Received: 29 April 2020 | Accepted: 24 August 2020

DOI: 10.1002/csc2.20319

Crop Science

SPECIAL ISSUE: ADAPTING AGRICULTURE TO CLIMATE CHANGE: A WALK ON THE WILD SIDE

Evaluation of durum wheat lines derived from interspecific crosses under drought and heat stress

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Assigned to Associate Editor Hannes Dempewolf.

Abstract

The productivity of durum wheat [*Triticum turgidum* subsp. *durum* (Desf.) van Slageren] is affected by drought and/or high temperatures, challenges to be amplified by climate change. Pre-breeding using wild relatives can supply useful traits for durum wheat improvement to adapt to major abiotic and biotic stresses. Sixty-seven lines issued from backcrosses of Cham5 and Haurani durum wheat varieties with accessions of *Triticum aegilopoides* (Link) Bal. ex Koern., *T. dicoccoides* Koern. ex Schweinf., *T. urartu* Thumanian ex Gandilyan, and *Aegilops speltoides* Tausch were evaluated for drought and heat tolerance. The trials were conducted during two seasons (2016–2017 and 2017–2018) at Tessaout, Morocco, under full irrigation (optimal conditions) and rainfed conditions (drought stressed) and at Wed Medani, Sudan, under full irrigation combined with heat stress. The recurrent parents, along with eight best cultivars and elite breeding lines, were used as checks. Drought reduced the grain yield by 62%. Grain yield and drought tolerance index were used to identify lines to be used by breeding programs to enhance drought and heat tolerance. The derivatives lines 142014 (Cham5*3/*T. aegilopoides*), 142074 (Cham5*3/*T. dicoccoides*), and 142015 along with the checks Icarachaz and Gidara 2 ranked among the best under heat stress. Under drought stress, the lines 141972 (Haurani*2/*T. urartu*) and 141973 (Cham5*2/*T. dicoccoides*) yielded 196 and 142% of their recurrent parents' yield, respectively. High variation was found for agronomic and phenology traits, with heading time explaining 16% of grain yield under drought, while thousand kernel weight accounted for 18% of the yield under heat. We conclude that gene introgression from wild relatives pays off and can increase wheat resilience to cope with climate change effects.

Abbreviations: BLUE, best linear unbiased estimation; BLUP, best linear unbiased prediction; BY, total biomass; DHE, days to heading; DMA, days to maturity; DTI, drought tolerance index; GFP, grain-filling period; GY, grain yield; HI, harvest index; PHT, plant height; SDSPK, number of seeds per spike; SPKM^2, number of spikes per square meter; TKW, thousand-kernel weight; TSIR, Tessaout under full irrigation; TSRF, Tessaout under rainfed conditions; WMD, Wed Medani.

1 INTRODUCTION

Core Ideas

- Drought and heat stresses are the major abiotic stresses affecting wheat productivity.
- Wheat wild relatives are a reservoir of valuable traits for wheat breeding.
- Pre-breeding should be supported to link conservation to use of crop wild relatives.

Durum wheat [*Triticum turgidum* subsp. *durum* (Desf.) van Slageren, $2n = 4x = 28$, AABB] is an economically important cereal crop cultivated in >21 countries over 13 million ha, with a global annual production of 36 Tg (Haile et al., 2019; Kadkol & Sissons, 2016; Tidiane Sall et al., 2019). Durum wheat is mainly used for pasta production in Europe and north America, whereas it is used for couscous, bourghul, and various types of bread in North African and West Asian countries (Troccoli, Borrelli, De Vita, Fares, & Di Fonzo, 2000). Around 75% of durum is cultivated around the Mediterranean basin, contributing 50% to the global production. However, climate change is expected to increase the temperature by 3–5 °C and to reduce precipitations by 4–27% during the cropping season (Flato et al., 2013; Li, Wu, Hernandez-Espinosa, & Peña, 2013), which will have drastic effects on crop production (Lobell et al., 2008). The global wheat area exposed to drought has doubled between 1979 and 2006 (Li, Ye, Wang, & Yan, 2009); in Australia, for example, the yield reduction associated with drought reached 47% in the year 2006 (Rauf, Al-Khayri, Zaharieva, Monneveux, & Khalil, 2016). Wheat yields worldwide are expected to decrease by 6% for each 1 °C increase in temperature (Asseng et al., 2015). Moreover, future yield losses associated with the predicted increase in heat and drought are expected to reach 10–30% by 2050 (Kumar et al., 2013; Lobell, Schlenker, & Costa-Roberts, 2011).

The development of productive and stress-resilient varieties will require the mobilization of novel diversity from landraces, primitive wheats, and wheat wild relatives to overcome the challenges associated to climate change, and to feed the growing human population (Nachit & Elouafi, 2004; Rajaram & Hettel, 1995). These genetic resources, having evolved under various natural biotic and abiotic challenges over long periods, should have accumulated genes for adaptation to drought- and heat-prone conditions (Zhang, Mittal, Leamy, Barazani, & Song, 2017).

A large number of *Triticum* and *Aegilops* species are included in the primary and secondary gene pools of durum wheat, including its direct progenitors [*Aegilops speltoides* Tausch, *T. urartu* Thumanian ex Gandilyan, *T. dicoccoides* Koern. ex Schweinf., and *T. dicoccum* (Schrank) Schübl.] (Faris, 2014). These species along with all other *Aegilops* species with S genomes and all primitive wheats with A, B, and G genomes constitute an important but still untapped reservoir of useful genes for genetic improvement of durum wheat (Ceoloni et al., 2017; Valkoun, 2001). They are regarded as last resort by most breeders because of reduced performance associated with undesirable genetic drags in the lines derived from interspecific crosses (Dempewolf et al., 2017; Mondal et al., 2016; Peng, Sun, & Nevo, 2011). However, several studies have reported on the value of introgression useful traits from primitive wheats and wild relative species, making wheat the second crop with the most cited uses of its wild relatives (Dempewolf et al., 2017; Mickelbart, Hasegawa, & Bailey-Serres, 2015; Zaïm et al., 2017; Zhang et al., 2017). The wheat wild relatives were mainly used as sources of resistance to major diseases in both durum and bread wheat (Anikster, Manisterski, Long, & Leonard, 2005; McIntosh, Hart, Devos, Gale, & Rogers, 2003; Monneveux, Rekika, & Zaharieva, 2000; Valkoun, Hammer, Kucerova, & Bartos, 1985) and insects (Bassi et al., 2019; Nsarellah, Amri, Nachit, El Bouhssini, & Lhaloui, 2003). Accessions of *Aegilops sharonensis* Eig, *A. searsii* M. Feldman & M. Kislev, *A. speltoides*, *Triticum aegilopoides* (Link) Bal. ex Koern., *T. dicoccum*, and *T. dicoccoides* showed good levels of tolerance to drought, cold, and salinity, and higher contents of proteins and micronutrients (Dempewolf et al., 2017; Monneveux et al., 2000; Nachit et al., 2015; Nevo & Chen, 2010). *Triticum aegilopoides* showed high level of drought tolerance (Mehrabad Pour-Benab, Fabriki-Ourang, & Mehrabi, 2019). Wild emmer *T. dicoccoides* harbors a rich allelic variation that can be used to enhance performances of durum wheat across diverse environments and constraints, as well as to improve the end-use qualities (Merchuk-Ovnat, Fahima, Krugman, & Saranga, 2016; Nachit and Elouafi, 2004). Drought tolerance is also found within *Ae. speltoides*, *Ae. longissima* Schweinf. & Muschl., and *Ae. searsii* (Waines, 1994), and salt tolerance is found in *T. dicoccum* (Hunsal, Balikai, & Viswanath, 1990).

The durum wheat improvement program at ICARDA (International Center for Agricultural Research in the Dry Areas) was among the few to extensively use primitive and wheat wild relative species in its breeding efforts (Nachit & Elouafi, 2004). A large number of lines issued from interspecific crosses are advanced every year for evaluation in the breeding program including for heat and drought tolerance.

Drought and heat tolerance are complex traits; their mechanisms are generally environment specific, and the strong genotype × environment interaction reduces the effectiveness of selection (Kaur, Singh, & Behl, 2016; Mickelbart et al., 2015). Therefore, breeding for heat and drought requires the integration of multiple disciplines and methodologies in plant science (Mwadzingeni, Shimelis, Dube, Laing, & Tsilo, 2016). Wheat wild relatives are generally assessed using physiological parameters associated with stress tolerance (Dulai et al., 2006; Mehrabad Pour-Benab et al., 2019; Pradhan et al., 2019; Sultan, Hui, Yang, & Xian, 2012; Zaharieva, Gaulin, Havaux, Acevedo, & Monneveux, 2001). For the derived lines, segregating populations, and elite lines, the evaluation of drought and heat tolerance can be done using empirical approach by assessing agronomic performance under typical environmental stresses and using stress tolerance and susceptibility indices (Mason et al., 2010; Mohammadi, Armion, Kahrizi, & Amri, 2010; Sio-Se Mardeh, Ahmadi, Poustini, & Mohammadi, 2006), or by measuring physiological parameters associated with tolerance to heat and drought (Araus, Slafer, Royo, & Serret, 2008; Reynolds & Langridge, 2016).

The objectives of this study were (a) to assess the contribution of wheat wild relatives to drought and heat tolerance through evaluation of durum wheat lines derived from interspecific crosses, and (b) to evaluate the effect of heat and drought on several morphological and agronomic traits of durum wheat derivatives.

2 MATERIALS AND METHODS

2.1 Plant material

The study was conducted with 77 lines of durum wheat (*Triticum turgidum* subsp. *durum*) including 67 lines derived from interspecific crosses, the two recurrent parents, and eight checks (Supplemental Table S1). The durum derivatives are the result of interspecific crosses between two durum wheat cultivars (Cham 5 and Haurani) and *Triticum turgidum* subsp. *dicoccoides* (syn. *Triticum dicoccoides*), *Triticum monococcum* subsp. *aegilopoides* (syn. *Triticum aegilopoides*), *Triticum urartu*, and *Aegilops speltoides* (Table 1). The scientific names of the wheat accessions used in the study are given based on the nomenclature proposed by van Slageren (1994). Valkoun (2001) described the procedure for the development of these lines where several backcrosses followed the interspecific hybridization to restore fertility and break the undesirable gene linkages. The list of wild parents used in the crosses is presented in Supplemental Table S2. Pedigree selection started at the (BC_2, BC_3, and BC_4) F_2 lines in 2002 and lasted until F_5, where the lines were advanced as bulk until F_{11}.

TABLE 1 Pedigree of the durum wheat derivatives evaluated for drought and heat tolerance

Pedigree	Wild parent genome	No of lines
Cham5*2/*T. aegilopoides*	A^mA^m	3
Cham5*2/*T. dicoccoides*	A^uA^uBB	6
Cham5*2/*T. urartu*	A^uA^u	3
Cham5*3/*T. aegilopoides*	A^mA^m	20
Cham5*3/*T. dicoccoides*	AABB	13
Cham5*3/*T. urartu*	A^uA^u	6
Cham5*4/*Ae. speltoides*	SS (BB)	7
Haurani*2/*T. aegilopoides*	A^mA^m	2
Haurani*2/*T. urartu*	A^uA^u	6
Haurani*3/*T. dicoccoides*	A^uA^uBB	1
Total	–	67

In addition to the pedigree and selection history (Supplemental Table S1), the derivatives lines and their recurrent parents were sequenced using DArTseqTM technology to assess their relatedness and diversity. The genotyping was done in collaboration with the International Center for Maize and Wheat Improvement (CIMMYT) at the Genetic Analysis Service for Agriculture (SAGA) facility in Mexico, to generate genomic profile of the germplasm. The genotypic raw data were filtered according to markers criterion; minor allele frequency $> 5\%$ and missing data $\leq 10\%$. This resulted in 6,196 DarTseq markers that were used to perform the principal component analysis (PCA) using the *pcaMethods* (Stacklies, Redestig, Scholz, Walther, & Selbig, 2007) package in R software.

