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Assessment of Heat Tolerance in Durum Wheat (*Triticum durum* Desf.) Landraces via Morphological and Physiological Traits

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Abstract

Changing climatic conditions with increasing global temperatures are among the factors causing significant yield losses in wheat. One of the main causes of these losses is high temperature stress. Wheat landraces, which have been cultivated from the past to the present and are still cultivated in certain regions due to their tolerance to all kinds of abiotic stress conditions, have important genetic resources in terms of tolerance to abiotic stresses. In this study, some practical, easily and quickly measurable physiological, morphological and yield related parameters that can be used in high temperature stress tolerance were investigated for use in durum wheat breeding programs in Southeast Anatolia region. In this context, 90 durum wheat landraces and 4 standard cultivars were used. The study was conducted for two years in the experimental field of GAP International Agricultural Research and Training Center under normal (optimum conditions) and late sowing (high temperature stress conditions) according to an augmented design under field conditions. As a result of the research, under high temperature stress conditions compared with optimum conditions, losses were recorded in flag leaf chlorophyll content (SPAD) of 5% in the first year and 8% in the second year, together with reductions of 1% (non-significant) and 6% in NDVI, 19% and 20% in flag leaf greening time, about 8% in plant height in both years, 16% and 20% in flag leaf area, about 4–5% in flag leaf erectability, and 20% and 17% in grain filling time. On the other hand, canopy temperature rose by 18% and 20% in the first and second years, respectively, while flag leaf curling increased by 25% and 9% and grain filling rate by 13% and 9% over the same period. Under both optimum and stress conditions, low vegetative temperature, high SPAD, flag leaf greening time, earliness in terms of spike time, flag leaf erection, flag leaf curling, flag leaf color, and grain filling time, which are among the morphological and physiological traits, can be used as selection criteria in stress-based breeding studies and research to be conducted in the region.

Keywords Landraces · Durum wheat · High temperature stress · Tolerance · Selection

Introduction

Durum wheat (*Triticum durum* L.), a cool-climate cereal, is highly sensitive to high temperature stress and is negatively affected by temperature stress at all stages of plant development (Akter and Islam 2017). It is estimated that temperature stress, which has increased globally with climate change, will continue throughout the 21st century and cause significant yield losses in wheat (Asseng et al. 2015). Rapid increases in wheat yields are needed to feed the growing world population and meet its nutritional needs (Fischer et al. 2014). However, high temperatures above 30 °C during wheat growth and development can significantly affect grain production, especially wheat yield (Dreccer et al. 2018). The life cycle of wheat is shortened due to increasing temperatures, resulting in low wheat yield and quality

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(Asseng et al. 2011). Therefore, it is important to develop temperature stress tolerant varieties along with new strategies to minimize the effects of temperature stress (Zandalinas et al. 2018). To improve tolerance to heat stress, it is necessary to elucidate the genetic variation and mechanisms associated with the stress in question (Thistlethwaite et al. 2015). In this context, Southeast Anatolia has both wild and landrace durum wheat genetic variation (Çakır et al. 2025). In particular, durum wheat landrace is still cultivated in the region due to its superior ability to adapt to abiotic stresses (Özberk et al. 2010). The areas under cultivation of wheat landraces, which are produced and can be a gene source, are shrinking or even disappearing from production due to various reasons. In order to achieve the goal of breeding studies quickly and effectively, it is very important to collect and characterize different landrace wheat gene resources, ensure that they are included in breeding programs as gene resources, and protect them in national gene banks (Akçura 2006).

Although there are many abiotic stresses that negatively affect the morphology, physiology, yield, and yield components of wheat, high temperature stress is one of the most important environmental factors that negatively affect the growth, development, and yield of wheat. In addition, high temperatures occurring during the grain filling phase are one of the most important stress factors limiting the yield of wheat, and high temperatures above 35 °C cause grain yield to decrease by up to 50% on genotype averages despite sufficient rainfall (Kılıç 2020). Similarly, there are significant decreases in gestation, spike, flowering, and physiological maturity periods of genotypes under late sowing conditions exposed to temperature stress compared to the normal sowing period (Alam et al. 2014). In addition, 24% of losses occurred in wheat under heat stress conditions compared to optimum conditions and late maturing genotypes are more affected by this stress as their grain filling periods are exposed to higher temperatures (Modhej et al. 2015). Under high temperature stress conditions, wheat genotypes have poor flower development, irregular flowering period, insufficient grain filling, leaf blight, pollen infertility, and permanent damage. However, to protect wheat from high temperature stress damage during the generative period, it should have morphological characteristics such as flag leaf curling, dark green color of the flag leaf, and erect flag leaf (Hunt et al. 2018). Characteristics such as plant height, grain weight, number of days to flowering, and grain filling time under field conditions during fertilization and grain filling periods were reported to decrease between 4 and 7% in flowering and grain yield for each 1 °C above 25 °C, and genotypes with more stay-green period of the flag leaf had higher yield, larger spike weight and more grain filling time (Ullah 2018). Under high temperature stress conditions, significant losses between 9 and 74% in morphological, physiological and phenological characters were observed in wheat, particularly 30, 25, 41 and 66% decreases in days to spike, plant height, number of spikes per plant and yield, respectively (Jamil et al. 2019).

The aim of this study was to determine some morphological, physiological and phenological characteristics of 90 landrace and 4 standard durum wheat genotypes collected from Southeast Anatolia region in response to high temperature stress. We hypothesized that specific local landraces possess superior, quantifiable physiological (e.g., prolonged stay-green) and morphological (e.g., flag leaf curling) adaptations to terminal heat stress compared to standard commercial cultivars, and that these traits can be utilized as reliable selection criteria. It is expected that the wheat landraces used in the study will contribute to the improvement of high temperature stress tolerance.

Material and Method

This research was conducted in the experimental field of GAP International Agricultural Research and Training Center Directorate. In this study, 90 durum wheat landraces and 4 standard durum wheat varieties (Diyarbakır-81, Fırat-93, Sümerli, Artuklu) collected from different provinces of the Southeastern Anatolia Region were used as material. The study was conducted for 2 years according to augmented experimental design. In order to determine the genotypes tolerant to high temperature, sowing was carried out in two periods as normal sowing and late sowing. Under field conditions, normal sowing was carried out on November 17, 2020 in the first year and November 16, 2021 in the second year, and late sowing was carried out on February 26, 2021 in the first year and February 21, 2022 in the second year. The plots were sown with a 6-row plot seeder at a seed rate of 500 seeds/m^2. The plots were 4.2 m2 (6 rows x 20 cm between rows x 3.5 m length) at sowing and 3 m^2 (6 rows x 20 cm between rows x 2.5 m length) at harvest. According to the results of soil analysis, fertilizers were applied as 6 kg/da of pure phosphorus and 12 kg/da of pure nitrogen per decare. The study was conducted under irrigated conditions to minimize the effect of drought stress on the genotypes.

Germplasm Characterization

Canopy Temperature: Canopy temperature (CTP) was measured in ºC with a portable infrared thermometer. During high temperature hours (11:00–14:00), the device was held at an angle of 30° from the ground (the most favorable angle with a dominant view of the leaves). Two measurements were taken for each plot, one from the north and one

