64	0.75	8.78
R^2		0.863	0.862	0.912	0.989	0.976	0.993	0.943
CV (%)		4.80	6.54	8.77	1.05	1.56	0.76	5.78

Note: PH = Plant height; SL = Spike length; PL = Peduncle length; DTH = Days to 50 % heading; DTF = Days to 50 % flowering; DTM = Days to maturity; GPS = Grains per spike; DF = Degrees of freedom; CV = Coefficient of variation; R^2 = Coefficient of determination; ns = non-significant; *, ** and *** indicate significance at $p < 0.05$, $p < 0.01$ and $p < 0.001$, respectively.

Table 2. Genotype × treatment interaction means and grouping based on LSD at 5 %

Genotype: Treatment	PH (cm)	SL (cm)	PL (cm)	DTH (days)	DTF (days)	DTM (days)	GPS
IC-252874 : NS	81.8^{fghi}	11.8^{h}	34.6	78^{ef}	84^{fg}	115^{e}	66^{a}
IC-252874 : LS	71.7^{k}	13.3^{efgh}	30.6	69^{i}	74^{j}	103^{g}	62^{a}
IC-252874 : RI	89.3^{cde}	17.1^{ab}	50.0	84^{a}	90^{a}	120^{c}	61^{a}
HD 2967 : NS	89.3^{cde}	13.1^{efgh}	33.0	76^{h}	85^{efg}	117^{d}	60^{b}
HD 2967 : LS	79.7^{ghij}	13.7^{defg}	30.4	69^{i}	74^{j}	102^{h}	45^{de}
HD 2967 : RI	92.9^{cd}	16.0^{bc}	49.2	82^{b}	88^{abc}	118^{d}	52^{c}
PBW 723 : NS	83.5^{efghi}	12.1^{gh}	30.4	77^{gh}	84^{gh}	117^{d}	46^{d}
PBW 723 : LS	77.7^{hijk}	14.1^{def}	31.2	67^{j}	72^{k}	102^{h}	35^{f}
PBW 723 : RI	87.2^{def}	15.8^{bc}	44.9	80^{c}	86^{cdef}	119^{c}	45^{de}
DH5-167 : NS	74.9^{jk}	14.5^{cde}	31.5	80^{cd}	85^{defg}	123^{a}	63^{a}
DH5-167 : LS	89.1^{cde}	12.3^{gh}	28.3	77^{fg}	82^{h}	114^{e}	45^{de}
DH5-167 : RI	100.4^{ab}	18.2^{a}	48.2	82^{b}	87^{bcd}	118^{d}	44^{de}
GIZA 168 : NS	84.3^{efgh}	12.9^{fgh}	34.7	79^{de}	79^{i}	116^{e}	64^{a}
GIZA 168 : LS	77.2^{ijk}	12.3^{gh}	30.8	65^{k}	70^{k}	103^{g}	40^{e}
GIZA 168 : RI	102.8^{a}	15.1^{cd}	53.5	80^{c}	87^{cde}	121^{c}	46^{d}
DH5-164 : NS	86.1^{defg}	12.1^{h}	34.1	80^{c}	86^{cdef}	120^{c}	61^{a}
DH5-164 : LS	82.8^{efghi}	14.1^{def}	31.6	67^{j}	72^{k}	101^{h}	45^{d}
DH5-164 : RI	95.1^{bc}	16.0^{bc}	48.2	82^{b}	89^{ab}	122^{c}	42^{de}
Mean ± SEm	85.9 ± 2.4	14.1 ± 0.5	37.5 ± 1.9	76 ± 1	82 ± 1	114 ± 1	51± 2
LSD (5 %)	6.9	1.5	5.5	1	2	1	5

PH = Plant height; SL = Spike length; PL = Peduncle length; DTH = Days to 50 % heading; DTF = Days to 50 % flowering; DTM = Days to maturity; GPS = Grains per spike; NS = Normal sown; LS = Late sown; RI = Restricted irrigation; SEm = Standard error of mean; LSD = Least significant difference (5 %). Different superscript letters within a column indicate significant differences at $p < 0.05$.

rather than genotype-specific responses. Such stem plasticity in wheat, where peduncle length responds strongly to environmental conditions rather than genetic differentiation, has been documented under contrasting water availability environments (19).

