

IMPACT OF WATER DEFICIT CONDITIONS ON MORPHOLOGICAL AND PHYSIOLOGICAL TRAITS OF SPRING WHEAT DURING EARLY AND LATE GROWTH STAGES

Original Article

Aziz Ullah^{1*}, Babar Islam², Khalil Ahmad³, Muhammad Majid⁴, Ilyas Ahmad⁵, Muhammad Omer Farooq⁶, Ubaid Ullah Anwar⁷, Muhammad Amir Amin⁸, Asia Batool⁸

¹Department of Plant Breeding and Genetics, College of Agriculture, University of Sargodha, Pakistan.

²Department of Plant Breeding and Genetics, Bahauddin Zakria University, Multan, Pakistan

³Vegetable Research Institute, Faisalabad, Pakistan.

⁴Lab Analyst GGAS Hi Tech Labs, Faisalabad, Pakistan.

⁵Pesticide Quality Control Laboratory, Multan, Pakistan.

⁶Department of Plant Breeding and Genetics, University of Agriculture Faisalabad, Pakistan.

⁷Molecular Plant Pathology Lab, Department of Plant Sciences, Quaid-e-Azam University Islamabad, Pakistan.

⁸Pulses Research Institute Faisalabad, Pakistan.

Corresponding Author: Aziz Ullah, Department of Plant Breeding and Genetics, College of Agriculture, University of Sargodha, Pakistan, drkr1367@gmail.com

Conflict of Interest: None

Grant Support & Financial Support: None

Acknowledgment: The authors acknowledge the support of the University of Sargodha's research facilities during this study.

ABSTRACT

Background: Wheat (*Triticum aestivum* L.) is one of the most essential cereal crops globally due to its nutritional value and wide consumption. However, drought stress significantly reduces wheat productivity, with grain yield losses reaching up to 40% in arid and semi-arid regions. Enhancing drought tolerance in wheat is critical for sustaining food security under climate variability. Screening and identification of drought-resilient genotypes form the foundation of drought-focused breeding programs.

Objective: This study aimed to evaluate the drought tolerance of fifty wheat genotypes through comprehensive physio-morphological assessments at seedling and reproductive stages under controlled and field drought conditions.

Methods: The experiment was conducted at the University of Sargodha over two consecutive growing seasons (2022–2024). Fifty genotypes were first evaluated at the seedling stage under two water treatments—100% and 50% field capacity—in a factorial arrangement with three replications. Traits measured included fresh and dry shoot weight and relative water content (RWC). Based on performance, seven genotypes were selected and assessed in the field using a split-plot design with three replications under normal and drought stress. Parameters recorded included days to flowering and maturity, plant height, number of grains per plant (NOG), 1000-grain weight (GW), and grain yield per plant (GYP).

Results: NR-583 recorded the highest RWC values (90.1% normal, 79.1% drought) and GYP (7.5 g normal, 6.9 g drought), followed by NR-582 (85.2%, 75.2%; 7.6 g, 6.5 g). NR-559 exhibited the most sensitivity, with the sharpest decline in RWC (65.1% to 50.1%) and GYP (7.5 g to 4.2 g). Grain weight dropped by 20–40% under drought across genotypes, while GYP decreased by up to 45%.

Conclusion: NR-582 and NR-583 showed exceptional drought resilience and yield stability, making them strong candidates for future wheat breeding in water-deficit environments.

Keywords: Drought Stress, Grain Yield, Plant Height, Relative Water Content, *Triticum aestivum*, Water Deficit, Wheat Breeding.

INTRODUCTION

Wheat (*Triticum aestivum* L.) stands as one of the world's most essential staple cereal crops, ranking second only to maize in terms of global cultivation and direct human consumption (1). Its centrality to global food systems is underscored by its diverse use in everyday diets, ranging from bread and pasta to cakes and confections, making it a vital component of nutritional security across regions. In Pakistan, wheat not only serves as the principal dietary staple but also plays a fundamental role in the agrarian economy. It is cultivated extensively across both irrigated plains and rainfed zones, thanks to its adaptability to varied agro-climatic conditions and significant nutritional value (2). The crop contributes meaningfully to the national Gross Domestic Product (GDP) and is a key source of livelihood for millions of rural households (2,3). Despite its national importance, wheat production in Pakistan remains below potential. While progressive farmers utilizing optimal agronomic practices report yields as high as 8,000 kg per hectare, the national average yield lingers around 2,600 kg per hectare (4,5). This yield disparity highlights systemic production constraints, including the use of low-quality seed, untimely sowing, suboptimal soil fertility management, and increasing vulnerability to climate-induced stressors. Among these challenges, water scarcity has emerged as one of the most pressing concerns. Pakistan, now officially classified as a water-deficit country, has seen its annual per capita water availability fall below 1,000 cubic meters due to climate variability, rapid population growth, and inadequate water resource management (6,7). These conditions pose a significant threat to wheat productivity, particularly during sensitive phenological stages such as seedling establishment, anthesis, and grain filling.

