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Hafid ABERKANE

Contribution of wild relatives to durum wheat (*Triticum turgidum* ssp. *durum*) improvement under climate change effects

Devant le JURY:

Zin El Abidine TRIQUI	**PES,** Faculté des Sciences, Université Mohammed V, Rabat	**Président/Rapporteur**
Mustapha ARBAOUI	**PH**, Institut Agronomique et Vétérinaire Hassan II, Rabat	**Rapporteur/ Examinateur**
Laila SBABOU	**PES**, Faculté des Sciences, Université Mohammed V, Rabat	**Rapporteur/ Examinatrice**
Abdelkarim FILALI-MALTOUF	**PES**, Membre correspondant de l'Académie Hassan II des Sciences et Techniques, Rabat	**Examinateur**
Zakaria KEHEL	**Expert**, International Center for Agricultural Research in the Dry Areas (ICARDA), Rabat	**Examinateur**
Abderrazek JILAL	**Expert**, Institut National de la recherche Agronomique (INRA), Rabat	**Examinateur**
Ahmed AMRI	**Expert**, International Center for Agricultural Research in the Dry Areas (ICARDA), Rabat	**Co-Directeur de thèse**
Bouchra BELKADI	**PES**, Faculté des Sciences, Université Mohammed V, Rabat	**Directrice de thèse**

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✉ Faculté des Sciences, avenue Ibn Battouta, BP. 1014 RP, Rabat –Maroc
☎ 00212(05) 37 77 18 76 🖷 00212(05) 37 77 42 61; http://www. fsr.um5.ac.ma

Dedication

To all those who were in my side during this journey

To my parents for their selfless support and for making me who I am,

My wife for her timely encouragements and endless patience,

My sisters and brothers for their support,

My friends who shared many moments of this journey.

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Aberkane, H., T. Payne, M. Kishi, M. Smale, A. Amri, et al. 2020. Transferring diversity of goat grass to farmers' fields through the development of synthetic hexaploid wheat. Food Sec. 12(5): 1017–1033. doi: 10.1007/s12571-020-01051-w.

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Abstract

Durum wheat (*Triticum turgidum* subsp *durum*) is affected by drought and heat stresses which are amplified by climate change. Coping with these challenges requires access to a rich reservoir of useful alleles which can be supplied by crop wild relatives (CWR). This study aimed to assess the contribution of CWR to improve drought/heat tolerance and yield stability under contrasted environments. For this purpose, sixty-seven lines derived from backcrossing of two durum wheat cultivars (Cham5 and Haurani) with *Aegilops speltoides, Triticum urartu, Triticum aegilopoides* and *Triticum dicoccoides* were used in the study along with eight checks and recurrent parents. Field trials were conducted in fifteen different environments in Morocco (13) and Sudan (2) between 2016 and 2018. Drought and heat tolerance screening were conducted under field conditions at Tessaout (Morocco) and Wad Medani (Sudan), respectively. Drought tolerant lines were identified in crosses with *T. dicoccoides* (141973) and *T. urartu* (141972), these lines yielded 142% and 196% of their recurrent parents, respectively. Under heat stress, several lines issued from crosses with *T. aegilopoides* (142014) and *T. dicoccoides* (142074) had high yields. The derivative lines exhibited high variation for agronomic and physiological drought/heat adaptive traits, allowing therefore to select lines combining different tolerance mechanisms. Stable genotypes were identified from different crosses using parametric and non-parametric approaches. The contribution of wild relatives was more pronounced under unfavorable environments to reduce yield losses. It was concluded that using wild relatives for durum wheat improvement can widen the genetic base for several traits.

Key words: Durum wheat *(Triticum turgidum* subsp *durum)*, Wheat wild relatives, drought tolerance, heat tolerance, yield stability.

Resumé

La culture du blé dur (*Triticum turgidum* subsp *durum*) est affectée par la sécheresse et le stress thermique, ces stress sont amplifiés par les effets des changements climatiques. Maintenir une production durable nécessite une large diversité génétique, qui peut provenir des espèces sauvages apparentées au blé. L'objectif de cette étude est d'évaluer la contribution des espèces sauvages à la tolérance à la sécheresse, au stress thermique, ainsi qu'à la stabilité du rendement du blé dur. Pour cela, Soixante-sept lignées issues des croisements interspécifiques de deux parents cultivés (Cham5 et Haurani) avec quatre ancêtres du blé dur (*Aegilops speltoides, Triticum urartu, Triticum aegilopoides* et *Triticum dicoccoides)* ont été évaluées avec huit témoins et les parents récurrents. Les expérimentations ont été conduites dans quinze environnements différents au Maroc (13) et au Soudan (2) entre 2016 et 2018. Les essais de tolérance à la sécheresse et au stress thermique ont été conduits à Tessaout et Wad Medani, respectivement. Des lignées issues des croisements avec *T. dicoccoides* (141973) et *T. urartu* (141972) ont montré une tolérance élevée à la sécheresse. Ces lignées ont eu des rendements significativement supérieurs aux parent récurrents. Des rendements élevés sont également observés chez des lignées provenant de *T. aegilopoides* (142014) et *T. dicoccoides* (142074) sous stress thermique. Les lignées dérivatives ont montré une variation élevée pour les paramètres agronomiques et physiologiques associés à la tolérance aux stress hydrique/thermique. L'étude de stabilité a identifié des génotypes stables issus des différents croisements, la contribution des espèces sauvages était plus prononcée dans les environnements stressés. Il a été conclu que l'utilisation des espèces sauvages peut contribuer à l'amélioration du blé sur face aux effets de la sécheresse et températures extrêmes.

Mots clés : Blé dur *(Triticum turgidum* subsp *durum)*, espèces sauvages, tolérance à la sécheresse, tolérance au stress thermique, stabilité de rendement

Résumé (détaillé)