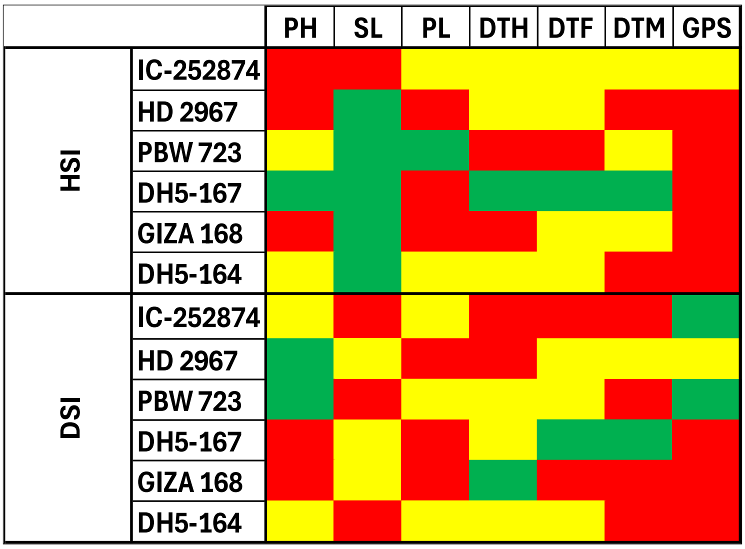
PH generally increased under RI, exceeding 100 cm in genotypes such as GIZA 168 and DH5-167, whereas late sowing reduced plant height to approximately 70 cm in IC-252874, indicating strong environmental modulation of vegetative growth. Similar increases in PH under regulated irrigation have been reported in wheat and commonly attributed to compensatory stem elongation following rewatering (10, 20, 21). SL also tended to increase under RI, likely reflecting improved assimilate partitioning and hormonal regulation during reproductive development. Rewatering after drought is known to restore ABA–cytokinin balance, thereby supporting spike growth and fertility (15). In contrast, LS consistently reduced spike growth, likely due to limited assimilate availability and shortened developmental duration under brief heat episodes (14, 22). Although PL did not exhibit a significant genotype × treatment interaction, its consistent increase under RI across genotypes indicates a common treatment-driven response rather than genotype-specific divergence.

Phenological development was accelerated under LS, with reductions in DTH, DTF and DTM, whereas RI delayed maturity relative to both LS and NS, extending the grain-filling period up to 120–123 days. Accelerated phenology under late sowing reflects the strong influence of elevated temperatures on developmental rates, whereby rapid thermal time accumulation initiates early anthesis and forces maturity (5). In contrast, restricted irrigation prolonged maturity and improved water use efficiency by allowing continued assimilate supply during reproductive development, consistent with responses reported under regulated irrigation regimes (10, 20, 21). Brief heat episodes associated with late sowing further accelerated senescence, thereby constraining grain filling and contributing to yield reduction (14, 22).

GPS declined under both stress treatments, with LS causing a more pronounced reduction than restricted irrigation. Under late sowing, sensitive genotypes showed a sharp decline in grains per spike to approximately 35–45 grains, whereas IC-252874 maintained around 60 grains per spike under both late sowing and restricted irrigation, indicating greater reproductive resilience. This differential response suggests that moderate water availability can partially buffer reproductive failure by supporting post-stress recovery processes. Reduced grains per spike under late sowing is consistent with the detrimental effects of brief heat stress on pollen viability, fertilization and early grain development (22). Hormonal adjustments during rewatering, particularly reduced abscisic acid levels and sustained cytokinin activity, may further contribute to stabilising grain set under restricted irrigation (15). Similar sensitivity of reproductive processes to elevated temperature during flowering has been widely reported in wheat, underscoring grains per spike as a key indicator of heat tolerance at the reproductive stage (23).

Stress susceptibility index (SSI)

While ANOVA and mean comparisons highlighted the overall treatment effects and genotype-specific responses, visualising these patterns across all traits and stress conditions provides a clearer perspective on genotype tolerance. Stress susceptibility was examined using the heat susceptibility index (HSI) for late-sown



		PH	SL	PL	DTH	DTF	DTM	GPS
HSI	IC-252874	🟥	🟥	🟨	🟨	🟨	🟨	🟨
	HD 2967	🟥	🟩	🟥	🟨	🟨	🟥	🟥
	PBW 723	🟨	🟩	🟩	🟥	🟥	🟨	🟥
	DH5-167	🟩	🟩	🟥	🟩	🟩	🟩	🟥
	GIZA 168	🟥	🟩	🟥	🟥	🟨	🟨	🟥
	DH5-164	🟨	🟩	🟨	🟨	🟨	🟥	🟥
DSI	IC-252874	🟨	🟥	🟨	🟥	🟥	🟥	🟩
	HD 2967	🟩	🟨	🟥	🟥	🟨	🟨	🟨
	PBW 723	🟩	🟥	🟨	🟨	🟨	🟥	🟩
	DH5-167	🟥	🟨	🟥	🟨	🟩	🟩	🟥
	GIZA 168	🟥	🟨	🟥	🟩	🟥	🟥	🟥
	DH5-164	🟨	🟥	🟨	🟨	🟨	🟥	🟥

Fig. 2. Classification of wheat genotypes for heat and drought stress tolerance using susceptibility indices relative to normal sown controls. Heatmap of stress tolerance in six wheat genotypes across seven traits, based on heat susceptibility index (HSI) and drought susceptibility index (DSI) relative to normal sown (NS) controls. HSI compares late sown (LS, heat stress) with NS and DSI compares restricted irrigation (RI, drought stress) with NS. Red indicates susceptibility (>1), yellow moderate tolerance (0.5–1) and green high tolerance (<0.5), enabling rapid evaluation of genotypic performance under heat and drought.

conditions and the drought susceptibility index (DSI) for restricted irrigation. The resulting heatmap revealed distinct genotype responses across morphological, phenological and yield traits (Fig. 2). For morphological traits (PH, SL, PL), susceptibility under LS (HSI) was most pronounced in IC-252874, HD 2967 and GIZA 168, whereas PBW 723 and DH5-167 were notably tolerant. For SL under LS, all genotypes except IC-252874 were grouped as tolerant. Under RI (DSI), HD 2967 and PBW 723 were tolerant to PH, while most genotypes for SL and PL ranged from moderately tolerant to susceptible.