Drought stress, characterized by prolonged water deficit during key developmental phases, is among the most severe abiotic factors impairing wheat growth. It disrupts fundamental physiological processes such as leaf turgor maintenance, stomatal regulation, photosynthetic capacity, and root-shoot development, ultimately compromising biomass accumulation and grain yield (8). Reports suggest that under extreme drought stress, wheat yield can be reduced by up to 90% compared to conditions with adequate irrigation (9,10). Given the recurring nature of droughts in arid and semi-arid regions like Pakistan, there is a growing urgency to develop wheat cultivars that are resilient to such conditions. Enhancing drought tolerance in wheat through genetic improvement has therefore become a pivotal goal of modern breeding programs. Current scientific consensus highlights that drought tolerance is a complex trait governed by a combination of physiological and morphological attributes. Traits such as relative water content (RWC), chlorophyll concentration, root system architecture, canopy temperature, and stomatal conductance are considered reliable indicators of a genotype's ability to withstand water-deficit environments (11,12). However, many breeding efforts have focused only on later developmental stages, often overlooking the importance of early-stage screening for drought responsiveness. There remains a gap in the comprehensive evaluation of genotypes across both early and late growth phases under drought conditions (13,14).

Addressing this knowledge gap, the present study evaluates a diverse set of wheat genotypes for their drought response at two critical growth stages: the seedling stage and maturity. Initially, genotypes were screened under controlled water stress for morpho-physiological traits such as shoot and root length, leaf area, RWC, and seedling chlorophyll content. Based on performance at this stage, selected genotypes were further assessed under prolonged drought stress during anthesis and physiological maturity, with additional parameters including flag leaf chlorophyll content, stomatal conductance, canopy temperature, yield components, and harvest index being measured. By integrating performance data across developmental stages, this study aims to identify genotypes exhibiting consistent drought resilience, offering promising candidates for future breeding programs focused on improving wheat productivity in water-limited environments. The objective of this research is to identify wheat genotypes with enhanced tolerance to drought by evaluating their physiological and morphological responses under water deficit conditions at both seedling and reproductive stages.

METHODS

Seedling Experiment: The seedling experiment was carried out in the research area of the Department of Plant Breeding and Genetics, University of Sargodha, during the 2022–2023 growing season. A total of fifty wheat (*Triticum aestivum* L.) genotypes were evaluated using a two-factor factorial design with three replications. Each replication consisted of five plants per genotype, maintained in individual sand-filled polythene bags measuring 30 cm in length and 15 cm in width. One seedling was planted per bag to ensure uniform growth conditions and avoid competition. The sowing was conducted on November 10, 2022. The average ambient temperature recorded during the experimental period was 28°C. A pressure membrane apparatus was employed to determine the field capacity of the sand medium. Two irrigation treatments were imposed: Treatment 1 (control) received 100% field capacity with 30 ml of water per bag, while Treatment 2 (stress) received 50% field capacity with 15 ml of water per bag, administered on alternate days. Drought stress was induced

by withholding water after 25 days of growth. At this stage, data were collected for key physiological parameters including fresh shoot weight, dry shoot weight, and relative water content (RWC). RWC was calculated using the formula:

$$\text{RWC (\%)} = [(\text{Fresh shoot weight} - \text{Dry shoot weight}) / (\text{Turgid weight} - \text{Dry shoot weight})] \times 100$$

All experimental conditions were maintained uniformly across replications to ensure comparability of results. Ethical approval was not required for this segment of the study as it involved no human or animal subjects. However, all procedures adhered to institutional biosafety guidelines.