Le blé dur *(Triticum turgidum* subsp *durum)* est une céréale importante avec une production annuelle de 40 millions tonnes. Celle-ci est principalement cultivée dans la région méditerranéenne qui se caractérise par plusieurs stress biotiques et abiotiques. Ces stress, particulièrement la sécheresse et les températures extrêmes, sont amplifiés par les changements climatiques, réduisant ainsi la production de blé dur. Le maintien d'une production durable nécessite une large diversité génétique, qui peut provenir des espèces sauvages apparentées au blé. L'objectif de cette étude est d'évaluer la contribution des espèces sauvages à la tolérance à la sécheresse, au stress thermique, ainsi qu'à la stabilité du rendement du blé dur. Pour cela, Soixante-sept lignées issues des croisements interspécifiques de deux parents cultivés (Cham5 et Haurani) avec quatre ancêtres du blé dur (*Aegilops speltoides, Triticum urartu, Triticum aegilopoides* et *Triticum dicoccoides)* ont été évaluées. Les deux parents récurrents ainsi que huit autres lignées ont servi de témoins. Les expérimentations ont été conduites dans quinze environnements différents au Maroc (13) et au Soudan (2) entre 2016 et 2018. La station Tessaout a servi pour évaluer la tolérance à la sécheresse à travers deux essais par saison. Le premier essai irrigué représentait un environnement optimal, et le deuxième sous conditions pluviales un environnement stressé. L'évaluation de la tolérance au stress thermique a été effectuée à Wad Medani (Soudan) où les essais étaient irrigués. Les autres environnements représentent le climat typique de la région méditerranéenne sous conditions pluviales. Les résultats ont montré une perte de rendement importante sous stress hydrique (62% en moyenne), ceci a permis d'identifier plusieurs lignées tolérantes à la sécheresse. Les deux lignées 141973 (Cham5*2/*T. dicoccoides*) et 141972 (Haurani*2/*T. urartu*) ont eu des rendements respectifs de 142% et 196% supérieurs à leurs parents récurrents. La tolérance à la sécheresse était associée d'une part à la précocité, et d'une autre part à une biomasse totale (BY) supérieure ainsi qu'un nombre de grains par épi (SDSPK) plus élevé. L'importance de ces traits s'est manifestée par le pourcentage du rendement qu'ils ont expliqué sous l'effet de la sécheresse (67%). Les indices de tolérance ont permis d'identifier des lignées qui combinent la tolérance à la sécheresse avec un potentiel de rendement élevé. Concernant le stress thermique, plusieurs lignées issues des croisements avec *T. aegilopoides* et *T. dicoccoides* ont montré une bonne tolérance aux températures élevées. Cette tolérance était associée au maintien de la fertilité des épis, ainsi qu'à une biomasse et un poids de mille grains élevés. Le taux de remplissage de grain a également montré une corrélation significative avec le rendement permettant de l'utiliser en sélection. Parmi les paramètres physiologiques, La fluorescence chlorophyllienne (Fv/Fm) était significativement corrélée au rendement sous stress hydrique (r^2=0.22) et thermique (r^2=0.4). Cependant, la faible héritabilité du Fv/Fm peut limiter son utilisation en sélection. La température du couvert végétal (CT) avait quant à elle une bonne héritabilité ainsi qu'une corrélation élevée avec le rendement et la biomasse totale. L'utilisation du CT pour la sélection peut donc identifier des lignées tolérantes à la sécheresse et aux températures élevées. Une variation génétique élevée était également observée pour l'indice de végétation par différence normalisé (NDVI) à WMD. Le NDVI a par ailleurs montré une corrélation significative avec le rendement et la biomasse totale. Ces résultats indiquent le potentiel du NDVI en sélection pour la tolérance au stress thermique. L'étude de stabilité a montré que l'interaction génotype x environnement était hautement significative. Chez les dérivatives de Cham5, l'utilisation des espèces sauvage a amélioré la stabilité sans affecter le potentiel de rendement. Les lignées dérivées de Haurani ont même présenté un avantage significatif par rapport au parent récurrent. Les analyses de stabilité ont identifié plusieurs lignées stables issues des différents parents sauvages. L'étude a conclu que l'exploitation des espèces sauvages peut élargir la base génétique pour l'amélioration du blé dur. La mobilisation des gènes des différents genepools doit être renforcée à travers le pre-breeding afin de faire face aux effets des changements climatiques.

Mots clés : Blé dur *(Triticum turgidum* subsp *durum)*, espèces sauvages, tolérance à la sécheresse, tolérance au stress thermique, stabilité de rendement

Abbreviations

AN: Annoceur experiment station

ANOVA: Analysis of Variance

ASV: AMMI stability value

AT: Sidi Allal Tazi experiment station

Bi: Regression coefficient

BLUE: Best linear unbiased estimation

BLUP: Best linear unbiased prediction

BY: Total biomass

CHL: Chlorophyll content

CIMMYT: International Maize and Wheat improvement Center

CT: Canopy temperature

CV: Coefficient of variation

CWR: Crop wild relatives

DHE: Days to heading

DMA: Days to maturity

DSI: Drought susceptibility index

DTI: Drought tolerance index

EV: Environment Variance

F_m: Maximum fluorescence

$F_{o:}$ Initial fluorescence

Fv/Fm: Maximum quantum yield of PSII

F_v/F_o: Ratio of variable to initial fluorescence

F_v: Variable fluorescence

GAI: Geometric adaptability index

GEI and GxE : Genotype by Environment Interaction

GFP: Grain-filling period

GFR: Grain filling rate

GY: Grain yield

HI: Harvest index

ICARDA: International Center for Agricultural Research in the Dry Areas

MCH: Marchouch experiment station

MP: Mean productivity

MSI: Mean score index

MsSTI: Modifies stress tolerance index

MZIR: Melk Zhar experiment station irrigated

MZRF: Melk Zhar experiment station under rainfed conditions

NDVI: Normalized difference vegetation index

PCA: Principal Component Analysis

PHT: Plant height

Pi: Superiority index

PSII: Photosystem II

QTLs: Quantitative Trait Loci

RCBD: Randomized complete block design

RFD: Rainfed conditions

S^2di: Squared deviation from regression

SDSPK: Number of seeds per spike

$S_i^{(1)}$: Sum of mean of the absolute rank differences of a genotype

$S_i^{(2)}$: Variance of the ranks of a genotype

$S_i^{(3)}$: Sum of absolute deviations

$S_i^{(6)}$: Relative sum of squares of rank for the genotype

SIPC: Absolute values of the IPCA scores

SIR: Supplementary irrigation

SPKM2: Number of spikes per square meter

TKW: Thousand-kernel weight

TOL: Tolerance

TSIR: Tessaout experiment station under full irrigation

TSRF: Tessaout experiment station under rainfed conditions

TST: Tessaout experiment station

WAAS: Weighed average of absolute scores

WAASY: Superiority index from weighed average of absolute scores and yield

Wi^2: Wrick Ecovalence

WMD: Wad Medani experiment station

σ_i^2: Shukla genotypic variance

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General introduction

Wheat production worldwide is affected by climate change adverse effects. The increase in global temperature and changes in precipitation amount and distribution reduced wheat yield in many regions of the world (Lobell et al., 2011; Challinor et al., 2014; Mall et al., 2017). Wheat is also among the crops which will be negatively impacted by global warming in the absence of adaptation strategy (Ainsworth and Ort, 2010). Durum wheat is grown widely in the semi-arid regions where it is exposed to rainfall fluctuations and several diseases. These effects have a significant impact on durum wheat production and limit the ability of breeders to increase yield while meeting the quality requirements (Able and Sissons, 2014).

Yield increase has been recognized as the most sustainable solution to meet future demands, especially with the reduction of arable lands. This was observed after the green revolution which had a significant impact on food supply and income of farmers, particularly in developing countries (Pinstrup-Andersen and Hazell, 1985). However, the current global yield gains in wheat are below 1%, which is insufficient to meet the projected needs by 2050 (Ray et al., 2013). The trends in wheat production also indicate that by 2050 the wheat yields will be short by 1 tone/ha (Mondal, 2016).