2.2 Experimental design and field conditions

The trials were carried out during two consecutive seasons (2016–2017 and 2017–2018) at two locations: the Tessaout experimental station (31°49′ N, 7°25′ E) in Morocco, characterized by a dry season with an average annual precipitation of 266 mm with frequent droughts, and Wed Medani (WMD) in Sudan (14°24′ N, 33°31′ E; 407 m asl), where heat is the major stress. In Tessaout, two trials were planted each season, one under full irrigation (TSIR) representing the non-stressed environment, the second under rainfed conditions considered as drought stressed environment (TSRF). The irrigated trials were irrigated six times every season; the first irrigation was done at sowing, whereas the others were supplemented at different growth stages (i.e. postemergence, tillering, jointing, booting, and grain filling). The rainfed trial received only one irrigation at sowing to ensure homogeneous and simultaneous germination with the TSIR trial. In Wed Medani, the trials were irrigated at an interval of 7–10 d.

Each trial was randomized as an incomplete block design (α-lattice) with two replications. Each replicate consisted of 11 blocks, with seven genotypes in each. The plots were laid out in four rows 2 m long with a sowing density of 300 seeds m^{-2}; the distance between rows was 0.30 m. The best agronomic practices (fertilizers, weeding, and fungicides) recommended for each location were applied.

2.3 | Data collecting

The phenology traits collected in this study were as follows. Days to heading (DHE) was recorded as the number of days from the first irrigation until 50% of the plants of each plot reached at heading. Days to maturity (DMA) was observed when 90% of the plants in each plot are dry. The grain-filling period (GFP) was calculated as the difference between DHE and DMA. The plant height (PHT) was recorded at maturity from the ground to the top of the stem excluding the spike. The number of seeds per spike (SDSPK) was estimated based on three spikes collected from the internal rows avoiding the borders. The number of spikes per square meter ($SPKM^2$) was calculated based on number of spikes in a homogenous portion of 0.25 m^2. The two internal rows of each plot were harvested to estimate the total biomass (BY), the grain yield (GY), and the harvest index (HI) expressed as the ratio of grain weight to BY. The thousand-kernel weight (TKW) was estimated by counting and weighing 500 seeds.

2.4 | Statistical analysis

To assess the genotype × environment interaction and compute the heritability of traits across years and locations, Meta-R software (Vargas et al., 2013) was used for the analysis of variance using linear mixed models. The location and year were combined into a single factor (environment) for this purpose. To compute the best linear unbiased predictions (BLUPs), both genotypes, environments, and genotype × environment interaction were considered as random effects to estimate the variance components and hence the heritability. In addition, the best linear unbiased estimations (BLUEs) were computed across years in each location (TSIR, TSRF, and WMD); for this purpose, the genotypes and their interaction with the environments were considered as fixed effects. The heritability across locations was estimated as follows:

$$H^2 = \frac{\sigma_g^2}{\sigma_g^2 + \frac{\sigma_{ge}^2}{E} + \frac{\sigma_{Er}^2}{RE}}$$

where σ_g^2 is the genotypic variance, σ_{ge}^2 is the genotype by environment interaction, σ_{Er}^2 is the error variance, E is the number of environments, and R is the number of replicates.

The BLUPs of genotypes in each location across years were computed using *sommer* package in R (Covarrubias-Pazaran, 2019). This time, the location, year, and their interaction were used as fixed effects, and the random effect of genotypes in each location was computed using diagonal variance structure across locations. The diagonal structure assumes that the variance is heterogenous between locations and years to provide an accurate estimate of the random effects. The replication and block effect were nested in each environment. In addition to replication and block effects, spatial analysis using row and column was performed as needed for the variance analysis of $SPKM^2$.

The heritability in each location was estimated as follows:

$$h^2 = \frac{\sigma_g^2}{\sigma_g^2 + \frac{\sigma_e^2}{r}}$$

where σ_g^2 is the genotypic variance, σ_e^2 is the error variance, and r is the number of replications.

Pearson correlation coefficients between the traits were computed using *Hmisc* Package version 4.3-0 (Harrell & Dupont, 2019). To estimate the contribution of different independent traits to GY, stepwise regression was conducted using *leaps* package (Lumley, 2017). Both correlation and stepwise regression analysis were performed using the BLUEs across years in each location. The formula for the stepwise regression is as follows:

$$\begin{aligned} GY \sim Intercept\ &+ BY + DHE + GFP + SPKM^2 \\ &+ SDSPK + TKW + PHT \end{aligned}$$

The GY reduction in TSRF was calculated as a percentage in comparison with GY in TSIR. The drought tolerance index (DTI) was computed using the BLUPs of GY in each location as follows:

$$\mathrm{DTI} = \frac{Y_s Y_p}{\bar{Y}_p^2}$$

where Y_s is the GY under drought stress, Y_p is the GY under optimal conditions (TSIR) and $\bar{Y}_p^2$ is the square of average GY under optimal conditions.

The plots were constructed using *ggplot2* (Wickham, 2016) and *corrplot* (Wei & Simko, 2017) package in R software.

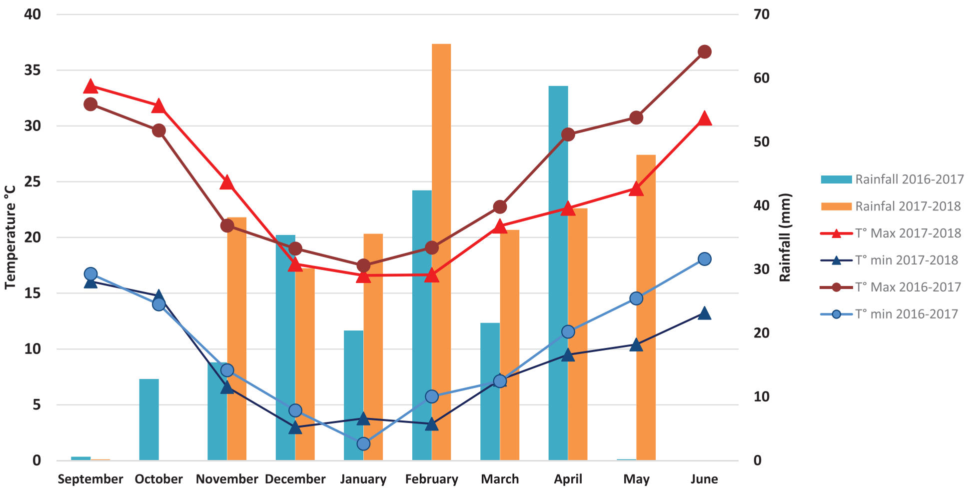

FIGURE 1 Precipitations (mm) and maximum and minimum temperatures (°C) registered at Tessaout during the cropping seasons of 2016–2017 and 2017–2018

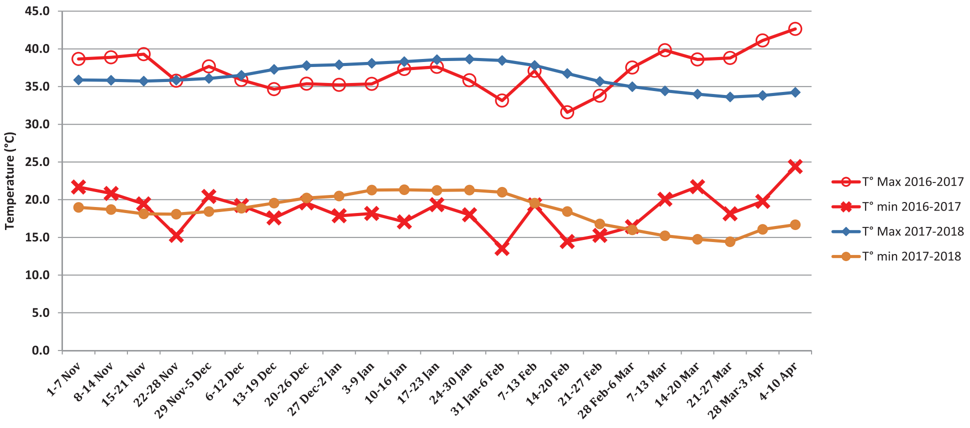

FIGURE 2 Minimum and maximum temperatures (°C) registered at Wed Medani during the cropping seasons of 2016–2017 and 2017–2018

2.5 | Climatic conditions

The total rainfall registered in Tessaout was 207 and 294 mm during the 2016–2017 and 2017–2018 seasons, respectively. The second season was more favorable, as the precipitations were evenly spread during the different growth stages of the crop (Figure 1). The first season at Tessaout was characterized by an increase in temperatures at the end of the cycle, which was associated with an absence of precipitation during the GFP.

In Wed Medani, no rainfall was registered during the two seasons. The average maximum and minimum temperatures were 37 and 18 °C, respectively. This range was consistent during the two seasons, and the maximum temperature was always higher than 30 °C (Figure 2). The average maximum temperature registered in both seasons was 37 °C. The first season (2016–2017) was characterized by higher temperatures at the end of the cycle.

3 | RESULTS

3.1 | Genotype × environment interaction

The combined ANVOA showed that the effect of genotypes was significant for all traits except for SPKM^2, which had the lowest heritability across environments (.40). The genotypes explained 5% of the variation in GY, 7% in TKW, and 14% in both HI and SDSPK. The environment effect was significant for all the traits and explained the highest ratio of the variance. The environment variance varied from 30% for SDSPK, to 75% for GY, to >95% for DHE and GFP. A high level of significance was observed for the genotype × environment interaction except for BY, which had a heritability of .54 across environments.

The phenological traits (DHE and GFP) had the same heritability of .56, which is relatively lower in comparison

TABLE 2 Combined ANOVA across environments for phenology and agronomic traits of durum wheat derivatives grown at Tessaout and Wed Madi experiment stations during the 2016–2017 and 2017–2018 seasons

Trait	G variance	G × ENV variance	ENV variance	H^2	CV
PHT	14.82**	17.41**	284.59**	.70	7.3
DHE	3.21**	12.74**	308.95**	.56	2.3
GFP	2.03**	3.35**	89.24**	.56	6.7
SPKM^2	68.02ns†	16,986,175.13*	5.26ns	.40	16.4
SDSPK	9.73**	5.24*	20.37ns	.69	13.6
TKW	4.988**	2.72**	39.64**	.74	11.5
HI	11.81**	13.61**	28.62*	.70	19.1
BY	490,327.13**	338,896.9ns	18,985,499.46**	.54	18.4
GY	230,539.29**	212,157.61**	3,470,507.06**	.71	23.2

Note. G, genotype; Env, environment; PHT, plant height; DHE, days to heading; GFP, grain-filling period; SPKM^2, number of seeds per square meter; SDSPK, number of seeds per spike; TKW, thousand-kernel weight; HI, harvest index; BY, total biomass; GY, grain yield.

*Significant at the .05 probability level.