Field Experiment: In the following year (2023–2024), the genotypes that exhibited superior physiological responses under drought stress at the seedling stage were further evaluated under field conditions. A total of seven genotypes were selected for this phase. The trial was conducted in a tunnel facility equipped for controlled irrigation treatments. A split-plot design was implemented under a randomized complete block design (RCBD) with three replications. The main plot factor was irrigation treatment (normal vs. drought), while genotype served as the subplot factor. Each subplot measured 1.8 m² with inter-row spacing maintained at 22 cm to allow adequate plant development. Drought stress in the experimental plots was simulated by withholding irrigation and shielding the tunnel area with a polythene sheet during rainfall events, thus preventing any unintended water input. Conversely, the control plots were regularly irrigated, and no polythene cover was applied to allow for normal precipitation and irrigation. Agronomic and yield-related parameters recorded at crop maturity included days to flowering, days to maturity, plant height (cm), number of grains per plant, 1000-grain weight (g), and grain yield per plant (g). Data from both experimental phases were subjected to statistical analysis using standard ANOVA procedures to evaluate the significance of genotype, treatment, and interaction effects. Statistical analysis software such as SPSS or R was used to ensure accurate interpretation of variance among treatments. While no direct ethical concerns were associated with this plant-based study, the trial was conducted in compliance with institutional standards for environmental and research safety.

RESULTS

Analysis of variance confirmed statistically significant differences among the fifty wheat genotypes for relative water content (RWC) under both normal and water-deficit conditions. A highly significant genotype $\times$ treatment interaction was also observed, demonstrating the varying drought tolerance capacities across genotypes. The genotype NR-583 exhibited the highest RWC values, maintaining 90.1% under normal irrigation and 79.1% under drought stress. This minimal reduction reflected strong drought resilience. NR-582 followed closely with 85.2% in normal and 75.2% in drought conditions, suggesting excellent adaptability. Urooj 22 showed moderate performance, with values of 81.2% and 71.2%, respectively, while Akbar 2019 and Chakwal 86 exhibited lower RWC under stress, indicating moderate tolerance. In contrast, NR-608 and NR-559 displayed the most significant declines, particularly NR-559, which dropped from 65.1% under normal conditions to 50.1% during drought, identifying it as the most drought-susceptible genotype. The reduction in RWC across genotypes aligned with previous findings, where water stress disrupted internal water balance and decreased cellular hydration (5,6). Physiological mechanisms such as osmotic adjustment was likely activated, concentrating compatible solutes like proline and sugars to retain water (7,8).

The field experiment conducted in the following season further validated these findings under controlled tunnel conditions. Seven genotypes were evaluated for physiological and yield traits under normal irrigation and complete water deficit until maturity. Grain yield per plant (GYP) was highest in NR-582 (7.6 g) and NR-583 (7.5 g) under normal conditions. Despite a decline under drought, both genotypes retained relatively high yields—6.5 g and 6.9 g, respectively—showing their drought resilience. NR-608 also performed well under normal conditions (7.4 g) but exhibited a larger drop to 5.5 g under stress. Urooj 22 experienced a notable yield loss from 6.9 g to 4.9 g, primarily due to a sharp decline in 1000-grain weight (from 24.5 g to 15.3 g). Akbar 2019 and Chakwal 86 exhibited early flowering and early maturity, suggesting a drought escape strategy. However, yield performance still dropped significantly under drought (Akbar 2019: 6.8 g to 4.8 g; Chakwal 86: 6.7 g to 5.4 g). NR-559, though initially high-yielding under normal conditions (7.5 g), showed the steepest reduction to 4.2 g, highlighting its poor adaptability to water stress. All genotypes showed reductions in plant height, grain number, and 1000-grain weight under drought. The average decrease in plant height ranged from 15 to 20 cm, while the number of grains per plant reduced by approximately 25%. The 1000-grain weight declined by 15–30%, depending on genotype. The reduction in these yield components indicated that drought stress significantly impaired reproductive development and photosynthate translocation during the grain-filling stage.

Shortened days to flowering (DOF) and days to maturity (DOM) were observed across genotypes under drought, consistent with a drought escape mechanism. For instance, NR-583 matured at 146.6 days under drought compared to 152.1 days under normal irrigation. A similar trend was seen in NR-582 (DOM: 145.3 vs. 153), Chakwal 86 (144.6 vs. 157), and Akbar 2019 (145.3 vs. 156.6). Early flowering and maturity allowed these genotypes to complete their lifecycle before peak water stress, partially mitigating yield losses. Overall, NR-583 and NR-582 consistently demonstrated superior performance across both physiological and agronomic traits, suggesting they are promising candidates for drought-prone environments. Their capacity to maintain RWC, grain number, and grain weight under water deficit conditions underlines their potential utility in breeding programs aimed at enhancing wheat drought resilience.