from the south and averaged. **Flag leaf chlorophyll content**: Measurements were recorded at flowering with a hand-held chlorophyll meter (SPAD, model 502). Five flag leaves were randomly selected from each plot for measurement and the data were averaged. **The normalized difference vegetation index (NDVI)**: Vegetation cover index (NDVI) was measured at full flowering using GreenSeeker (Handheld crop) device at 11.00–15.00 time period when the plant surface was not wet, there was no wind and sunlight was high. The measurement was carried out by walking along the plot with the device at the same height and distance (approximately 90 cm) from the vegetation and in the center of the plot for approximately five seconds. **Days to heading**: It was determined by calculating the number of days between the date of emergence and the date when ½ of the spike emerged from the flag leaf sheath in 70% of the plants in each plot. **Stay-green period of the flag leaf**: It was determined as the number of days between the emergence of the flag leaf and the period when the leaf turned yellow approximately 95% of the time. **Plant height**: It was determined by measuring 10 random stems with 10 spikelets from each plot from the soil level to the tip of the top spikelet. **Flag Leaf Area**: Once the flag leaf on the main stem of the plants had finished developing, its area in cm² was determined by measuring the width and length of the flag leaf of ten plants from each plot and multiplying by a factor of 0.72. **Leaf Erectness**: The angle of the leaf blade to the stem (0–90°) was used as a scale to determine its effect on the plant's ability to receive sunlight and tolerate heat. Measurements were taken visually during the spike period. **Flag leaf color** was determined between the beginning and end of flowering (Zadoks 60–69) using a 1–3 scale (1: lightest color; 3: darkest color). **Flag leaf curling (rolling)**: Observations of flag leaf rotation were taken twice daily during the milking period (early morning before 10:00 a.m. and noon between 1:00 and 4:00 p.m.). The rate of leaf rotation (folding) was determined by averaging the two daily observations using a 0–3 scale (0 = no folding, 1 = leaf slightly curled at the tip, 2 = leaf moderately curled, and 3 = leaf tightly curled). **Grain filling time**: It was calculated as the number of days from flowering to physiological maturity. **Grain filling rate**: It was calculated by dividing the average single grain weight by the grain filling time. Spike waxiness: It was determined between the beginning and end of flowering (Zadoks 60–69) on a scale of 1–9 (1 = None or very weak; 3 = Weak; 5 = Moderate; 7 = Strong; 9 = Very strong). Waxy stem: It was determined between Zadoks stages 60 and 69 according to a 1–9 scale (1 = none or very weak, 3 = weak, 5 = moderate, 7 = strong, 9 = very strong).

Data Analysis

Statistical analyses of the data obtained in the study were performed using the JMP Pro13 program (Copyright © 2007 SAS Institute Inc.). Because an augmented experimental design was used, with unreplicated test genotypes and replicated check cultivars, analyses were conducted separately for each year and sowing condition. The check cultivars (Diyarbakır-81, Fırat-93, Sümerli, Artuklu) provided the error estimate for the design, and one-way ANOVA was applied to the augmented-design adjusted (BLUE) means of the test genotypes to assess genotypic variation according to augmented experimental design (Federer 1956). The sowing-date effect was evaluated separately for each growing season using a paired t-test, with the 90 landraces serving as the pairing unit to compare normal and late sowing. Differences were considered significant at $P < 0.05$ and are denoted in the figures as * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$. To determine the relationship between traits, a scatterplot matrix was used to perform a pairwise correlation analysis in the JMP Pro13 package program. Since an augmented experimental design was used in the study, year combining was not performed. Thus, heat stress treatments and landraces were evaluated separately for each year.

Results

Impact of High-Temperature Stress on Canopy Thermal Regulation and Photosynthetic Integrity

Analysis of variance revealed statistically significant differences at the $P \leq 0.01$ level among genotypes for canopy temperature (CTP) and flag leaf chlorophyll content (SPAD) under both normal sowing (NS) and late sowing (LS) conditions in both trial years. All figures were independently regenerated from the trait means in the Supplementary Tables; correspondence between each figure and its underlying data is verifiable therein.

High-temperature stress significantly increased canopy temperature. Mean canopy temperature under late sowing rose by 18% in the first year and 20% in the second year relative to normal sowing. A wide variation in stress response was observed among genotypes. For instance, landraces 1, 2, and 3 exhibited high CTP values under both sowing conditions, indicating greater stress impact, whereas landraces 82 and 84 minimized the effect of stress with low CTP values. While the mean CTP of standard cultivars was similar to the landrace average, the highest and lowest CTP values were recorded among the landraces, highlighting the extensive genetic diversity within the local population (Fig. 1).

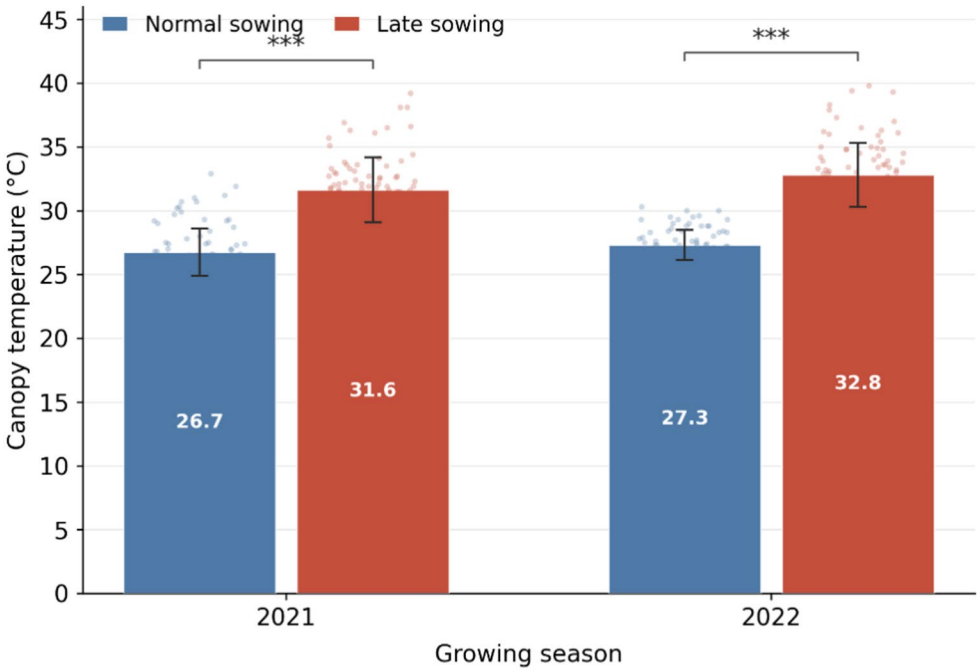

Fig. 1 Canopy temperature (°C) of 90 durum wheat landraces under normal and late (terminal heat-stress) sowing during the 2021 and 2022 growing seasons. Bars represent the mean ± standard deviation of the augmented-design adjusted means across the 90 landraces; individual points denote single landraces. Canopy temperature was 18% higher in 2021 and 20% higher in 2022 under late sowing

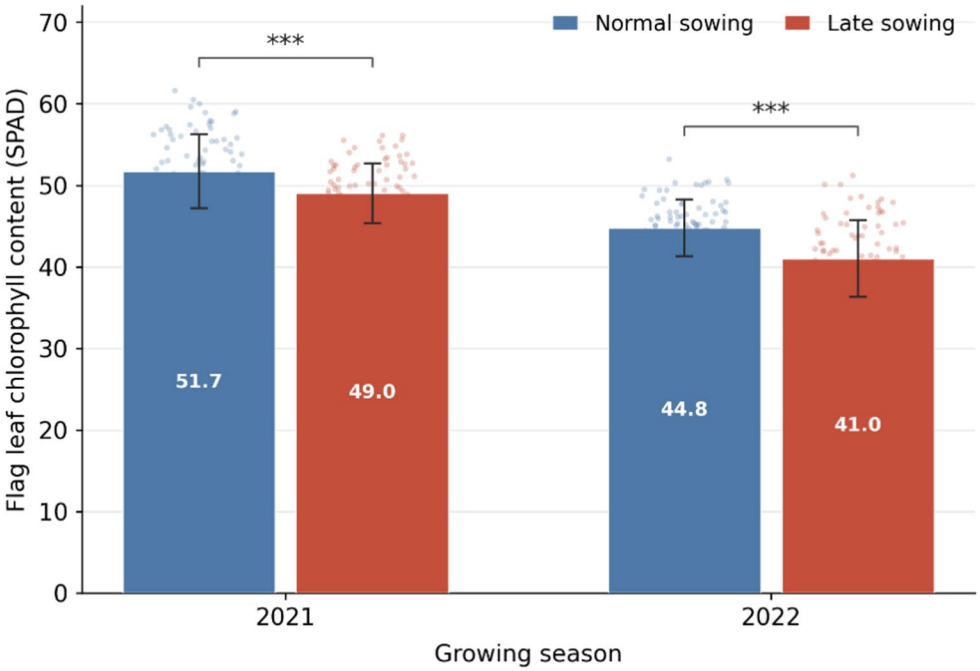

Fig. 2 Flag leaf chlorophyll content (SPAD) of 90 durum wheat landraces under normal and late (terminal heat-stress) sowing during the 2021 and 2022 growing seasons. Bars represent the mean ± standard deviation of the augmented-design adjusted means across the 90 landraces; individual points denote single landraces. Chlorophyll content was 5% lower in 2021 and 8% lower in 2022 under late sowing

Conversely, flag leaf chlorophyll content (SPAD) decreased under high-temperature stress. Mean SPAD declined by 5% in the first year and 8% in the second year under late sowing. In terms of SPAD values, landraces 59 and 104, along with the standard cultivar Sümerli, performed well under both conditions, while landraces 72, 16, 89, and 8 showed lower SPAD values. Although the highest and lowest SPAD values were obtained from landraces, the overall average for landraces was lower than that of the standard cultivars (Fig. 2).