Yield stagnation was long overcome by a strategic use of available diversity to increase the genetic gains in wheat breeding (Rajaram, 1999; Ogbonnaya et al., 2013). However, there is a genetic bottleneck for several traits, which requires access to a broader gene pool to improve adaptive morpho-physiological traits (Reynolds et al., 2009; Jha et al., 2014; Reynolds and Langridge, 2016). Wheat wild relatives evolved over thousands of years in a wide range of environments. This allowed them to develop adaptive traits which can be useful to widen the genetic base for wheat improvement (Nevo and Chen, 2010). The literature reports an extensive use of wheat wild relatives, they served as sources of disease/pest resistance, tolerance to abiotic stresses and to improve quality characteristics. Genes were introgressed from nearly 52 wild species into wheat background (Hajjar and Hodgkin, 2007; Dempewolf et al., 2017).

Despite the confirmed value of CWR for wheat improvement, breeders are reluctant to use them in their programs. This is associated with several crossing barriers, linkage drag, limited information about ex-situ collections, and the cost of developing useful germplasm from wild

material. In this context, “pre-breeding” becomes essential in the process of linking conservation to use of CWR. Pre-breeding aims to integrate the useful traits from CWR into adapted genetic background that can be used directly by breeders (Mujeeb-Kazi et al., 1995; Moore, 2015; Dempewolf et al., 2017).

Historically, some of the wild relatives revolutionized wheat breeding and their contribution was mainly associated with resistance to major diseases. For instance, the introgression of leaf rust resistance from *Aegilops umbellulata* saved the US wheat production in the 1960s (Reynolds et al., 2012). The 2NS translocation from *Aegilops ventricosa* is used widely since the 1990s in wheat breeding, the 2NS segment possesses many resistance genes to major wheat diseases (Gao et al., 2020). Wheat breeding also exploited the 1RS/1BL translocation from rye (*Secale cereale* L.) on large scales. This translocation served as a source of resistance to several diseases, more recently its contribution to yield especially under drought was reported (Howell et al., 2014; Aguirre-Rojas et al., 2017).

For quantitative traits such as yield, quality characteristics and tolerance to drought and heat stresses, the use of CWR was less pronounced. This is due to the complex inheritance of these traits and the difficulty to break linkage drag. In addition, the weedy form of wild relatives does not allow direct screening for agronomic performance under field conditions (Zhang et al., 2017). Physiological screening identified several *Aegilops* ssp and wild *Triticum* ssp with the potential to improve physiological adaptive traits for drought and heat tolerance. Heat and drought tolerance in these species was associated with improved chlorophyll content and photosynthetic activity (Rekika et al., 1997; Zaharieva et al., 2001; Dulai et al., 2006), expression of genes responsible for antioxidant enzymes (Mehrabad Pour-Benab et al., 2019) and higher proline and relative water content (Sultan et al., 2012).

The contribution of wild relatives to the agronomic performance under drought and heat stresses can only be assessed in the lines derived from interspecific crosses. Monneveux et al., (2000) reported that progenies from heat tolerant *Triticum dicoccoides* expressed high level of heat tolerance. Drought resistance in *T. dicoccoides* derived lines was associated with higher spike productivity, higher total biomass and improved harvest index (Peleg et al., 2009). The identification of adaptive traits in lines derived from wide crosses is still limited in durum wheat compared to bread wheat. More recently, the assessment of the usefulness of deploying CWR in

durum wheat breeding showed their value on farm. The assessment findings reported a significant contribution of CWR to improve yield under heat conditions (El Haddad et al., 2021).

Improvement of yield stability is another major challenge for durum wheat breeding worldwide. Low stability has been recognized as a major factor for the gap between potential and actuals yields (De Vita et al., 2010). Insufficient stability is a result of high genotype by environment interaction (GEI), which was amplified by climate change in the last decades (Turner et al., 2014; Xiong et al., 2020). Wild relatives (e.g., *T. monococcum, T. dicoccoides* and *Ae. speltoides*) showed high potential to simultaneously improve yield stability and yield potential across a wide range of environments. The contribution of wild relatives was associated with higher resistance to major disease and improved tolerance to terminal drought and high temperatures (Nachit and Elouafi, 2004; Zaïm et al., 2017).

Breeding for yield stability requires also integrating appropriate statistical approaches to account for the high GEI and improve selection accuracy (Mohammadi and Amri, 2008). The importance of these approaches is related to the complex GEI in multi-environment trials, the changes in yields and also the changes in ranks between environments (cross over interaction) (Xiong et al., 2020). In this view, several approaches were proposed to select stable genotypes for specific environments or for broad adaption. Some of these approaches use yield responses (parametric stability) (Roemer, 1917; Finlay and Wilkinson, 1963; Eberhart and Russell, 1966; Gauch, 1988; Sneller et al., 1997) while others rely on the ranking of genotypes in each environment (non-parametric stability) (Huehn, 1979; Nassar and Huehn, 1987).

Breeding for durum wheat resilience requires therefore the integration of different disciplines. It starts by harnessing diversity from different gene pools, which can be facilitated by available characterization/evaluation data and molecular technics. The implementation of suitable phenotyping technics to screen pre-breeding germplasm for different stresses such as drought and heat. Finally, the use of suitable statistical approaches to account for the high GEI and select stable high yielding genotypes (Crossa, 1990; Mondal, 2016).

Rational and specific objectives

The general aim of this thesis is to assess the role of pre-breeding in harnessing the mobilization of useful traits from wheat wild relatives. This is approached by evaluating a set of durum wheat lines derived from crosses with wild relatives for adaptation to stresses associated with climate change effects. Special focus is given to heat and drought tolerance as they are the major abiotic stresses with significant effect on durum wheat production under the Mediterranean region. The specific objectives are as follow:

1- Evaluation of the agronomic performance of durum wheat derivatives under drought and heat stresses to understand the contribution of CWR to yield and its components.
2- Assess the physiological response of the lines derived from wide crosses under heat and drought. Selection of tolerant genotypes using physiological parameters and drought tolerance indices.
3- Use and compare different parametric and non-parametric stability approaches to assess the yield stability of durum wheat derivatives under a wide range of environments.

Chapter 1: Literature review

1.1. Importance and challenges for wheat production

Wheat is the first cereal in terms of area as it is cultivated over more than 200 million hectares in the world. The annual wheat production exceeded 700 million tons since 2013, the increase in production is mainly associated with the yield gains since the cultivation area is stable since the 1960s (Figure 1-1) (Faostat, 2021). Wheat supplies 20% of the total protein and calories to human nutrition, it is also an important source of micronutrients (Zinc, iron and manganese) and vitamins B and E for millions of people worldwide (Goel et al., 2018; Sansaloni et al., 2020).