**Significant at the .01 probability level. †ns, not significant.

TABLE 3 Descriptive statistics and heritability of days to heading (DHE), grain-filling period (GFP), plant height (PHT), and harvest index (HI) at Tessaout under optimal conditions (TSIR) and drought stress (TSRF)

	TSIR				TSRF			
Trait	Min.	Max.	Mean	h^2	Min.	Max.	Mean	h^2
DHE	105	106	105	.69	96	109	102	.81
GFP	51	56	53	.48	45	54	50	.72
PHT	98	121	110	.75	73	92	83	.72
HI	31	46	39	.71	16	30	24	.81

with heritabilities of the other yield components such as TKW (.74) and SDSPK (.69) (Table 2).

The effect of the year on GY and other agronomic traits was important at all locations, with higher impact in the stressed environments (Figure 3). At TSRF, higher values were recorded for all traits in the second season except for DHE and GFP that remained the same. The average GY in TSRF increased from 2,253 kg ha^{-1} in 2016–2017 to 4,557 kg ha^{-1} in 2017–2018. Simultaneously, BY, HI, SPKM^2, and TKW showed higher values in the second season at TSRF (Figure 3). The same findings were observed in WMD as the GY increased from 1,380 kg ha^{-1} the first season to 2,183 kg ha^{-1} during the second. All the other traits increased; TKW went from 29 to 36 g, whereas the HI increased to an average of 31% in the second year. Despite the effect of year on the stressed environments (TSRF and WMD), the performance in the optimal conditions (TSIR) was not affected by the year (Figure 3). In the second season, the average GY at TSIR, for example, was 13% higher than TSRF, despite that the second season was more favorable for the rainfed trial.

3.2 | Screening for drought tolerance

3.2.1 | Drought effect on agronomic traits

The comparison of performance between TSIR and TSRF revealed that drought stress reduced different traits measured. The genotypic expression of the phenological traits increased under drought stress. The heritability of DHE varied from .69 in TSIR to .80 in TSRF. Similarly, GFP heritability increased from .48 under optimal conditions to .72 under drought. On average, the heading time was reduced by 4 d (Table 3), whereas PHT was reduced by 25% at TSRF. The reduction in PHT has affected the BY.

The yield losses due to drought across the years was 62%; this was associated with a significant decrease in all yield components measured (Figure 4). Under optimal conditions, the GY ranged between 4,075 and 7,971 kg ha^{-1} with a heritability of .51 and an average of 5,954 kg ha^{-1}. Icarachaz was the highest yielding line at TSIR with a GY of 7,971 kg ha^{-1}, followed by the line 142064 (7,491 kg ha^{-1}) that yielded 33% higher than its recurrent parent (Haurani)

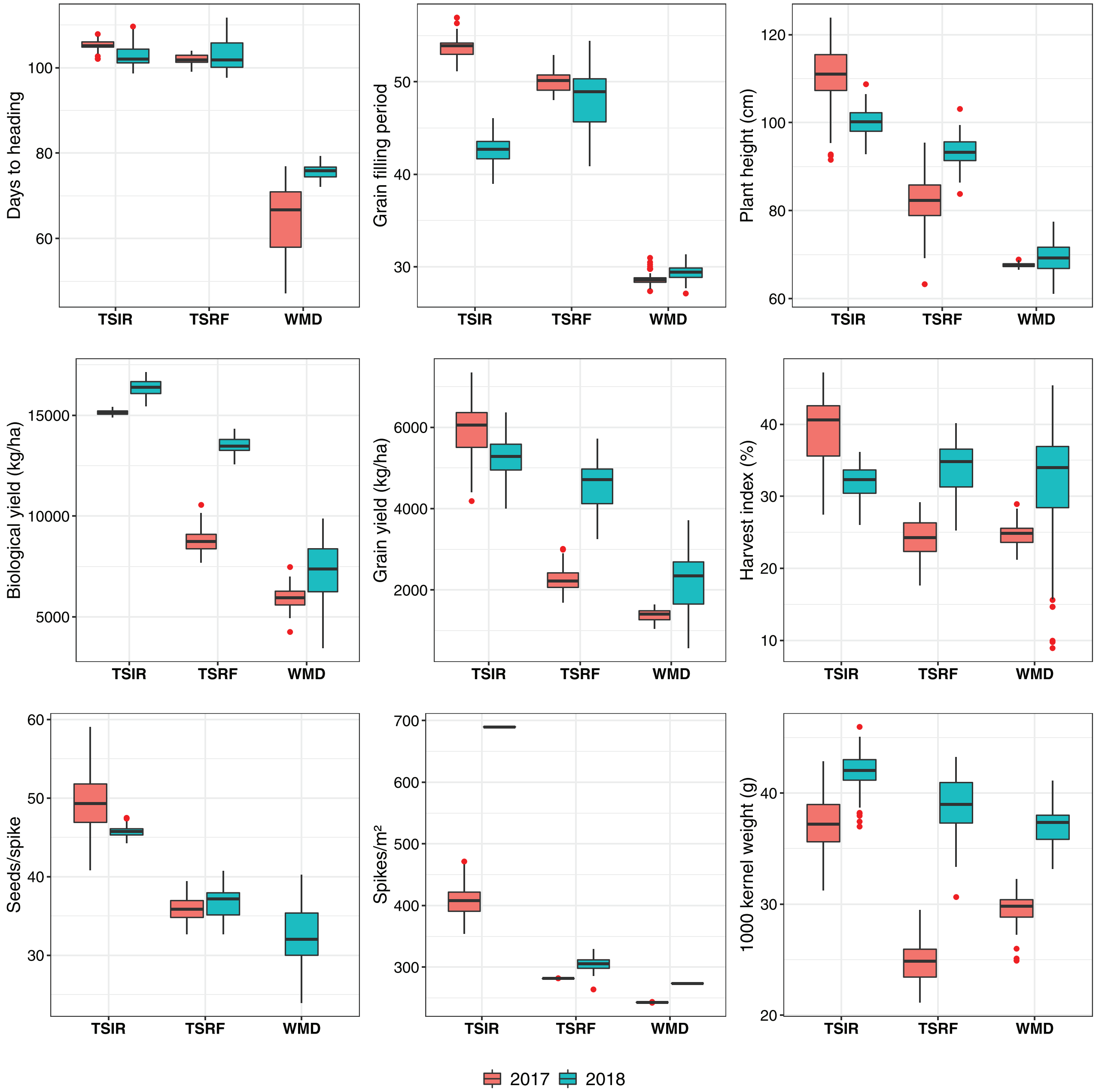

FIGURE 3 Boxplots of the best linear unbiased predictions (BLUPs) of the phenology and agronomic traits of durum wheat derivatives at Tessaout under irrigated (TSIR) and rainfed conditions (TSRF) and Wed Medani (WMD) during the 2016–2017 and 2017–2018 seasons

at TSIR. The line 141999 (Haurani*2/*T. urartu*) yielded 7,174 kg ha^{-1} in TSIR; this was significantly higher that the recurrent parent by 27% (Supplemental Table S3).

Under drought stress, all the lines with GY higher than 3,000 kg ha^{-1} were derived from interspecific crosses. The highest GY in TSRF was 3,628 kg ha^{-1} recorded by a line derived from a cross of Cham 5 to *Triticum dicoccoides* (141973), it outyielded significantly its recurrent parent by 42%. It was followed by lines derived from crosses of both recurrent parents to *Triticum aegilopoides*, *Triticum urartu*, and *Aegilops speltoides* (Supplemental Table S4).

The two genotypes, 142013 and 129080 (Cham1), were more stable as their BLUPs were high under both rainfed and irrigated conditions. The GY heritability at TSRF increased to .61, which implies an increase of the genotypic effect under stress.

Total biomass was the second trait most affected by drought; the observed losses were 43%, and the gap between optimal and stressed conditions was highly significant (Figure 3). The relatively low heritability is shown in the density plot where the range is small at both TSIR and TSRF. Harvest index showed higher ability to

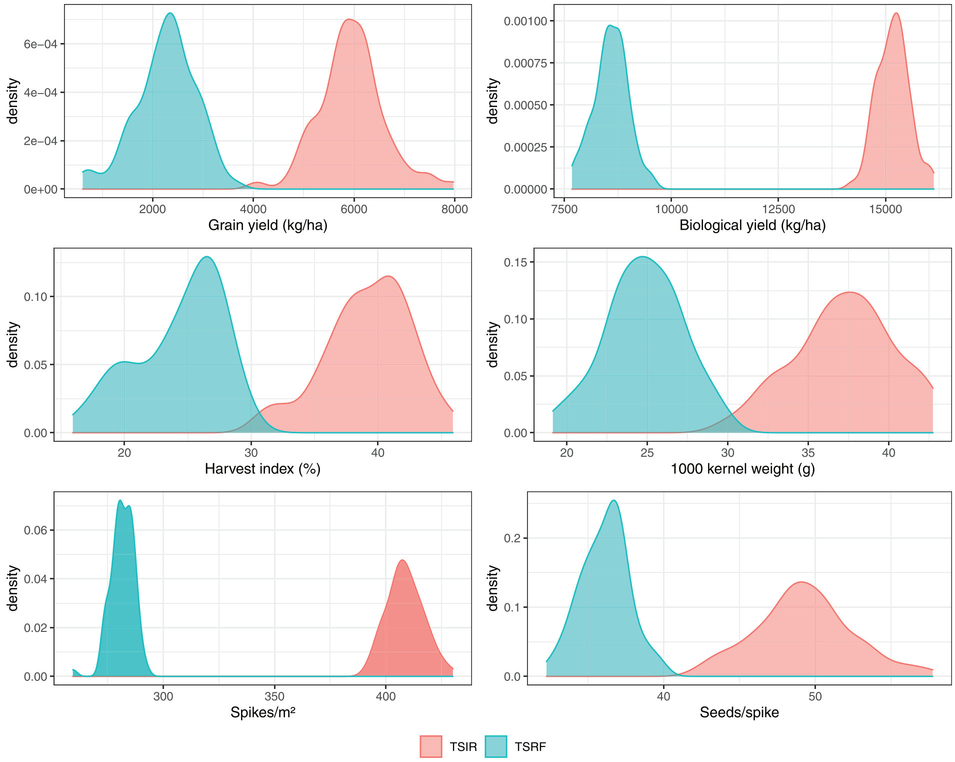

FIGURE 4 Density plots for the best linear unbiased predictions (BLUPs) of grain yield, biological yield, harvest index, 1000-kernel weight, spikes m^{-2}, and seeds $spike^{-1}$ under optimal conditions (TSIR) and drought stress (TSRF) at the Tessaout experiment station

distinguish genotypes, as the heritabilities were high under both optimal conditions ($h^2 = .71$) and drought stress ($h^2 = .81$). The HI reduction due to drought was 37%.

Among yield components, SPKM^2 had the lowest heritability at both TSIR (.20) and TSRF (.38). The mean SPKM^2 decreased significantly from 408 at TSIR to 281 (31% reduction) at TSRF due to drought (Figure 4). The low heritability did not allow us to discriminate the most desirable genotypes for SPKM^2 at TSIR. The trait least affected by drought was SDSPK which showed a reduction of 26%, on average, and higher genotypic expression in the optimal conditions ($h^2 = .43$).