For phenological traits (DTH, DTF, DTM), stress responses were generally moderate. DH5-167 exhibited consistent tolerance under both LS and RI, whereas IC-252874 was moderately tolerant under LS but susceptible under RI. For the yield trait (GPS), most genotypes were highly susceptible under heat stress, except IC-252874, which was moderately tolerant. Under drought stress, IC-252874 and PBW 723 showed tolerance, HD 2967 was moderately tolerant and the remaining genotypes were susceptible. Overall, DH5-167 emerged as the most tolerant across multiple traits under both stresses, particularly for morphological and phenological attributes. However, it did not retain this advantage for yield, clustering with DH5-164 and GIZA 168 as the most susceptible. These results highlight the complexity of stress responses and the importance of trait-group–based selection for identifying robust genotypes. Abiotic stress can readily disrupt assimilate supply during grain filling, explaining why genotypes stable for vegetative traits (e.g., DH5-167) may still fail to maintain yield, underscoring the challenge of achieving both resilience and yield stability (24).

Correlation coefficient analysis

Overall correlation patterns based on pooled data revealed strong integration among phenological traits and coordinated relationships between structural and developmental attributes, indicating tight coupling of growth and timing across environments (Fig. 3). The strongest association occurred between DTF and DTH (r = 0.953***), reflecting close synchrony between these developmental stages. Such tight coordination among phenological phases suggests that temperature increases can compress successive stages of development, thereby amplifying stress effects and limiting phenological plasticity under adverse conditions (5). Structural traits also showed strong interrelationships, with peduncle length positively correlated with plant height (r = 0.747***) and spike length (r = 0.669***). These positive associations of peduncle length with both plant height and spike length are consistent with previous observations in wheat and indicate coordinated architectural development of stem and spike components (25). Such architectural coordination likely reflects shared assimilate pathways and common growth regulation mechanisms, which may become disrupted under environmental stress conditions.

Phenological traits showed modest but significant associations with GPS, with DTM exhibiting the strongest relationship (r = 0.375**), indicating that longer developmental duration can support spike fertility. A previous study on three wheat genotypes reported stronger correlations between phenological traits and total grain yield, highlighting phenological timing as a key determinant of reproductive performance (26). The comparatively weaker associations observed here likely reflect the inclusion of a broader set of six genotypes, contrasting stress treatments (LS heat and RI drought) and the focus on GPS rather than total yield. Vegetative growth was also closely coordinated with phenological progression, with taller genotypes generally exhibiting longer vegetative phases, indicating tight coupling between growth dynamics and developmental timing**.** These findings suggest that extended phenology enhances reproductive success under favourable conditions but that this advantage is moderated under abiotic stress due to limitations in source–sink balance.

Treatment-wise correlation analysis showed that the strength and direction of trait associations varied markedly among NS, LS and RI, demonstrating that environmental stress reshapes trait coordination and reveals genotype × environment interactions (Fig. 3). Trait-specific patterns further varied with treatment, as evident from the colour-coded scatterplots and density distributions (Fig. 3). The association between PH and DTH was significant only under LS (r = 0.574*), indicating that taller plants tend to head earlier under heat stress. In contrast, a significant correlation between PH and PL emerged only under RI (r = 0.505*),