Effects of High-Temperature Stress on Plant Senescence Dynamics

The Normalized Difference Vegetation Index (NDVI) and the stay-green period of the flag leaf illustrate the impact of high-temperature stress on plant senescence processes. Significant differences at the $P \leq 0.01$ level were found among genotypes for both traits.

NDVI showed a season-dependent response under late sowing: the first-year change was negligible and

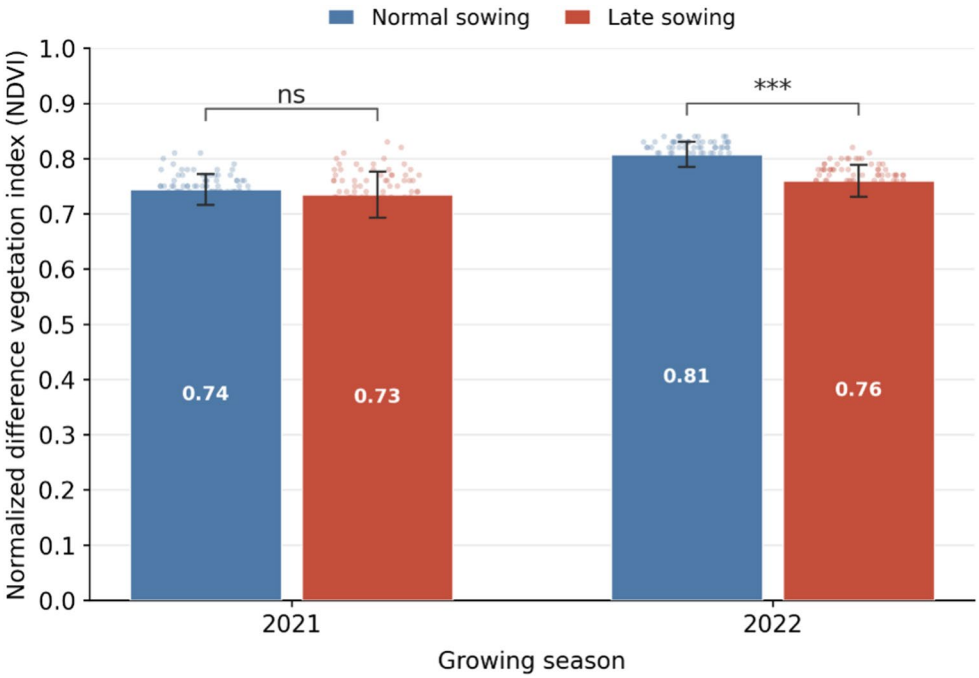

Fig. 3 Normalized difference vegetation index (NDVI) of 90 durum wheat landraces under normal and late (terminal heat-stress) sowing during the 2021 and 2022 growing seasons. Bars represent the mean ± standard deviation of the augmented-design adjusted means across the 90 landraces; individual points denote single landraces. NDVI was essentially unchanged in 2021 (−1%) and 6% lower in 2022 under late sowing

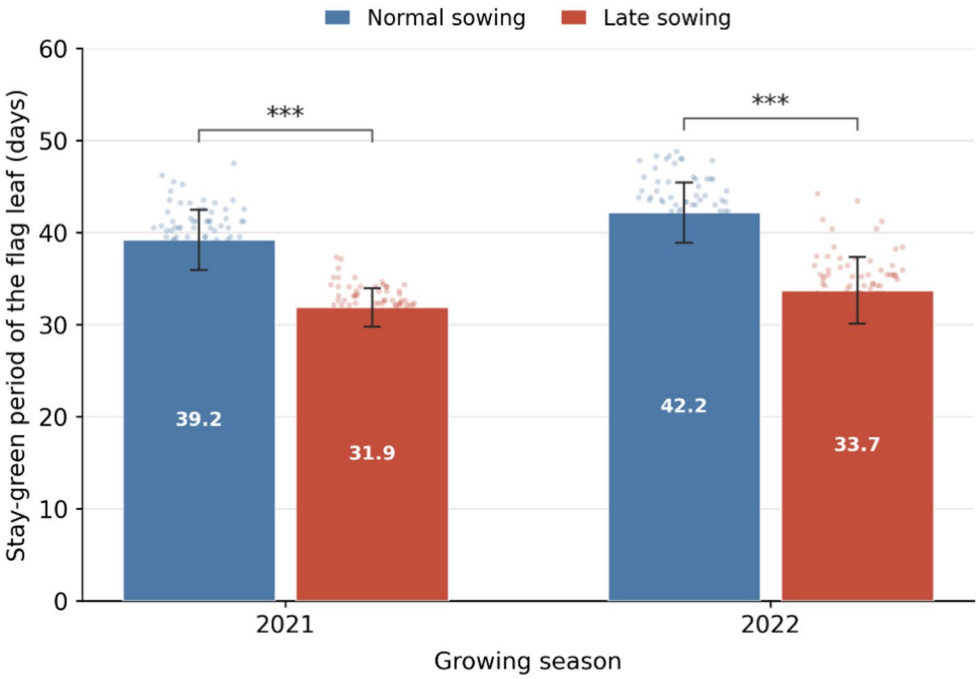

Fig. 4 Stay-green period of the flag leaf (days) of 90 durum wheat landraces under normal and late (terminal heat-stress) sowing during the 2021 and 2022 growing seasons. Bars represent the mean ± standard deviation of the augmented-design adjusted means across the 90 landraces; individual points denote single landraces. The stay-green period was 19% shorter in 2021 and 20% shorter in 2022 under late sowing

non-significant (−1%), whereas a significant decline of 6% occurred in the second, hotter season. The post-flowering decline in NDVI was evident mainly in the hotter second season. Landraces 27, 98, 101, and 106 exhibited high NDVI values, whereas landraces 1, 4, 58, and 83 showed lower values. Overall, landraces demonstrated a more prominent performance for NDVI compared to standard cultivars (Fig. 3).

The stay-green period of the flag leaf was significantly and negatively affected by high-temperature stress. Under late sowing, the stay-green period was shortened by 19% in the first year and 20% in the second year compared to normal sowing, indicating that heat stress caused marked curtailment of the functional life of the flag leaf. Landraces 99, 103, and 104, along with the standard cultivar Sümerli, excelled in maintaining a longer stay-green period under both conditions, while landraces 51, 58, 68, and 72 had shorter durations. In general, the standard cultivars had longer stay-green periods than the landraces (Fig. 4).

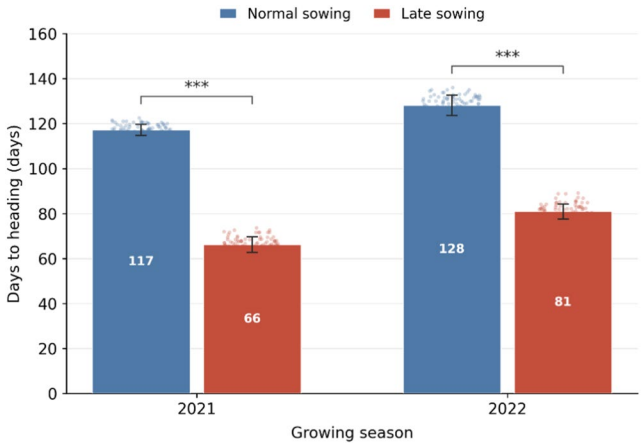

Fig. 5 Emergence-to-heading interval (days) of 90 durum wheat landraces under normal and late (terminal heat-stress) sowing during the 2021 and 2022 growing seasons. Bars represent the mean ± standard deviation of the augmented-design adjusted means across the 90 landraces; individual points denote single landraces. Normal and late sowing were compared within each season by paired t-test (*** $P < 0.001$). The emergence-to-heading interval was on average 51 days shorter in 2021 and 47 days shorter in 2022 under late sowing, primarily reflecting development under warmer temperatures and longer photoperiods rather than constitutive genotypic earliness

Phenological and Architectural Responses to High-Temperature Stress

High-temperature stress significantly altered the phenological calendar and plant architecture of wheat. Significant differences at the $P \leq 0.01$ level were detected among genotypes for days to heading and plant height in both years and under both sowing conditions.