3.2.2 | Selection of drought-tolerant genotypes

The comparison of GY at TSIR and TSRF revealed a negative correlation between the two environments; most of the genotypes with high yield potential showed low drought tolerance, and vice versa (Figure 5a). However, two interesting groups of genotypes were identified with respect to drought tolerance (Figure 5b). In the first group combining drought tolerance and high yield potential, the line 142013 had the second highest DTI (0.52) and yielded 6,829 kg ha^{-1} under optimal conditions. Similar findings are observed with other lines: 142060 (DTI = 0.44), 142008 (DTI = 0.43), 141997 (DTI = 0.42), and 142046 and 142018 (DTI = 0.40). The second group represents the low-yield-potential genotypes with good performance under drought. The most distinguished line in this group was 141973 (Cham5*2/*T. dicoccoides* ICWT 601116) with the highest DTI (0.53). This group includes the lines with the highest GY at TSRF (141973, 141996,142020, 142055, 141972, and 141990; Supplemental Table S5). However, these lines did not respond positively to the favorable conditions at TSIR. (Figure 5).

3.3 | Screening for heat stress

The screening for heat tolerance was approached by comparing the performance of entries under continuous heat stress prevailing at WMD. Phenological traits, especially the heading time, showed a good potential to identify desirable genotypes for heat stress. The heritabilities of DHE and GFP were .68 and .50, respectively (Table 4). Earliness was an important trait for the lines with high yield at WMD. For example, the two checks Marzak and Louiza reached heading after 60 d only. The lines 142001 and 142015 (both derived from *T. urartu*) headed after 58 and 67 d, respectively. The line 142007, also derived from *T. urartu,*

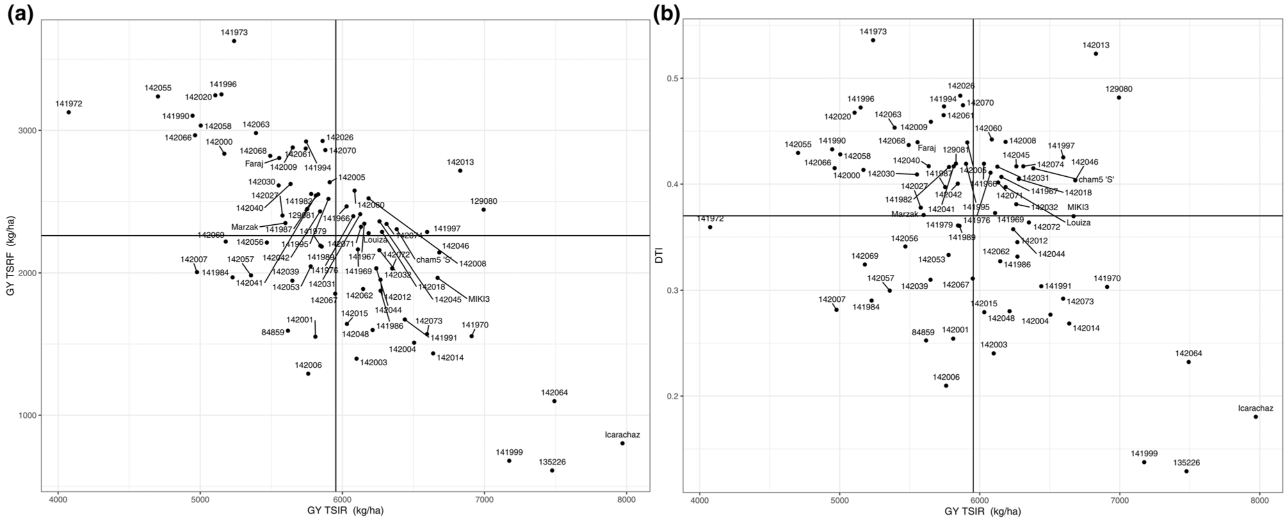

FIGURE 5 Biplot of (a) grain yield (GY) at Tessaout under irrigated (TSIR) and rainfed (TSRF) and (b) drought tolerance index (DTI) plotted against the GY at TSIR of durum wheat lines

TABLE 4 Descriptive statistics for phenology and agronomic traits under heat stress at Wed Medani across the two seasons of 2016–2017 and 2017–2018

Statistic	DHE	GFP	PHT	SPKM^2	SDSPK	TKW	BY	GY	HI
Min.	55	27	63	238	28	26.59	4,271	634	17
Max.	70	31	72	247	44	32.23	7,276	2,082	29
Mean	64	29	68	243	36	29.52	5,922	1,377	24
h^2	.68	.50	.48	.10	.67	.36	.47	.60	.37

Note. DHE, days to heading; GFP, grain-filling period; PHT, plant height; SPKM^2, number of seeds per square meter; SDSPK, number of seeds per spike; TKW, thousand-kernel weight; BY, total biomass; GY, grain yield; HI, harvest index.

headed 13 d before its recurrent parent (Haurani) (Supplemental Table S5).

In terms of yield components, SPKM^2 had the lowest heritability (.10); the range of the BLUPs was small and did not allow to distinguish desirable genotypes for this trait. The heritabilities of TKW and SDSPK were .36 and .67, respectively. The SDSPK ranged between 28 and 44 seeds per spike; this range allowed us to identify some lines with high spikelet fertility under heat stress. The check Louiza and the recurrent parent Haurani had the highest SDSPK (44), and Haurani derivatives had lower seeds per spike at WMD compared to their recurrent parent. The BY averaged 5,922 kg ha^{-1} at WMD with a heritability of .47 (Table 4). Louiza, Marzak, and the line 142074 were the most distinguished lines for BY; their BY was >7,000 kg ha^{-1} (Supplemental Table 5).

The average GY in WMD was 1,377 kg ha^{-1} with a heritability of .60 (Table 4). The maximum yield was 2,082 kg ha^{-1}, which was obtained by the line 142015 (Cham5*2/*T. urartu*) (Supplemental Table S5). In addition to the checks Marzak and Louiza, other lines derived from crosses with *T. aegilopoides* and *T. dicoccoides* were among the highest yielding under heat stress (Supplemental Table S5).

A biplot of GY among TSIR, TSRF, and WMD was performed to identify suitable lines combing high yield potential with heat and drought tolerance (Figure 6). Several lines combining heat tolerance and high yield potential were identified. Interestingly, the checks Gidara 2 (IG 135226) and Icarachaz combined high yield under heat (1,930 and 1,831 kg ha^{-1}) with the high GY at TSIR (7,476 and 7,971 kg ha^{-1}) (Figure 6a). The line 142001 (Haurani*2/*T. urartu*) showed a potential for breeding for tolerance to heat stress. Most of the stable genotypes with respect to heat stress are derived from crosses of both recurrent parents to *Triticum urartu*, *Triticum dicoccoides*, and *Triticum aegilopoides.*

In terms of combining heat and drought tolerance, three interesting lines derived from the same cross of Cham 5 to *Triticum aegilopoides* were identified (142009,142066, and 142068). Another two lines derived from *Triticum urartu* (142026) and *Aegilops speltoides* (142055) showed suitability for breeding to both drought and heat (Figure 6b).

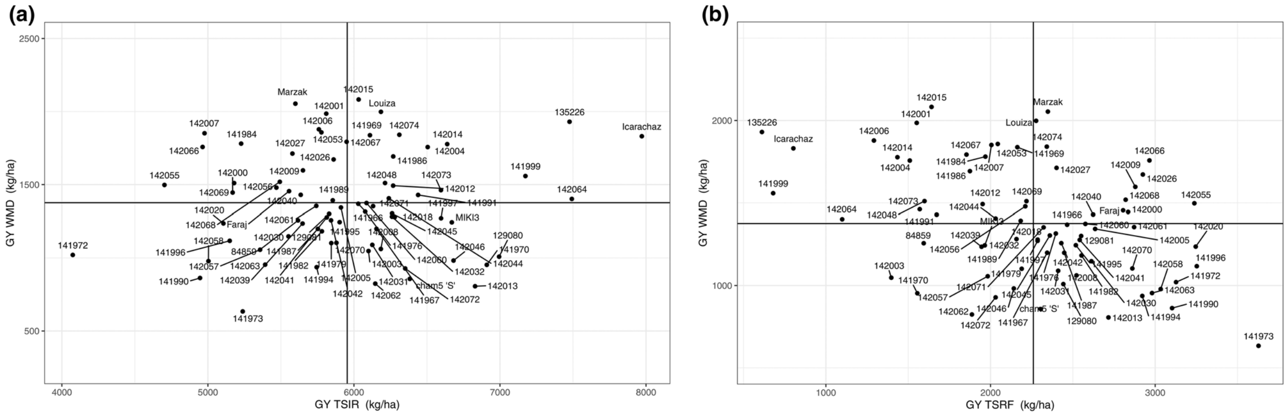

FIGURE 6 Biplot of (a) grain yield (GY) at Wed Medani (WMD) plotted against GY at Tessaout under irrigated conditions (TSIR), and (b) GY at WMD plotted against GY at Tessaout under rainfed conditions (TSRF)

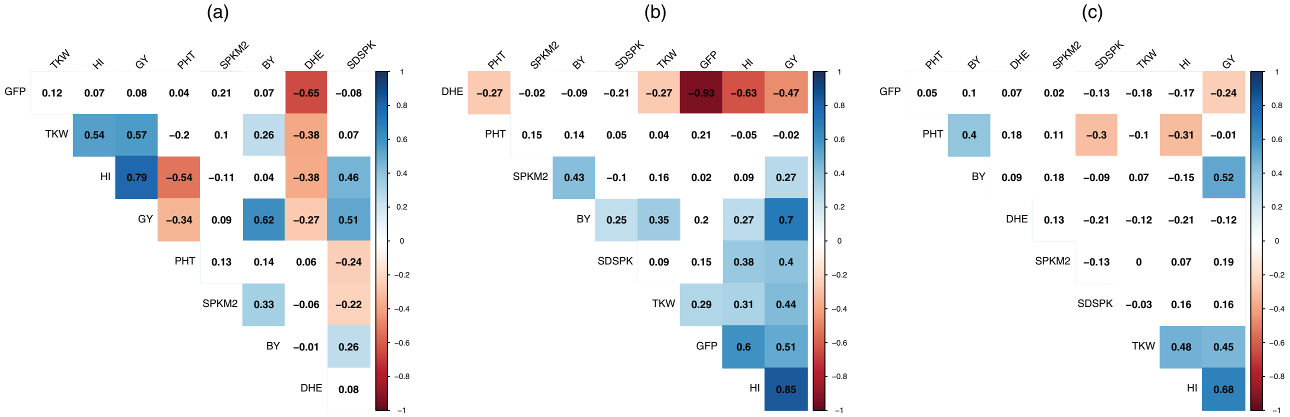

FIGURE 7 Pearson correlation coefficients between the different traits in the three environments under (a) optimal conditions, (b) drought stress, and (c) heat stress. Level of significance α = .05. GFP, grain-filling period; TKW, thousand-kernel weight; HI, harvest index; GY, grain yield; PHT, plant height; SPKM^2, number of spikes per square meter; BY, total biomass; DHE, days to heading; SDSPK, number of seeds per spike

3.4 | Correlation and stepwise regression analyses results

At TSIR, GY was positively correlated to TKW (r^2 = .57), HI (r^2 = 079) BY (r^2 = .82), and SDSPK (r^2 = .51). The DHE was negatively associated with GFP (r^2 = −.65), TKW (r^2 = −.38), HI (r^2 = −.38), and GY (r^2 = −.27). Under drought stress (TSRF), an important cluster composed of interrelated traits (HI, GFP, TKW, and SDSPK) showed significant correlations with GY (Figure 7). Very high negative correlation was observed between DHE and GFP (r^2 = −.93). This later showed significant positive correlation with TKW (r^2 = .29).

At WMD, GY was negatively correlated with GFP (r^2 = −.24), but positively correlated with HI (r^2 = .68), TKW (.45), SPKM^2, and BY. The DHE affected negatively the SDSPK and HI. The correlation between DHE and GFP was not significant.

