

Seedling-stage Heat Stress Adaptation in Indian Dwarf Wheat (*Triticum sphaerococcum* Perc.): Implications for Wheat Improvement

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Abstract

Heat stress is a major limitation to wheat establishment and productivity, particularly under increasing global temperatures. Seventy *Triticum sphaerococcum* genotypes along with nine bread wheat checks were evaluated at the seedling stage for heat tolerance using physiological (root and shoot length, relative water content, membrane stability index, seed vigour) and biochemical (proline, total protein, nitrogen content) traits. Heat stress significantly affected growth, water relations, and metabolic stability; however, several TS lines, notably TS 70, TS 31, and TS 21, outperformed bread wheat checks, including C 306 and PBW 677. Correlation analyses identified root length, MSI, RWC, proline content, and seed vigour as key determinants of tolerance. K-means clustering effectively distinguished tolerant and sensitive genotypes. The results highlight the inherent adaptive potential of *T. sphaerococcum* and its utility as a genetic resource for breeding heat-resilient wheat. Elite TS lines identified in this study can serve as donor material in early-generation crossing programs aimed at developing cultivars capable of maintaining physiological stability and productivity under heat stress, contributing to climate-resilient wheat improvement.

Keywords: *Triticum sphaerococcum*, heat stress, proline, membrane stability, wheat breeding, seedling vigour

1. Introduction

Wheat (*Triticum aestivum* L.) is one of the most important cereal crops worldwide, contributing nearly 20% of the dietary calories and protein consumed by the global population (Shewry, 2009). India ranks second in global wheat production, emphasizing the critical role of wheat in national food security and agricultural sustainability (FAO, 2022). However, wheat productivity is increasingly threatened by abiotic stresses, particularly heat stress, which has emerged as a major constraint under changing climatic conditions. Recent terminal heat waves have already resulted in substantial yield losses in major wheat-growing regions, including northwestern India,

highlighting the vulnerability of current cultivars to temperature extremes.

Wheat is highly sensitive to elevated temperatures during key developmental stages such as anthesis and grain filling (Farooq *et al.*, 2011). Predictive models suggest that wheat yield declines by approximately 6% for every 1 °C increase above the optimum growing temperature (Asseng *et al.*, 2015). Global mean surface temperature has already increased by about 0.85 °C since the pre-industrial era and is projected to rise further during the twenty-first century, posing serious challenges to the sustainability of wheat production systems (Wheeler and Braun, 2013). These trends underscore the urgency of developing wheat



genotypes capable of maintaining physiological stability and productivity under heat stress.

Heat stress affects wheat growth and yield through multiple physiological and biochemical disruptions, including reduced photosynthetic efficiency, loss of cellular water balance, membrane destabilization, and excessive accumulation of reactive oxygen species (ROS) (Xu *et al.*, 2020; Sharma *et al.*, 2021). To counteract these effects, wheat plants activate a suite of adaptive mechanisms such as enhanced antioxidant enzyme activity, osmolyte accumulation (e.g., proline), and stabilization of cellular membranes. Consequently, physiological parameters including relative water content (RWC), membrane stability index (MSI), and seedling vigor, together with biochemical indicators such as antioxidant enzymes, have been widely employed as reliable screening tools for identifying heat-tolerant wheat genotypes (Blum 2011; Gupta *et al.*, 2020). Despite these advances, the genetic base for heat tolerance in modern bread wheat cultivars remains narrow, necessitating the exploration of alternative and under utilized genetic resources.

Land races represent valuable reservoirs of genetic diversity shaped by long-term natural and farmer-led selection under diverse environmental conditions (Zeven, 1998; Dwivedi *et al.*, 2016). Among these, *Triticum sphaerococcum* Percival, commonly referred to as Indian dwarf wheat, is an indigenous hexaploid wheat subspecies historically cultivated in the northwestern Indian subcontinent. Archaeological evidence suggests its early domestication in regions characterized by warm, drought-prone, and marginal soils, indicating inherent adaptation to environmental stresses (Lone *et al.*, 2014). The species is characterized by early flowering, short stature, spherical grains, and relatively high grain protein content, traits that reflect adaptation to stressful agro-ecological conditions (Howard and Howard 1910; Singh 1946).