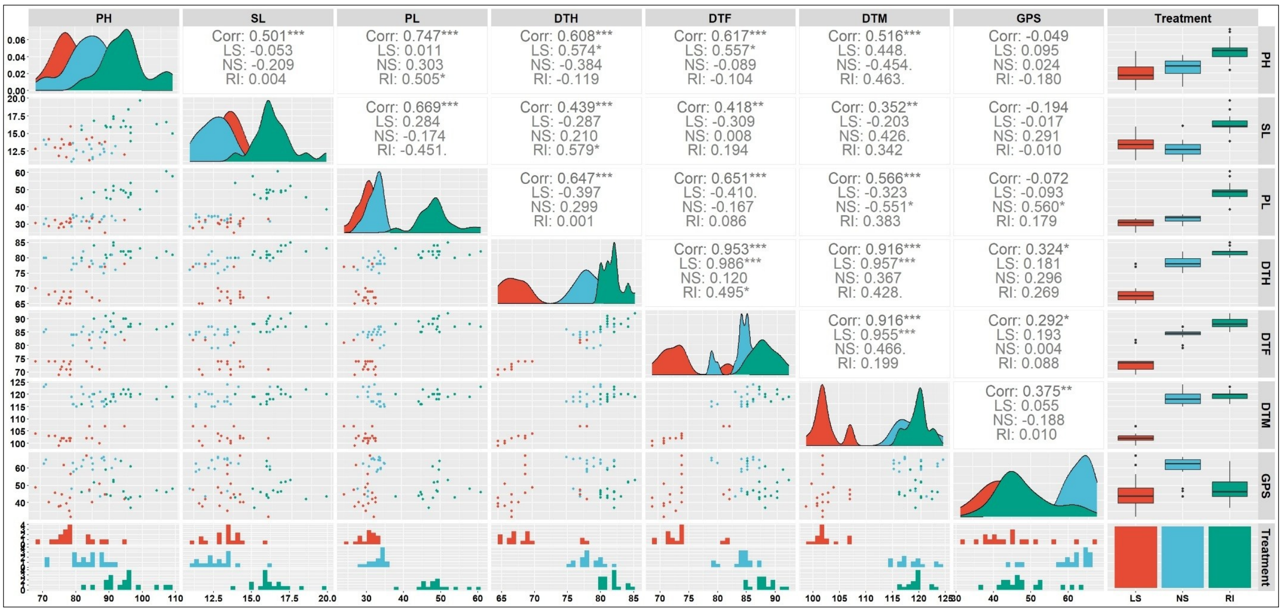


Fig. 3. Pairwise correlation and trait distribution matrix across treatments. Scatterplots, correlation coefficients and density plots are shown for traits under late sown (LS), normal sown (NS) and restricted irrigation (RI). Diagonal panels show trait distributions; off-diagonal plots depict trait associations by treatment. Correlation coefficients with significance (*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$) are reported separately for LS, NS and RI. Boxplots on the right compare trait values across treatments. LS, NS and RI are represented by red, blue and green, respectively.

suggesting altered coordination of vegetative growth under water limitation. These stress-specific relationships indicate that environmental constraints reorganise trait dependencies, exposing conditional linkages that are not apparent under optimal growing conditions (17).

DTH and DTF exhibited exceptionally strong synchrony under LS (r = 0.986***), indicating pronounced compression of early reproductive development under heat stress. This stress-induced synchronisation reflects rapid thermal time accumulation, which accelerates successive phenological phases and limits developmental plasticity during the reproductive period (5). In contrast, phenological coordination was weaker under NS and RI conditions, underscoring that tight coupling of heading and flowering is a characteristic response to elevated temperature stress. Overall, stress conditions such as LS and RI altered both the strength and coordination of phenological trait relationships compared with NS, highlighting the dominant role of environmental stress in reshaping trait interactions.

Distribution plots further illustrate treatment-dependent variation in trait expression (Fig. 3). GPS exhibited greater variability and a higher frequency of outliers under LS, reflecting the heightened sensitivity of reproductive traits to heat stress. Under RI, DTM showed a slightly bimodal distribution, indicating heterogeneous genotypic responses to water limitation. Boxplots revealed clear treatment effects, with PH reaching its highest values under RI, while GPS displayed the widest dispersion under late sowing. Together, these patterns indicate that both vegetative growth and yield components respond strongly to environmental conditions, reinforcing the influence of genotype × environment interactions on phenotypic expression. The correlation and distribution analyses collectively highlight coordinated relationships among developmental and morphological traits that are differentially modulated by environmental stress, underscoring the importance of evaluating genotypes under realistic stress scenarios to capture biologically meaningful variation relevant for stress-resilient breeding.

Principal component analysis

Principal component analysis (PCA) was used to reduce data dimensionality by transforming correlated variables into a smaller set of principal components that capture most of the variation in the dataset (27). PCA was conducted for the six wheat genotypes under NS, LS and RI conditions. The first two principal components had eigenvalues greater than one (4.45 for PC1 and 1.60 for PC2) and together explained 86.38 % of the total variation, with PC1 and PC2 accounting for 63.59 % and 22.79 %, respectively. Eigenvalues declined sharply after the second component (Table 3), indicating diminishing contribution of subsequent components (28, 29). Each of the remaining components explained less than 8 % of the total variability and was therefore considered negligible and only the first two components were retained for further interpretation based on the Kaiser criterion.

The PCA biplot showed a clear separation of genotypes primarily according to treatment rather than genotype, underscoring the dominant influence of environmental stress on phenotypic expression (Fig. 4). Genotypes under LS clustered along the negative axis of PC1, corresponding to reduced values for GPS and accelerated phenology (DTH, DTF and DTM), reflecting consistent suppressive effects of heat stress. In contrast, genotypes under RI were more widely distributed along the positive PC1 axis and the negative PC2 axis, indicating heterogeneous phenological and growth responses likely driven by genotype-specific tolerance to water limitation. Genotypes grown under NS clustered closer to the positive PC2 axis and near the GPS vector, indicating better spike fertility and more stable performance under non-stress conditions.