The results of the stepwise regression showed that BY explained the highest portion of GY variation in the three environments, accounting for 38, 49, and 26% at TSIR, TSRF, and WMD, respectively. The highest variation of GY explained by DHE was 16% under drought conditions. Under heat stress at WMD, the contribution of DHE was not significant. However, GFP was important under heat, explaining 3.65% of GY at WMD. In the two other environments, GFP contribution was not significant. The yield components were important under optimal conditions and heat stress, as 18.24% of the GY was explained by SDSPK and TKW at TSIR, and 17.62 and 4.93% of the GY was explained by TKW and SDSPK at WMD, respectively. In addition, 1.61% of the GY under heat was associated with SPKM^2, whereas this trait was not important at TSIR and TSRF. The SDSPK was more important than TKW under drought stress at TSRF, since it explained 2.30% of the GY variation (Figure 8).

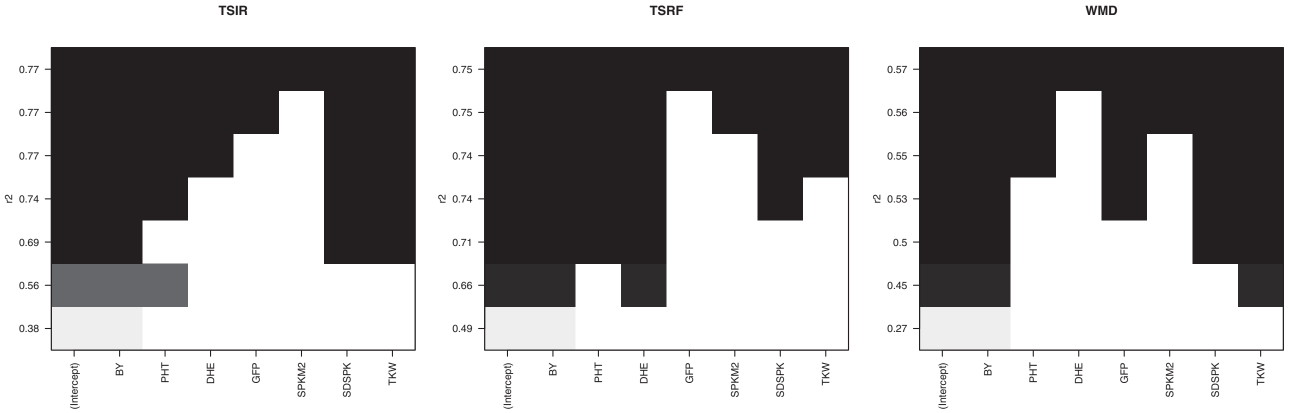

FIGURE 8 Stepwise regression for biomass, phenology, and yield components of durum wheat derivatives at Tessaout under irrigated conditions (TSIR), Tessaout under rainfed conditions (TSRF) and Wed Medani (WMD). BY, total biomass; PHT, plant height; DHE, days to heading; GFP, grain-filling period; SPKM^2, number of spikes per square meter; SDSPK, number of seeds per spike; TKW, thousand-kernel weight

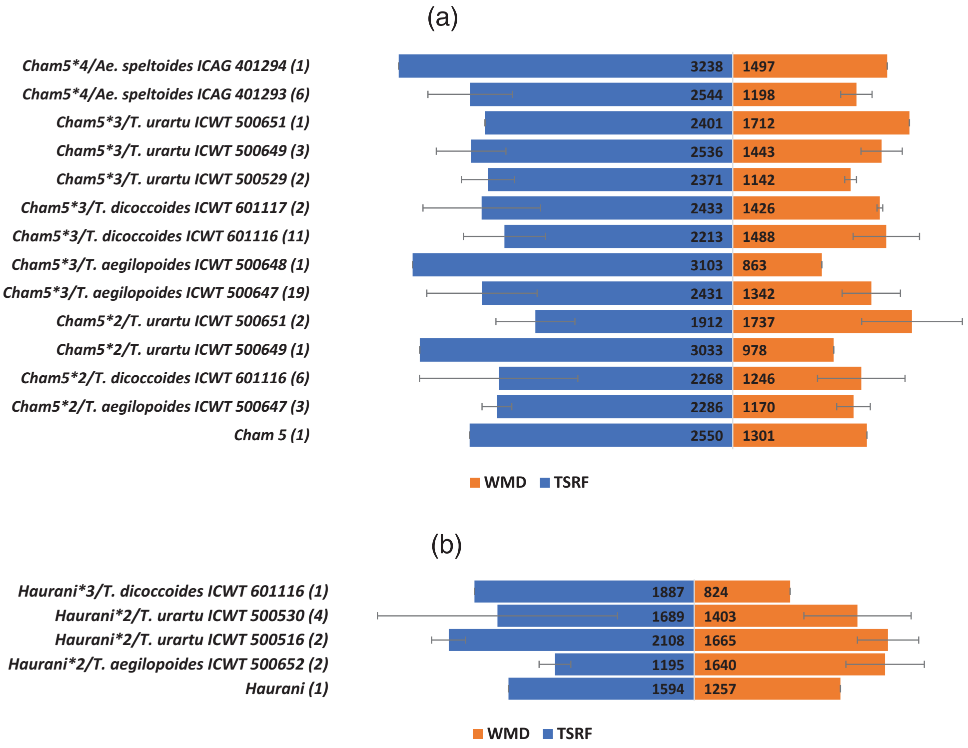

FIGURE 9 Average and standard deviation of the grain yield (GY, kg ha^{-1}) of durum wheat derivatives lines from crosses with (a) Cham 5 and (b) Haurani by pedigree with their recurrent parents at Wed Medani (WMD) and Tessaout under rainfed conditions (TSRF). The number between parentheses represents the number of lines derived from each cross

3.5 | Comparison of the derivatives to the recurrent parents

The comparison of the durum wheat derivatives with their recurrent parents revealed high variability among the durum wheat derivatives. The highest variation in GY under drought was observed in lines derived from interspecific crosses with *Triticum dicoccoides*. The lines derived from *Aegilops speltoides* yielded higher than Cham 5 under both stresses. *Triticum urartu* is also a potential source of combined tolerance to drought and heat (Figure 9). The most interesting lines in TSRF were 141973 and 141996; they are derived from crosses with *Triticum dicoccoides* and *Aegilops speltoides*, respectively.

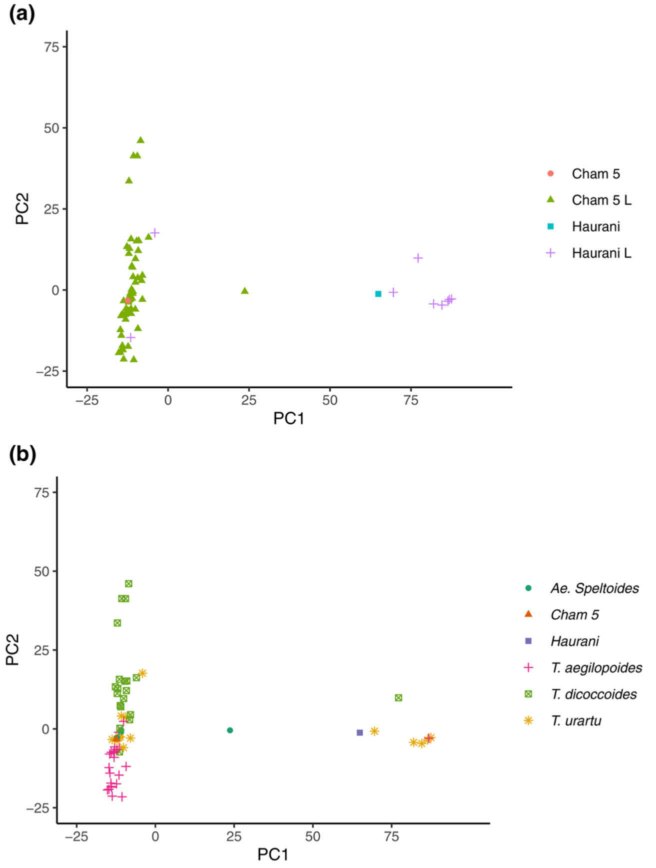

FIGURE 10 Biplot of the first two principal components (PCs) of the principal component analysis using DarTseq markers colored by (a) the cultivated parent and (b) the wild parent. Cham 5 L = lines derived from Cham 5; Haurani L = lines derived from Haurani

The accession 142015 (Cham5*2/*T. urartu* ICWT 500651) had a GY of 2,082 kg ha^{-1}, which was 60% higher than its recurrent parent Cham 5 under heat stress. Many lines derived from *Triticum dicoccoides* were ranked among the best performing under heat stress.

The GY of Haurani derivatives lines from crosses with *Triticum urartu* were higher than their recurrent parent under both heat and drought stresses. In TSRF, the GY of the line 141972 was almost twice (196%) the GY of Haurani. At WMD, the genotypes 142001 (Haurani*2/*T. urartu*) and 142006 (Haurani*2/*T. aegilopoides*) yielded 50% more than their recurrent parent. The line derived from *Triticum dicoccoides* did not show significant increase in comparison with Haurani in TSRF.

The principal component analysis based on the DarTseq markers showed that the first five components explained 61% of the genotypic variance in the population. The biplot of the two first components (explaining 49%) revealed that the genotypes are clustered mainly according to the recurrent parent (Figure 10a), and then following the wild parents (Figure 10b). Two lines derived from Haurani (142065 and 142001) were included within the cluster of lines derived from Cham 5. The second level clusters followed the genome of the wild parents; the lines derived from *Triticum urartu* and *Triticum aegilopoides* (AA genome) were clustered together, whereas lines derived from *Triticum dicoccoides* (AABB genome) were different. Four lines derived from the same cross of Cham 5 to *T. dicoccoides* were distinguished from the other lines. The genotypes derived from *Aegilops speltoides* were grouped together, except for the accession 142055, which was different. No pattern was observed with respect to the number of backcrosses.

4 | DISCUSSION

The climatic data showed differences between the two seasons in terms of precipitation distribution at Tessaout; however, the first season has allowed us to screen the germplasm for both terminal drought and heat, whereas the second season has allowed us to screen the germplasm for mild drought. These stresses are the major factors affecting cereal production under Mediterranean climates, which explains the year-to-year fluctuations (Zhang et al., 2018) and the genotype × environment interactions showing the need for selecting genotypes with wide yield stability. The yield losses at TSRF due to drought (62%) are similar to those reported previously by Sukumaran, Reynolds, and Sansaloni (2018). This penalty depends on the growth stage, but mostly on the duration of crop exposure to stress (Balla et al., 2019; Nezhadahmadi, Prodhan, & Faruq, 2013). It can be concluded that the distribution of rainfall in the Mediterranean region is more determinant than the amount of precipitation during the cropping season. The evaluation of breeding germplasm under irrigated and nonirrigated conditions at Tessaout will allow breeders to select lines combining yield potential with drought tolerance, which could be advanced to later stages of yield evaluation under multiyear, multilocation trials to assess their yield stability.

The average maximum temperature registered at WMD is higher than the optimal temperature for wheat growth during both vegetative (20–30 °C; Balla et al., 2019) and reproductive stages, where the optimal temperature during anthesis is 23 ± 1.15 °C while for the optimal temperature for grain filling is 21.3 ± 1.27 °C (Farooq, Bramley, Palta, & Siddique, 2011). High temperature has been associated with reductions or lengthening of the durum wheat cycle (Bauer et al., 1988; Villegas et al., 2016). This is also in line with the fact that high temperature shortens the growth stages and accelerates the plant growth (Parent & Tardieu, 2012; Reynolds et al., 2017). These reported findings were observed on phenology and cycle duration at WMD.