Several distinctive morphological and adaptive traits of *T. sphaerococcum* have been linked to the pleiotropic *Sphaerococcum 1 (S1)* locus located on chromosome 3D, which influences plant architecture and has been associated with stress adaptation (Konzak 1977; Matsuoka 2011). Despite its potential value, *T. sphaerococcum* has remained largely under utilized in modern wheat breeding programs following the widespread adoption of high-yielding cultivars during the Green Revolution

(Peng *et al.*, 2011). As a result, systematic evaluations of its physiological and biochemical responses to heat stress remain limited.

Given its evolutionary background and historical cultivation under warm environments, *T. sphaerococcum* represents a promising but under explored genetic resource for improving heat stress tolerance in wheat. The present study was therefore undertaken to evaluate a diverse panel of *T. sphaerococcum* genotypes for their physiological and biochemical responses under controlled heat stress conditions. By assessing key traits related to water status, membrane stability, osmotic adjustment, antioxidant defense, and seedling vigor, this work aims to identify heat-tolerant genotypes and to generate trait-based insights that could facilitate the effective utilization of *T. sphaerococcum* in wheat improvement programs targeting climate resilience.

2. Materials and methods

2.1 Plant material and experimental site

The experiment was conducted at the Wheat Molecular Laboratory, Department of Plant Breeding and Genetics, Punjab Agricultural University (PAU), Ludhiana, India during 2022-2025. A total of 70 genotypes of *Triticum sphaerococcum* Percival were procured from the Indian Institute of Wheat and Barley Research (IIWBR), Karnal, and evaluated for heat stress tolerance. In addition, 9 bread wheat check cultivars with well-characterized responses to heat and salinity stress were included for comparative assessment. These included heat-tolerant (e.g. C 306), moderately tolerant (e.g. PBW 343, HD 3086), and sensitive checks (e.g. HD 2329, HD 2339).

2.2 Seedling growth conditions and heat stress treatment

Seeds of uniform size and without visible damage were surface sterilized using 0.1% mercuric chloride followed by thorough washing with distilled water. Seeds were subsequently treated with 70% ethanol for 1–2 min and rinsed again with distilled water. Seedlings were raised using the cigar roll method, with fifteen seeds per genotype placed on autoclaved moist germination paper and rolled vertically. Rolls were maintained in plastic containers with 6–8 cm of water at the base to ensure adequate moisture. After germination, seedlings were grown under two temperature regimes: control (25 ± 2 °C) and heat stress (40 °C), following established protocols for inducing heat



stress at the seedling stage (Iqbal *et al.*, 2021). Seedlings were exposed to the respective temperature treatments for 10 days, after which physiological and biochemical observations were recorded.

2.3 Growth and physiological traits

All seedling growth parameters were measured using standard procedures. Shoot and Root Length was measured from base to tip in cm after 10 days of emergence. Seedling Fresh and Dry Weight (SFW, SDW) was calculated after seedlings were weighed before and after drying at 65°C. Germination Percentage (GP) was calculated after 7 days using standard formula. Seedling Vigour Index (SVI) was calculated as:

$$\text{SVI} = \text{GP} \times \text{Seedling Length} / 100 \text{ (Abdul-Baki\& Anderson, 1973).}$$

Membrane Stability Index (MSI) was measured following heat-induced electrolyte leakage (Martineau *et al.*, 1979). Relative Water Content (RWC) was calculated using fresh, turgid, and dry weights (Turner, 1986).

2.4 Biochemical analyses

Free proline content was estimated from dried leaf tissue using the acid ninhydrin method described by Bates *et al.* (1973). Absorbance was measured at 520 nm, and proline concentration was calculated using a standard curve and expressed as $\mu\text{mol g}^{-1}$ dry weight.

Total nitrogen content was determined using the Kjeldahl method (Kjeldahl 1883). Dried and finely ground leaf samples were digested with concentrated sulfuric acid in the presence of a catalyst mixture, followed by distillation

and titration. Nitrogen content was expressed on a dry weight basis.

2.5 Calculation of heat tolerance index (HTI)

Heat Tolerance Index was calculated as per Fernandez (1992) on the basis of seedling dry weight of the genotypes under stressed and control environments.

2.6 Statistical analysis

The experiment was conducted using a completely randomized design with control and heat stress treatments. All measurements were performed with appropriate replication. Data were subjected to analysis of variance (ANOVA) and K-means clustering using R statistical software to test the significance of genotypic and treatment effects. Mean comparisons were performed at appropriate significance levels.