Late sowing markedly shortened the emergence-to-heading interval, which was on average 51 days shorter in the first year and 47 days shorter in the second year compared with normal sowing. It must be noted, however, that late sowing was performed approximately 100 days after normal sowing (February vs. November), so plants under the late-sown treatment developed under progressively warmer temperatures and longer photoperiods. The shortened emergence-to-heading interval therefore reflects an environmental rather than a purely genotypic response, and should not be interpreted directly as heritable early-heading ability. Within the late-sown treatment, however, meaningful genotypic variation in heading time was still observed: landraces 83, 103, and 104, along with the standard cultivar Artuklu, were notable for their relative earliness under both sowing conditions, suggesting these genotypes possess genuine phenological plasticity. In contrast, landraces 12, 41, 42, and 52 exhibited comparatively later heading. On average, the standard cultivars headed earlier than the landraces (Fig. 5).

Plant height was reduced under heat stress. Plant height decreased by approximately 8% under late sowing in both seasons (7.5% and 7.8%, respectively). The landraces used in the study were generally taller than the standard cultivars, which raised the overall average plant height of the trial. For example, landraces 38, 41, and 42 showed high plant height values, while landraces 83, 87, 88, and 99, along with the standard cultivars, were shorter (Fig. 6).

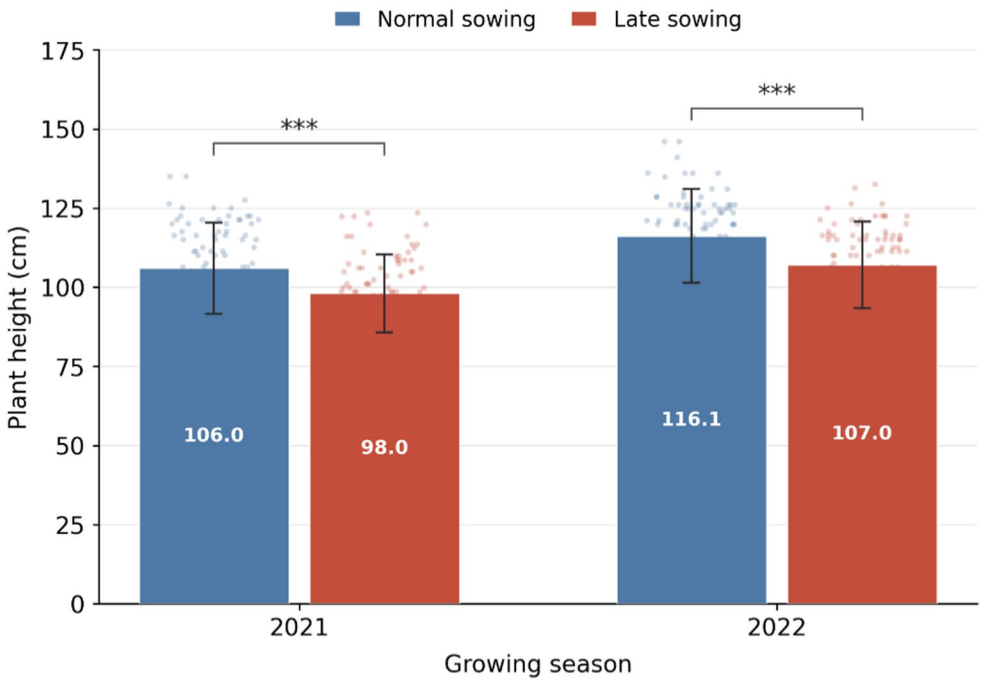

Fig. 6 Plant height (cm) of 90 durum wheat landraces under normal and late (terminal heat-stress) sowing during the 2021 and 2022 growing seasons. Bars represent the mean ± standard deviation of the augmented-design adjusted means across the 90 landraces; individual points denote single landraces. Plant height was reduced by approximately 8% under late sowing in both seasons

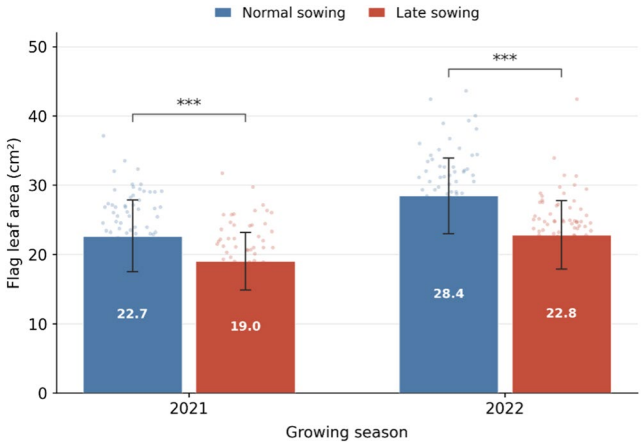

Fig. 7 Flag leaf area (cm²) of 90 durum wheat landraces under normal and late (terminal heat-stress) sowing during the 2021 and 2022 growing seasons. Bars represent the mean ± standard deviation of the augmented-design adjusted means across the 90 landraces; individual points denote single landraces. Flag leaf area was 16% smaller in 2021 and 20% smaller in 2022 under late sowing

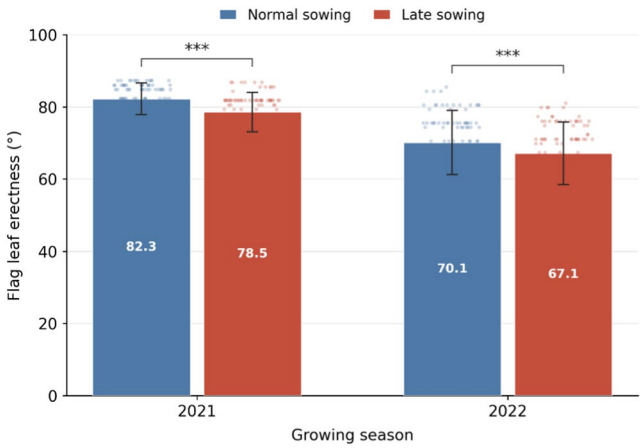

Fig. 8 Flag leaf erectness (°) of 90 durum wheat landraces under normal and late (terminal heat-stress) sowing during the 2021 and 2022 growing seasons. Bars represent the mean ± standard deviation of the augmented-design adjusted means across the 90 landraces; individual points denote single landraces. Flag leaf erectness declined modestly under late sowing, by about 4–5% in both seasons

Alterations in Flag Leaf Morphology Caused by High-Temperature Stress

As the primary source of photosynthates during grain filling, the morphology of the flag leaf is critically important. Significant genotypic differences were found for flag leaf area ($P \leq 0.01$ in both years) and for flag leaf erectness ($P \leq 0.05$ in 2021 and $P \leq 0.01$ in 2022).

