



A comparison of drought responses in wild wheat relatives and domesticated wheat grown under irrigated and rainfed field conditions

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ABSTRACT

Context: Domestication and breeding processes for developing modern wheat plants from diverse wild relatives and landraces have had unintended effects of loss of genetic diversity. This reduction in genetic variation undermines the ability of modern wheat cultivars to tolerate environmental stresses such as drought. Wheat wild relatives possess untapped genetic potential for tolerating abiotic stress, especially drought. Yet, their morpho-physiological adaptation and drought stress resilience mechanisms remain underexplored.

Objective: This study aimed to investigate the adaptive responses of plants within the *Triticum* spp. gene pool, encompassing wheat wild relatives, landraces, and modern cultivars to drought stress under rainfed and irrigated field conditions.

Methods: From an initial pool of 110 genotypes screened during the first growing season in 2022, 20 best performing genotypes, including modern cultivars for comparison, were selected for a second growing season in 2023 based on their relative yield performance. Two different treatment conditions, irrigated and rainfed, were applied during both growing seasons. This experiment observed single plants per replicate. Multiple parameters, including days to heading and flowering, plant height, number of spikes per plant, spike length, spike weight per plant, straw weight per plant, aboveground biomass per plant, grain yield per plant, thousand kernel weight, harvest index, stomatal conductance, and vegetation indices, were assessed on the selected genotypes.

Results: Taking averages measured across both growing seasons, we observed significant genotypic variation across several parameters: days to heading and flowering, plant height, number of spikes per plant, spike length, spike and straw weight per plant, aboveground biomass per plant, grain yield per plant, thousand kernel weight, harvest index, stomatal conductance, and vegetation indices. Water stress during the rainfed treatment significantly reduced grain yield (by 21 %) and stomatal conductance (by 45 %). Stomatal conductance was associated with grain yield and yield-related traits under rainfed conditions. Diverse physiological drought tolerance mechanisms associated with stomatal regulation were identified, revealing genotype-specific responses to drought stress. Genotypes such as *T. dicoccoides* (G242), *T. urartu* (G45), *T. boeoticum* (G27) and *T. araraticum* (G221) exhibited isohydric adaptation, whereas *T. monococcum* *sinskajae* (G89) and *T. durum* cv. Sambadur (G41) exhibited anisohydric adaptation.

Conclusion: Some genotypes of *T. dicoccoides*, *T. urartu*, *T. boeoticum* and *T. araraticum* exhibited isohydric adaptation, while *T. monococcum* *sinskajae* and *T. durum* cv. Sambadur exhibited anisohydric adaptation under drought stress which needs further verification. These genotypes can serve as donors for introducing drought tolerance traits within wheat improvement programs.

Abbreviations: ARI2, anthocyanin reflectance indices; BM, aboveground biomass per plant; CRI1, carotenoid reflectance index 1; DTF, days to flowering; DTH, days to heading; SPP, number of spikes per plant; gsw, stomatal conductance; GY, grain yield per plant; HI, harvest index; Lic2, Lichtenthaler index 2; NDVI, normalized difference vegetation index; PCA, principal component analysis; PH, plant height; PRI, photochemical reflectance index; SIPI, structure insensitive pigment index; SL, spike length; Spwt, spike weight per plant; Stwt, straw weight per plant; TKW, thousand kernel weight; PhiPS2, photosystem II efficiency.

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Implications: These findings holds great significance in improving drought tolerance in modern wheat breeding programs.

1. Introduction

Drought is a major abiotic stress that threatens crop productivity worldwide (IPCC, 2023), with climate change causing more severe and unpredictable droughts that adversely affect plant growth (Munné-Bosch and Villadangos, 2023). Drought stress affects plants in complex ways (Badaeva et al., 2022; Khadka et al., 2020; Nevo and Chen, 2010), which vary according to their phenological stage as well as the intensity and duration of drought stress (Chaouachi et al., 2023; Mohammadi, 2018). Wheat requirements for satisfying the food demands of a growing global population will inevitably increase (Bapela et al., 2022; Khadka et al., 2020; OECD-FAO, 2020). Environmental stresses may also constrain production (Kulkarni et al., 2017). This issue could be resolved by breeding cultivars with enhanced drought tolerance. Therefore, an understanding of the mechanisms underlying drought tolerance and the development of well-adapted, drought-tolerant varieties are critical needs.

Common wheat (*Triticum aestivum* L., $2n = 6x = 42$, BBAADD) is a major staple food crop for underpinning global food security, contributing approximately 20 % of total dietary calories in human nutrition (Shiferaw et al., 2013). Recent studies have explored the complexities of wheat evolution and taxonomy (Feldman and Levy, 2023; Sharma et al., 2021; Zeibig et al., 2022). Only four naturally occurring wild *Triticum* species have been found: *Triticum urartu* Thumanjan ex Gandilyan ($2n = 2x = 14$, AA), *T. boeoticum* Boiss. ($2n = 2x = 14$, AA, wild einkorn) and two wild tetraploid species, *T. dicoccoides* (Körn. ex. Asch. & Graebner) Schweinf. ($2n = 4x = 28$, BBA⁴A⁴, wild emmer), and *T. araraticum* Jakubz. ($2n = 4x = 28$, GGA⁴A⁴).

Genetic diversity has been reduced within many breeding pools through crop domestication and improvement, resulting in a genetic bottleneck (Dempewolf et al., 2017). Moreover, the loss of genetic diversity in cultivated varieties has limited their ability to withstand various environmental (biotic and abiotic) stresses (Nevo and Chen, 2010; Peng et al., 2011; Sharma et al., 2021). Wheat wild relatives provide important genetic source material in modern wheat breeding programs (Kilian et al., 2021; Leigh et al., 2022). They are well-adapted to harsh environments and contain potentially useful alleles that can improve drought tolerance in wheat cultivars (Ahmadi et al., 2018; Nevo and Chen, 2010). Some studies that have evaluated agronomical and physiological traits associated with drought tolerance in wild emmer wheat *T. dicoccoides*, and have identified certain genotypes as potential donors for introducing drought tolerance traits (Budak et al., 2013; Peng et al., 2011; Suneja et al., 2019; Zhang and Kirkham, 1994). By contrast, *T. araraticum* (GGA⁴A⁴) has received less attention despite its potential value in plant breeding (Badaeva et al., 2022). Sultan et al. (2012) found that it is less tolerant to drought than other species, but their study only examined one accession of *T. araraticum* under artificially imposed drought conditions at the early seedling stage. Other taxa, such as *T. urartu* and *T. boeoticum* (Ahmadi et al., 2018; Pour-Aboughadareh et al., 2017) as well as *T. monococcum*, *T. carthlicum*, *T. dicoccon*, and *T. durum* (Zhang and Kirkham, 1994), exhibit drought tolerance primarily via antioxidant defense mechanisms at the seedling stage.

When exposed to drought stress, plants exhibit both short-term and long-term responses (Oguz et al., 2022). Short-term responses to drought stress include changes in stomatal conductance, water potential, turgor pressure, and biochemical composition. The long-term response is the cumulative effect of short-term effects, which include changes in plant morphology, phenology, and grain yield caused by disruption of the plant's entire physiology (Oguz et al., 2022). Adaptive mechanisms under drought stress include maintenance of stomatal

conductance and retention of photosynthetic pigments (Aspinwall et al., 2015; Kulkarni et al., 2017; Suneja et al., 2019). Stomatal regulation in wheat varies between isohydric (water-saving) and anisohydric (water-wasting) drought adaptation strategies (Guizani et al., 2023). According to the prevailing conceptual model explaining isohydric and anisohydric strategies, the degree of stomata closure is a response to water stress (Martínez-Vilalta and Garcia-Forner, 2017). Isohydric plants minimize water loss and can maintain leaf water potential under water stress conditions by rapidly reducing stomatal conductance. By contrast, anisohydric plants keep their stomata open and increase transpiration in response to water stress and maintain their photosynthetic rate (Bandurska, 2022). An anisohydric strategy supports growth and development during short-term drought, whereas an isohydric response prioritizes passive survival during prolonged drought conditions (Martínez-Vilalta and Garcia-Forner, 2017; Sade et al., 2012). Understanding drought-related adaptive phenotypic traits that contribute to yield is a first and fundamental step toward advancing understanding of complex physiological and biochemical mechanisms (Mwadingeni, et al., 2016) and constitutes the basis for selecting drought-tolerant wheat genotypes (Reynolds et al., 2009; Sallam et al., 2019).