3. Results

3.1 Analysis of variance

Analysis of variance revealed *highly significant genotypic differences* ($p < 0.01$) among the 70 *Triticum sphaerococcum* genotypes for all ten morpho-physiological and biochemical traits evaluated under stress conditions (Table 1), indicating the presence of substantial genetic variability.

Among the traits, root length (RL) exhibited the highest F-value ($F = 126.24$), followed by proline content (PR) ($F = 67.86$) and seedling dry weight (SDW) ($F = 59.90$), reflecting strong genotypic control over root development, osmotic adjustment, and biomass accumulation under stress.

Table 1: Analysis of Variance (ANOVA) for all observed traits

| Trait | DF | MSS | F- Value | p- Value |
|-------|----|----------|----------|-----------|
| GP | 69 | 2907.384 | 3.97** | 1.03E-13 |
| MS | 69 | 1714.491 | 5.43** | 1.22E-19 |
| RWC | 69 | 3133.062 | 8.64** | 3.26E-30 |
| TP | 69 | 25.146 | 26.38** | 1.33E-61 |
| PR | 69 | 189.954 | 67.86** | 9.16E-92 |
| SL | 69 | 605.293 | 24.21** | 5.55E-59 |
| RL | 69 | 917.987 | 126.24** | 2.20E-112 |
| SFW | 69 | 27782.08 | 42.46** | 1.50E-76 |
| SDW | 69 | 363.731 | 59.9** | 1.12E-87 |
| SV | 69 | 29001558 | 28.34** | 8.18E-64 |

GP=Germination Percentage, MS=Membrane Stability, RWC=Relative Water Content, TP=Total Protein, PR=Free Proline Content, SL=Shoot Length, RL=Root Length, SFW= Seedling Fresh Weight, Seedling Dry Weight, SV=Seed Vigour, MSS=Mean Sum of Squares**=Significant at $\alpha=0.01$



Significant variation was also observed for seedling fresh weight (SFW) ($F = 42.46$), seed vigour (SV) ($F = 28.34$), total protein content (TP) ($F = 26.38$), and shoot length (SL) ($F = 24.21$). Relative water content (RWC) ($F = 8.64$) and membrane stability index (MSI) ($F = 5.43$) showed moderate but significant genotypic differences, highlighting variability in plant water status and membrane integrity under stress.

Although grain protein content (GPC) recorded the lowest F-value ($F = 3.97$), the variation remained statistically significant, indicating differential genotype

responses for quality traits under stress. Overall, the ANOVA results confirm the suitability of the evaluated traits for discriminating stress-responsive genotypes in *T. sphaerococcum*.

3.2 Correlation analysis

Pearson's correlation analysis revealed several significant associations among morpho-physiological traits of *Triticum sphaerococcum* genotypes under stress conditions (Fig. 1), indicating coordinated physiological and growth responses.