High-temperature stress caused a substantial reduction in flag leaf area. Compared with normal sowing, flag leaf area under late sowing decreased by 16% in the first year and 20% in the second year. Wide variation was observed for this trait, with landraces 41, 42, 45, and 73 generally having

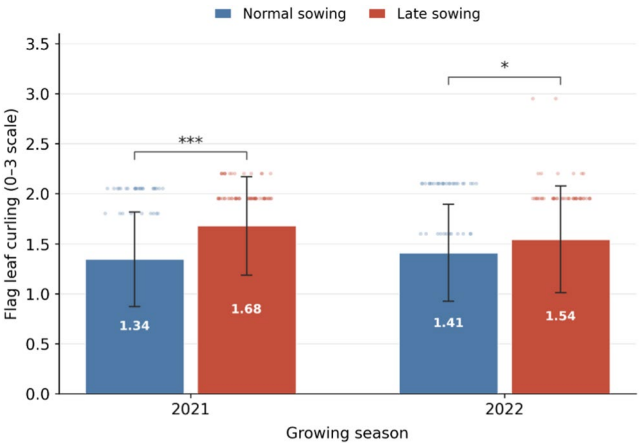

Fig. 9 Flag leaf curling (0–3 scale) of 90 durum wheat landraces under normal and late (terminal heat-stress) sowing during the 2021 and 2022 growing seasons. Bars represent the mean ± standard deviation of the augmented-design adjusted means across the 90 landraces; individual points denote single landraces. Flag leaf curling increased by 25% in 2021 and 9% in 2022 under late sowing

larger flag leaf areas, while landraces 51, 62, 84, and 86 had smaller leaves (Fig. 7).

Flag leaf erectness was also negatively affected by heat stress, with leaves shifting from an erect to a more recumbent and drooping position as temperatures increased. Flag leaf erectness declined only modestly under late sowing, by about 4–5% in both seasons (4.5% and 4.3%, respectively). Landraces 82 and 83, along with the standard cultivars Sümerli and Artuklu, generally maintained a more erect leaf posture under both conditions. The leaves of the standard cultivars were, on average, more erect than those of the landraces (Fig. 8).

Adaptive Morphological Traits Observed Under Stress Conditions

Plants exhibit various morphological adaptations to high-temperature stress, including flag leaf curling, flag leaf color, and spike/stem waxiness. Significant differences at the $P \leq 0.01$ level were found among genotypes for flag leaf curling under both conditions. Similarly, a significant difference at the $P \leq 0.01$ level was found for spike waxiness.

Flag leaf curling increased markedly under heat stress, with an increase of 25% in the first year and 9% in the second year under late sowing compared to normal sowing. In general, landraces showed higher rates of flag leaf curling than standard cultivars, suggesting potentially more effective stress avoidance mechanisms (Fig. 9).

Flag leaf color and spike/stem waxiness were determined to be traits unaffected by sowing time and stable across sowing dates. Therefore, data for these traits are presented from a single growing season. Because these are visually scored,

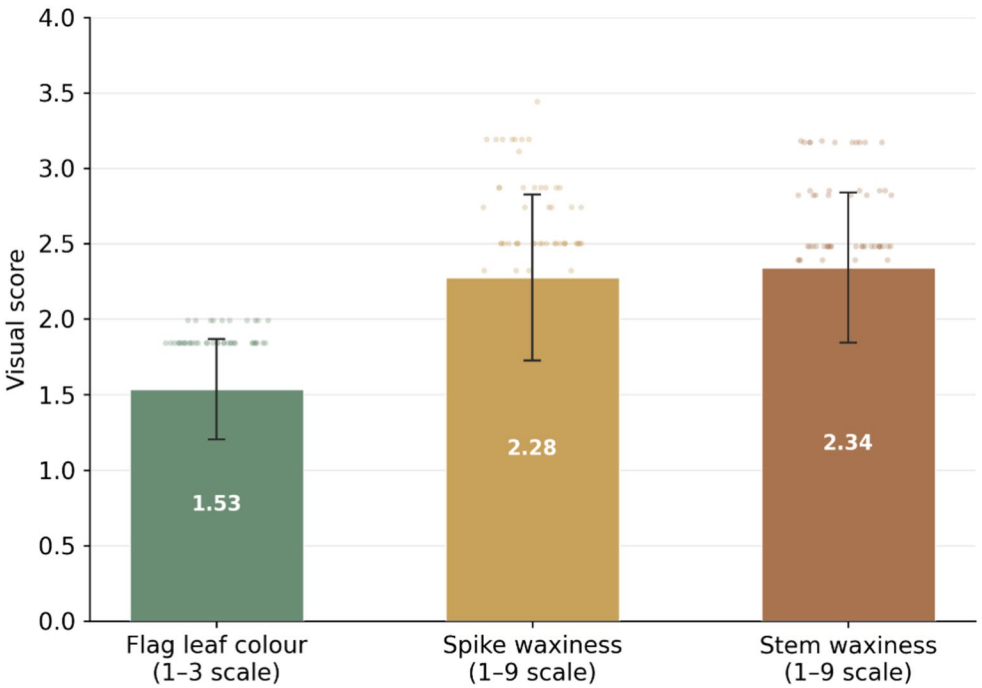

Fig. 10 Flag leaf colour (1–3 scale) and epicuticular waxiness of the spike and stem (1–9 scale) of 90 durum wheat landraces. Bars show the mean ± standard deviation across the 90 landraces; individual points denote single landraces. Because these traits were stable across sowing dates, values from a single season are presented (mean: flag leaf colour 1.53, spike waxiness 2.28, stem waxiness 2.34)

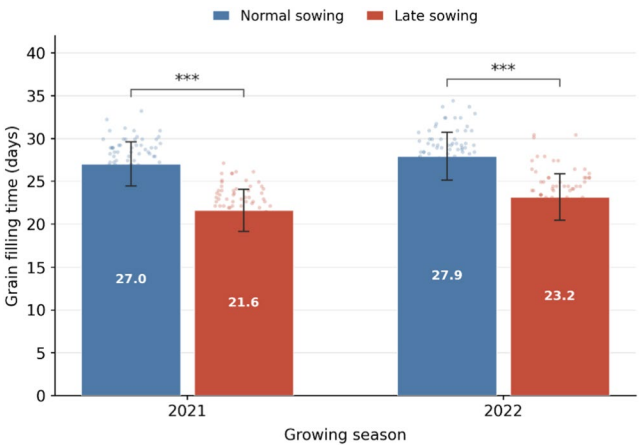

Fig. 11 Grain filling duration (days) of 90 durum wheat landraces under normal and late (terminal heat-stress) sowing during the 2021 and 2022 growing seasons. Bars represent the mean ± standard deviation of the augmented-design adjusted means across the 90 landraces; individual points denote single landraces. Grain filling duration was 20% shorter in 2021 and 17% shorter in 2022 under late sowing

single-season observations without formal statistical testing between cultivars and landraces, claims of cultivar superiority should be interpreted with appropriate caution; they are presented as descriptive tendencies rather than statistically verified differences. Observations of flag leaf color indicated a tendency for standard cultivars to have darker green leaves than the landraces. Significant variation was also observed for spike and stem waxiness, with genotypes exhibiting a prominent waxy layer also tending to perform well in other morphological and physiological parameters (Fig. 10).

Consequences of High-Temperature Stress on Grain Filling Dynamics

Grain filling duration and grain filling rate are critical components that directly influence yield. Significant differences at the $P \leq 0.01$ level were detected among genotypes for both traits under all conditions.

High-temperature stress significantly shortened the grain-filling duration. Grain filling duration was reduced by 20% in the first year and 17% in the second year under late sowing, demonstrating that heat stress curtails the wheat life cycle and constrains yield potential. Landraces 16, 82, 83, and 98 stood out for their longer grain filling duration under both conditions, while landraces 1, 2, 52, and 66 had shorter durations (Fig. 11).

In contrast to the shortened duration, the grain filling rate increased. Grain filling rate increased by 13% in the first year and 9% in the second year under late sowing. This suggests an attempt by the plant to mobilize assimilates more rapidly to fill the grain within the shortened timeframe. The genotypes with the highest grain filling rates included landraces 41, 46, 52, and 106, while the lowest rates were observed in landraces 82, 88, 99, and 103 (Fig. 12).