Most studies on drought tolerance in wheat wild relatives have been limited to examining plant physiology within a few taxa or samples per taxon during the seedling stage, without considering the effect of drought stress on grain yield. Moreover, there is a paucity of studies that have used wheat wild relatives under field conditions. Furthermore, these studies have not attended to the morphological and physiological traits contributing to yield-related traits. Therefore, we investigated the genetic variation underlying drought adaptation within a diverse collection of wheat wild relatives, landraces, and modern wheat cultivars under field conditions through an analysis of morphological and physiological traits associated with yield components. Accordingly, we conducted field experiments in a drought-prone location in Germany under two different moisture conditions: irrigated and rainfed. We tested the following hypotheses: (a) large variations in morphological and physiological traits exist within the *Triticum* gene pool; (b) these variations in morphology and physiology contribute to variations in drought tolerance; and (c) wheat wild relatives demonstrate greater drought tolerance than modern cultivars. The findings of this study will benefit future breeding programs aimed at developing drought-tolerant wheat cultivars in arid regions.

2. Materials and methods

2.1. Plant material

During the 2022 growing season, 110 wild and domesticated wheat (*Triticum*) genotypes were used in a screening experiment. They comprised 60 genotypes from 4 wild taxa, 44 genotypes from 20 landrace taxa, and 6 modern winter wheat varieties (Table S1). The wheat species were classified according to the classification system outlined in a previous study (Zeibig et al., 2024b), with slight modification. The modern winter wheat cultivars included in the study were 4 bread wheat cultivars: cv. Apostel (I.G. Pflanzenzucht), cv. Julius (KWS SAAT SE & Co.), cv. Nordkap (SAATEN UNION), and cv. RGT Reform (RAGT Saaten) and 2 durum wheat cultivars: cv. Sambadur (Hauptsaaten) and cv. Wintergold (SAATEN UNION). Twenty genotypes were selected for further testing during the 2023 growing season according to the results of the screening experiment conducted during the 2022 growing season. These genotypes belonged to 11 taxa comprising 4 wild taxa (11

genotypes), 6 landrace taxa (one genotype each), and 3 modern cultivars (two of bread wheat and one of durum wheat). The selection of genotypes for the 2023 growing season was primarily based on their relative grain yield performance during the 2022 growing season (Table S2).

2.2. Experimental conditions and treatments

Field experiments were conducted during two winter wheat growing seasons (October 2021–June 2022 and October 2022–June 2023) in the sandy loam soil of the Gross Gerau experimental station at Justus Liebig University Giessen in Germany (49°56'N, 8°30'E; 92 m above sea level). The field capacity of the soil at the experimental location was classified as very low (0–130 mm / 100 cm) according to the classification of the Ministry of Nature Protection, Environment and Geology of the State of Hesse (HLNUG, 2024). Data on precipitation, temperature, and relative humidity were collected daily during the growing seasons from November to June (Figs. 1A and 1B). The total precipitation amounts during the 2022 and 2023 growing seasons were 281 mm and 294 mm, respectively. The minimum and maximum average temperatures were -1.8°C and 24.4°C , respectively, and the average relative humidity was 74 % during the 2022 growing season. In 2023, the minimum and maximum average temperatures were -3.4°C and 23.4°C , respectively, and the average relative humidity was 76 %. The maximum temperatures were 37°C in 2022 and 38°C in 2023, both were recorded at the end of June during the physiological maturity of the crop.

During both growing seasons, the seedlings were germinated using the procedure described by Zeibig et al. (2024a). Briefly, eight single seeds per genotype were sown in Quickpot trays and kept in a vernalization chamber for 48 hours at 5°C and at a relative humidity of 60 %–70 %. They were subsequently transferred to a greenhouse with a 10 h:14 h light/dark photoperiod and day/night temperatures of $15^{\circ}\text{C}/10^{\circ}\text{C}$. Lastly, they were acclimatized outdoors for two days before being transplanted into the field. Seeds used for the 2022 growing

season were sown on October 5, 2021 and subsequently transplanted on November 8, 2021. Seeds used for the 2023 growing season were sown on October 4, 2022 and transplanted on November 1, 2022. The plant-to-plant and row-to-row distances of transplanted seedlings were 75 cm and 1 m, respectively. The topsoil was sandy and loose, with hard rocks below 45 cm, making it prone to drought stress. Therefore, wider spacing was used to prevent plants from competing for water at shallow depth. A gap of 2.5 m was maintained between the irrigated and rainfed plots to prevent any seepage of irrigation water to the rainfed plots.

A randomized split plot experimental design was used with four replications (a single plant per replicate) under two treatment conditions: rainfed and irrigated during both growing seasons. Throughout the winter, no irrigation was applied for the rainfed or irrigated treatments. Only the irrigated plot received supplemental irrigation, and the water stress conditions were solely rainfed throughout the cropping seasons. Irrigation was applied using an automated overhead sprinkler. The plants in the irrigated plots were watered four times during both growing seasons between April 20, 2022 and June 8, 2022 and between May 26, 2023 and June 16, 2023. Irrigation ensured that water limitations did not constrain normal crop performance in the irrigated plots, considering the precipitation pattern. During the 2022 growing season, the irrigated plots received a total of 130 mm of supplemental irrigation at the jointing stage when the plants reached stage 33 of Zadoks growth scale (Z33; Zadoks et al., 1974), the heading (Z49), flowering (Z65), and grain-filling (Z80) stages. During the 2023 growing season, 83 mm of supplemental irrigation, in total, was applied at the flowering (Z61), late flowering (Z69), early grain-filling (Z77), and dough (Z85) stages of growth.

Soil moisture was measured using an HH2 moisture meter, version 4.2 (Delta-T Devices Ltd., Cambridge, UK) after irrigation commenced. The measurements were taken at different soil depths of approximately 6 cm and 30 cm at a randomly selected location in each replication for both treatment conditions. After the onset of irrigation, they were taken

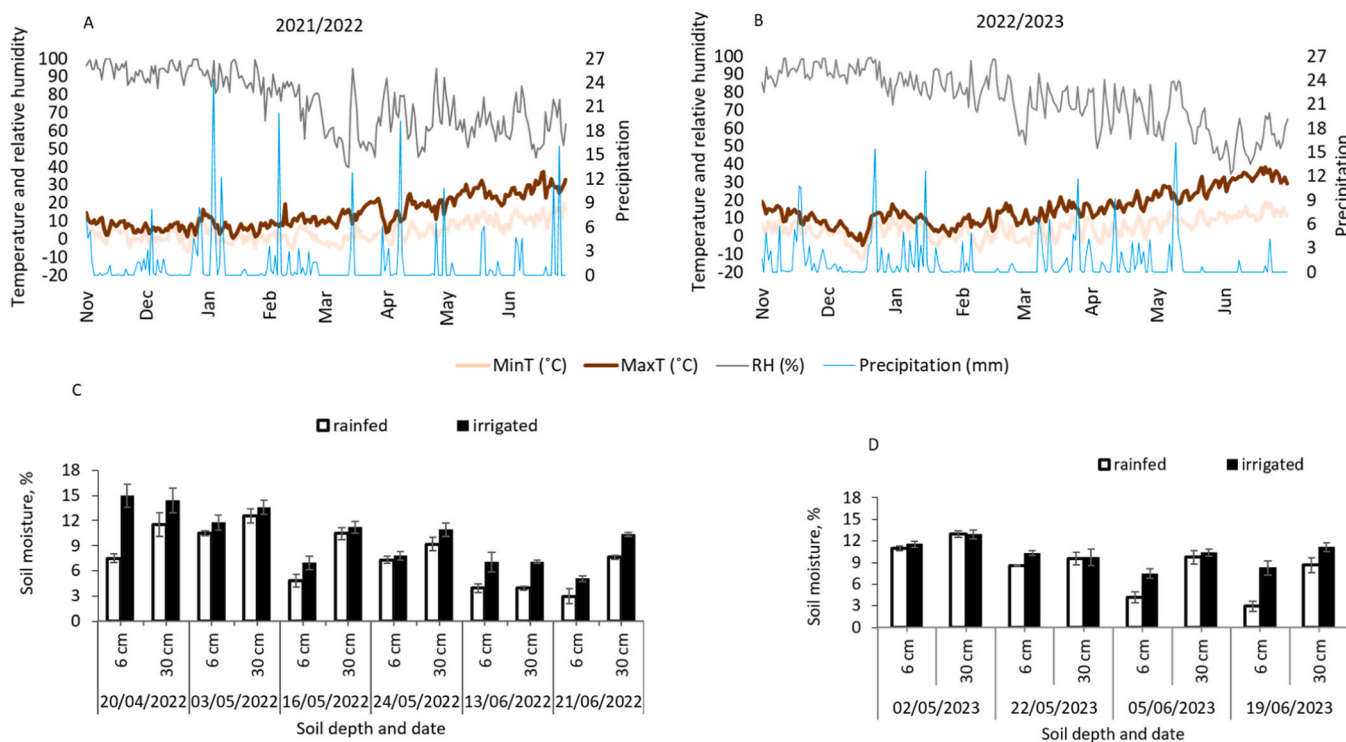


Fig. 1. Weather data, and soil moisture status during the crop growing periods at the research station in Gross Gerau, Germany. Average daily temperatures, precipitation, and humidity levels during the 2022 growing season (A) and the 2023 growing season (B). The percentage of soil moisture was measured on different dates at different soil depths during the 2022 growing season (C) and the 2023 growing season (D). The soil moisture under irrigated and rainfed conditions are depicted as black and white bars, respectively, and the values are means \pm standard errors ($n=4$).

on different dates during the crop season. For both growing seasons, all the plants were harvested by the second week of July when they were fully matured.