Durum wheat is grown on 17 million hectares representing 8.5% of the total wheat area, its annual production reaches 40 million tons (Beres et al., 2020). Most of the durum wheat growing area is in the Mediterranean region which produces more than 60% of the world durum wheat. Countries of the Mediterranean region are also the first importers of durum wheat and its derived products. Other countries such as Canada and the USA are among the top producers of durum wheat, it also has the potential to be grown in parts of sub-Saharan Africa (Lidon et al., 2014; Tidiane Sall et al., 2019; Xynias et al., 2020). The importance of durum wheat is derived from the unique characteristics of its grains. These characteristics in addition to protein content and gluten strength allow to produce several products such as semolina, pasta, bourghul, couscous and others (Hammami and Sissons, 2020).

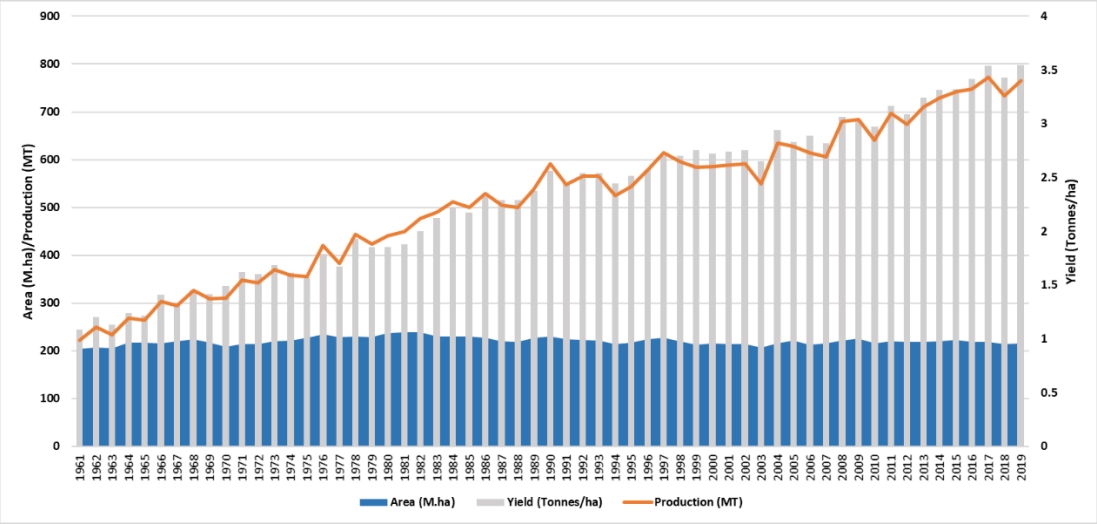

Figure 1-1. Evolution of wheat area (million hectares), production (million tons) and yield (tons/ha) in the world between 1961 and 2019 (Faostat 2021).

Durum wheat is well adapted to arid and semi-arid regions and it can tolerate high temperatures more than bread wheat. Nevertheless, its productivity faces several challenges associated with climate change such as drought, heat, diseases and pests pressure (Challinor et al., 2014). Drought and heat are increasing in terms of frequency and severity which pose an immense challenge to wheat production, especially in the Mediterranean region (Ceccarelli et al., 2010). In fact, heat already slowed the wheat yields in many wheat growing areas. At the same time, each 1°C increase in temperature reduce the production by 6% (Asseng et al., 2015; Akter and Rafiqul Islam, 2017). The wheat area exposed to drought increased from 12% to 20% between 1960 and 2000, and it is expected to increase in the future. Additionally, the highest proportion of yield fluctuations in the Mediterranean region is associated with drought events (Araus et al., 2003; Li et al., 2009).

Several insects and diseases are also responsible for significant yield losses in durum wheat (Able and Sissons, 2014). These pests and diseases are directly responsible of 20% and 40% of the wheat yield losses in the world, respectively. For instance, the yield damage caused by Hessian fly (*Mayetiola destructor*) can reach up to 33% in Morocco in normal season (Lhaloui et al., 1992). Russian wheat aphids caused $800 million losses in the USA between 1987 and 1993 (Haley et al., 2004). These insects are evolving, and new biotypes are emerging with more virulence which can break the existing resistance genes (Harvey et al., 1999; Caubel et al., 2017; Aguirre-Rojas et al., 2017). Diseases such as leaf rust and yellow rust are responsible for important economic losses. For instance, the yield losses caused by a new race of leaf rust in Mexico were estimated at US$32 million in 2001 (Ordoñez and Kolmer, 2007; Caubel et al., 2017). These pathogens are dynamic and keep evolving which increase the challenges to maintain the productivity of durum wheat under changing climate (Ericson et al., 1999).

1.2. Wheat evolution and domestication

Wheat was first domesticated in the fertile crescent 10.000 years ago as a part of the Neolithic Revolution. The first wheat ancestor to be domesticated was the diploid Einkorn; *Triticum monococcum* ssp *monococcum* ($2n=2x=14$, A^mA^m). It was domesticated from *Triticum monococcum* ssp *aegilopoides* following a mutation in the gene responsible for spikelet shattering in the A genome (*Br* to *br*). Tetraploid wheat (2n = 4x = 28) is divided into two species, *Triticum turgidum* (AABB) and *Triticum timopheevii* (AAGG). Each of these species is derived from a

different amphiploids with two evolutionary lineages (Dvořák et al., 1993; Jiang and Gill, 1994; Ciaffi et al., 2000; Faris, 2014).

Triticum turgidum belongs to the emmer lineage, it resulted from hybridization of *Triticum urartu* (AA) and *Aegilops speltoides* ssp (SS) or one of its close relatives from the sitposis section (Dhaliwal, 1977; Dvorak and Zhang, 1990; Daud and Gustafson, 1996; Kilian et al., 2007; Gornicki et al., 2014; Miki et al., 2019). Domestication of *Triticum turgidum* started with the emmer (*Triticum turgidum* ssp *dicoccum*) after acquiring the non-brittle rachis on A and B genomes (*br*) from *Triticum turgidum* ssp *dicoccoides* (Huang et al., 2002). The domesticated *Triticum turgidum* ssp *dicoccum* has non-brittle rachis, however the seeds were hulled. The free threshing was acquired after the mutation of the Q^{5A} gene that was the second major event in wheat domestication. The hexaploid *Triticum aestivum* (2n = 6x = 42, AABBDD) resulted from the second hybridization in the emmer lineage, this amphiploid hybridization included one of the tetraploid species (*Triticum turgidum* ssp) and the wild diploid *Aegilops tauschii* (DD) (Figure 1-2). The derived *Triticum aestivum* ssp *spelta* had the tough glumes from *Aegilops tauschii*, a mutation in the gene responsible for this trait lead to *Triticum aestivum* ssp *aestivum* which covers now more than 90% of the total wheat area (Mcfadden and Sears, 1946; Huang et al., 2002).