Table 1: Mean values of wheat genotypes of yield and yield related traits under normal and drought conditions

Genotypes	Trt	DOF m±S.E	DOM m±S.E	PH (cm) m±S.E	NOG P ⁻¹	1000 GW (g) m±S.E	GYP ⁻¹ (g) m±S.E
NR-583	N	99.6±0.98	152.1±0.91	109.3±0.59	79.6±0.74	35.8±0.81	7.5±0.69
	D	90±0.89	146.6±0.85	91.4±0.88	47.3±0.54	27.5±0.86	6.9±0.56
NR-582	N	98±0.88	153±0.87	109.2±0.84	78.6±0.54	35.8±0.80	7.6±0.64
	D	92.3±0.7	145.3±0.82	90.3±0.59	46.3±0.87	26.8±0.74	6.5±0.56
Urooj 22	N	91.3±0.85	154.3±0.75	108.6±0.51	78.3±0.52	24.5±0.42	6.9±0.56
	D	87.6±0.87	143.6±0.74	89.76±0.62	45.3±0.87	15.3±0.42	4.9±0.58
Akbar 2019	N	84.3±0.75	156.6±0.75	107.5±0.67	77.6±0.53	22.3±0.84	6.8±0.56
	D	83.6±0.68	145.3±0.76	88.7±0.62	44.3±0.87	15.3±0.87	4.8±0.58
Chakwal 86	N	91.3±0.74	157±0.78	107.6±0.63	65.3±0.52	21.4±0.89	6.7±0.56
	D	86.3±0.68	144.6±0.79	88.1±0.57	43.3±0.87	15.3±0.78	5.4±0.35
NR-608	N	98.3±0.47	151.3±0.71	111.7±0.91	81.6±0.57	23.5±0.62	7.4±0.54
	D	95.6±0.52	145.3±0.73	95.4±0.54	54.3±0.53	16.1±0.48	5.5±0.52
NR0559	N	99.6±0.57	153±0.72	110.6±0.52	77.6±0.53	26.8±0.45	7.5±0.81
	D	94.6±0.53	149.6±0.71	95.2±0.54	53.3±0.87	18.5±0.58	4.2±0.89

Table 2: Wheat Genotype Performance Data

Genotype	Normal GYP	Drought GYP	Normal RWC	Drought RWC
NR-583	7.5	6.9	90.1	79.1
NR-582	7.6	6.5	85.2	75.2
Urooj 22	6.9	4.9	81.2	71.2
Akbar 2019	6.8	4.8	75.2	65.1
Chakwal 86	6.7	5.4	70.2	60.1
NR-608	7.4	5.5	67	55
NR-559	7.5	4.2	65.1	50.1

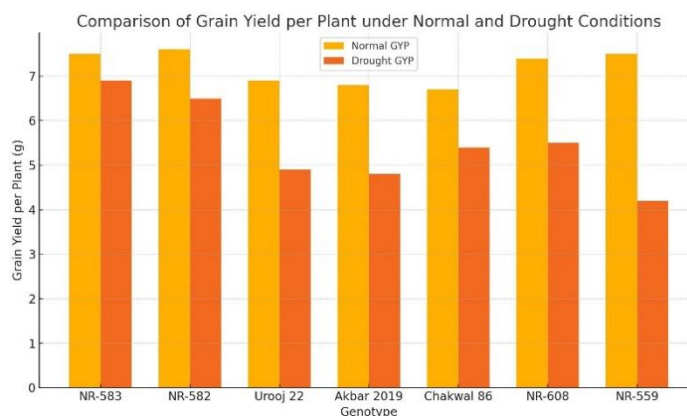


Figure 1 Comparison of Grain Yield Per Plant Under Normal and Drought Conditions

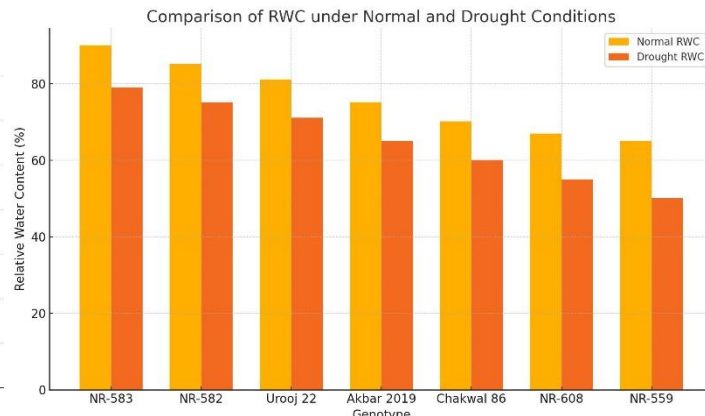


Figure 2 Comparison of RWC Under Normal and Drought Conditions

Mean Comparison of selected wheat genotypes for RWC at 50% FC and 100% FC.