Therefore, the Wed Medani station can serve breeders to screen for specific adaptation to continuous heat stress. The selected lines could combine tolerance mechanisms to heat in both vegetative and reproductive stages; this presents an important and valuable advantage, as most of the studies focus on heat effect at the reproductive stage only (Balla et al., 2011; El Hassouni et al., 2019; Farooq et al., 2011; Stone & Nicolas, 1995). Due to its latitude and photoperiod, the germplasm to be generated could better fit sub-Saharan African countries, where wheat cultivation is expanding (Tidiane Sall et al., 2019). In addition, this site could serve to study the in situ mechanisms of heat tolerance in wheat and other crops.

Although many lines are derived from similar crosses, high heritability was observed for GY across environments ($h^2 = .71$), which suggests that some lines could be adapted to more than one environment simultaneously. For example, many lines showed their potential to be used as parental material to breed for both heat stress and yield potential. Other lines combined tolerance to heat and drought stresses. These findings demonstrate the potential of crop wild relatives to enhance durum wheat yield potential, simultaneously with the improvement of tolerance to abiotic stresses. Most of the traits introgressed from crop wild relatives in wheat focused on improvement of resistance to pests and diseases with limited emphasis on yield, abiotic stresses, and quality attributes (Hajjar & Hodgkin, 2007; Zaïm et al., 2017). The contribution of the wheat progenitors was observed directly in the GY, where many lines were as performant as the best checks, or by improving the yield components. For example, *Triticum aegilopoides*-derived lines showed the potential to improve the grain number per spike under all the environments. Under heat stress, the line 142007 (Haurani*2/*T. urartu*) was early with high TKW, which makes it a potential line for earliness and high grain-filling rate under continuous heat stress. This finding highlights the ability to include such lines in the breeding programs to improve specific adaptive traits to heat and drought stresses.

Comparing the genotypic performance under both stresses suggests that the mechanisms of heat and drought tolerance could be different. This was observed in the correlation and stepwise regression analysis under each environment. The BY showed strong correlation to GY under all environments, as it explained the greatest part of variation in GY. Furthermore, the second largest decrease associated with drought was observed in BY, which is in line with the results reported by Zhang et al. (2018) in their meta-analysis. Moreover, yield losses under drought were associated with a lower supply of assimilates to support the reproductive stages and seed growth (Zhang et al., 2018). Therefore, the development of germplasm with higher biomass through early vigor and higher tillering capacity could lead to higher yields under heat and drought. The advantage in yield can be explained by greater remobilization of assimilates to the grains during the reproductive stage. Reynolds et al. (2017) also suggested the aboveground biomass as a criteria for selecting the parents to breed for adaptation to heat-prone environments. They suggested using landraces and wild relatives as a source of higher biomass.

Phenology was important under both stresses. At WMD, five of the highest yielding lines reached heading before 60 d, which highlights the importance of earliness in escaping more severe heat stress in later stages. Earliness is also important in escaping terminal drought combined with heat stress experienced at TSRF as confirmed by stepwise regression analysis. These results confirm that earliness is one of the most effective strategies in breeding for environment characterized by terminal abiotic stresses (Araus et al., 2008). Mondal, Joshi, Huerta-Espino, and Singh (2015) also concluded that earliness under Mediterranean conditions allows the plants to escape terminal heat stress in addition to promoting an efficient use of available resources under continuous heat stress. However, very early germplasm might result in show low yield potential (Blum & Jordan, 1985). Based on the significant negative correlation between GY and GFP at WMD, achieving high yield under continuous heat stress will require a combination of earliness with high grain-filling rate. Grain-filling rate was suggested as a selection criteria for heat stress tolerance, as it affects the TKW (Baillot, Girousse, Allard, Piquet-Pissaloux, & Le Gouis, 2018; Wu, Tang, Li, & Wu, 2018). The two lines 142057 and 142007 derived from crosses of *Triticum urartu* to both recurrent parents combined earliness with high TKW under heat stress, which suggests their value as parental material to improve these traits towards achieving higher heat tolerance.

Under drought conditions (TSRF), the GFP has significant positive correlation with GY. This phase is reported as the most vulnerable stage of wheat to water deficit, (Guoth et al., 2009; Jha, Bohra, & Singh, 2014; Sehgal et al., 2018). Therefore, selecting early genotypes with long GFP could lead to selecting lines with good levels of drought tolerance.

In terms of yield components, drought stress affected the spike fertility, which in turn reduced the grain number per spike. This trait had higher heritability at WMD (.67), which highlights the ability of SDSPK to discriminate heat-susceptible and heat-tolerant lines. This is confirmed by the stepwise regression analysis, where 5% of GY under heat was explained by SDSPK, making it the third most important trait after BY and TKW. These findings confirm the results of other studies highlighting the contribution of the number of grains per spike to higher yields under drought and heat stresses (El Hassouni et al., 2019; Fábián, Sáfrán, Szabó-Eitel, Barnabás, & Jäger, 2019; Leilah & Al-Khateeb, 2005; Villegas, García del Moral, Rharrabti, Martos, & Royo, 2007; Zhang et al., 2018). Vahamidis, Karamanos, and Economou (2019) reported high plasticity of seed number per spike in wheat, which can allow breeders to achieve genetic gains under drought and heat stresses using this trait. We found high variability for SDSPK in *Triticum aegilopoides* and *Triticum dicoccoides* derivatives at all environments. Under drought stress, the lines 141996, 141999, and 142000 derived from *Aegilops speltoides, Triticum urartu*, and *Triticum dicoccoides* can be used as sources to improve this trait. Other studies have shown that *Triticum dicoccoides* was found to have high plasticity for phenology, biomass, and spike dry matter under terminal drought stress, and accessions of *Triticum dicoccoides* showed advantage in spike productivity (Peleg et al., 2005; Suneja, Gupta, & Bains, 2019).

The correlation and stepwise regression results showed the strong association between TKW and GY at all environments. The TKW is among the key traits that contributed to genetic gain in wheat breeding under drought, as confirmed by several studies (Leilah & Al-Khateeb, 2005; Mohammadi, Farshadfar, & Amri, 2016). However, this trait was not largely exploited to select for heat tolerance (Lopes et al., 2012). Under heat stress in WMD, this trait explained the highest ratio of GY; therefore, selection for higher TKW under the continuous heat stress can result in higher GY. Several lines derived from *Triticum urartu* showed the potential for use to improve this trait under both drought and heat stresses. However, some of the interspecific-derived lines with winter growth habit had shown low yields despite the high TKW.

Under TSRF, the highest number of $SPKM^2$ was reached by lines derived from *Triticum dicoccoides*, followed by those derived from crosses with *Triticum aegilopoides*. The $SPKM^2$ showed positive correlation with GY under heat at WMD. Despite the low heritability across environments, this trait showed some variation under drought stress. Many lines derived from crosses with *Triticum dicoccoides* and *Triticum aegilopoides* had high $SPKM^2$ at TSRF. These two species, in addition to *Aegilops speltoides*, were reported as potential sources of drought tolerance (Djanaguiraman et al., 2019; Sultan et al., 2012). The high tillering capacity of *Triticum dicoccoides* (Peleg et al., 2005) can be exploited to increase the effective tillers, and therefore $SPKM^2$, under drought. The low heritability of this trait under heat did not allow us to assess the value of this trait for breeding for heat tolerance.

The comparison of durum wheat derivatives with their respective recurrent parents was used to show the potential contribution of wheat wild relatives to improve heat and drought tolerance. All interspecific crosses have resulted in a wide range of variability under different environments for all traits measured. This shows the potential of using crop wild relatives to broaden the genetic base of wheat. No clustering pattern was observed with respect to the number of backcrosses when using molecular markers. The best lines for different traits could be found in different backcrossing populations, showing that the selection could start after BC_2 unless the purpose is to develop isogenic lines of the recurrent parent. Fewer backcrosses are needed in the case of interspecific crosses involving primitive wheats and wild relatives that are in Gene pool 1. In fact, some genotypes showed an advantage for high yield potential in comparison with the recurrent parent with only two backcrosses (142064, 141999, and 141970). The primary gene pool species can present an important advantage when breeding for traits with polygenic inheritance; such is the case for heat and drought tolerance. The recombination of homologous chromosomes allows simultaneous transfer of genes from multiple chromosomes (Valkoun, 2001). The use of these species is made easy, as the rate of success in the crosses is high and does not require the use of advanced technics. The derived lines can be supplied in a short time period to supply the breeders with new diverse germplasm. Therefore, direct progenitors of wheat present an ideal germplasm for wheat improvement against abiotic stresses.

However, when crosses are done with species in the secondary and tertiary gene pools, more backcrosses might be needed to avoid the effect of genetic drag and to reduce the length of any translocated chromosome segment of the wild species. Nevo and Chen (2010) reported other species from the secondary and tertiary gene pools with potential contribution to drought tolerance. *Aegilops geniculata* was also identified as a source of heat and drought tolerance; the population evaluated showed high biomass production under those stresses (Zaharieva et al., 2001). The geographic distribution of wild relatives affects their level of drought tolerance (Peleg et al., 2005; Zaharieva et al., 2001). Therefore, targeted selection of accessions in ex situ collections and collection of new accessions in drought- and heat-stressed environments will allow broader and novel diversity to improve tolerance to these stresses.

Pre-breeding efforts are needed to supply sources of valuable traits needed by the breeders to develop elite germplasm that will adapt to climate change effects and respond to requirements of farmers and consumers. The use of crop wild relatives should not be restricted to pest and diseases resistance; it should cover their contribution to improve nutritional value and industrial quality, in addition to efficient use of inputs. The evaluation and use of wild relatives and their derived pre-breeding germplasm should be strengthened to ensure the link between conservation and the use of crop wild relatives.