2.3. Trait measurements

A total of 19 traits were investigated during the 2022 and 2023 growing seasons. These traits covered several categories. Two phenological traits were measured: days to heading (DTH) and days to flowering (DTF). Nine of the traits were morphological and yield-related: plant height (PH), number of spikes per plant (SPP), spike length (SL), spike weight per plant (Spwt), straw weight per plant (Stwt), above-ground biomass per plant (BM), grain yield per plant (GY), thousand kernel weight (TKW) and harvest index (HI). The remaining eight traits were physiological: stomatal conductance (gsw), photosystem II efficiency (PhiPS2), normalized difference vegetation index (NDVI), Lichenthaler index 2 (Lic2), photochemical reflectance index (PRI), anthocyanin reflectance indices (ARI2), structure insensitive pigment index (SIPI), and carotenoid reflectance index 1 (CRI1). During the 2022 growing season, three replicates were used for measuring physiological traits, whereas all other measurements were obtained using four replicates. However, during the 2023 growing season, four replications were included for all of the above measurements.

During both growing seasons, phenological data (DTH and DTF) were recorded following the Zadoks growth scale (Zadoks et al., 1974) as soon as the individual plant reached Z50 and Z60, respectively. Phenological traits were recorded with reference to the seed sowing date for the respective phenological stages. PH was measured post-flowering from the soil surface to the tip of the spike, excluding the awns. SL was measured from the base to the tip of the spike, excluding the awns. The main tiller of the plant was considered for both phenological and morphological trait measurements. SPP were counted during the physiological maturity period (Z90). Single plants for each genotype were harvested when fully mature. BM was determined after the harvested samples were oven dried at 30 °C to attain a constant weight. The spikes were threshed using an electric coffee mill. GY per plant and TKW were subsequently measured. The HI for each plant was calculated by dividing GY per plant by BM per plant.

Spectral reflectance measurements (vegetation indices) were recorded using a Polypen RP 410 portable instrument (Photon Systems Instruments, Drasov, Czech Republic). Of the many vegetation indices described in the literature, the following were selected: NDVI = $(R780 - R630)/(R780 + R630)$; Lic2 = $R440/R690$ (Begum et al., 2020); PRI = $(R531 - R570)/(R531 + R570)$ (Sims and Gamon, 2002); ARI2 (anthocyanin reflectance indices) = $R790/(1/R550 - 1/R700)$ (Gitelson and Merzlyak, 1997); CRI1 = $1/R510 - 1/R700$ (Gitelson et al., 2003); and SIPI = $(R790 - R450)/(R790 - R650)$ (Peñuelas et al., 1995). A portable handheld LI-600 porometer system integrated with a fluorometer (LI-COR, Lincoln, Nebraska, USA) was used to measure gsw and PhiPS2 between 10:00 h and 14:00 h on a sunny day. All of these physiological traits were measured at the flowering stage (Z60), after clipping the middle portion of the leaf below the flag leaf of the main tiller. We used the leaf below the flag leaf for measurements because the flag leaf of some species was too narrow for the LI-600 sensor.

2.4. Data analysis

To rank the genotypes for drought tolerance, a “relative value” was calculated for each genotype as described by Bouslama and Schapaugh (1984) but with slight modifications. The relative value was calculated as the ratio of the rainfed value of the individual genotype to the average irrigated value of the same genotype for each studied trait. Relative values provide an effective way to rank morphologically diverse genotypes, as the stress levels were interpreted relative to their initial conditions. The statistical analysis was performed in R version 4.2.0 (www.r-project.org). The effects of genotype and treatment and their

interaction were obtained from the model fitted with lmer from the lme4 package (Kuznetsova et al., 2017), with genotype and treatment treated as fixed factors; year and replication by treatment by year interaction were treated as a random effects. Multiple test comparisons were performed with the emmeans function. Principal component analysis (PCA) was performed using FactoMineR and Factoextra in R. To obtain Pearson's correlation, the Hmisc package was used in R. Figures were generated with ggplot2 and Microsoft Excel.

3. Results

3.1. Soil moisture under irrigated and rainfed conditions

During the respective growing seasons in 2022 and 2023, the rainfed treatment area received approximately 31 % and 22 % less water than the irrigated treatment area, which benefited from supplemental irrigation. Therefore, relative to the irrigated condition, the soil moisture was reduced under the rainfed condition, decreasing on average by 25 % and 20 %, respectively, during the growing seasons in 2022 (Fig. 1C) and 2023 (Fig. 1D).

3.2. Genotypic variations exist in the Triticum gene pool under both irrigated and rainfed conditions

We investigated genotypic variation in 110 genotypes during the 2022 growing season, mainly considering two yield-related traits: BM and GY (Table 1). Significant genotypic differences in BM and GY were detected in wild wheats and landraces under both irrigated and rainfed conditions. A significant genotypic effect on GY in modern cultivars only occurred under rainfed conditions.

The relative GY values ranged between 0.17 and 2.12 for wild wheats, 0.32 and 3.00 for landraces, and 0.40 and 1.53 for modern cultivars, averaged across all genotypes within a genetic group during the 2022 growing season. The 110 genotypes were ranked from 1 to 110 according to the average relative BM and GY values, where a rank value of 1 indicated the most drought-tolerant genotype, and a rank value of 110 indicated the most drought-sensitive genotype (Table S2). We observed highly significant treatment effects on both BM and GY for all genetic groups when averaged across all genotypes during the 2022 growing season (Table 1). However, the genotype-by-treatment effect was significant for both BM and GY in the landrace group but not in wild wheats and modern cultivars. The average values of phenological, morphological, and yield-related traits for 110 genotypes grown under irrigated and rainfed conditions during the 2022 growing season are shown in Table S6.

3.3. Effects of drought stress on physiological, morphological, and yield traits

We evaluated morphological, physiological, and yield-related traits in 20 genotypes over two growing seasons in 2022 and 2023 (Table 2). We intentionally selected genotypes of wild relatives and landraces that exhibited high relative performance based on GY and BM in the screening experiment conducted in 2022 (Table S2) to compare them with contemporary modern cultivars. We then analysed the physiological parameters of those genotypes across two seasons. The average values decreased for all the measured traits except PhiPS2 under rainfed conditions compared with those grown under irrigated conditions due to water stress, when averaged across 20 genotypes over two growing seasons (Table 2, S3 and S4). Water stress caused significant reductions in gsw, GY, Spwt, SL, NDVI, PRI, ARI2, CRI1, and SIPI under rainfed conditions. Notably, gsw and GY decreased by more than 20 %, whereas other traits decreased by less than 20 %. The effect of genotype was highly significant for GY and all yield-related traits. However, among the yield-related traits, only GY was significantly affected by the treatment-by-genotype interaction. All the physiological traits apart

Table 1

Performances of 110 genotypes from different genetic groups under irrigated and rainfed conditions during the 2022 growing season.

	Wild			Landrace			Modern cultivar					
	df	Irrig.	Rain	Rv	df	Irrig.	Rain	Rv	df	Irrig.	Rain	Rv
Aboveground biomass per plant (BM), g												
Minimum		15.57	10.98	0.25		33.69	18.37	0.39		62.27	30.24	0.41
Maximum		93.01	66.77	1.46		210.90	223.33	1.80		130.19	108.28	1.39
Mean		47.59	31.38	0.67		101.45	73.42	0.75		85.73	68.15	0.85
Standard error		1.94	1.41	0.03		4.77	3.82	0.04		12.14	8.69	0.04
Genotype	59	**	***		43	***	***		5	ns	ns	
Treatment	1		**		1		***		1		***	
Genotype: Treatment	59		ns		43		*		5		ns	
Grain yield per plant (GY), g												
Minimum		3.67	2.18	0.17		5.32	5.78	0.32		30.44	13.14	0.40
Maximum		24.33	15.66	2.12		83.07	88.92	3.00		64.74	50.31	1.53
Mean		10.86	6.93	0.67		35.76	25.31	0.75		41.24	32.84	0.87
Standard error		0.49	0.35	0.03		1.87	1.58	0.05		6.19	4.88	0.14
Genotype		*	*			***	***			ns	*	
Treatment	1		***		1		***		1		***	
Genotype: Treatment	59		ns		43		*		5		ns	
Treatment												

Notes: Irrig. = irrigated, Rain = rainfed, df = degree of freedom, Rv= relative value calculated as the ratio of rainfed to the mean value for the irrigated condition for individual plants. *, **, and *** denote significance at $p < 0.05$, $p < 0.01$, and $p < 0.001$, respectively; ns = nonsignificant.

from PhiPS2 also exhibited highly significant genotypic differences, and the genotype-by-treatment interaction was significant for gsw, PhiPS2, SIPI, Lic2, PRI, and CRI1. Moreover, the genotype effect, but not the treatment or the genotype-by-treatment interaction effects on DTH, DTF, and PH were highly significant.