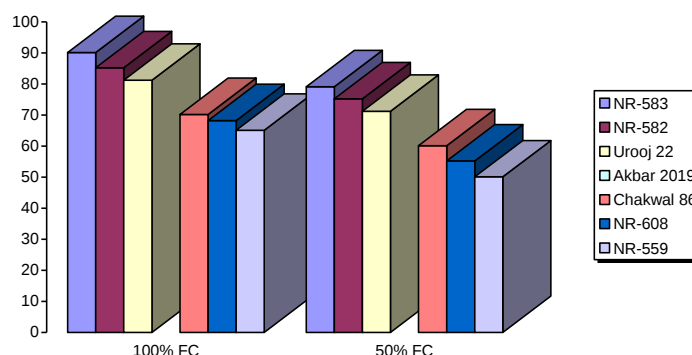


Figure 3 Mean Comparison of Selected Wheat Genotypes for RWC at 50% FC and 100% FC

DISCUSSION

The findings of this study demonstrate substantial genotypic variation in wheat response to drought stress, particularly in terms of relative water content (RWC), grain yield per plant (GYP), and other yield-related attributes. The genotype NR-583 consistently showed superior performance under both normal and water-deficit conditions, affirming its potential as a drought-resilient variety. This observation is in agreement with recent research emphasizing the importance of physiological traits like RWC and 1000-grain weight in identifying drought-tolerant wheat cultivars (15,16). The ability of NR-583 and NR-582 to maintain higher RWC and grain yield under drought conditions reflects strong osmotic adjustment capacity, which is a crucial trait for sustaining cellular hydration and metabolic function during periods of water scarcity. The use of RWC as a primary indicator of drought tolerance aligns with earlier findings and continues to be validated by recent literature. RWC remains one of the most reliable physiological indicators for drought assessment due to its direct association with plant water status and stomatal behavior (17,18). Under drought conditions, genotypes like NR-583 that retained higher RWC also showed reduced reduction in grain yield, confirming the critical link between physiological stability and agronomic performance. This study also highlighted that, genotypes employing a drought escape mechanism, such as early flowering and maturity observed in Akbar 2019 and Chakwal 86, may offer partial protection against drought stress by completing the life cycle before peak stress periods. However, their yield performance under stress conditions did not match that of NR-583 or NR-582, suggesting that drought escape alone may not be sufficient for stable productivity (19).

The observed decline in 1000-grain weight across all genotypes under drought stress is consistent with existing evidence that water deficit during grain filling reduces assimilate accumulation and hinders translocation processes (20). Photosynthesis inhibition due to stomatal closure and oxidative stress further disrupts source-sink dynamics, contributing to lower grain weight and overall yield loss (21,22). Moreover, the variability in the extent of yield reduction among genotypes underscores the presence of genetic diversity in stress adaptability, which can be exploited in breeding programs. One of the key strengths of this study lies in its two-phase approach, beginning with a controlled seedling evaluation and extending to a field-based assessment under realistic drought simulation. This structure provided a comprehensive understanding of genotype performance across different developmental stages. The use of both physiological and agronomic parameters strengthened the interpretability and applicability of results, ensuring that selected genotypes are not only physiologically resilient but also agronomically viable.

However, several limitations must be acknowledged. The study did not incorporate molecular or biochemical analyses such as proline accumulation, antioxidant enzyme activity, or gene expression profiling, which could provide deeper insights into the mechanisms underlying drought tolerance. Additionally, important physiological traits like stomatal conductance, canopy temperature, and water-use efficiency were not evaluated, limiting the physiological resolution of the findings. These omissions, while not diminishing the value of the study, highlight areas for future research that could enrich the phenotypic data with mechanistic understanding. Another limitation was the lack of multi-environment trials. The study was confined to a single location and two cropping seasons, which may not capture the full extent of genotype $\times$ environment interactions. Future studies should incorporate diverse agro-ecological zones and seasonal variations to confirm the stability of identified drought-tolerant genotypes. Furthermore, inclusion of large-scale yield trials under farmer field conditions would enhance the translational value of the research and support the integration of top-performing genotypes into commercial breeding programs (23).