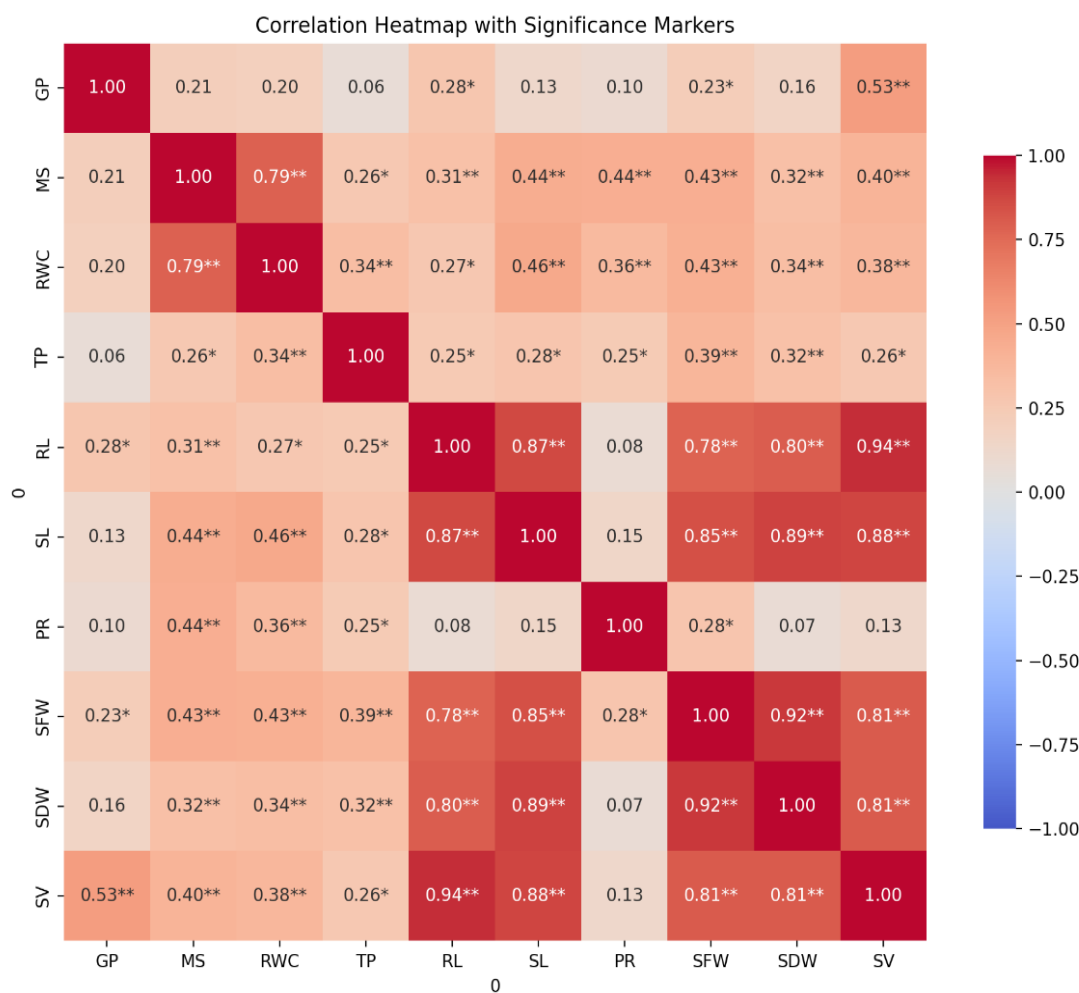


Fig. 1. Correlation matrix for all observed traits

Membrane stability index (MSI) showed a strong positive correlation with relative water content (RWC) ($r = 0.79$, $p < 0.01$) and a moderate positive association with seedling length (SL) ($r = 0.44$, $p < 0.01$). RWC was positively correlated with total protein content (TP) ($r = 0.34$, $p < 0.01$) and SL ($r = 0.46$, $p < 0.01$).

Root length (RL) exhibited highly significant positive correlations with SL ($r = 0.87$), seedling fresh weight (SFW) ($r = 0.78$), seedling dry weight (SDW) ($r = 0.80$), and seed vigour (SV) ($r = 0.94$) ($p < 0.01$). Similarly, SL was strongly correlated with SFW ($r = 0.85$), SDW ($r = 0.89$), and SV ($r = 0.88$) ($p < 0.01$).



Seed vigour (SV) showed strong positive associations with RL ($r = 0.94$), SL ($r = 0.88$), SFW ($r = 0.81$), and SDW ($r = 0.81$) ($p < 0.01$). Proline content (PR) was positively correlated with MSI ($r = 0.44$), RWC ($r = 0.36$) ($p < 0.01$), and TP ($r = 0.25$, $p < 0.05$), while showing weak or non-significant associations with growth-related traits.

In contrast, grain protein content (GPC) exhibited a significant negative correlation with SV ($r = -0.53$, $p < 0.01$) and RL ($r = -0.28$, $p < 0.05$). Additional moderate

positive correlations were observed between MSI and TP ($r = 0.26$, $p < 0.05$), TP and RWC ($r = 0.34$, $p < 0.01$), and TP and SFW ($r = 0.39$, $p < 0.01$).

3.3 K-means clustering on the basis HTI

K-means clustering based on Heat Tolerance Index (HTI) classified the *Triticum sphaerococcum* genotypes and bread wheat checks into *two distinct clusters*, representing contrasting heat stress responses (Table 2; Fig. 2).