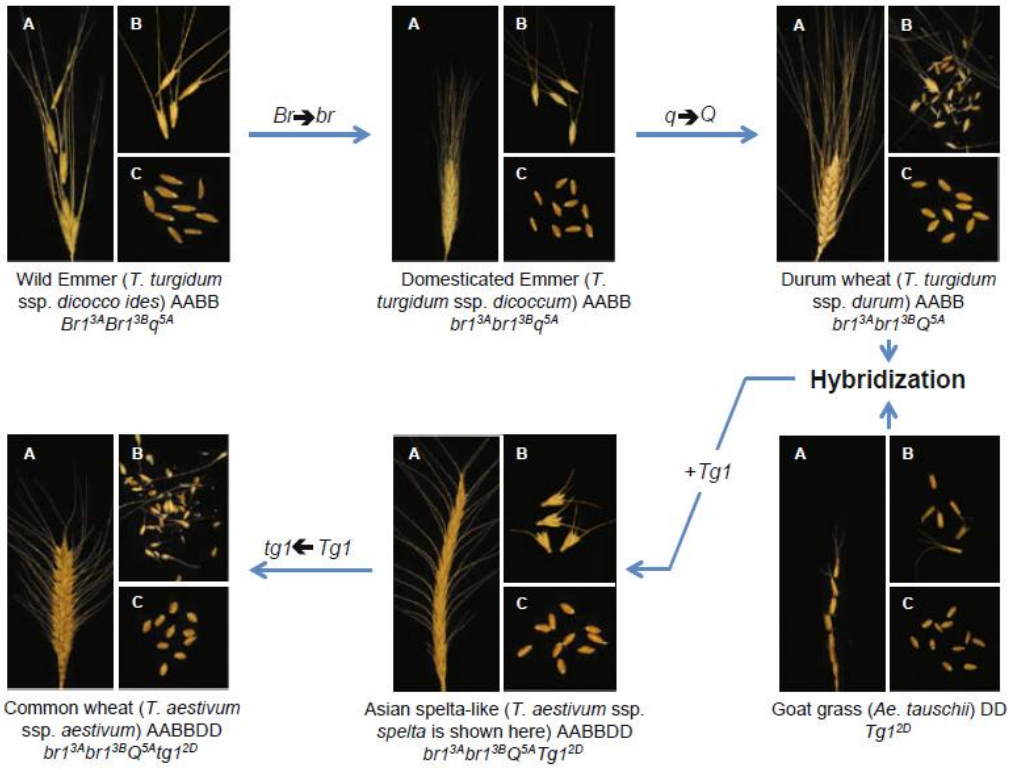

Figure 1-2. Evolution of the tetraploid and hexaploid wheat species from the emmer lineage with the major gene mutations involved in the domestication. shattering (*Br* = brittle rachis; *br* = non-brittle rachis), threshing (*q* = non-free-threshing; *Q* = free-threshing), tough glumes (*Tg* = tough glume; *tg* = soft glume). A, Spike; B, spikelet following moderate hand threshing; C, seeds (Faris, 2014).

The process of domestication resulted in a genetic bottleneck which reduced diversity in the cultivated species. The domestication bottleneck is driven by the small initial sample selected from the wild species and from further selection pressure (Cox, 1997; Tanksley and McCouch, 1997; Buckler et al., 2001) (Figure 1-3). The loss of diversity was reported to be higher in durum wheat (84%) than bread wheat (69%) compared to their wild progenitors (Haudry et al., 2007). The bottleneck effect was amplified by breeding effects and lower diversity was registered in the breeding populations compared to the landraces and CWR (Warburton et al., 2006; Wang et al., 2014).

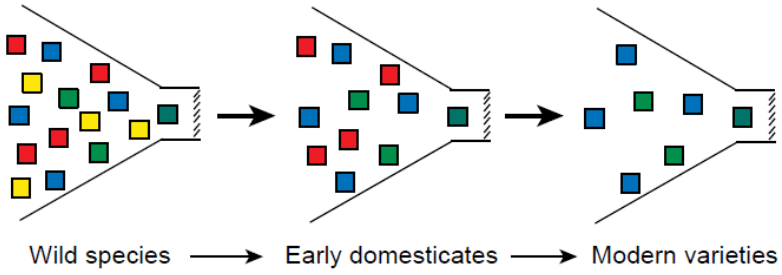

Figure 1-3. Representation of the genetic bottleneck imposed during domestication and modern crop breeding. The colored squares represent the allelic diversity (Tanksley and McCouch, 1997).

1.3. Gene pool of durum wheat

The gene pool concept was introduced by Harlan and De Wet (1971), it suggests that there is a potential pool of diversity available for use within species of each crop. The species related to each crop are classified into primary, secondary, and tertiary gene pools based on their crossing ability and survival of their hybrids.

1.3.1. Primary gene pool

Hybridization and gene transfer from the primary gene pool species are generally easy and chromosome recombination with the cultivated one is possible. In durum wheat, the primary gene pool includes the cultivated landraces, the diploid donors of the A genome (*Triticum urartu*, *Triticum monococcum* ssp *aegilopoides*, and *Triticum monococcum* ssp *monococcum*) and the tetraploid *Triticum turgidum* ssp from the emmer lineage (Harlan and De Wet, 1971; Feuillet et al., 2007). For instance, chromosomes of A and B genomes from *Triticum turgidum* ssp *dicoccoides* have high homology with those of durum wheat which makes gene transfer for quantitative traits possible (Valkoun, 2001).

1.3.2. Secondary gene pool

The secondary gene pool includes distantly related species whose full genome is not homologous with A and B genomes (Harlan and De Wet, 1971). Diploid *Aegilops* species (e.g *Aegilops speltoides*) with the S genome and some *Triticum* species (e.g. *Triticum timopheevi* AAGG) belongs to the secondary gene pool of wheat. Transfer of genes from these species is possible if they are located on the homologous genome (Feuillet et al., 2007). Hybrids resulting from crosses

with secondary gene pool can be sterile, weak and the recovery of desirable lines in the advanced generations require additional efforts (Harlan and De Wet, 1971).

1.3.3. Tertiary gene pool

Species from the tertiary gene pool are generally referred to as alien species, this gene pool is composed of all the *Triticeae* species carrying a genome other than A, B, and D. Homologous recombination with alien species is not possible and gene transfer requires the use of advanced cytogenetic techniques (Qi et al., 2007). Radiation, chromosome doubling and embryo rescue to avoid endosperm abortion of the hybrids can enhance gene transfer from alien species (Ceoloni and Jauhar, 2005; Kishii, 2019). *Ph1* is a gene located on the 5B wheat chromosome and it controls homeologous chromosomes pairing. The use of *Ph1* mutants allow homeologous recombination with genetically distant species (Aghaee-Sarbarzeh et al., 2000).