ACKNOWLEDGMENTS

This work was undertaken as part of the initiative "Adapting Agriculture to Climate Change: Collecting, Protecting and Preparing Crop Wild Relatives," which is supported by the Government of Norway. The project is managed by the Global Crop Diversity Trust with the Millennium Seed Bank of the Royal Botanic Gardens, Kew, and implemented in partnership with national and international gene banks and plant breeding institutes around the world. For further information, see the project website: http://www.cwrdiversity.org/.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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REFERENCES

Anikster, Y., Manisterski, J., Long, D. L., & Leonard, K. J. (2005). Leaf rust and stem rust resistance in *Triticum dicoccoides* populations in Israel. *Plant Diseases*, *89*, 55–62. https://doi.org/10.1094/PD-89-0055

Araus, J. L., Slafer, G. A., Royo, C., & Serret, M. D. (2008). Breeding for yield potential and stress adaptation in cereals. *Critical Reviews in Plant Sciences*, *27*, 377–412. https://doi.org/10.1080/07352680802467736

Asseng, S., Ewert, F., Martre, P., Rötter, R. P., Lobell, D. B., Cammarano, D., … Zhu, Y. (2015). Rising temperatures reduce global wheat production. *Nature Climate Change*, *5*(2), 143–147. https://doi.org/10.1038/nclimate2470

Baillot, N., Girousse, C., Allard, V., Piquet-Pissaloux, A., & Le Gouis, J. (2018). Different grain-filling rates explain grain-weight differences along the wheat ear. *PLOS ONE*, *13*(12). https://doi.org/10.1371/journal.pone.0209597

Balla, K., Karsai, I., Bónis, P., Kiss, T., Berki, Z., Horváth, Á., … Veisz, O. (2019). Heat stress responses in a large set of winter wheat cultivars (*Triticum aestivum* L.) depend on the timing and duration of stress. *PLOS ONE*, *14*(9). https://doi.org/10.1371/journal.pone.0222639

Balla, K., Rakszegi, M., Li, Z., Békés, F., Bencze, S., & Veisz, O. (2011). Quality of winter wheat in relation to heat and drought shock after anthesis. *Czech Journal of Food Science*, *29*, 117–128. https://doi.org/10.17221/227/2010-CJFS

Bassi, F. M., Brahmi, H., Sabraoui, A., Amri, A., Nsarellah, N., Nachit, M. M., … El Bouhssini, M. (2019). Genetic identification of loci for Hessian fly resistance in durum wheat. *Molecular Breeding*, *39*(2). https://doi.org/10.1007/s11032-019-0927-1

Bauer, A., Garcia, R., Kanemasu, E. T., Blad, B. L., Hatfield, J. L., Major, D. J., … Hubbard, K. G. (1988). Effect of latitude on phenology of 'Colt' winter wheat. *Agricultural and Forest Meteorology*, *44*, 131–140. https://doi.org/10.1016/0168-1923(88)90012-3

Blum, A., & Jordan, W. R. (1985). Breeding crop varieties for stress environments. *Critical Reviews in Plant Sciences*, *2*, 199–238. https://doi.org/10.1080/07352688509382196

Ceoloni, C., Kuzmanović, L., Ruggeri, R., Rossini, F., Forte, P., Cuccurullo, A., & Bitti, A. (2017). Harnessing genetic diversity of wild gene pools to enhance wheat crop production and sustainability: Challenges and opportunities. *Diversity*, *9*(4). https://doi.org/10.3390/d9040055

Covarrubias-Pazaran, G. (2019). *Quantitative genetics using the sommer package*. Vienna: Comprehensive R Archive Network.

Dempewolf, H., Baute, G., Anderson, J., Kilian, B., Smith, C., & Guarino, L. (2017). Past and future use of wild relatives in crop breeding. *Crop Science*, *57*, 1070–1082. https://doi.org/10.2135/cropsci2016.10.0885

Djanaguiraman, M., Prasad, P. V. V., Kumari, J., Sehgal, S. K., Friebe, B., Djalovic, I., … Gill, B. S. (2019). Alien chromosome segment from *Aegilops speltoides* and *Dasypyrum villosum* increases drought tolerance in wheat via profuse and deep root system. *BMC Plant Biology*. *19*(1). https://doi.org/10.1186/s12870-019-1833-8

Dulai, S., Molnár, I., Prónay, J., Csernák, Á., Tarnai, R., & Molnár-Láng, M. (2006). Effects of drought on photosynthetic parameters and heat stability of PSII in wheat and in *Aegilops* species originating from dry habitats. *Acta Biologica Szegediensis*, *50*, 11–17.

El Hassouni, K., Belkadi, B., Filali-Maltouf, A., Tidiane-Sall, A., Al-Abdallat, A., Nachit, M., & Bassi, F. M. (2019). Loci controlling adaptation to heat stress occurring at the reproductive stage in durum wheat. *Agronomy*, *9*(8). https://doi.org/10.3390/agronomy9080414

Fábián, A., Sáfrán, E., Szabó-Eitel, G., Barnabás, B., & Jäger, K. (2019). Stigma functionality and fertility are reduced by heat and drought co-stress in Wheat. *Frontiers in Plant Science*, *10*. https://doi.org/10.3389/fpls.2019.00244

Faris, J. D. (2014). Wheat domestication: Key to agricultural revolutions past and future. In R. Tuberosa, A. Graner, & E. Frison (Eds.), *Genomics of plant genetic resources* (pp. 439–464). Dordrecht, the Netherlands: Springer. https://doi.org/10.1007/978-94-007-7572-5_18

Farooq, M., Bramley, H., Palta, J. A., & Siddique, K. H. M. (2011). Heat stress in wheat during reproductive and grain-filling phases. *Critical Reviews in Plant Sciences*, *30*, 491–507. https://doi.org/10.1080/07352689.2011.615687

Flato, G., Marotzke, J., Abiodun, B., Braconnot, P., Chou, S. C., Collins, W. J., … Rummukainen, M. (2013). Evaluation of climate models. In In T. F. Stocker, et al. (Eds.), *Climate change 2013: The physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (Vol. 5, pp. 741–866). Cambridge, UK, and New York: Cambridge University Press.

Guoth, A., Tari, I., Csiszar, J., Pecsvaradi, A., Cseuz, L., & Erdei, L. (2009). Comparison of the drought stress responses of tolerant and sensitive wheat cultivars during grain filling: Changes in flag leaf photosynthetic activity, ABA levels, and grain yield. *Journal of Plant Growth Regulation*, *28*, 167–176. https://doi.org/10.1007/s00344-009-9085-8

Haile, J. K., N'Diaye, A., Walkowiak, S., Nilsen, K. T., Clarke, J. M., Kutcher, H. R., … Pozniak, C. J. (2019). Fusarium head blight in durum wheat: Recent status, breeding directions, and future research prospects. *Phytopathology*, *109*, 1664–1675. https://doi.org/10.1094/PHYTO-03-19-0095-RVW

Hajjar, R., & Hodgkin, T. (2007). The use of wild relatives in crop improvement: A survey of developments over the last 20 years. *Euphytica*, *156*, 1–13. https://doi.org/10.1007/s10681-007-9363-0

Harrell, Jr, F. E., & Dupont, C. (2019). Hmisc: Harrell Miscellaneous. R package version 4.3-0. Comprehensive R Archive Network. Retrieved from https://CRAN.R-project.org/package=Hmisc

Hunsal, C. S., Balikai, R. B., & Viswanath, D. P. (1990). *Triticum dicoccum*: Its performance in comparison with barley under salinity. *Journal of Maharashtra Agricultural University*, *125*, 376–377.

Jha, U. C., Bohra, A., & Singh, N. P. (2014). Heat stress in crop plants: Its nature, impacts and integrated breeding strategies to improve heat tolerance. *Plant Breeding*, *133*, 679–701. https://doi.org/10.1111/pbr.12217

Kadkol, G. P., & Sissons, M. (2016). Durum wheat: Overview. In C. W. Wrigley, H. Corke, & K. Seetharaman (Eds.), *Encyclopedia of food grains* (pp. 117–124). Amsterdam: Elsevier.

Kaur, V., Singh, S., & Behl, R. K. (2016). Heat and drought tolerance in wheat: Integration of physiological and genetic platforms for better performance under stress. *Ekin Journal of Crop Breeding and Genetics*, *2*, 1–14.

Kumar, S., Kumari, P., Kumar, U., Grover, M., Singh, A. K., Singh, R., & Sengar, R. S. (2013). Molecular approaches for designing heat tolerant wheat. *Journal of Plant Biochemistry and Biotechnology*, *22*, 359–371. https://doi.org/10.1007/s13562-013-0229-3

Leilah, A. A., & Al-Khateeb, S. A. (2005). Statistical analysis of wheat yield under drought conditions. *Journal of Arid Environments*, *61*, 483–496. https://doi.org/10.1016/j.jaridenv.2004.10.011

Li, Y., Ye, W., Wang, M., & Yan, X. (2009). Climate change and drought: A risk assessment of crop-yield impacts. *Climate Research*, *39*, 31–46. https://doi.org/10.3354/cr00797

Li, Y.-F., Wu, Y., Hernandez-Espinosa, N., & Peña, R. J. (2013). Heat and drought stress on durum wheat: Responses of genotypes, yield, and quality parameters. *Journal of Cereal Science*, *57*, 398–404. https://doi.org/10.1016/j.jcs.2013.01.005

Lobell, D. B., Burke, M. B., Tebaldi, C., Mastrandrea, M. D., Falcon, W. P., & Naylor, R. L. (2008). Prioritizing climate change adaptation needs for food security in 2030. *Science*, *319*, 607–610. https://doi.org/10.1126/science.1152339

Lobell, D. B., Schlenker, W., & Costa-Roberts, J. (2011). Climate trends and global crop production since 1980. *Science*, *333*, 616–620. https://doi.org/10.1126/science.1204531

Lopes, M. S., Reynolds, M. P., Manes, Y., Singh, R. P., Crossa, J., & Braun, H. J. (2012). Genetic yield gains and changes in associated traits of CIMMYT spring bread wheat in a "historic" set representing 30 years of breeding. *Crop Science*, *52*, 1123–1131. https://doi.org/10.2135/cropsci2011.09.0467

Lumley, T. (2017). leaps: Regression Subset Selection. Comprehensive R Archive Network. Retrieved from https://CRAN.R-project.org/package=leaps

Mason, R. E., Mondal, S., Beecher, F. W., Pacheco, A., Jampala, B., Ibrahim, A. M. H., & Hays, D. B. (2010). QTL associated with heat susceptibility index in wheat (*Triticum aestivum* L.) under short-term reproductive stage heat stress. *Euphytica*, *174*, 423–436. https://doi.org/10.1007/s10681-010-0151-x

McIntosh, R. A., Hart, G. E., Devos, K. M., Gale, M. D., & Rogers, W. J. (2003). *Catalogue of gene symbols for wheat*. USDA-ARS. Retrieved from http://wheat.pw.usda.gov/ggpages/wgc/98/

Mehrabad Pour-Benab, S., Fabriki-Ourang, S., & Mehrabi, A.-A. (2019). Expression of dehydrin and antioxidant genes and enzymatic antioxidant defense under drought stress in wild relatives of wheat. *Biotechnology and Biotechnological Equipment*, *33*, 1063–1073. https://doi.org/10.1080/13102818.2019.1638300

Merchuk-Ovnat, L., Fahima, T., Krugman, T., & Saranga, Y. (2016). Ancestral QTL alleles from wild emmer wheat improve grain yield, biomass and photosynthesis across environments in modern wheat. *Plant Science*, *251*, 23–34. https://doi.org/10.1016/j.plantsci.2016.05.003

Mickelbart, M. V., Hasegawa, P. M., & Bailey-Serres, J. (2015). Genetic mechanisms of abiotic stress tolerance that translate to crop yield stability. *Nature Reviews Genetics*, *16*, 237–251. https://doi.org/10.1038/nrg3901

Mohammadi, R., Armion, M., Kahrizi, D., & Amri, A. (2010). Efficiency of screening techniques for evaluating durum wheat genotypes under mild drought conditions. *International Journal of Plant Production*, *4*, 11–24. https://doi.org/10.22069/IJPP.2012.677

Mohammadi, R., Farshadfar, E., & Amri, A. (2016). Path analysis of genotype × environment interactions in rainfed durum wheat. *Plant Production Science*, *19*, 43–50. https://doi.org/10.1080/1343943X.2015.1128100

Mondal, S., Joshi, A. K., Huerta-Espino, J., & Singh, R. P. (2015). Early maturity in wheat for adaptation to high temperature stress. In Y. Ogihara, S. Takumi, & H. Handa (Eds.), *Advances in wheat genetics: From genome to field* (pp. 239–245). Tokyo: Springer Japan. https://doi.org/10.1007/978-4-431-55675-6_26

Mondal, S., Rutkoski, J. E., Velu, G., Singh, P. K., Crespo-Herrera, L. A., Guzmán, C., … Singh, R. P. (2016). Harnessing diversity in wheat to enhance grain yield, climate resilience, disease and insect pest resistance and nutrition through conventional and modern breeding approaches. *Frontiers in Plant Science*, *7*. https://doi.org/10.3389/fpls.2016.00991.