Table 2: TS lines in various clusters as per K-means clustering

| Cluster | Genotype |
|--------------------------------|--|
| Cluster 0 (Heat intolerant) | TS 38, TS 32, TS 66, TS 15, TS 7, TS 55, TS 16, TS 24, TS 4, TS 6, TS 54, TS 50, TS 68, TS 19, TS 20, TS 8, TS 61, TS 46, TS 13, TS 37, TS 10, TS 43, TS 26, TS 57, TS 44, TS 36. |
| Cluster 1 (Heat tolerant) | TS 23, TS 17, TS 52, TS 12, TS 63, TS 53, TS 39, TS 62, TS 69, TS 34, TS 51, TS 27, TS 48, TS 33, TS 29, TS 11, TS 28, TS 58, TS 67, TS 64, TS 41, TS 14, TS 9, TS 30, TS 59, TS 40, TS 42, TS 25, TS 56, TS 47, TS 18, TS 45, TS 60, TS 3, TS 22, TS 49, TS 1, TS 2, TS 65, TS 5, TS 35, TS 21, TS 31, TS 70. |

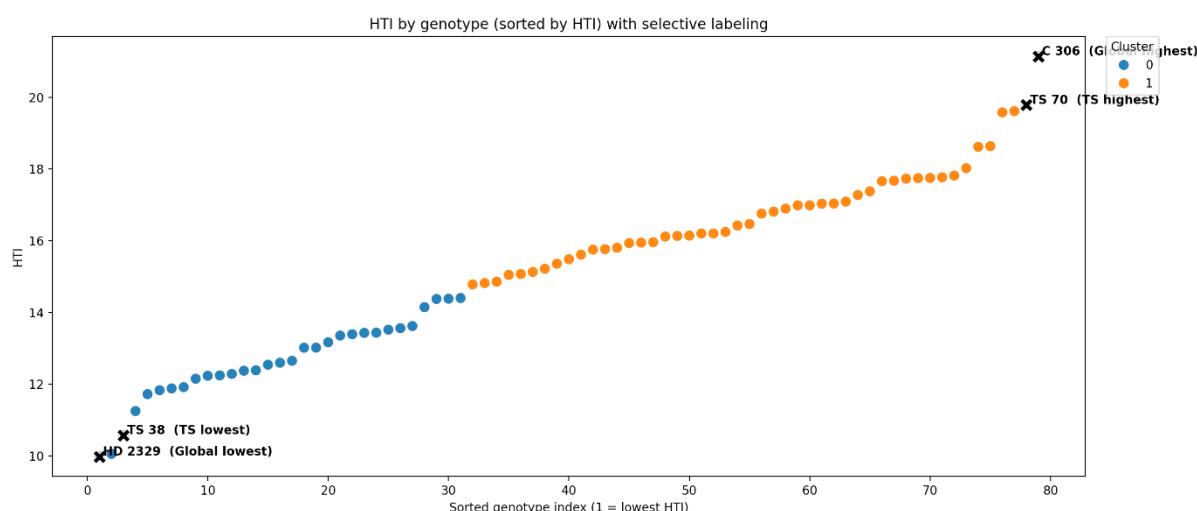


Fig 2. Clustering of genotypes on the basis of Heat Tolerance Index (HTI)

Cluster I consisted of 31 genotypes with lower HTI values (9.98–14.40) and predominantly represented heat-susceptible responses. This cluster included all major susceptible and moderately susceptible bread wheat checks, namely HD 2329, PBW 343, PBW 660, PBW 869, and HD 3086, validating the effectiveness of HTI in discriminating stress response. A subset of TS lines (e.g., TS 38, TS 32, TS 66, TS 15, TS 7, TS 55) clustered with these checks, indicating comparable or lower heat tolerance relative to cultivated bread wheat.

In contrast, Cluster II comprised 39 genotypes with moderate to high HTI values (14.78–21.14) and represented heat-tolerant responses. Importantly, this cluster included

the heat-tolerant bread wheat checks C 306 (HTI = 21.14) and PBW 677 (HTI = 14.82), serving as benchmarks for tolerance. Several *T. sphaerococcum* lines such as TS 70, TS 31, TS 21, TS 35, TS 5, TS 65, TS 2, TS 1, TS 49, TS 22, and TS 3 exhibited HTI values equal to or exceeding those of the tolerant bread wheat checks, indicating superior or comparable heat tolerance.

Notably, the highest HTI values were predominantly observed in TS genotypes, with TS 70 (19.78), TS 31 (19.61), TS 21 (19.58), TS 35 (18.64), and TS 5 (18.62) outperforming most bread wheat checks except C 306. This suggests that *T. sphaerococcum* harbours novel and



stronger heat tolerance mechanisms not fully exploited in modern bread wheat cultivars.