1.4. Linking conservation to use of crop wild relatives

Genebanks have two major roles, the first is to conserve species from different gene pools to reduce the loss of biodiversity. The second role is to characterize and distribute this germplasm for direct use in research and breeding (Smale and Jamora, 2020). The global strategy for wheat conservation highlighted the need to prioritize the conservation of crop wild relatives, especially with the advanced techniques to improve their use in breeding (International Maize and Wheat Improvement Center (CIMMYT), 2007). Over 460,456 accessions of wheat and its relatives are recorded in Genesys (accessed 28-04-2021), this germplasm is conserved in 86 institutes over 44 countries. Half of this germplasm is conserved in three research institutions; CIMMYT (146,005 accessions), the national small grain germplasm collection in the united states (62,028 accessions) and the international center for agricultural research in the dry areas (ICARDA) (44,026 accessions) (“Data accessed through Genesys Global Portal on Plant Genetic Resources,” 2021). ICARDA conserves 8335 wild accessions of *Aegilops* and *Triticum* wild species representing 15% of its wheat collection. This collection covers the geographic distribution of *Aegilops* and wild *Triticum* which goes from North Africa to West Asia (Figure 1-4) (ICARDA documentation system 2021).

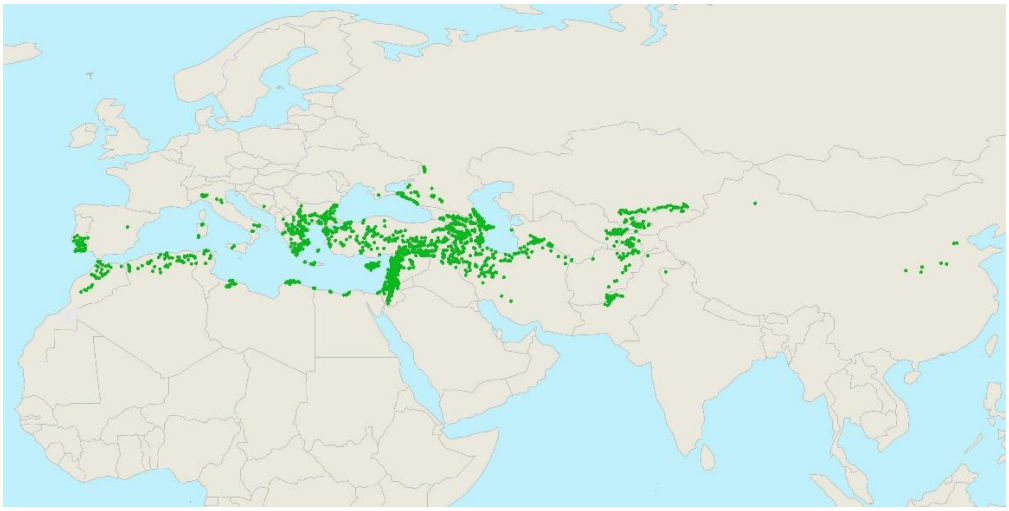

Figure 1-4. Geographic distribution of *Aegilops* ssp and wild *Triticum* ssp conserved at ICARDA genebeank (Source. ICARDA database 2021)

The direct use of CWR from genebank collections by the breeders is constrained by the time required for gene introgression and the high frequency of linkage drag. To overcome these constraints, pre-breeding becomes a key step in the process of gene discovery and introgression from wild relatives. Pre-breeding uses CWR to develop and supply the breeders with an immediately usable parental germplasm. This pre-breeding germplasm should address breeding challenges while increasing diversity in the elite gene pool (Dempewolf et al., 2017). Pre-breeding is a long-term investment that aims to face different challenges ahead of the modern agriculture (Kilian et al., 2021).

1.5. Contribution of wild relatives to wheat improvement

1.5.1. Disease and pest resistance

Wheat is the second crop with most reported potential and confirmed uses of CWR to cope with biotic stresses (Hajjar and Hodgkin, 2007; Dempewolf et al., 2017). Resistance to major diseases (i.e. leaf rust, yellow rust, stem rust and powdery mildew) were transferred to cultivated wheat from *Triticum dicoccoides, Triticum timopheevi, Aegilops speltoides, Aegilops sharonensis, and Aegilops kotschyi* (Dyck, 1994; Anikster et al., 2005; Cherukuri et al., 2005; Marais et al., 2005b; Knott et al., 2005; Hovhannisyan et al., 2011; Vikas et al., 2014; Millet et al., 2014; Sadeghabad et al., 2017). Resistance to Hessian fly (*Mayetiola destructor*) was found in several *Aegilops* species collected from the Mediterranean region (El Bouhssini et al., 2008). High variation for

resistance to Hessian fly, wheat stem sawfly, and Russian wheat aphid was found in wheat lines derived from *Aegilops speltoides* (Crespo-Herrera et al., 2019). These examples are corroborated by several other studies that reported the transfer of disease and pest resistance genes from wheat wild relatives (Table 1-1).

Table 1-1. Examples of resistance genes transferred from *Aegilops* ssp and *Triticum* ssp into cultivated wheat.

Pest/disease	**Source**	**Genes**	**Reference**
Leaf rust	Ae. *speltoides* (SS)	*Lr28, Lr47, Lr51, LrS2427*	(Helguera et al., 2000 ; 2005; Vikal et al., 2004; Niranjana et al., 2017)
	T. timopheevi (AAGG)	*Lr18*	(Sadeghabad et al., 2017)
	T. dicoccoides (AABB)	*Lr53*	(Marais et al., 2005b)
	Ae. tauschii (DD)	*Lr22a*	(Hiebert et al., 2007)
Stem rust	*Ae. speltoides* (SS)	*Sr47*	(Klindworth et al., 2017)
	Ae. sharonensis ($S^{sh}S^{sh}$)	*Sr-1644-1Sh* and *Sr-1644-5Sh*	(Yu et al., 2017)
Stripe rust	*T. dicoccoides* (AABB)	*Yr15, YrG303, YrH52*	(Klymiuk et al., 2020)
	Ae. ventricosa (DDMM)	*Yr17*	(Niranjana et al., 2017)
Hessian fly	*Ae. tauschii* (DD)	*H13*	(Miranda et al., 2010)
	T. turgidum ssp. *Dicoccum* (AABB)	*Hdic*	(Liu et al., 2005)
	Ae. triuncialis (UC)	*H30*	(Martín-Sánchez et al., 2003)
	T. araraticum (AAGG)	*QHara.icd-6B*	(Bassi et al., 2019)

1.5.2. Abiotic stresses

Several abiotic stresses affect wheat productivity, the major stresses associated with climate change are drought, heat, and salinity. These stresses cause more losses in wheat yields than pests and diseases. The effect of these abiotic stresses on wheat yields is related to the growth stage of occurrence, duration, and severity (Asseng et al., 2015; Cao et al., 2015; Abhinandan et al., 2018). Several studies investigated the contribution of wheat wild relatives to improve tolerance to abiotic major abiotic stresses.