PC1 primarily captured variation associated with phenological and architectural traits, with high contributions from DTF (20.08 %), DTH (19.90 %), DTM (17.64 %), PL (16.74 %) and PH (15.05 %), while PC2 was dominated by GPS (49.26 %) and SL (17.88 %), reflecting differences in reproductive efficiency and spike morphology (Table 3). Similar separation of structural and reproductive traits along major principal components has been reported in cereal crops (30, 31). The clustering patterns indicate that treatment effects exerted a stronger influence on phenotypic variability than genotypic differences alone, consistent with

Table 3. Eigenvalues, percentage of variance and cumulative percentage of variance explained by all seven principal components (PCs) for the studied wheat traits

PC	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Eigen value	4.45	1.60	0.54	0.25	0.10	0.04	0.03
Percentage of variance	63.59	22.79	7.67	3.58	1.40	0.56	0.41
Cumulative percentage of variance	63.59	86.38	94.05	97.63	99.03	99.59	100.00
Percentage contribution of traits to principal components							
PC	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**
PH	15.05	7.77	16.96	37.68	20.42	-	-
SL	10.02	17.88	42.40	9.13	17.52	-	-
PL	16.74	8.23	7.25	12.18	55.20	-	-
DTH	19.90	5.18	0.27	3.59	1.45	-	-
DTF	20.08	3.67	2.15	3.89	0.01	-	-
DTM	17.64	8.02	6.28	12.28	2.97	-	-
GPS	0.57	49.26	24.68	21.25	2.45	-	-

PH = Plant height; SL = Spike length; PL = Peduncle length; DTH = Days to 50 % heading; DTF = Days to 50 % flowering; DTM = Days to maturity; GPS = Grains per spike.

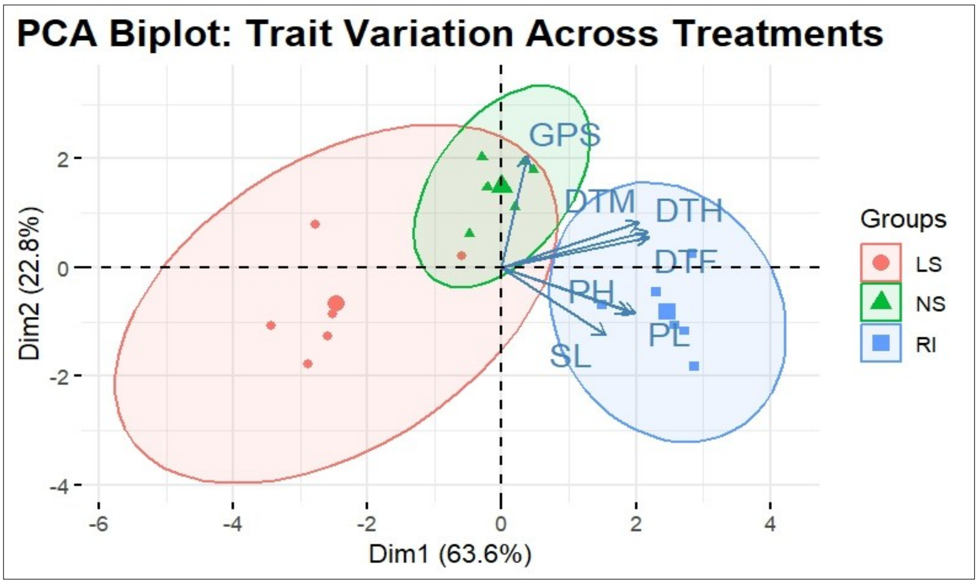


Fig. 4. Principal component analysis (PCA) biplot showing trait distribution and genotype clustering under different treatments. Dim1 and Dim2 represent the first two principal components. Treatments: LS = Late sown, NS = Normal-sown, RI = Restricted irrigation.