3.4. Genotypic responses to drought stress in the *Triticum* gene pool

We compared treatment effects on individual genotypes using data for 20 genotypes averaged over two seasons in 2022 and 2023. *T. dicoccon* (G198) and *T. compactum* (G213) showed significant decreases in BM (Fig. 2A). The treatment significantly affected GY in *T. dicoccon* (G198), *T. compactum* (G213), *T. aestivum* (G10), *T. aestivum* cv. Apostel (G134), and *T. aestivum* cv. Nordkap (G181) (Fig. 2B). BM and GY measurements revealed that *T. durum* cv. Sambadur (G41) had the highest water stress tolerance, followed by *T. dicoccoides* (G242), *T. monococcum* *sinskajae* (G89), *T. araraticum* (G221), *T. urartu* (G45), and *T. boeoticum* (G27), each with an average relative value of 1. The treatment effect on HI or TKW was non-significant for any of the genotypes (Figs. 2C and 2D). However, *T. dicoccon* (G198), *T. compactum* (G213), and *T. aestivum* cv. Nordkap (G181) exhibited significant decreases in Spwt induced by the treatment (Figure S1A), with the greatest relative changes observed in *T. durum* cv. Sambadur (G41) and *T. dicoccoides* (G242), each with an average relative value of 1. Treatment effects on Stwt were significant for *T. dicoccon* (G198), *T. compactum* (G213) and *T. aestivum* (G10) (Figure S1B). The highest relative Stwt values were observed for *T. urartu* (G45) and *T. dicoccoides* (G90), each with an average relative value of 1.8.

Most of the genotypes from wild *T. boeoticum* (G27 and G33), *T. urartu* (G45), and *T. dicoccoides* (G242 and G248), as well as the landrace, *T. carthlicum* (G159), showed a significant decrease in stomatal conductance due to water stress (Fig. 3A). However, *T. spelta* (G109) and *T. araraticum* (G189) exhibited low stomatal responses. NDVI significantly decreased for *T. araraticum* (G161) and *T. araraticum* (G205) (wild), *T. aestivum* (G10) (a landrace) and *T. durum* cv. Sambadur (G41) due to water stress. By contrast, *T. compactum* (G213) and *T. carthlicum* (G159), had the highest average relative value of 1 (Fig. 3C). All the genotypes belonging to the landrace group except those in *T. aestivum* (G10) and all three modern cultivars, namely *T. aestivum* and *T. durum* taxa showed an increase in Lic2 under rainfed conditions relative to irrigated conditions. However, water stress caused a decrease in Lic2 in all the genotypes of the wheat wild relatives (Fig. 3D).

The genotype effect on DTH (Fig. 4A) was only significant for

T. urartu (G45), with none of the other genotypes exerting significant effects on DTF or PH (Figs. 4B and 4C). SPP decreased significantly in *T. aestivum* (G10) (Fig. 4D), and *T. urartu* (G45) had the highest relative SPP, followed by *T. durum* cv. Sambadur (G41). The treatment effect on SL was significant for *T. boeoticum* (G27), while *T. dicoccoides* (G242) and *T. araraticum* (G205) had the highest relative value of 1 (Figure S1C).

3.5. Correlation analysis under irrigated and rainfed conditions

A correlation analysis was performed on the 19 traits measured under irrigated (Fig. 5A) and rainfed conditions (Fig. 5B) over two seasons, including those for the dataset of 20 genotypes. Under both irrigated and rainfed conditions, yield-related traits, namely Spwt, Stwt, BM, GY, HI, and TKW exhibited significant positive correlations with each other, with the exception of Stwt with HI under both conditions and with TKW under rainfed conditions. PH was significantly negatively correlated with HI and TKW under irrigated conditions and with GY, HI, and TKW under rainfed conditions. There were significant positive correlations of DTH and DTF with Stwt, Spwt, BM, and GY under rainfed conditions. Under irrigated conditions, DTF was significantly correlated with Stwt and BM but not with Spwt or GY.

Strikingly, under rainfed conditions, gsw was significantly positively correlated with most yield-related traits. However, no such correlation was found under irrigated conditions. Significant positive correlations were observed between gsw and GY and between HI and TKW. There was no strong correlation between the NDVI and yield-related traits under either irrigated or rainfed conditions, with few exceptions. The NDVI was significantly positively correlated with Stwt under rainfed conditions and significantly negatively correlated with GY and TKW under irrigated conditions. CRI1 and SIPI were negatively correlated with yield-related traits. CRI1 was significantly negatively correlated with Spwt, BM, GY, HI, and TKW under irrigated conditions and with GY, HI, and TKW under rainfed conditions. Similarly, there were significant negative correlations between the SIPI and Spwt, GY, HI, and TKW under both irrigated and rainfed conditions.

3.6. Principal component analysis

PCA was also performed to examine the relationships between morphological, physiological, and yield-related traits and the diversity of genotypes under irrigated and rainfed conditions. The first five PCs explained 88.6 % of the total variation, and their eigenvalues were > 1

Table 2
Summary statistics for 20 genotypes averaged over two growing seasons in 2022 and 2023.

Traits	Mean Squares			Treatment Means (Standard Deviation)	
	Treatment	Genotype	Treatment × Genotype	Irrigated	Rainfed
	df: 1	df: 19	df: 19		
Days to heading	0.9 ^{ns}	552 ^{***}	11.4 ^{ns}	220 (8.9)	220 (9.8)
Days to flowering	2.7 ^{ns}	634 ^{***}	11.6 ^{ns}	229 (10.5)	228 (11.6)
Plant height (cm)	876 ^{ns}	3500 ^{***}	122 ^{ns}	99 (21.3)	95 (21.6)
Number of spikes per plant	57 ^{ns}	1409 ^{***}	68 ^{ns}	23 (13.8)	22 (13.6)
Spike length (cm)	16*	78 ^{***}	2.5 ^{ns}	10.4 (3.0)	9.6 (2.3)
Spike weight per plant (g)	1306 ^{***}	2753 ^{***}	439 ^{ns}	38.2 (25.7)	32.3 (20.3)
Straw weight per plant (g)	713 ^{ns}	2281 ^{***}	214 ^{ns}	30.5 (20.4)	26.0 (17.3)
Aboveground biomass per plant (g)	39134 ^{ns}	8891 ^{***}	1221 ^{ns}	68.7 (44.6)	58.1 (35.7)
Grain yield per plant (g)	914*	2179 ^{***}	269 ^{**}	22.3 (19.4)	17.5 (14.1)
Thousand kernel weight (g)	59.5 ^{ns}	1533 ^{***}	14.7 ^{ns}	30.0 (10.7)	28.9 (10.48)
Harvest index	0.002 ^{ns}	0.13 ^{***}	0.004 ^{ns}	0.29 (0.10)	0.28 (0.12)
Stomatal conductance (mmol m ⁻² s ⁻¹)	77297 ^{***}	2951 ^{**}	2400*	103 (52.7)	57 (30.5)
Photosystem II efficiency	0.001 ^{ns}	0.016 ^{ns}	0.028*	0.42 (0.16)	0.43 (0.16)
Normalized difference vegetation index	0.143 ^{***}	0.015 ^{***}	0.007 ^{ns}	0.57 (0.06)	0.52 (0.10)
Lichtenthaler index 2	0.023 ^{ns}	0.239 ^{***}	0.026 ^{***}	0.86 (0.13)	0.85 (0.21)
Photochemical reflectance index	0.002 ^{***}	0.002 ^{***}	0.0004 ^{**}	-0.007 (0.016)	-0.01 (0.022)
Anthocyanin reflectance indices	0.55*	0.52 ^{***}	0.07 ^{ns}	-0.05 (0.23)	0.06 (0.43)
Carotenoid reflectance index 1	4.28 ^{**}	4.77 ^{***}	0.62 ^{**}	2.53 (0.77)	2.19 (0.91)
Structure insensitive pigment index	0.096 ^{***}	0.028 ^{***}	0.004*	0.62 (0.05)	0.58 (0.08)

Notes: Mean values are shown for irrigated and rainfed conditions and mean square values of all the investigated traits between treatments, genotypes, and genotype-by-treatment interactions. The values inside parentheses denote standard deviations associated with the corresponding mean values.

*p < 0.05

** p < 0.01

*** p < 0.001

ns = nonsignificant.

under irrigated conditions (Table S5). Additionally, under rainfed conditions, the first four PCs had eigenvalues >1 and explained 88.5 % of the total variation (Table S5). Moreover, under rainfed conditions, the first two PCs contributed 67.1 % of the total variation, with PC1 explaining 44.6 % of the variation and PC2 explaining 22.5 % of the variation (Figure S2B). Of the traits examined, the major contributors to these two PCs were HI, TKW, GY, DTH, DTF, Stwt, NDVI, SIPI, CRI1, PH, and ARI2. The first two PCs explained 61.9 % of the variation (PC1: 41.9 % and PC2: 20 %) under irrigated conditions (Figure S2A). The

major contributing traits in these two PCs were GY, TKW, CRI1, SIPI, NDVI, DTF, DTH, BM, and Spwt.