Overall, the clustering analysis highlights that while several TS lines exhibit susceptibility similar to bread wheat, a substantial proportion of *T. sphaerococcum* genotypes surpass commonly used bread wheat checks in heat tolerance, underscoring their value as *donor parents for introgression of heat stress resilience into bread wheat breeding programs*.

3.4 Key tolerant genotypes

Based on Heat Tolerance Index (HTI) and K-means clustering, several *Triticum sphaerococcum* genotypes were

identified as *key heat-tolerant lines*, exhibiting performance comparable to or exceeding standard bread wheat checks. The highest HTI was recorded for the tolerant check *C 306* (HTI = 21.14), followed closely by multiple TS genotypes, indicating strong intrinsic tolerance within *T. sphaerococcum* germplasm.

Among the TS lines, *TS 70* (HTI = 19.78), *TS 31* (19.61), *TS 21* (19.58), *TS 35* (18.64), and *TS 5* (18.62) consistently ranked among the top performers under heat stress. These genotypes surpassed widely used bread wheat checks such as PBW 677, PBW 826, PBW 660, PBW 869, and HD 3086, demonstrating superior heat stress resilience (Fig 3).

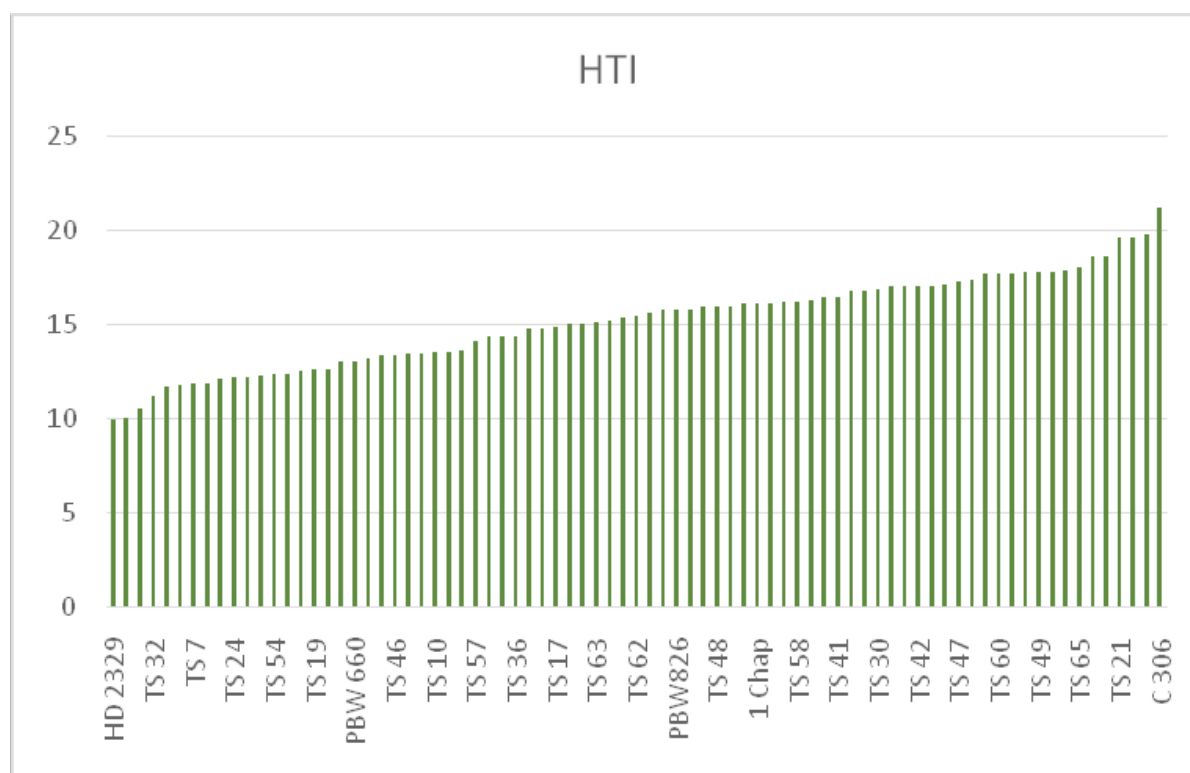


Fig. 3. Heat tolerance Index of all genotypes (incl. Checks)

In addition, TS genotypes including TS 65, TS 2, TS 1, TS 49, TS 22, TS 3, TS 60, and TS 45 showed HTI values comparable to the tolerant check PBW 677, reinforcing their potential utility as donor lines. The predominance of *T. sphaerococcum* genotypes among the top HTI ranks suggests that this under utilized wheat subspecies harbours novel adaptive traits conferring enhanced tolerance to high-temperature stress.