Despite these limitations, the study provides valuable contributions to drought tolerance research in wheat. It reinforces the role of early screening in identifying promising genotypes and supports the integration of both physiological and agronomic parameters in selection protocols. The findings have practical implications for breeding programs aimed at enhancing wheat productivity in arid and semi-arid regions, where water availability is increasingly unpredictable due to climate change. Moreover, the observed variability in yield response among genotypes suggests opportunities for pyramiding multiple traits—such as high RWC, stable grain weight, and early maturity—into elite lines to achieve durable drought resilience. Advancements in high-throughput phenotyping, genomics, and crop modeling can further enhance the screening and selection processes. Genomic selection approaches, combined with precise physiological trait data, could accelerate the development of varieties tailored to specific drought-prone environments. The integration of this study's findings into such frameworks can contribute meaningfully to climate-resilient agriculture and national food security strategies.

CONCLUSION

This study identified NR-582 and NR-583 as the most promising wheat genotypes, demonstrating stable performance and resilience across both normal and drought conditions. Their ability to maintain grain yield and critical physiological traits under water stress highlights their potential for cultivation in drought-prone regions. NR-608 also showed strong yield capacity, though with slightly less stress adaptability, while Urooj 22, Akbar 2019, and Chakwal 86 displayed moderate tolerance. NR-559 proved highly sensitive to drought, indicating limited suitability for water-limited environments. These findings provide valuable direction for future breeding programs focused on improving wheat productivity and stability under climate-induced water scarcity, contributing to food security in vulnerable agro-ecosystems.

AUTHOR CONTRIBUTION

Author	Contribution
Aziz Ullah*	Substantial Contribution to study design, analysis, acquisition of Data
	Manuscript Writing
	Has given Final Approval of the version to be published
Babar Islam	Substantial Contribution to study design, acquisition and interpretation of Data
	Critical Review and Manuscript Writing
	Has given Final Approval of the version to be published

Author	Contribution
Khalil Ahmad	Substantial Contribution to acquisition and interpretation of Data Has given Final Approval of the version to be published
Muhammad Majid	Contributed to Data Collection and Analysis Has given Final Approval of the version to be published
Ilyas Ahmad	Contributed to Data Collection and Analysis Has given Final Approval of the version to be published
Muhammad Omer Farooq	Substantial Contribution to study design and Data Analysis Has given Final Approval of the version to be published
Ubaid Ullah Anwar	Contributed to study concept and Data collection Has given Final Approval of the version to be published
Muhammad Amir Amin	Writing - Review & Editing, Assistance with Data Curation
Asia Batool	Writing - Review & Editing, Assistance with Data Curation