The genotype distribution determined via PCA revealed distinct clustering patterns under rainfed and irrigated conditions (Figure S2). All the genotypes of *T. dicoccoides* and *T. araraticum* (wild tetraploid species) were clustered together under the irrigation condition, while the genotypes of *T. boeoticum* and *T. urartu* (wild diploid species) occupied unique positions. Conversely, under rainfed conditions, *T. boeoticum* was dispersed from wild tetraploids. Notably, *T. urartu* held an intermediate position between *T. dicoccoides* and *T. araraticum* (the wild tetraploids) and *T. boeoticum* (the wild diploid). Landrace taxa and modern cultivars formed distinct clusters under both conditions, with the exception of diploid landraces of *T. monococcum* and the tetraploid landrace of *T. compactum*, which were more closely related to *T. boeoticum* and modern cultivars, respectively.

4. Discussion

4.1. Impact of water stress on grain yield

In this study, we evaluated the water stress response in the *Triticum* spp. genepool, initially in a diverse set of 110 genotypes grown in 2022 (Table S1) and subsequently in 20 genotypes selected for a second growth season in 2023 (Table S2). Most of the *Triticum* taxa used in this study have already shown good adaptability to the Central European climate (Zeibig et al., 2024a). Among the yield components, GY was the most affected trait (Table 2). Our finding of a 21 % average decrease in GY is aligned with the findings of previous studies (Farooq et al., 2014; Wang et al., 2017), in which the GY of wheat decreased by 19 % and 28 %, respectively, during - drought stress. Our results fell within the range reported in these studies, indicating that plants experienced drought stress at critical reproductive stages, such as heading, flowering, and grain filling, which occurred between May and June in our study. Essentially, the reproductive stage is a crucial period, and water stress during this phase could result in a severe reduction in GY by affecting pollination and fertilization and causing inadequate grain filling (Farooq et al., 2014).

4.2. Genotypic variation in morpho-physiological traits within the *Triticum* genepool

Our first hypothesis was that there is wide variation in morphological and physiological traits within the *Triticum* genepool. To test this hypothesis, we measured various agro-morphological and physiological traits. Our results clearly showed significant genotypic differences (p < 0.001) in the *Triticum* taxa assessed using morphological, physiological (except for PhiPS2), GY, and yield-related traits (Tables 1 and 2). Previous studies have also reported such variation for a number of morphological and physiological traits within the *Triticum* genepool (Reynolds et al., 2007; Suneja et al., 2017; Wang et al., 2017). This finding highlights that *Triticum* genepool provides a valuable repository of genetic diversity, which could potentially be used to improve drought tolerance in elite cultivars within breeding programs. However, no variation in PhiPS2 might indicate that this trait is highly conserved and is likely more dependent on environmental conditions, which requires further confirmation. However, the genotype-by-treatment effect was significant in this study.

4.3. Morpho-physiological responses to water stress and their impact on yield traits

The second hypothesis in this study was that variations in drought tolerance occur within the *Triticum* genepool. To test this hypothesis, we examined the impact of drought on agro-morphological and physiological traits to elucidate diverse drought stress responses among the evaluated genotypes. Previous studies have shown that drought stress

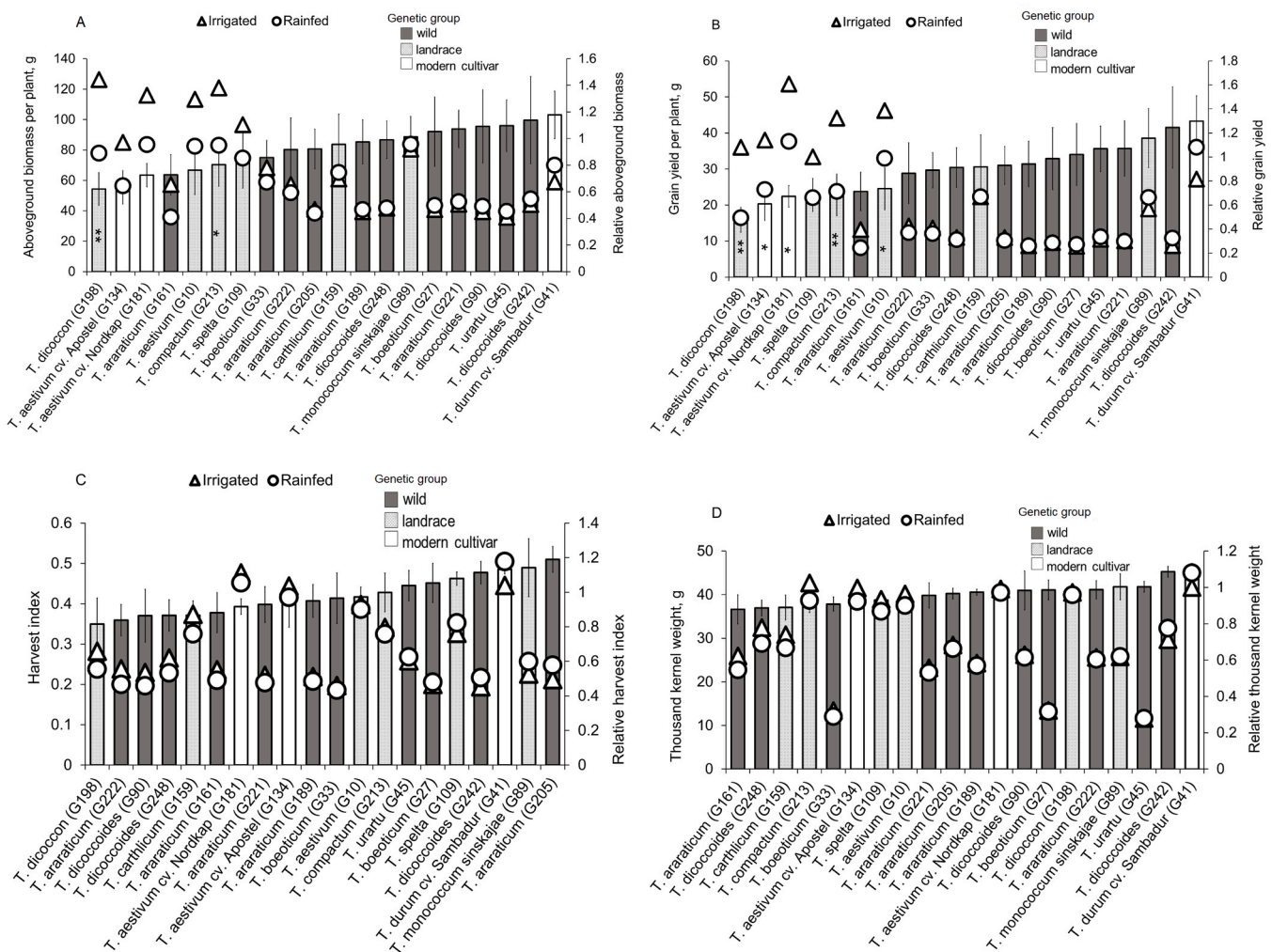


Fig. 2. Effect of drought stress on yield-related traits in 20 wheat genotypes. Aboveground biomass per plant (A), grain yield per plant (B), harvest index (C) and thousand kernel weight (D). The primary vertical axis depicts the means under rainfed and irrigated conditions. The data are presented as average values across two growing seasons in 2022 and 2023. Open circles and triangles indicate means under rainfed and irrigated conditions, respectively. The asterisks within the vertical bar indicate significant differences between rainfed and irrigated conditions (treatment effect) for the same genotype (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$). Mean relative values \pm standard errors of the means are depicted on the secondary vertical axis represented by bars. The genotypes are arranged in ascending order from low relative values (left) to high relative value (right). The different shades indicate the genotypes' genetic groups.

significantly decreases GY (Shokat et al., 2023; Wang et al., 2017). They support our finding that water stress significantly affects GY and other yield-related traits, such as Spwt and SL (Table 2). The results of our correlation analysis and PCA (Fig. 5 and S3) revealed a positive correlation between GY and other yield-related traits, such as Spwt, BM, HI, and TKW that was consistent across irrigated and rainfed conditions. This finding endorsed the previous study (Zhang et al., 2019), which reported a positive correlation between GY and yield-related traits such as TKW. Yield traits are important components for enhancing GY in wheat (Qaseem et al., 2019), however their usually low heritability might pose a challenge for plant breeders (Chen et al., 2012).