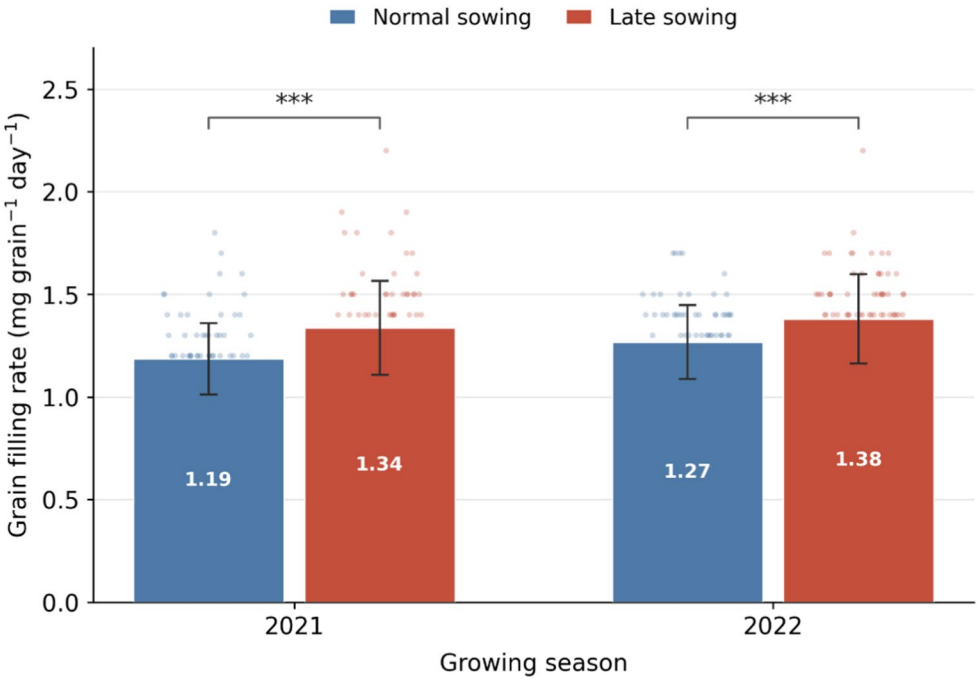

Fig. 12 Grain filling rate (mg grain^{-1} day^{-1}) of 90 durum wheat landraces under normal and late (terminal heat-stress) sowing during the 2021 and 2022 growing seasons. Bars represent the mean ± standard deviation of the augmented-design adjusted means across the 90 landraces; individual points denote single landraces. Grain filling rate increased by 13% in 2021 and 9% in 2022 under late sowing

Discussion

Canopy Coolness and Photosynthetic Stability: The Cornerstones of High-Temperature Tolerance

The finding that lower canopy temperature (CTP) and maintained flag leaf chlorophyll content (SPAD) are associated with heat tolerance reflects fundamental physiological resilience. The observed 18–20% increase in CTP under stress is consistent with the principle that heat stress induces stomatal closure to conserve water, thereby reducing transpirational cooling (Koutroubas and Sfatkic 2022). Landraces 82 and 84, which maintained cooler canopies, likely possess superior root water uptake or more efficient stomatal regulation, making CTP a powerful integrative trait for plant-water relations (Koutroubas and Sfatkic 2022). The 5–8% reduction in SPAD values under stress is a direct consequence of heat-induced damage to chloroplasts (Wollenweber et al. 2003) and accelerated chlorophyll degradation (Ullah 2018). Genotypes like 59 and 104 that maintained high SPAD values possess more stable thylakoid membranes, a key indicator of intrinsic heat tolerance that allows them to sustain a higher photosynthetic potential, which is strongly linked to final grain yield (Ristic et al. 2007). These two traits — CTP and SPAD — are not independent indicators but form a causal chain: tolerant genotypes maintain transpirational cooling → cooler canopy temperature → reduced chloroplast thermal damage → higher, more stable SPAD → sustained photosynthesis and superior yield outcomes (Koutroubas and Sfatkic 2022; Ristic et al. 2007). Selecting for low CTP in large-scale screening identifies genotypes where this entire physiological cascade is functioning optimally.

The Dual Strategy of Heat Escape and Functional Stay-Green to Sustain Productivity

Two complementary mechanisms underpin yield maintenance under terminal heat stress: phenological plasticity enabling a shorter growing cycle under late-sowing conditions, and functional tolerance via extended stay-green duration. Genotypes combining both traits may shift grain-filling into a relatively cooler window while sustaining the photosynthetic source capacity needed to fill it effectively. It should be noted, however, that the shortened emergence-to-heading interval observed in this study is primarily an environmental response to the warmer, longer-day conditions associated with late sowing rather than a direct measure of constitutive genotypic earliness; the potential breeding value of this phenological plasticity, particularly differences among genotypes within the late-sown treatment, requires verification in dedicated earliness experiments.

Genotypes that headed earlier within the late-sown treatment may benefit from decoupling their critical reproductive phase from peak summer temperatures — a well-established adaptive mechanism in heat-prone environments (Karaman 2017; Ullah 2018). Interpreting this advantage requires caution, however: because the overall shortening of the emergence-to-heading interval is driven by the environmental shift to warmer conditions and longer photoperiods under late sowing, genotypic differences in heading time observed in this study reflect relative phenological plasticity rather

than constitutive early-heading ability per se. Concurrently, the 19–20% reduction in stay-green duration observed under stress reveals the metabolic cost of heat on chloroplast integrity and nitrogen remobilization. Genotypes resisting this accelerated senescence maintain functional rubisco activity and membrane stability longer, directly prolonging assimilate supply to the developing grain (Kamal et al. 2019; Ali et al. 2020). Pairwise correlation analysis indicated a tendency for higher early-season NDVI to be associated with relatively faster heading within the late-sown treatment, suggesting that vigorous canopy establishment may be linked to phenological progression; however, formal correlation coefficients and significance levels for this association are not available in the present dataset and this observation should be regarded as exploratory (Ramya et al. 2015; Lopes and Reynolds 2012).

The optimal ideotype is not the earliest-heading genotype, but one that balances earliness with maximized source capacity — heading early enough to escape damaging temperatures while retaining sufficient canopy area and functional duration for effective grain-filling. Extreme earliness truncates vegetative biomass accumulation, reducing the assimilate pool available for translocation; extreme lateness exposes grain-filling to lethal temperatures. Genotypes such as 103 and 104, exhibiting both early heading and prolonged stay-green, appear to have resolved this trade-off. Mapping the genetic architecture underlying this phenological optimization — particularly QTLs co-regulating heading time and senescence rate — would enable environment-specific fine-tuning of crop life cycles beyond the reductive "earlier is better" selection framework (El-basyoni et al. 2024; Tahmasebi et al. 2021).

Plant Architecture as a Mediator of High-Temperature Stress

Plant architecture traits function as the primary interface between the crop and its thermal micro-environment, with each trait encoding a distinct physiological trade-off under heat stress. The 8% reduction in plant height reflects heat-mediated inhibition of gibberellin-driven cell elongation, while simultaneously reducing lodging risk — though excessive height reduction compromises canopy competitiveness and biomass accumulation (Shah et al. 2019). The 16–20% decrease in flag leaf area represents an active reduction in transpiring surface, a response mechanistically driven by elevated vapor pressure deficit (VPD): even under irrigated conditions, high temperatures create an atmospheric drought by amplifying the leaf-to-air water potential gradient, triggering stomatal closure and ultimately leaf area limitation (Rsaliyev et al. 2024). This reveals that heat and drought tolerance pathways converge at the level of water balance regulation. The more modest 4–5% decline in flag leaf erectness reflects a partial loss of turgor, while genotypes maintaining erect posture (e.g., 82, 83) benefit from two compounding effects — more uniform light distribution within the canopy and reduced direct solar irradiance on the adaxial leaf surface, lowering leaf temperature and protecting photosystem II integrity (Tekdal 2012).

These traits present an inherent ideotype dilemma: larger flag leaves maximize light interception and carbon assimilation under optimal conditions, yet become a liability under heat-induced high VPD; taller plants build greater source biomass but increase lodging susceptibility. The landrace diversity in this collection offers a path to resolving these conflicts by identifying genotypes that combine moderately sized but photosynthetically efficient flag leaves with erect posture and structurally sound stems. This reframes breeding targets from simple morphometric optima toward functional indices — photosynthetic efficiency per unit leaf area and lodging resistance — enabling selection for architectures resilient across variable stress intensities rather than optimized for a single scenario.