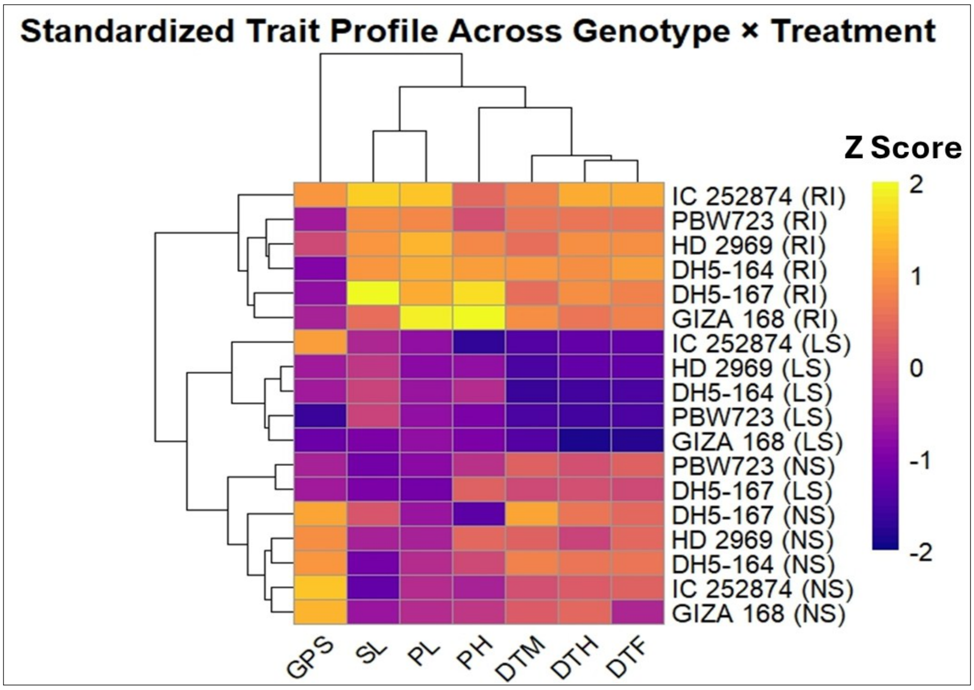


Fig. 5. Standardised trait profile heatmap across wheat genotype × treatment combinations. Heatmap shows standardised trait values (Z scores, ~ -2 to + 2) for genotypes under normal sown (NS), late sown (LS) and restricted irrigation (RI). Traits (vertical axis) and genotype-treatment combinations (horizontal axis) are clustered hierarchically. Yellow–red denotes higher Z scores and blue–purple denotes lower values, indicating relative trait expression.

previous reports highlighting the predominant role of environmental factors and genotype × environment interactions in shaping wheat performance (32, 33). The tight grouping of RI genotypes reflects the uniform and suppressive impact of water stress, whereas the broader dispersion of genotypes under LS suggests diverse heat response strategies, potentially mediated by genotype-specific physiological mechanisms.

Hierarchical clustering heatmap of standardised trait profiles

The PCA results, highlighting major trait contributions and treatment-driven separation of genotypes, were further complemented by hierarchical clustering of standardized trait profiles across genotype × treatment combinations (Fig. 5). The heatmap revealed clear treatment-driven groupings, with most genotypes subjected to RI clustering together and characterised by elevated PH and PL. Late-sown genotypes formed a distinct cluster marked by generally reduced trait values and accelerated phenological development, whereas NS entries clustered separately, reflecting comparatively stable trait expression under non-stress conditions. These treatment-based patterns were largely consistent across genotypes, except for DH5-167 under late sowing, which clustered with normal-sown entries rather than its late-sown counterparts. This deviation highlights genotype-specific buffering capacity within broad treatment effects and demonstrates the utility of hierarchical clustering in identifying both dominant environmental influences and atypical genotype responses.

Trait clustering further revealed biologically meaningful associations among measured traits. SL and PL were clustered together, indicating their coordinated regulation of spike architecture and assimilate transport. PH forms a separate branch, suggesting a more independent pattern of variation relative to spike -associated traits. The phenological traits (DTH, DTF and DTM) clustered tightly, reflecting their strong interdependence in controlling developmental timing, consistent with previous reports of close phenological co-regulation in wheat (34). In contrast, GPS formed a distinct cluster, underscoring its relative independence from phenological and architectural traits and highlighting its sensitivity to stress during reproductive development. Together, these clustering patterns emphasise that phenology-related traits exhibit strong coordinated responses, whereas architectural and yield-related traits display more differentiated and stress-dependent variation across genotypes and treatments. From a breeding perspective, the dominance of treatment effects over genotypic differences highlights the importance of environment-specific selection strategies. The strong clustering of genotypes by stress treatment indicates that performance rankings are not stable across environments, underscoring the need to evaluate breeding materials directly under target stress conditions. In particular, selection for late-sown heat tolerance or restricted irrigation adaptation should be conducted within the respective stress environments, rather than relying on performance under optimal conditions, to capture traits that confer resilience under realistic field scenarios.

Conclusion

Late sowing-induced heat stress and restricted irrigation-induced drought exerted distinct impacts on wheat performance. Heat stress accelerated phenology and sharply reduced grains per spike (GPS), whereas drought delayed maturity but still penalised yield. Genotype DH5-167 exhibited strong vegetative resilience under combined stress but failed to sustain reproductive performance, indicating a trade-off between growth and yield stability. In contrast, IC 252874 maintained higher GPS despite moderate vegetative susceptibility. These findings emphasise the need to integrate traits that secure reproductive resilience under heat with those that prolong grain filling under drought, to enhance yield stability in stress-prone environments.

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Authors' contributions

RK conceived and designed the study, supervising and providing critical revisions. TM conceived and designed the study, conducted the experiments, analysed the data, drafted the manuscript, supervised and provided critical revisions. AM drafted the manuscript, supervising and providing critical revisions. All authors read and approved the final manuscript.