The significant genotype-by-treatment interaction effects observed across multiple traits, especially gsw and GY in this study reveals the diverse responses among genotypes under water stress (Table 2). Similar interactions were reported for wheat in previous drought stress studies (Lopes et al., 2012; Suneja et al., 2017). This finding highlights the need to consider specific genotypes for optimizing crop yields, especially under diverse environmental conditions. Drought stress did not affect GY in certain genotypes from different genetic groups. These were *T. boeoticum* (G27), *T. urartu* (G45), *T. dicoccoides* (G242), and *T. araraticum* (G221) from the wild group; *T. monococcum* *sinskajae* (G89) from the landrace group; and *T. durum* cv. Sambadur (G41) from

the modern cultivar group, which also exhibited high relative values for yield-related traits, such as BM, Spwt, Stwt, and HI. Therefore, these genotypes showed greater tolerance in terms of yield traits than other genotypes. Conversely, compared with other genotypes, those from *T. dicoccon*, *T. compactum*, and *T. aestivum* (G10) and the modern bread wheat cultivars, *T. aestivum* cv. Apostel (G134) and cv. Nordkap (G181) showed lower tolerance with significant and greater decreases in GY and other yield traits, such as BM, Spwt, and Stwt. Genotypes from taxa such as *T. boeoticum*, *T. urartu*, *T. dicoccoides*, *T. monococcum*, and *T. durum*, have previously been reported to be drought tolerant (Aberkane et al., 2021; Ahmadi et al., 2018; Suneja et al., 2017; Zhang and Kirkham, 1994).

4.4. Drought stress adaptation: differential stomatal regulation in the *Triticum* genotype

The gsw trait enables stomata to control the exchange of gases, primarily water vapor and carbon dioxide between the plant and its surroundings (McAusland et al., 2020). Stomatal closure is one of the first responses to drought stress in plants and strongly influences the characteristics associated with photosynthesis and transpiration (Li et al., 2017). A previous study reported a significant positive correlation

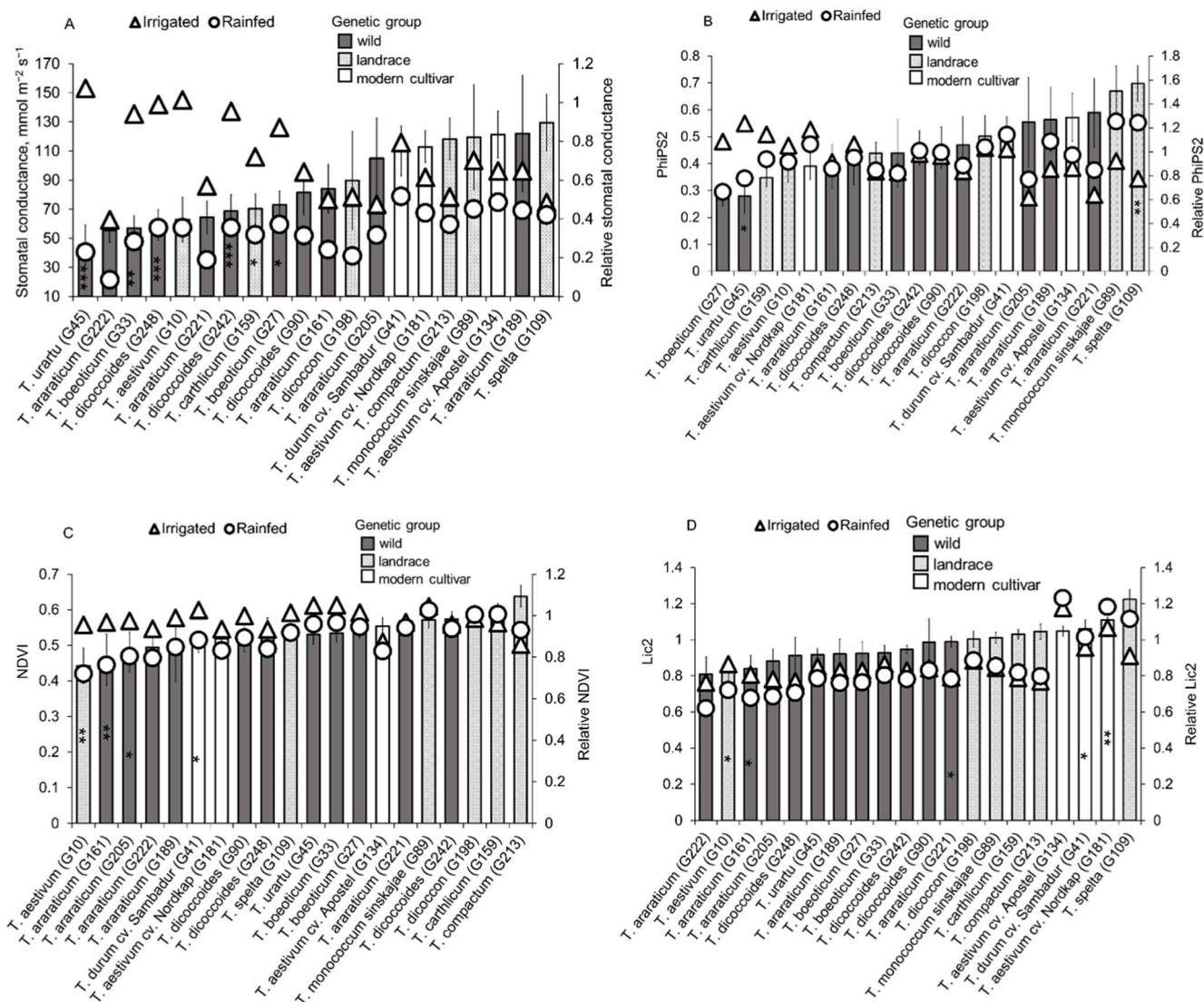


Fig. 3. Effect of drought stress on physiological traits in 20 wheat genotypes; stomatal conductance (A), PhiPS2 (B), NDVI (C) and Lic2 (D). The primary vertical axis represents the means under rainfed and irrigated conditions. Open circles and triangles indicate means under rainfed and irrigated conditions respectively. The data are presented as average values over two growing seasons in 2022 and 2023. Mean relative values \pm standard errors of the means are shown on the secondary vertical axis represented by bars. The genotypes are arranged in ascending order from low relative values (left) to high relative value (right). The different shades indicates the genotypes' genetic groups. The asterisks inside the vertical bar indicate significant differences arising from the treatment effect (rainfed and irrigated conditions) for the same genotype (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$). PhiPS2 = photosystem II efficiency, NDVI = normalized difference vegetation index, Lic2 = Lichtenthaler index 2.

between gsw and GY under both irrigated and water stress conditions (Aminian et al., 2011). In contrast, we observed a significant positive correlation between gsw and GY and yield-related traits only under water stress conditions.

In our study, a significant reduction in gsw occurred due to water stress (Table 2). This finding is consistent with those of previous studies (Pour-Aboughadareh et al., 2017; Saiedi and Abdoli, 2015), which reported a significant decrease in gsw caused by drought stress. Notably, at the species level, gsw reduction in *T. urartu* was 74 %, that was highest among all species included in our study, which contradicts the findings of Pour-Aboughadareh et al. (2017), who reported a 26 % lower reduction in gsw in *T. urartu* at the seedling stage compared with gsw reduction in other wild wheats and in *T. aestivum*. These contrasting results could be explained by dynamic, stage-dependent developmental responses of gsw to moisture stress within *Triticum* taxa, indicating the complexity of their adaptive mechanisms.

A significantly greater reduction in gsw was observed in species such as *T. urartu*, *T. dicoccoides*, and *T. boeoticum*, despite lower reductions in

yield traits. The most tolerant genotypes with an isohydric adaptive mechanism were *T. dicoccoides* (G242), *T. urartu* (G45), *T. boeoticum* (G27), and *T. araraticum* (G221), whose GY and yield-related traits were maintained but whose gsw reduction exceeded the average gsw reduction. This process can be an isohydric adaptive mechanism for maintaining yield traits through efficient water management entailing stomata closure. Isohydric wheat genotypes prioritize water preservation, leading to reduced photosynthesis and subsequent decreases in grain yield (Guizani et al., 2023). However, efficient water management directly enhances resilience to drought stress, ensuring a consistent yield even in unpredictable climatic conditions, which could be associated with stomatal morphology (Bertolino et al., 2019). Therefore, the finding of a large reduction in gsw in some wild wheat genotypes in this study could indicate improved water use efficiency through the maintenance of water potential, which requires further verification. However, not all the genotypes of the wild species exhibited isohydric adaptation, which suggests that adaptation in wheat is genotype specific rather than species dependent, as proposed in a previous study