Adaptive Morphological Mechanisms for Direct Heat and Radiation Avoidance

Morphological traits act as a primary physical defense against thermal damage by actively altering the leaf surface to manage heat load. The 9–25% increase in flag leaf curling is an avoidance mechanism that physically reduces the surface area exposed to solar irradiance, thereby lowering leaf temperature and restricting transpirational water loss (Karaman 2017; Kadioglu et al. 2012; Ali et al. 2022). Similarly, epicuticular wax on the stem and spike provides a glaucous layer that increases surface albedo, reflecting UV and near-infrared radiation to reduce the total solar energy absorbed by the tissues (Mondal et al. 2015). When combined with darker green foliage—which indicates higher chlorophyll density and strong baseline photosynthetic capacity (Öztürk 2011; Bandyopadhyay et al. 2021)—these structural adaptations form a highly effective defense system.

Mechanistically, these physical traits provide "passive" cooling, which reduces the plant's reliance on "active" physiological cooling via transpiration. While non-waxy, flat leaves must expend large amounts of water through open stomata to cool down—or risk dangerous internal temperatures when stomata close to conserve moisture—curled and waxy leaves inherently absorb less heat. This lower baseline heat load allows stomata to remain open longer, sustaining CO2 uptake and carbon assimilation without excessive water loss. Because traits like waxiness are highly heritable and easily scored visually, they serve as a valuable structural

"thermal armor" that breeding programs can seamlessly integrate to elevate baseline environmental resilience.

Source-Sink Dynamics and Grain Filling Under Terminal High-Temperature Stress

Terminal heat stress induces accelerated leaf senescence, truncating the grain-filling duration by 17–20% (Hays et al. 2007; Akter and Islam 2023). The grain-filling rate, computed here as single grain weight divided by grain-filling duration (see Methods), increased by 9–13% under late sowing. It is important to note that because grain-filling duration was shortened by 17–20%, a part of this computed rate increase is arithmetically expected: a shorter denominator elevates the ratio even if numerator grain weight is unchanged or reduced. In the absence of direct thousand-kernel weight (TKW) data in the present study, it cannot be determined what proportion of the rate increase reflects genuine accelerated assimilate flux versus this arithmetic artefact. Consequently, the commonly invoked "panic filling" interpretation (Farooq et al. 2011) should be regarded as tentative; future studies should measure TKW directly to evaluate whether accelerated rates translate to maintained or reduced final grain weight. Subject to this qualification, the pattern is consistent with compensatory mobilization of assimilates within a compressed timeframe. If grain weight is indeed compromised under stress — as widely reported in the literature (Dias et al. 2009) — this dynamic suggests that heat-stressed yield is fundamentally source-limited rather than sink-limited; the primary bottleneck is the functional lifespan of the photosynthetic machinery, not the grain's physical capacity to store starch (Al-Khateeb et al. 2019; Luo et al. 2022; Gaju et al. 2023). Genotypes that maintain a longer filling duration successfully extend their source activity through interconnected traits like cooler canopies and functional stay-green. When current carbon assimilation inevitably declines under intense heat, the efficient remobilization of non-structural stem reserves becomes critical to finish grain development (Meena et al. 2024). Consequently, breeding programs should pivot away from targeting rapid filling rates and instead select for upstream mechanisms that prolong source duration, utilizing diverse landraces to shift crop improvement from a sink-driven to a source-driven approach.

Synthesis and Implications for Breeding High-Temperature Tolerant Durum Wheat

The genetic diversity within Southeast Anatolian landraces offers a robust reservoir for developing climate-resilient durum wheat. Because terminal heat stress induces complex physiological bottlenecks, breeding programs must shift from singular yield metrics to a multi-trait selection index that pyramids specific phenological and functional mechanisms. The superior genotypes identified in this study (e.g., 82, 83, 87, 99, 103, 104) successfully integrate heat escape, passive cooling, and sustained source activity.

To systematically capture these mechanisms, a tiered breeding strategy is recommended:

1. **(High-Throughput Screening**: Canopy Temperature (CTP) (Koutroubas and Sfatkic 2022) and Days to Heading (El-basyoni et al. 2024; Tahmasebi et al. 2021) should be used for initial, large-scale screening of breeding populations. These traits capture the core strategies of physiological tolerance and phenological escape.
2. **Physiological Confirmation**: Selected lines should be evaluated for SPAD maintenance/stay-green characteristics (Ristic et al. 2007; Ali et al. 2020) and visually scored for adaptive morphological traits like Leaf Erectness (Tekdal 2012) and Waxiness (Mondal et al. 2015). These traits confirm the underlying resilience of the photosynthetic system and protective structures.
3. **Yield Component Analysis**: In the most promising lines, Grain Filling Duration (Hays et al. 2007) and Thousand Kernel Weight should be analyzed to confirm that the selected physiological traits translate into stable yield components under stress.

Ultimately, these landraces provide the foundational genetic architecture for mapping specific QTLs through genomic studies. By employing marker-assisted selection to pyramid alleles controlling these interconnected morphological and physiological traits, breeders can strategically design wheat ideotypes optimized for high-temperature environments (El-basyoni et al. 2024).

Conclusion and Recommendations

Late-sown terminal heat stress imposes a severe physiological bottleneck on durum wheat by accelerating ontogeny and prematurely degrading photosynthetic source capacity. The observed truncation of the grain-filling duration (17–20%), coupled with significant reductions in stay-green period and chlorophyll retention, forces a compensatory but ultimately insufficient acceleration in grain-filling rate (9–13%). This accelerated rate is a stress-driven remobilization response—a symptom of early senescence—rather than a true marker of physiological efficiency (Hays et al. 2007; Farooq et al. 2011; Akter and Islam 2023). However, the extensive genetic variation among the 90 Southeast Anatolian landraces reveals robust, exploitable adaptive strategies. Superior genotypes (e.g., landraces 82, 83, 87, 99, 103, 104 and cultivars Artuklu, Sümerli) successfully buffer

thermal stress through a synchronized tripartite mechanism: phenological plasticity associated with a shorter growing cycle under late-sowing conditions (which may partly reflect a genotypic capacity for relative earliness but is also driven by the warmer environment of late sowing), passive structural avoidance via leaf curling and epicuticular wax to reduce incident radiative heat load, and sustained physiological function via cooler canopies and extended stay-green to prolong assimilate translocation (Tekdal 2012; Mondal et al. 2015; Koutroubas and Sfatkic 2022).

Because heat tolerance relies on these interconnected pathways, breeding programs must transition from singular yield-based metrics to a multi-trait selection index. This index should systematically integrate high-throughput phenological and thermal screening (heading time and canopy temperature) with secondary confirmations of structural "armor" (waxiness, leaf erectness, curling) and source longevity (SPAD maintenance, grain-filling duration). Furthermore, the high-performing landraces identified herein represent indispensable genetic reservoirs for high-resolution genomic mapping. Dissecting the quantitative trait loci (QTLs) governing these adaptive plant architectures will enable the deployment of marker-assisted selection, allowing breeders to efficiently introgress these complex, multi-genic tolerance mechanisms into elite durum wheat cultivars to secure regional and global climate resilience (Tahmasebi et al. 2021; El-basyoni et al. 2024).

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Declarations

Conflict of interest The authors declared that they have no conflict of interest to this work. We declare that we do not have any commercial or associative interest that represents a conflict of interest in connection with the work submitted.