Compliance with ethical standards

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

Ethical issues: None

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the author used generative AI (ChatGPT) to improve the grammar, clarity and readability of the text. No data, results, or scientific content were generated by the tool. The author reviewed and edited all content and takes full responsibility for the accuracy and integrity of the manuscript.

References

1. Acevedo M, Zurn JD, Molero G, Singh P, He X, Aoun M, et al. The role of wheat in global food security. In: Agricultural development and sustainable intensification: technology and policy challenges in the face of climate change. 1st ed. New York: Routledge; 2018. p. 81–110. https://doi.org/10.4324/9780203733301-4
2. Zhang Q, Men X, Hui C, Ge F, Ouyang F. Wheat yield losses from pests and pathogens in China. Agric Ecosyst Environ. 2022;326:107821. https://doi.org/10.1016/j.agee.2021.107821
3. Luo X, Yang Y, Lin X, Xiao J. Deciphering spike architecture formation towards yield improvement in wheat. J Genet Genomics. 2023;50(11):835–45. https://doi.org/10.1016/j.jgg.2023.02.015
4. Mani M, Bandyopadhyay S, Chonabayashi S, Markandya A. South Asia's hotspots: the impact of temperature and precipitation changes on living standards. Washington DC: World Bank Publications; 2018. https://doi.org/10.1596/978-1-4648-1155-5