Overall, these key TS genotypes represent promising genetic resources for wheat improvement, particularly

for introgression of heat tolerance into elite bread wheat backgrounds without compromising adaptability.

4. Discussion

Heat stress at the seedling stage poses a major constraint to wheat establishment by impairing membrane integrity, water relations, and metabolic stability (Farooq *et al.*, 2011). In the present study, significant genotypic variation among *Triticum sphaerococcum* lines for morpho-physiological and biochemical traits under heat stress highlights the adaptive potential of this under utilized wheat subspecies.



Highly significant differences across all traits indicate substantial genetic diversity, a prerequisite for effective selection under stress environments (Blum, 2011). Root length exhibited the strongest genotypic control, emphasizing the importance of root system architecture in stress avoidance through improved water uptake and maintenance of plant water status (Lopes and Reynolds, 2010). The strong positive associations between root and shoot traits further underline the coordinated role of below- and above-ground growth in sustaining seedling performance under heat stress.

Membrane Stability Index (MSI) and Relative Water Content (RWC) emerged as key physiological determinants of tolerance. Their strong positive correlation suggests that maintenance of cellular hydration is critical for preserving membrane integrity under high temperature stress. Heat-induced oxidative damage leads to lipid peroxidation and increased electrolyte leakage, making MSI a reliable indicator of cellular stability (Sairam and Tyagi, 2004; Hasanuzzaman *et al.*, 2013). Genotypes with higher MSI likely possess more efficient antioxidant defence systems, enabling better protection of membrane lipids and proteins.

Proline accumulation showed positive associations with MSI, RWC, and total protein content, reinforcing its role in osmotic adjustment, membrane stabilization, and protection of cellular proteins under stress (Bates *et al.*, 1973; Szabados and Savouré, 2010). However, its weak correlation with growth traits suggests that proline primarily contributes to biochemical protection rather than directly promoting biomass accumulation, a trend consistent with previous studies in wheat (Ashraf and Foolad, 2007).

Strong positive correlations among root length, shoot length, biomass traits, and seed vigour indicate that heat tolerance is an integrated response involving morphological robustness and physiological stability. Seed vigour emerged as a reliable integrative trait reflecting early seedling establishment under stress, supporting its utility as a rapid screening parameter (Farooq *et al.*, 2009). Conversely, the negative association between grain protein content and seed vigour suggests a trade-off between stress adaptation and quality traits, likely due to stress-induced shifts in assimilate partitioning (Stone and Nicolas, 1996).

K-means clustering based on Heat Tolerance Index effectively differentiated tolerant and susceptible genotypes. Several *T. sphaerococcum* lines, notably *TS 70*, *TS 31*, *TS 21*, *TS 35*, and *TS 5*, clustered with or outperformed bread wheat checks such as C 306 and PBW 677. The superior performance of these TS lines highlights the presence of novel adaptive alleles within *T. sphaerococcum*, shaped by its indigenous origin and adaptation to marginal environments (Dvorak *et al.*, 2006; Mujeeb-Kazi *et al.*, 2013).

Overall, the integration of physiological, biochemical, and multivariate analyses proved effective in identifying heat-tolerant genotypes. Traits such as root length, MSI, RWC, proline content, and seed vigour can serve as reliable selection criteria in early-generation screening. The elite *T. sphaerococcum* genotypes identified in this study represent valuable genetic resources for introgression of heat tolerance into bread wheat, contributing to the development of climate-resilient cultivars.

5. Conclusion

Significant genetic variation was observed among *T. sphaerococcum* lines for seedling-stage traits linked to heat tolerance, including root length, membrane stability, relative water content, proline accumulation, and seed vigour. Several TS lines outperformed bread wheat checks, highlighting their potential as donors of heat-resilient traits. Multivariate analysis confirmed that elite TS genotypes cluster with or surpass tolerant checks like C 306, reflecting coordinated physiological and metabolic adaptation. These results underscore *T. sphaerococcum* as a valuable genetic resource for breeding wheat with improved resilience to rising temperatures.

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Author contributions

All the authors contributed in the generation of data and development of the variety.

Conflict of interest

The authors declare no conflict of interest.

Ethical Approval

The article doesn't contain any study involving ethical approval.



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No

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