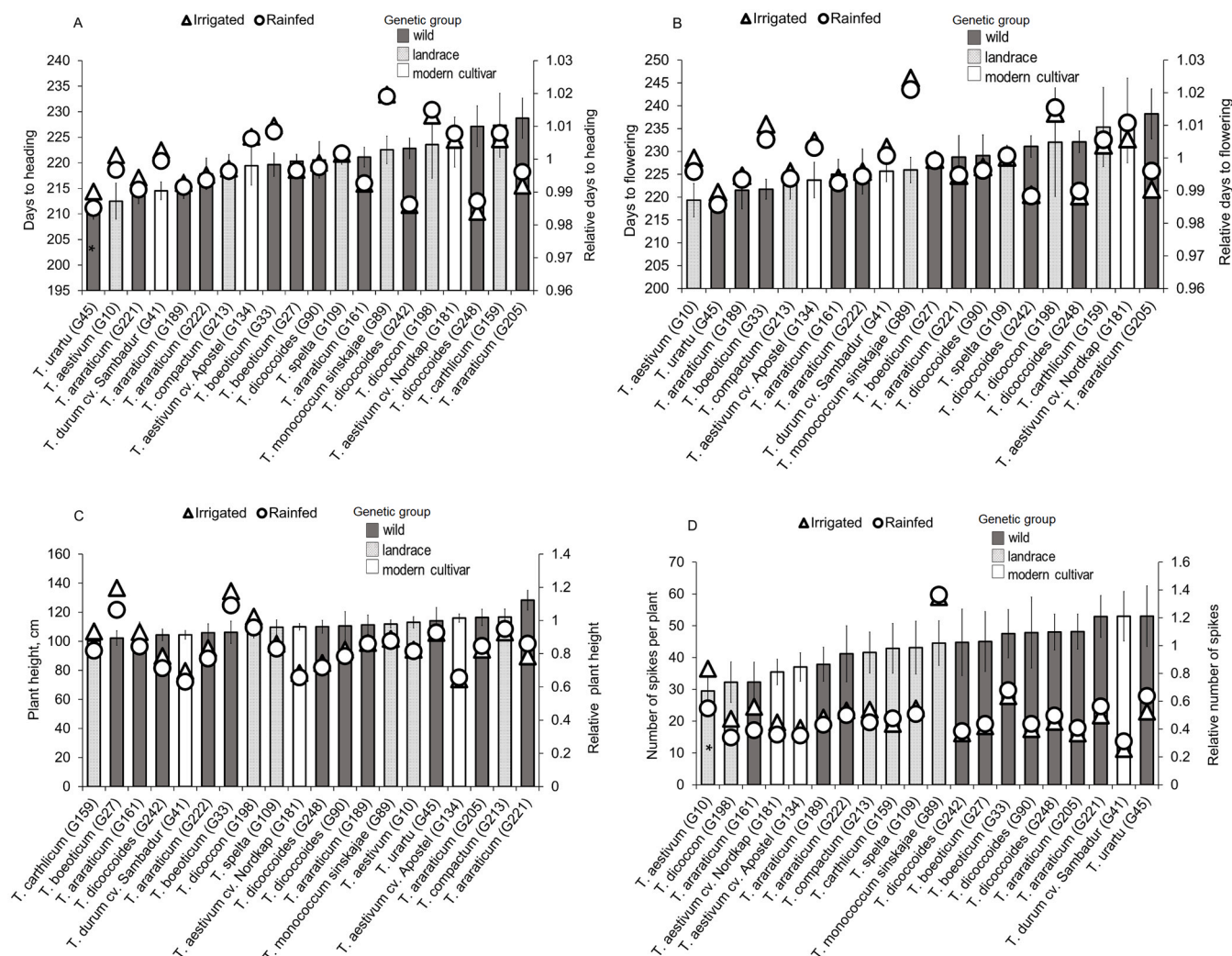


Fig. 4. Effect of drought stress on phenological and morphological traits in 20 wheat genotypes; days to heading (A), days to flowering (B), plant height (C) and number of spikes per plant (D). The primary vertical axis shows the means under rainfed and irrigated conditions. Open circles and triangles indicate means under rainfed and irrigated conditions, respectively. The data are presented as average values over two growing seasons in 2022 and 2023. The mean relative value \pm standard errors of the means are shown on the secondary vertical axis presented by bars. The genotypes are arranged in ascending order from low relative values (left) to high relative value (right). The different shades denote the genetic groups of the genotypes. The asterisks inside the vertical bar indicate significant differences arising from the treatment effect (rainfed and irrigated conditions) for the same genotype. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

(Onyemaobi et al., 2021).

The most tolerant genotypes from the landrace group, *T. monococcum* sinkajae (G89), and the modern durum wheat cultivar, *T. durum* cv. Sambadur (G41), exhibited anisohydric behavior, with a decline in gsw below the average, with maintenance of GY and yield traits in line with those reported in previous studies (Guizani et al., 2023; Onyemaobi et al., 2021). This indicates drought-tolerant wheat genotypes deploying anisohydric adaptation to maintain yield traits through osmotic adjustment. Both isohydric and anisohydric strategies are beneficial for plants under drought stress conditions (Bandurska, 2022) and they can be linked with the root morphology (Saradadevi et al., 2014). Isohydric wheat genotypes might be associated with root signals for stomatal closure, while anisohydric wheat genotypes may have deep root systems that might help to maintain stomatal conductance, by having access to water in deeper soil layers. However, as this study did not include root traits, their roles remain unclear. Additionally, higher planting density might influence this result. Stomatal closure during the reproductive stage improves grain set in wheat, and genetic variations influencing stomatal conductance are presumed to affect a plant’s ability to adapt to limited water conditions (Onyemaobi et al., 2021).

We found strong correlations between phenological traits (DTH and DTF) and BM and GY, consistent with those reported by Gizaw et al. (2016), indicating positive correlations between phenological days and BM. Positive associations between phenological traits and GY under rainfed conditions support the importance of crop phenology in a water stress environment in line with previous findings (Lopes et al., 2012). For instance, a diploid landrace of *T. monococcum*, which has a prolonged vegetative period, exhibited advantages of BM accumulation and GY maintenance under water stress, which could ultimately contribute to increased photosynthesis and a decreased reduction in gsw. Our results revealed that individual genotypes within the *Triticum* gene pool under investigation exhibited diverse trait combinations rather than consistent combinations of all the positive traits in a single genotype, indicating variability in drought tolerance (Figs. 2, 3, 4, S1 and S2). Such genotypic variations in drought adaptation among different genotypes and species have previously been studied in wheat (Aberkane et al., 2021; Lopes et al., 2014; Suneja et al., 2017).

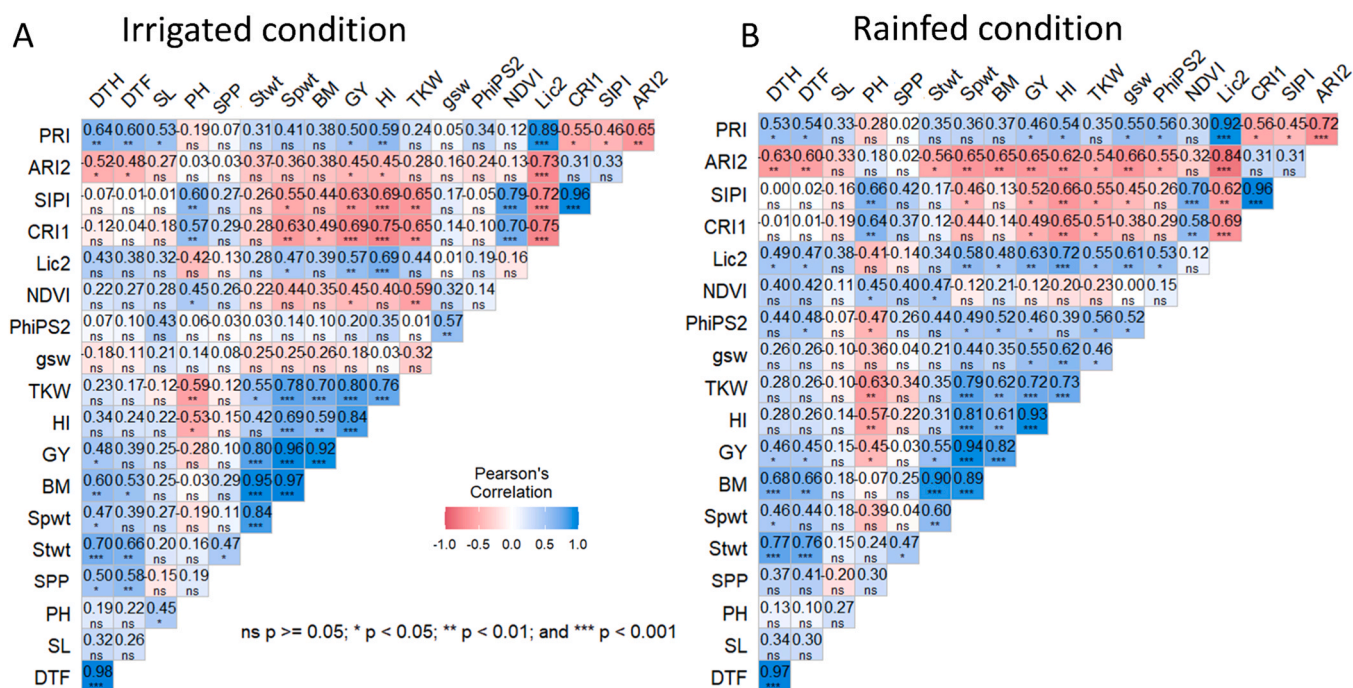


Fig. 5. Pearson's correlation between the 19 measured traits for irrigated (A) and rainfed conditions (B). DTH = days to heading, DTF = days to flowering, PH = plant height, SL = spike length, SPP = number of spikes per plant, Spwt = spike weight per plant, Stwt = straw weight per plant, BM = above ground biomass per plant, GY = grain yield per plant, TKW = thousand kernel weight, HI = harvest index, gsw = stomatal conductance, PhiPS2 = photosystem II efficiency, NDVI = normalized difference vegetation index, Lic2 = Lichtenthaler index 2, SIPI = structure insensitive pigment index, CRI1 = carotenoid reflectance index1, PRI = photochemical reflectance index, and ARI2 = anthocyanin reflectance indices.