1.5.2.1. Drought tolerance

Triticum dicoccoides harbors rich genetic diversity for agronomic and physiological drought adaptive traits (Budak et al., 2013; Peng et al., 2013; Suneja et al., 2019). Under water limited conditions, wild emmer accessions collected from hot and dry environments showed higher biomass and spike productivity compared to durum wheat. These traits were combined with early heading which allow to combine escaping drought stress with higher availability of assimilates for grain filling (Peleg et al., 2005). Interspecific hybridization of durum wheat with *T. dicoccoides, T. urartu, and T. aegilopoides* produced lines showing good productivity during a dry season (Valkoun, 2001). Several quantitative trait loci (QTLs) were associated with drought tolerance in a recombinant inbred lines (RIL) population from durum wheat and *T. dicoccoides*. These QTLs were identified for morpho-physiological traits, phenology, yield, and yield components (Peleg et al. 2009). Other *Triticum* ssp and *Aegilops* ssp were identified as donors for useful traits under drought. For instance, *T. aegilopoides* showed small decrease in water relative content under drought, *Aegilops geniculata* can increase tillering capacity with deeper rooting system (Kara et al., 2000; Sultan et al., 2012). Chlorophyll content and photosynthetic parameters involved in drought tolerance can be improved using *Ae. speltoides, Ae. geniculata* and *Ae. tauschii* (Zaharieva et al., 2001; Dulai et al., 2006). The contribution of *Ae. tauschii* was observed in its derived synthetic hexaploid wheat which exhibited high variation for drought tolerance in bread wheat (Reynolds et al., 2006).

1.5.2.2. Heat tolerance

The limited variability for heat tolerance in cultivated wheat suggest the need to harness the allelic variation in CWR. High potential to improve heat tolerance was identified in *Ae. speltoides, Ae.*

tauschii, Ae. geniculata and *T. dicoccoides*. These species had improved spike fertility and grain weight under heat stress (Khanna-Chopra and Viswanathan, 1999; Pradhan et al., 2012b). Higher kernel weight and yield under heat was also reported in bread wheat lines derived from *Triticum dicoccum*. This increase in kernel weight was associated with higher contribution from the emmer genome (Ullah et al., 2018). Several *Aegilops* ssp and *Triticum* ssp showed more potential than cultivated to improve heat tolerance during vegetative stage. This means that they can be used for breeding to continuous heat stress which requires different adaptive mechanisms (Monneveux et al., 2000).

1.5.2.3. Other abiotic stresses

Screening several *Aegilops* species under salinity stress found that *Aegilops* ssp with DD and CD genome were highly tolerant. *Aegilops tauschii* and *Aegilops ovata* showed high survival under different salt concentrations while *Triticum dicoccoides* was as tolerant as barley for salinity (Farooq et al., 1989; Nevo et al., 1993). *Triticum dicoccoides* involved different mechanisms related to growth rate and Na+ exclusion in salt tolerance (Shavrukov et al., 2010). The D genome *Aegilops* ssp were also identified as potential donors for frost tolerance in addition to *Triticum timopheevi* and other *Aegilops* ssp with S genome (Monneveux et al., 2000).

1.5.2.4. Yield and quality characteristics

Crop wild relatives were generally regarded as a source of stress resistance/tolerance, however they can also contribute to yield improvement under a wide range of environments. Yield potential is in fact the major reason behind the large adoption of varieties derived from synthetic hexaploid wheat in China (Aberkane et al., 2020). Higher yields were observed in durum wheat lines derived from interspecific hybridization, the high yield was combined with better quality than elite lines (Zaïm et al., 2017). The use of *Triticum dicoccoides* and *Triticum monococcum* in pre-breeding allowed to double the yield in durum wheat (Nachit and Elouafi, 2004). Protein, Zinc, and Iron concentrations in *Triticum dicoccoides* were twice higher than durum wheat. The content of these nutrients was not affected by yield which suggests the possibility to improve nutritional quality under different environments (Chatzav et al., 2010). In fact, protein content in some *Triticum dicoccoides* accessions was higher than 20%, which is considerably higher than what is found in the cultivated durum wheat (Peng et al., 2013). The screening of bread wheat substitution lines

revealed high potential of chromosomes 6A, 6B and 5B from *Triticum dicoccoides* to improve iron and zinc concentrations in cultivated wheat. *Triticum aegilopoides* is also a potential source to improve micronutrients concentration (Cakmak et al., 2000; 2004).

1.6. Methodologies of yield stability assessment

The different biotic and abiotic stresses result in a considerable change in the environment, which in turn increase the variation of the genotypic performance under unpredictable conditions. These variations increase the genotype by environment interaction (GEI) and reduce the stability over a wide range of environments (Padovan, 2020; Xiong et al., 2020). In fact, low stability has been recognized as a major factor for the gap between potential and actual yield in drought affected environments (De Vita et al., 2010). In many cases, the GEI results in changing the ranks of genotypes across environments, this is referred to as crossover interaction. Non crossover interaction refers to the parallel response of all genotypes to changes in the environments with no change in the ranks (Figure 1-5).

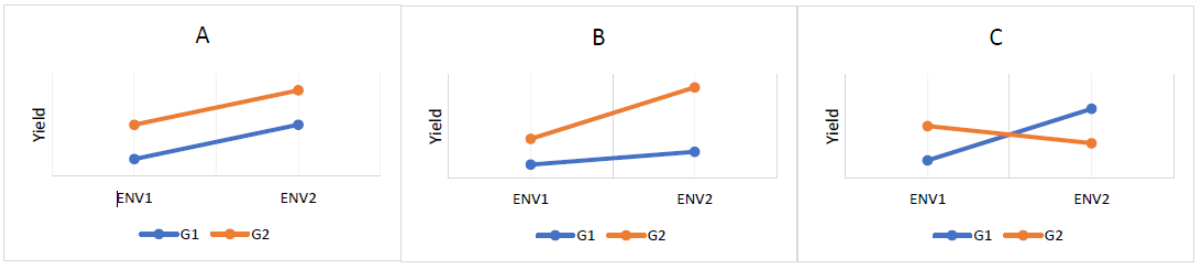

Figure 1-5. Genotype by environment interactions (GEI); A, absence of interaction; B, Presence of GEI with no change in ranks (non-crossover GEI); C, Presence of interaction with change in the ranks (crossover GEI).

There are two stability concepts which select different types of genotypes. The “biological concept” selects genotypes having consistent performance with a minimal variation across environments. In general, these genotypes will not respond to improvement in the environmental conditions and increase the yield in favourable environments. The “agronomic concept” defines a stable genotype as the one with minimum contribution to the GEI. Stable genotypes according to the agronomic concept will respond to change in the environments (Becker, 1981; Becker and Leon, 1988). Several statistical approaches were developed to dissect the GEI and estimate the phenotypic stability for both concepts.