Monneveux, P., Rekika, D., & Zaharieva, M. (2000). The utilisation of *Triticum* and *Aegilops* species for the improvement of durum wheat. In C. Royo, M. Nachit, N. Di Fonzo, & J. L. Araus (Eds.), *Durum wheat improvement in the Mediterranean region: New challenges* (pp. 71–81). Zaragoza, Spain: CIHEAM.

Mwadzingeni, L., Shimelis, H., Dube, E., Laing, M. D., & Tsilo, T. J. (2016). Breeding wheat for drought tolerance: Progress and technologies. *Journal of Integrative Agriculture*, *15*, 935–943. https://doi.org/10.1016/S2095-3119(15)61102-9.

Nachit, M. M., & Elouafi, I. (2004). Durum adaptation in the Mediterranean dryland: Breeding, stress physiology, and molecular markers. In S. C. Rao & J. Ryan (Eds.), *Challenges and strategies of dryland agriculture* (pp. 203–218). Madison, WI: CSSA and ASA. https://doi.org/10.2135/cssaspecpub32.c13

Nachit, M. M., N, Nsarellah, Motowaj, J., Kehel, Z., Pagnott, M., Mondi, I., … Amri, A. (2015). Use of durum landraces and *Triticum* wild relatives to breed robust durum cultivars for Mediterranean environmental conditions. In *From seed to pasta & beyond: A sustainable durum wheat chain for food security and healthy lives. Abstracts*. Bologna, Italy: Avenue Media.

Nevo, E., & Chen, G. (2010). Drought and salt tolerances in wild relatives for wheat and barley improvement. *Plant, Cell and Environment*, *33*, 670–685. https://doi.org/10.1111/j.1365-3040.2009.02107.x

Nezhadahmadi, A., Prodhan, Z. H., & Faruq, G. (2013). Drought tolerance in wheat. *Science World Journal*, *2013*, 1–12. https://doi.org/10.1155/2013/610721

Nsarellah, N., Amri, A., Nachit, M. M., El Bouhssini, M., & Lhaloui, S. (2003). New durum wheat with Hessian fly resistance from *Triticum araraticum* and *T. carthlicum* in Morocco. *Plant Breeding*, *122*, 435–437. https://doi.org/10.1046/j.1439-0523.2003.00871.x

Parent, B., & Tardieu, F. (2012). Temperature responses of developmental processes have not been affected by breeding in different ecological areas for 17 crop species. *New Phytologist*, *194*, 760–774. https://doi.org/10.1111/j.1469-8137.2012.04086.x

Peleg, Z., Fahima, T., Abbo, S., Krugman, T., Nevo, E., Yakir, D., & Saranga, Y. (2005). Genetic diversity for drought resistance in wild emmer wheat and its ecogeographical associations. *Plant, Cell and Environment*, *28*, 176–191. https://doi.org/10.1111/j.1365-3040.2005.01259.x

Peng, J. H., Sun, D. F., & Nevo, E. (2011). Wild emmer wheat, *Triticum dicoccoides*, occupies a pivotal position in wheat domestication process. *Australian Journal Crop Science*, *5*, 1127–1143.

Pradhan, S., Babar, M. A., Robbins, K., Bai, G., Mason, R. E., Khan, J., & Bernardo, A. (2019). Understanding the genetic basis of spike fertility to improve grain number, harvest index, and grain yield in wheat under high temperature stress environments. *Frontiers in Plant Science*, *10*. https://doi.org/10.3389/fpls.2019.01481

Rajaram, S., & Hettel, G. P. (1995). *Wheat breeding at CIMMYT: Commemorating 50 years of research in Mexico for global wheat improvement.* Mexico City: CIMMYT.

Rauf, S., Al-Khayri, J. M., Zaharieva, M., Monneveux, P., & Khalil, F. (2016). Breeding strategies to enhance drought tolerance in crops. In J. M. Al-Khayri, S. M. Jain, & D. V. Johnson (Eds.), *Advances in plant breeding strategies: Agronomic, abiotic and biotic stress traits* (pp. 397–445). Cham: Springer International Publishing.

Reynolds, M., & Langridge, P. (2016). Physiological breeding. *Current Opinion in Plant Biology*, *31*, 162–171. https://doi.org/10.1016/j.pbi.2016.04.005

Reynolds, M. P., Pask, A. J. D., Hoppitt, W. J. E., Sonder, K., Sukumaran, S., Molero, G., & Joshi, Arun K. (2017). Strategic crossing of biomass and harvest index—source and sink—achieves genetic gains in wheat. *Euphytica*, *213*(11). https://doi.org/10.1007/s10681-017-2040-z

Sehgal, A., Sita, K., Siddique, K. H. M., Kumar, R., Bhogireddy, S., Varshney, R. K., & Nayyar, H. (2018). Drought or/and heat-stress effects on seed filling in Food Crops: Impacts on functional biochemistry, seed yields, and nutritional quality. *Frontiers in Plant Science*, *9*. https://doi.org/10.3389/fpls.2018.01705

Sio-Se Mardeh, A., Ahmadi, A., Poustini, K., & Mohammadi, V. (2006). Evaluation of drought resistance indices under various environmental conditions. *Field Crops Research*, *98*, 222–229. https://doi.org/10.1016/j.fcr.2006.02.001

Stacklies, W., Redestig, H., Scholz, M., Walther, D., & Selbig, J. (2007). pcaMethods: A bioconductor package providing PCA methods for incomplete data. *Bioinformatics*, *23*, 1164–1167. https://doi.org/10.1093/bioinformatics/btm069

Stone, P., & Nicolas, M. (1995). A survey of the effects of high temperature during grain filling on yield and quality of 75 wheat cultivars. *Australian Journal of Agricultural Research*, *46*, 475–492. https://doi.org/10.1071/AR9950475

Sukumaran, S., Reynolds, M. P., & Sansaloni, C. (2018). Genome-wide association analyses identify QTL hotspots for yield and component traits in durum wheat grown under yield potential, drought, and heat stress environments. *Frontiers in Plant Science*, *9*. https://doi.org/10.3389/fpls.2018.00081

Sultan, M., Hui, L., Yang, L. J., & Xian, Z. H. (2012). Assessment of drought tolerance of some *Triticum* L. species through physiological indices. *Czech Journal of Genetics and Plant Breeding*, *48*, 178–184.

Suneja, Y., Gupta, A. K., & Bains, N. S. (2019). Stress adaptive plasticity: *Aegilops tauschii* and *Triticum dicoccoides* as Potential donors of drought associated morpho-physiological traits in wheat. *Frontiers in Plant Science*, *10*. https://doi.org/10.3389/fpls.2019.00211

Tidiane Sall, A., Chiari, T., Legesse, W., Seid-Ahmed, K., Ortiz, R., van Ginkel, M., & Bassi, F. M. (2019). Durum wheat (*Triticum durum* Desf.): Origin, cultivation and potential expansion in sub-Saharan Africa. *Agronomy*, *9*(5). https://doi.org/10.3390/agronomy9050263

Troccoli, A., Borrelli, G. M., De Vita, P., Fares, C., & Di Fonzo, N. (2000). Mini review: Durum wheat quality: A multidisciplinary concept. *Journal of Cereal Science*, *32*, 99–113. https://doi.org/10.1006/jcrs.2000.0322

Vahamidis, P., Karamanos, A. J., & Economou, G. (2019). Grain number determination in durum wheat as affected by drought stress: An analysis at spike and spikelet level. *Annals of Applied Biology*, *174*, 190–208. https://doi.org/10.1111/aab.12487

Valkoun, J., Hammer, K., Kucerova, O., & Bartos, P. (1985). Disease resistance in the genus *Aegilops* L.: Stem rust, leaf rust, stripe rust and powdery mildew. *Kulturpfianze*, *33*, 133–153.

Valkoun, J. J. (2001). Wheat pre-breeding using wild progenitors. *Euphytica*, *119*, 17–23. https://doi.org/10.1023/A:1017562909881

van Slageren, M. W. (1994). *Wild wheats: A monograph of Aegilops L. and Amblyopyrum (Jaub. & Spach) Eig (Poaceae).* Wageningen, the Netherlands: Wageningen Agricultural University and ICARDA.

Vargas, M., Combs, E., Alvarado, G., Atlin, G., Mathews, K., & Crossa, J. (2013). META: A suite of SAs programs to analyze multi-environment breeding trials. *Agronomy Journal*, *105*, 11–19. https://doi.org/10.2134/agronj2012.0016

Villegas, D., Alfaro, C., Ammar, K., Cátedra, M. M., Crossa, J., García del Moral, L. F., & Royo, C. (2016). Daylength, temperature and solar radiation effects on the phenology and yield formation of spring durum wheat. *Journal of Agronomy and Crop Science*, *202*, 203–216. https://doi.org/10.1111/jac.12146

Villegas, D., García del Moral, L. F., Rharrabti, Y., Martos, V., & Royo, C. (2007). Morphological traits above the flag leaf node as indicators of drought susceptibility index in durum wheat. *Journal of Agronomy and Crop Science*, *193*, 103–116. https://doi.org/10.1111/j.1439-037X.2006.00246.x

Waines, J. G. (1994). High temperature in wild wheats and spring wheats. *Australian Journal of Plant Physiology*, *21*, 705–715.

Wei, T., & Simko, V. (2017). R package “corrplot”: Visualization of a correlation matrix (version 0.84). GitHub. Available from Retrieved from https://github.com/taiyun/corrplot

Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. New York: Springer. Retrieved from https://ggplot2.tidyverse.org

Wu, X., Tang, Y., Li, C., & Wu, C. (2018). Characterization of the rate and duration of grain filling in wheat in southwestern China. *Plant Production Science*, *21*, 358–369. https://doi.org/10.1080/1343943X.2018.1518722

Zaharieva, M., Gaulin, E., Havaux, M., Acevedo, E., & Monneveux, P. (2001). Drought and heat responses in the wild wheat relative *Aegilops geniculata* Roth: Potential interest for wheat improvement. *Crop Science*, *41*, 1321–1329. https://doi.org/10.2135/cropsci2001.4141321x

Zaïm, M., El Hassouni, K., Gamba, F., Filali-Maltouf, A., Belkadi, B., Sourour, A., … Bassi, F. M. (2017). Wide crosses of durum wheat (*Triticum durum* Desf.) reveal good disease resistance, yield stability, and industrial quality across Mediterranean sites. *Field Crops Res*, *214*, 219–227. https://doi.org/10.1016/j.fcr.2017.09.007

Zhang, H., Mittal, N., Leamy, L. J., Barazani, O., & Song, B.-H. (2017). Back into the wild-Apply untapped genetic diversity of wild relatives for crop improvement. *Evolutionary Applications*, *10*, 5–24. https://doi.org/10.1111/eva.12434

Zhang, J., Zhang, S., Cheng, M., Jiang, H., Zhang, X., Peng, C., … Jin, J. (2018). Effect of drought on agronomic traits of rice and wheat: A meta-analysis. *International Journal of Environmental Research and Public Health*, *15*(5). https://doi.org/10.3390/ijerph15050839

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Aberkane H, Amri A, Belkadi B, et al. Evaluation of durum wheat lines derived from interspecific crosses under drought and heat stress. *Crop Science*. 2020;1–18. https://doi.org/10.1002/csc2.20319