5. Dubey R, Pathak H, Chakrabarti B, Singh S, Gupta DK, Harit RC. Impact of terminal heat stress on wheat yield in India and options for adaptation. Agric Syst. 2020;181:102826. https://doi.org/10.1016/j.agsy.2020.102826
6. Zulfiqar U, Ahmad M, Valipour M, Ishfaq M, Maqsood MF, Iqbal R, et al. Evaluating optimum limited irrigation and integrated nutrient management strategies for wheat growth, yield and quality. Hydrology. 2023;10(3):56. https://doi.org/10.3390/hydrology10030056
7. Gupta DK, Bhatia A, Das TK, Singh P, Kumar A, Jain N, et al. Economic analysis of different greenhouse gas mitigation technologies in rice–wheat cropping system of the Indo-Gangetic plains. Curr Sci. 2016;110(5):867–74.
8. Mahmood N, Arshad M, Kächele H, Ma H, Ullah A, Müller K. Wheat yield response to input and socioeconomic factors under changing climate: evidence from rainfed environments of Pakistan. Sci Total Environ. 2019;688:1275–85. https://doi.org/10.1016/j.scitotenv.2019.06.266
9. Kumar V, Nameirakpam B, Murugesh T, Pragya P, Mishra A, Panigrahi S, et al. Comprehensive analysis of wheat starch synthase III revealed existence of two copies differentially expressed under heat stress. Cereal Res Commun. 2025;53(1):193–209. https://doi.org/10.1007/s42976-024-00553-z
10. Bao X, Liu X, Hou X, Yin B, Duan W, Wang Y, et al. Single irrigation at the four-leaf stage in the spring optimizes winter wheat water consumption characteristics and water use efficiency. Sci Rep. 2022;12(1):14257. https://doi.org/10.1038/s41598-022-18446-8
11. Si Z, Qin A, Liang Y, Duan A, Gao Y. A review on regulation of irrigation management on wheat physiology, grain yield and quality. Plants. 2023;12(4):692. https://doi.org/10.3390/plants12040692
12. Wang Z, Zhang B, Li J, Lian S, Zhang J, Shi S. Effects of deficit-regulated irrigation on root-growth dynamics and water-use efficiency of winter wheat in a semi-arid area. Water. 2024;16(18):2678. https://doi.org/10.3390/w16182678
13. Shoukat Hafiza B, Ishaque W, Ahmad S, Ali S, El-Sheikh MA. Optimizing wheat productivity and water productivity through deficit irrigation strategies in semi-arid environments. Sci Rep. 2025;15(1):20630. https://doi.org/10.1038/s41598-025-04618-9
14. Sattar A, Nanda G, Singh G, Jha RK, Bal SK. Responses of phenology, yield attributes and yield of wheat varieties under different sowing times in Indo-Gangetic plains. Front Plant Sci. 2023;14:1224334. https://doi.org/10.3389/fpls.2023.1224334
15. Duvnjak J, Lončarić A, Brkljačić L, Šamec D, Šarčević H, Salopek-Sondi B, et al. Morpho-physiological and hormonal response of winter wheat varieties to drought stress at stem elongation and anthesis stages. Plants. 2023;12(3):418. https://doi.org/10.3390/plants12030418
16. Fischer RA, Maurer R. Drought resistance in spring wheat cultivars. I. Grain yield responses. Aust J Agric Res. 1978;29(5):897–912. https://doi.org/10.1071/AR9780897
17. Sareen S, Budhlakoti N, Mishra KK, Bharad S, Potdukhe NR, Tyagi BS, et al. Resilience to terminal drought, heat and their combination stress in wheat genotypes. Agronomy. 2023;13(3):891. https://doi.org/10.3390/agronomy13030891
18. Vaezi B, Arzani A, Roberts TH. How do drought, heat stress and their combination impact stem reserve mobilization in wheat genotypes? Agronomy. 2024;14(8):1867. https://doi.org/10.3390/agronomy14081867
19. Wang T, Su N, Lu J, Zhang R, Sun X, Weining S. Genome-wide association studies of peduncle length in wheat under rain-fed and irrigating field conditions. J Plant Physiol. 2023;280:153854. https://doi.org/10.1016/j.jplph.2022.153854
20. Mu Q, Cai H, Sun S, Wen S, Xu J, Dong M, et al. The physiological response of winter wheat under short-term drought conditions and the sensitivity of different indices to soil water changes. Agric Water Manag. 2021;243:106475. https://doi.org/10.1016/j.agwat.2020.106475
21. Mu Q, Xu J, Yu M, Guo Z, Dong M, Cao Y, et al. Physiological response of winter wheat (Triticum aestivum L.) during vegetative growth to gradual, persistent and intermittent drought. Agric Water Manag. 2022;274:107911. https://doi.org/10.1016/j.agwat.2022.107911
22. Xu J, Lowe C, Hernandez-Leon SG, Dreisigacker S, Reynolds MP, Valenzuela-Soto EM, et al. The effects of brief heat during early booting on reproductive, developmental and chlorophyll physiological performance in common wheat (Triticum aestivum L.). Front Plant Sci. 2022;13:886541. https://doi.org/10.3389/fpls.2022.886541
23. Prasad PVV, Pisipati SR, Momčilović I, Ristic Z. Independent and combined effects of high temperature and drought stress during grain filling on plant yield and chloroplast EF-Tu expression in spring wheat. J Agron Crop Sci. 2011;197(6):430–41.
24. Kumar H, Chugh V, Kumar M, Gupta V, Prasad S, Kumar S, et al. Investigating the impact of terminal heat stress on contrasting wheat cultivars: a comprehensive analysis of phenological, physiological and biochemical traits. Front Plant Sci. 2023;14:1189005. https://doi.org/10.3389/fpls.2023.1189005
25. Ghaffar Y, Ashraf W, Akhtar N, Zeshan MA, Ghani MU, Fatima S, et al. Estimation of statistical parameters in candidate wheat genotypes for yield-related traits. J King Saud Univ Sci. 2022;34(8):102364. https://doi.org/10.1016/j.jksus.2022.102364
26. Semnaninejad H, Nourmohammadi G, Rameeh V, Cherati A. Correlation and path coefficient analyses of phenological traits, yield components and quality traits in wheat. Rev Bras Eng Agrícola Ambient. 2021;25(9):597–603. https://doi.org/10.1590/1807-1929/agriambi.v25n9p597-603
27. Birla D, Ramgiry SR. AMMI analysis to comprehend genotype-by-environment (G×E) interactions in rainfed grown soybean [*Glycine max* (L) Merrill]. Indian J Agric Res. 2015;49(1):39–45. http://doi.org/10.5958/0976-058X.2015.00005.0
28. Kaiser HF. The application of electronic computers to factor analysis. Educ Psychol Meas. 1960;20(1):141–51. https://doi.org/10.1177/001316446002000116
29. Jolliffe IT. Principal component analysis. In: Lovric M, editor. International encyclopedia of statistical science. Berlin, Heidelberg: Springer; 2011. p. 1094–6. https://doi.org/10.1007/b98835
30. Yano K, Morinaka Y, Wang F, Huang P, Takehara S, Hirai T, et al. GWAS with principal component analysis identifies a gene comprehensively controlling rice architecture. Proc Natl Acad Sci U S A. 2019;116(42):21262–7. https://doi.org/10.1073/pnas.1904964116
31. Verma A, Chauhan A, Pant A, Gupta P. Principal component analysis (PCA) of wheat genotypes concerning morphological responses to heat stress. J Adv Biol Biotechnol. 2025;28(2):443–53. https://doi.org/10.9734/jabb/2025/v28i22004
32. Yue H, Wang Y, Chen Z, Zhu J, Behera PP, Liu P, et al. Assessing the role of genotype by environment interaction of winter wheat cultivars using envirotyping techniques in North China. Front Plant Sci. 2025;16:1538661. https://doi.org/10.3389/fpls.2025.1538661
33. Sallam M, Ghazy A, Al-Doss A, Al-Ashkar I. Combining genetic and phenotypic analyses for detecting bread wheat genotypes of drought tolerance through multivariate analysis techniques. Life. 2024;14(2):183. https://doi.org/10.3390/life14020183
34. Rathod ST, Pole SP, Gawande SM. Correlation and path analysis for quality and yield contributing traits in wheat (*Triticum aestivum* L.). Int J Curr Microbiol Appl Sci. 2019;8(6):456–61. https://doi.org/10.20546/ijcmas.2019.806.051

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