References

Akçura M (2006) Türkiye kışlık ekmeklik buğday genetik kaynaklarının karakterizasyonu. Dissertation, Selçuk University

Akter N, Islam MR (2017) Heat stress effects and management in wheat: a review. Agron Sustain Dev 37:1–17. https://doi.org/10.1007/s13593-017-0443-9

Akter N, Islam MR (2023) Heat stress in wheat: a global challenge to feed billions in the current era of the changing climate. Front Sustain Food Syst 7:1203721

Al-Khateeb AA, Al-Abdallat AM, Al-Tawaha AR, Al-Issa TA (2019) Heat stress effects on source–sink relationships and metabolome dynamics in wheat. Funct Plant Biol 46:999–1013

Alam MN, Mannaf MA, Sarker MAZ, Akhter MM (2014) Effect of terminal high temperature imposed by late sowing on phenological traits of wheat (*Triticum aestivum* L). Int J Agron Agric Res 3:6–10

Ali M, Mubeen M, Hussain N, Ali L, Farid HU, Anjum MA (2020) Deciphering the role of stay-green trait to mitigate terminal heat stress in bread wheat (*Triticum aestivum* L). Agronomy 10:1001

Ali A, Ali Q, Javid M, Iqbal MS, Ahmad MQ (2022) Leaf rolling dynamics for atmospheric moisture harvesting in wheat plant as an adaptation to arid environments. Environ Sci Pollut Res 29:66959–66973

Asseng S, Foster I, Turner NC (2011) The impact of temperature variability on wheat yields. Glob Change Biol 17:997–1012. https://doi.org/10.1111/j.1365-2486.2010.02262.x

Asseng S, Ewert F, Martre P, Rötter RP, Lobell DB, Cammarano D, Zhu Y (2015) Rising temperatures reduce global wheat production. Nat Clim Change 5:143–147

Bandyopadhyay T, Saha S, Kumar A, Singh AK, Kumar S (2021) Association of leaf chlorophyll content with the stay-green trait and grain yield in wheat grown under heat stress. Czech J Genet Plant Breed 57:161–169

Çakır E, Alsaleh A, Bektas H, Özkan H (2025) Wild emmer (*Triticum turgidum* ssp. *dicoccoides*) diversity in southern Turkey: evaluation of SSR and morphological variations. Life 15:203. https://doi.org/10.3390/life15020203

Dias AS, Lidon FC, Ramalho JC (2009) Evaluation of grain filling rate and duration in bread and durum wheat, under heat stress after anthesis. J Agron Crop Sci 195:137–147

Dreccer MF, Fainges J, Whish J, Ogbonnaya FC, Sadras VO (2018) Comparison of sensitive stages of wheat, barley, canola, chickpea and field pea to temperature and water stress across Australia. Agric Meteorol 248:275–294

El-basyoni I, El-maghraby M, Al-ashkar I, Al-suhaibani N, Al-otaibi S, Al-qahtani S, Mourad M (2024) Identification of novel marker–trait associations for agronomic traits in bread wheat under WANA environments through GWAS. PLoS ONE 19:e0309838. https://doi.org/10.1371/journal.pone.0309838

Farooq M, Bramley H, Palta JA, Siddique HM (2011) Heat stress in wheat during reproductive and grain-filling phases. Crit Rev Plant Sci 30:1–17. https://doi.org/10.1080/07352689.2011.615687

Federer WT (1956) Augmented (or Hoonuiaku) designs. Hawaii Planters' Record 55:191–208

Fischer RA, Byerlee D, Edmeades GO (2014) Crop yields and global food security: will yield increase continue to feed the world? Australian Centre for International Agricultural Research, Canberra

Gaju O, Reynolds MP, Murchie EH (2023) Sink strength: a key determinant of yield potential in wheat. J Exp Bot 74:40–55

Hays DB, Do JH, Mason RE, Morgan G, Finlayson SA (2007) Heat stress induced ethylene production in developing wheat grains induces kernel abortion and increased maturation. Plant Sci 172:1113–1123

Hunt JR, Hayman PT, Richards RA, Passioura JB (2018) Opportunities to reduce heat damage in rain-fed wheat crops based on plant breeding and agronomic management. Field Crops Res 224:126–138. https://doi.org/10.1016/j.fcr.2018.05.012

Jamil M, Aamir A, Alvina G, Awan A, Napar A, Amir İ, Naveed N, Yasin N, Mujeeb-Kazi A (2019) Genome-wide association studies of seven agronomic traits under two sowing conditions in bread wheat. BMC Plant Biol 19:149. https://doi.org/10.1186/s12870-019-1754-6

Kadioglu A, Terzi R, Saruhan N, Saglam A (2012) Current advances in the investigation of leaf rolling caused by biotic and abiotic stress factors. Plant Sci 192:13–20

Kamal NM, Gorafi YSA, Abdel-ghany HM, El-basyoni ISM (2019) Stay-green trait: a prospective approach for yield potential, and drought and heat stress adaptation in cereals. Agronomy 9:837

Karaman M (2017) Makarnalık buğdayda fizyolojik ve morfolojik parametrelerin verim ve kalite ile olan ilişkisinin belirlenmesi. Dissertation, Dicle University

Kılıç H (2020) Durum buğday genotiplerinin (*Triticum durum* L.) yüksek sıcaklık şartlarında verim ve bazı kalite özellikleri yönünden değerlendirilmesi. Int J Pure Appl Sci 6:17–32. https://doi.org/10.29132/ijpas.721877

Koutroubas SD, Sfatkic D (2022) Canopy temperature depression for drought- and heat-stress tolerance in wheat breeding. Vavilov J Genet Breed 26:196–201

Lopes MS, Reynolds MP (2012) Stay-green in spring wheat can be determined by spectral reflectance measurements (normalized difference vegetation index) independently from phenology. J Exp Bot 63:3789–3798

Luo Z, Liu H, Xie J, Liu S, Li X, Zhang A (2022) Source–sink relations and responses to sink–source manipulations during grain filling in wheat. Agronomy 12:1198

Meena MK, Singh AK, Kumar S, Singh R, Kumar A (2024) Stay-green and stem reserve mobilization: key physiological traits for improving grain filling in wheat under abiotic stress. Front Plant Sci 15:1541944

Modhej A, Farhoudi R, Afrous A (2015) Effect of post-anthesis heat stress on grain yield of barley, durum and bread wheat genotypes. In Proceedings of the 10th International Barley Genetics Symposium. Apr 2008. (230). Alexandria, Egypt ICARDA

Mondal S, Singh RP, Crossa J, Huerta-Espino J, Sharma I, Chatrath R, Joshi AK (2015) Association of canopy temperature and stay-green trait with grain yield and its components in wheat under late-sown, high-temperature stress. Field Crops Res 179:1–10

Özberk İ, Zencirci N, Özkan H, Özberk F, Eser V (2010) Dünden bugüne makarnalık buğday ıslahı ve geleceğe bakış. In: Makarnalık Buğday ve Mamulleri Konferansı. Ankara, pp 43–66

Öztürk İ (2011) Ekmeklik buğday (*Triticum aestivum* L.) genotiplerinde kurağa etkilerinin karakterizasyonu ve kalite ile ilişkileri. Dissertation, Namık Kemal University

Ramya KT, Jain N, Ramya P, Singh PK, Arora A, Singh GP, Prabhu KV (2015) Genotypic variation for normalized difference vegetation index and its relationship with grain yield in wheat under terminal heat stress. Indian J Genet Plant Breed 75:174–182

Ristic Z, Bukovnik U, Prasad PV (2007) Correlation between heat stability of thylakoid membranes and loss of chlorophyll in winter wheat under heat stress. Crop Sci 47:2067–2073. https://doi.org/10.2135/cropsci2006.10.0674

Rsaliyev SS, Urazaliev RA, Ziyaev ZM, Yusupov NK (2024) Drought tolerance in winter wheat cultivars grown in Kazakhstan and Uzbekistan. SABRAO J Breed Genet 56:1918–1928. https://doi.org/10.54910/sabrao2024.56.5.15

Shah L, Yahya M, Shah SMA (2019) Improving lodging resistance: using wheat and rice as classical examples. Agronomy 9:612

Tahmasebi S, Heidari B, Pakniyat H, McIntyre CL (2021) A major QTL on chromosome 7D for terminal drought and heat escape in wheat (*Triticum aestivum* L). Theor Appl Genet 134:175–193

Tekdal S (2012) Makarnalık buğdaylarda (*Triticum durum* Desf.) sıcaklık stresine toleransın belirlenmesinde kullanılabilecek fizyolojik ve morfolojik parametrelerin araştırılması. Dissertation, Dicle University

Thistlethwaite RJ, Tan DK, Buckley TN, Trethowan RM (2015) Identification of genetic variation in heat stress and mechanisms of tolerance in wheat. Procedia Environ Sci 29:30

Ullah S (2018) The influence of AB genome variation on the high-temperature tolerance of wheat. Dissertation, University of Sydney

Wollenweber B, Porter JR, Schellberg J (2003) Lack of interaction between extreme high-temperature events at vegetative and reproductive growth stages in wheat. J Agron Crop Sci 189:142–150

Zandalinas SI, Mittler R, Balfagón D, Arbona V, Gómez-Cadenas A (2018) Plant adaptations to the combination of drought and high temperatures. Physiol Plant 162:2–12

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