REFERENCES

1. Prasanna BM, Cairns JE, Zaidi PH, Beyene Y, Makumbi D, Gowda M, et al. Beat the stress: breeding for climate resilience in maize for the tropical rainfed environments. *Theor Appl Genet.* 2021;134(6):1729-52.
2. Aliyeva DR, Gurbanova UA, Rzayev FH, Gasimov EK, Huseynova IM. Biochemical and Ultrastructural Changes in Wheat Plants during Drought Stress. *Biochemistry (Mosc).* 2023;88(11):1944-55.
3. Lamom SF, Abdelghany AM, Farouk AS, Alwakel ES, Makled KM, Bukhari NA, et al. Biochemical and yield response of spring wheat to drought stress through gibberellic and abscisic acids. *BMC Plant Biol.* 2025;25(1):5.
4. Langridge P, Reynolds M. Breeding for drought and heat tolerance in wheat. *Theor Appl Genet.* 2021;134(6):1753-69.
5. Hafeez A, Ali S, Javed MA, Iqbal R, Khan MN, Çiğ F, et al. Breeding for water-use efficiency in wheat: progress, challenges and prospects. *Mol Biol Rep.* 2024;51(1):429.
6. Zhang X, Li C, Lu W, Wang X, Ma B, Fu K, et al. Comparative analysis of combined phosphorus and drought stress-responses in two winter wheat. *PeerJ.* 2022;10:e13887.
7. Sallam A, Alqudah AM, Dawood MFA, Baenziger PS, Börner A. Drought Stress Tolerance in Wheat and Barley: Advances in Physiology, Breeding and Genetics Research. *Int J Mol Sci.* 2019;20(13).
8. Li S, Zhang Y, Liu Y, Zhang P, Wang X, Chen B, et al. The E3 ligase TaGW2 mediates transcription factor TaARR12 degradation to promote drought resistance in wheat. *Plant Cell.* 2024;36(3):605-25.
9. Meng Y, Lv Q, Li L, Wang B, Chen L, Yang W, et al. E3 ubiquitin ligase TaSDIR1-4A activates membrane-bound transcription factor TaWRKY29 to positively regulate drought resistance. *Plant Biotechnol J.* 2024;22(4):987-1000.
10. Poggi GM, Corneti S, Aloisi I, Ventura F. Environment-oriented selection criteria to overcome controversies in breeding for drought resistance in wheat. *J Plant Physiol.* 2023;280:153895.
11. Bapela T, Shimelis H, Tsilo TJ, Mathew I. Genetic Improvement of Wheat for Drought Tolerance: Progress, Challenges and Opportunities. *Plants (Basel).* 2022;11(10).
12. Nouraei S, Mia MS, Liu H, Turner NC, Yan G. Genome-wide association study of drought tolerance in wheat (*Triticum aestivum* L.) identifies SNP markers and candidate genes. *Mol Genet Genomics.* 2024;299(1):22.
13. Correia PMP, Cairo Westergaard J, Bernardes da Silva A, Roitsch T, Carmo-Silva E, Marques da Silva J. High-throughput phenotyping of physiological traits for wheat resilience to high temperature and drought stress. *J Exp Bot.* 2022;73(15):5235-51.
14. Feng W, Zhang H, Cao Y, Liu Y, Zhao Y, Sun F, et al. Maize ZmBES1/BZR1-1 transcription factor negatively regulates drought tolerance. *Plant Physiol Biochem.* 2023;205:108188.
15. Peršić V, Ament A, Antunović Dunić J, Drezner G, Cesar V. PEG-induced physiological drought for screening winter wheat genotypes sensitivity - integrated biochemical and chlorophyll a fluorescence analysis. *Front Plant Sci.* 2022;13:987702.
16. Moosavi SS, Abdi F, Abdollahi MR, Tahmasebi-Enferadi S, Maleki M. Phenological, morpho-physiological and proteomic responses of *Triticum boeoticum* to drought stress. *Plant Physiol Biochem.* 2020;156:95-104.

17. Mokhtari N, Majidi MM, Mirlohi A. Physiological and antioxidant responses of synthetic hexaploid wheat germplasm under drought. *BMC Plant Biol.* 2024;24(1):747.
18. Wahab A, Abdi G, Saleem MH, Ali B, Ullah S, Shah W, et al. Plants' Physio-Biochemical and Phyto-Hormonal Responses to Alleviate the Adverse Effects of Drought Stress: A Comprehensive Review. *Plants (Basel).* 2022;11(13).
19. Yi Y, Hassan MA, Cheng X, Li Y, Liu H, Fang W, et al. QTL mapping and analysis for drought tolerance in rice by genome-wide association study. *Front Plant Sci.* 2023;14:1223782.
20. Gill RA, Ahmar S, Ali B, Saleem MH, Khan MU, Zhou W, et al. The Role of Membrane Transporters in Plant Growth and Development, and Abiotic Stress Tolerance. *Int J Mol Sci.* 2021;22(23).
21. Wang D, Zhang X, Cao Y, Batool A, Xu Y, Qiao Y, et al. TabHLH27 orchestrates root growth and drought tolerance to enhance water use efficiency in wheat. *J Integr Plant Biol.* 2024;66(7):1295-312.
22. Du L, Huang X, Ding L, Wang Z, Tang D, Chen B, et al. TaERF87 and TaAKS1 synergistically regulate TaP5CS1/TaP5CR1-mediated proline biosynthesis to enhance drought tolerance in wheat. *New Phytol.* 2023;237(1):232-50.
23. Hussain S, Wang J, Asad Naseer M, Saqib M, Siddiqui MH, Ihsan F, et al. Water stress memory in wheat/maize intercropping regulated photosynthetic and antioxidative responses under rainfed conditions. *Sci Rep.* 2023;13(1):13688.