4.5. Uncertain genotypic effects on photo-spectral indices under drought stress

Photosynthetic pigment indices reflect physiological changes in plants (Sims and Gamon, 2002). As a measure of chlorophyll content and its spectrum, the NDVI is used to predict green biomass (Liu et al., 2019). Chlorophyll absorbs light, which is integral for the photosynthetic process. Previous studies (Lopes et al., 2014; Raun et al., 2001) demonstrated that NDVI measurements of winter wheat at the reproductive or late flowering stages do not provide reliable predictions of GY and biomass production. These findings support our results, indicating an absence of associations between the NDVI and GY under water stress conditions (Fig. 5B). In contrast, Zhang et al., (2019) revealed that NDVI measured at the flowering and the mid-grain filling stages was positively correlated with yield in wheat under both irrigated and water stress conditions. Therefore, further study is needed considering alternative growth stages of the vegetation indices associated with the chlorophyll index. This can provide a more accurate representation of the relationship between the NDVI and GY under different environmental conditions (Lopes et al., 2014).

Our finding that drought stress does not significantly impact PhiPS2 endorses that of Sommer et al. (2023), who reported that drought stress does not affect PhiPS2 except when the stress is severe or when it is mild, which prompts the activation of several protective mechanisms. Chlorophyll tends to decline more rapidly than carotenoids when plants are under stress (Merzlyak et al., 1999; Sims and Gamon, 2002). The lack of a significant effect of the chlorophyll-to-carotenoid ratio (Lic2) on the plants in our study was likely due to stress conditions during the reproductive stage. However, a complex scenario emerged with a genotype-by-treatment interaction effect on PhiPS2, Lic2, and NDVI, indicating the diverse responses of individual genotypes. Consequently, traits such as PhiPS2, Lic2, and NDVI may lack consistency and may not therefore be reliable criteria for selecting drought-tolerant genotypes under drought stress. Further investigations are required to explore

tolerance mechanisms in specific genotypes, considering diverse growth stages and dynamic drought scenarios to elucidate how these physiological traits reflect drought tolerance in different genotypes.

4.6. Genotype-specific drought adaptation in the *Triticum* gene pool

Our third hypothesis proposed that drought tolerance is greater in wild wheats than in modern wheat cultivars. To test this hypothesis, we undertook a comprehensive comparison of the drought response of wild wheat genotypes with those of modern cultivars. We found that drought tolerance in the *Triticum* gene pool is genotype specific, which challenges our assumption of the uniform superiority of wheat wild relatives over modern cultivars. This finding emerged during the screening experiment in 2022 (Table S2 and S3) and through the performance of a two-season experiment evaluating the drought response of various genotypes via their morphological and physiological traits (Figs. 2, 3, and 4). This might be because the breeding efforts for high yield may also incorporate useful traits for abiotic and biotic stress tolerance (Mohammadi, 2018). However, in our two-season experiment, *T. urartu* (G45) exhibited greater tolerance than *T. aestivum* cv. Apostel (G134) and cv. Nordkap (G181), and excluding *T. durum* cv. Sambadur. These findings are aligned with those of a previous study (Pour-Aboughadareh et al., 2017), which reported that *T. urartu* is drought tolerant. Additionally, one study showed that introgression lines derived from *T. urartu* produced greater yields under drought stress than their parental lines (Aberkane et al., 2021). *T. boeoticum* has also been reported to be drought tolerant (Liu et al., 2015; Mehrabad Pour-Benab et al., 2019). Notably, these diploid wild species exhibited greater drought tolerance than bread wheat genotypes.

Our results indicated that *T. dicoccoides* (G90, G242, G248) exhibited superior drought tolerance relating to GY and other yield-related traits, such as BM, Spwt, Stwt, and HI, compared with *T. aestivum* cv. Apostel (G134) and cv. Nordkap (G181) and excluding *T. durum* cv. Sambadur (Fig. 2B). These findings are aligned with those of previous studies

(Peleg et al., 2005, 2009; Suneja et al., 2017; Zhang and Kirkham, 1994), which identified *T. dicoccoides* as being drought tolerant. *T. dicoccoides* has evolved rich genetic diversity and developed adaptations to adverse environmental stresses, including limited water availability (Budak et al., 2013; Peleg et al., 2005). Our findings support the suggestion of earlier studies that *T. dicoccoides* could potentially be a donor for improving drought tolerance (Aberkane et al., 2021; Merchuk-Ovnat et al., 2016).

In our two-season experiment, 45 % of the wild genotypes belonged to *T. araraticum* and exhibited greater tolerance than modern bread wheat cultivars but less tolerance than *T. durum* cv. Sambadur. This finding contrasts with that of a previous study (Sultan et al., 2012), which reported that *T. araraticum* is less tolerant than bread wheat at an early vegetative growth stage. According to our results, compared with other wild wheat species, *T. araraticum* was less tolerant than *T. dicoccoides*, *T. urartu*, and *T. boeoticum*. However, tolerance varied between the genotypes. We found that *T. araraticum* (G221) was more tolerant than *T. urartu* (G45) and *T. boeoticum* (G27 and G33) but less tolerant than *T. dicoccoides* (G242). The collection sites of *T. araraticum* and *T. dicoccoides* genotypes were, respectively, Iraq and Israel, whereas *T. urartu* and *T. boeoticum* genotypes were respectively collected from Syria and Turkey. Therefore, variations in drought tolerance within wild taxa can be explained by the diverse environments of their regions of origin, which are primarily characterized by a semi-arid to arid climate with hot and dry summers (Jaradat, 2017). Northern Iraq is the center of diversity and the origin of *T. araraticum* (Badaeva et al., 2022). This may suggest that genotypes of *T. araraticum* collected from these areas might have greater drought tolerance, which needs further testing. The *T. araraticum* taxa could augment the diversity of drought tolerance traits in the *Triticum* gene pool along with other wild taxa. They are potentially of considerable value for improving bread and durum wheat (Badaeva et al., 2022). Although, Ayed, et al. (2021) reported that *T. araraticum*-derived lines did not outperform their parent under terminal drought stress, our results suggest that the *T. araraticum* taxa merit further attention as potential candidates for imparting drought tolerance. However, elucidating drought tolerance mechanisms remains challenging, and additional studies are warranted to explore these mechanisms.

5. Conclusion

This study revealed significant variation in morphological and physiological traits within the *Triticum* gene pool in response to water deficit. For example, significant genotype-by-treatment interactions occurred for gsw and GY per plant, as well as vegetation indices. The differential response in terms of gsw and their link to drought-tolerance warrants further investigation and confirmation in plants grown in a community rather than single plants. This study identified some genotypes as potential donors of drought adaptive traits from the wild wheat group, such as *T. dicoccoides* (G242), *T. urartu* (G45), *T. boeoticum* (G27), and *T. araraticum* (G221) in terms of GY per plant with a high response to gsw. Moreover, a landrace, *T. monococcum* *sinskajae* (G89), and the modern durum wheat cultivar, *T. durum* cv. Sambadur (G41) exhibited low GY loss per plant with a low response in terms of gsw. While wild genotypes were not found to be superior, *per se*, to domesticated ones in terms of drought adaptation, the selected genotypes could potentially be used as donors of traits that could contribute to drought tolerance in domesticated wheat. We recommend further studies exploring the transfer of such traits to domesticated wheat.

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CRedit authorship contribution statement

Sumitra Pantha: Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **Hakan Özkan:** Writing – review & editing, Resources. **Benjamin Kilian:** Writing – review & editing, Validation. **Michael Frei:** Writing – review & editing, Supervision, Resources, Methodology, Conceptualization. **Frederike Zeibig:** Writing – review & editing, Investigation.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Sumitra Pantha reports financial support was provided by German Academic Exchange Service. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Code availability

Not applicable

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.fcr.2024.109678](https://doi.org/10.1016/j.fcr.2024.109678).

Data availability

Data will be made available on request.

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