1.6.1. Parametric stability approaches

The parametric stability approaches rely on the absolute data, these approaches are affected by data distribution and some assumptions should be met with regards to the effects of genotypes, environment and their interaction (Mohammadi and Amri, 2008). The combined analysis of variance (ANOVA) is used as a routine to select superior genotypes from multi-environment trials. The ANOVA divides the variation between additive effects (genotypes and environments effects) and non-additive effects of the GEI. The conventional ANOVA assumes that the error variance is homogenous which can be a limitation as the GEI is generally complex with heterogenous variance (Crossa, 1990). The use of linear mixed models for the combined ANOVA can increase the accuracy and account for heterogenous variance between environments (Friesen et al., 2016). The joint regression analysis (Finlay and Wilkinson, 1963; Eberhart and Russell, 1966) was extensively used for the selection of stable genotypes based on the regression coefficient (Bi) and the squared deviation from regression (S^2di). The environment variance (EV) (Roemer, 1917) and the coefficient of variation (CV) (Francis and Kannenberg, 1978) measure stability according to the biological concept. Lin and Binns (1988) proposed the genotypic superiority index (Pi) to measure the agronomic stability. The superiority index is measured using the squared distance between each genotype and the maximum response in the environment. Shukla stability variance (σ_i^2) (Shukla, 1972) and Wricke ecovalence (Wi^2) (Wricke, 1962) measure the stability by estimating the contribution of each genotype to the GEI. These indices are similar for the ranking of genotypes with stable genotypes being the ones with lower contribution to the GEI. Table 1-2 summarizes the formulas to compute each of these parametric stability indices.

Table 1-2. Formulas for the calculation of different parametric stability indices

Index	Formula
Regression coefficient	$B_i = \sum_{j=1}^{n}(X_{ij} - \bar{X}_i)(\bar{X}_j - \bar{X}) / \sum_{j=1}^{n}(\bar{X}_j - \bar{X})^2$
Squared deviation from the regression	$S^2di = \frac{1}{(E-2)}\left[\sum_i(X_{ij} - \bar{X}_i - \bar{X}_j + \bar{X}) - (bi-1)^2 \sum(X_j - \bar{X})^2\right]$
Wrick ecovalence	$W_{i^2} = \sum_{j=1}^{n}(X_{ij} + \bar{X}_i + X_j + \bar{X})^2$
Geometric adaptability index	$GAI = \sqrt[E]{(\bar{X}_1)(\bar{X}_2)\ldots(\bar{X}_i)}$
Superiority index	$P_i = \frac{\sum_{j=1}^{n}(X_{ij} - Mj)^2}{2E}$
Environment variance	$EV = \frac{\sum(X_{ij} - \bar{X}_i)}{(E-1)}$

X_{ij}, Performance of the i_{th} genotype in the jth environment; $\bar{X}_i$, average performance of the i_{th} genotype; $\bar{X}_j$, average in the j_{th} environment; $\bar{X}$, grand mean; E, Number of environments; Mj; genotype with the maximum response. ($\bar{X}_1$) and ($\bar{X}_2$) represent the yields of the genotype in the first and second environments, respectively.

1.6.2. Multivariate parametric approaches

Multivariate approaches are proposed to summarize, understand the data structure, and eliminate the noise from the data patterns. The additive main effects and multiplicative interaction (AMMI) (Zobel et al., 1988; Gauch, 1988) is the most known multivariate model for the analysis of multi-environment trials. The AMMI model combines the analysis of variance for the additive effects of genotypes and environment with the principal component analysis (PCA) to dissect the non-

additive GEI. The interaction principal component from the AMMI model was used to compute several stability indices. The AMMI stability value (ASV) (Purchase et al., 2000) considers the first two components while the sums of the absolute values of the IPCA scores (SIPC) (Sneller et al., 1997) uses all the components with significant effects. These indices consider stable genotypes as the ones with low contribution to the GEI. The weighted average of absolute scores (WAAS) was recently developed using mixed models to dissect the GEI, the interpretation of WAAS is like ASV and SIPC. A superiority index (WAASY) can be computed based on WAAS and yield in order to balance between adaptability and productivity for the selection of superior genotypes (Olivoto et al., 2019).

Table 1-3. Formulas for the stability indices derived from the parametric multivariate models

Index	**Formula**
AMMI stability value (ASV)	$ASV = \sqrt{[\frac{SSIPC1}{SSIPC2}(IPC1)]^2 + (IPC2)^2}$
sums of the absolute values of the IPCA scores (SIPC)	SIPC=$\sum_{k=1}^{P} \lvert\lambda_k^{0.5}\alpha_{ik}\rvert$
Weighted average of absolute scores	$WAAS = \frac{\sum_{k=1}^{p} \lvert \mathrm{IPCA}_{ik} \times EP_k \rvert}{\sum_{k=1}^{p} EP_k}$
Superiority index from Weighed average of absolute scores	$WAASY = \frac{(rG_i \times \theta_Y) + (rW_i \times \theta_s)}{\theta_Y + \theta_s}$

SSIPC1, Sum of squares of the first interaction component; SSIPC2, sum of squares of the second interaction component; IPC1, score of the first interaction principal component; IPC2, score of the second interaction principal component; λ_k, the eigenvalue of the k_{th} PC; α_{ik}, score of the i_{th} Genotype for the k_{th} IPC; PCA_{ik} is the score of the i_{th} genotype in the k_{th} IPCA, and EP_k is the amount of the variance explained by the k_{th} IPCA; *rGi* and *rWi* are the rescaled values for GY and WAAS, ΘY and ΘS are the weights for grain yield and stability, respectively.

1.6.3. Non-parametric stability approaches

Non-parametric stability approaches do not require the use of absolute data, these approaches are based on the changes in the ranking between the environments. Therefore, no assumptions need to be met for data distribution which makes the non-parametric approaches less affected by the presence of outliers (Mohammadi and Amri, 2008). Four non-parametric indices were proposed by Huehn (1979) and Nassar and Huehn, (1987) to select for both biological and agronomic stability. $S_i^{(1)}$ represents the sum of mean of the absolute rank differences of a genotype over the environments, $S_i^{(2)}$ represents the variance of the ranks, $S_i^{(3)}$ is the sum of absolute deviations and $S_i^{(6)}$ is calculated as the relative sum of squares of rank for the genotype. correlation of non-parametric and parametric approaches from the literature suggest that they can be used interchangeably to select for yield stability (Fasahat, 2015).

Chapter 2: Materials and Methods

2.1. Plant Material

The plant material used for this research consisted of a population derived from interspecific crosses of two durum wheat cultivars (Haurani and Cham5) with four wheat wild progenitors. Three of the wild parents, *Triticum dicoccoides* (2n=4x=28), A^uA^uBB), *Triticum monococcum* ssp *aegilopoides* (2n=14, A^uA^u) and *Triticum urartu* (2n= A^mA^m) belong to the primary gene pool. Only *Aegilops speltoides* (2n=14, SS) belongs to the secondary gene pool, however recombination of its chromosomes with the wheat B genome is possible. The initial development of the population was done at ICARDA genetic resources unit (1995). The wild parents were selected based on origin of the accession and available disease information. The recurrent parent Haurani is a Syrian landrace locally adapted while Cham5 is a line selected from ICARDA durum wheat breeding germplasm and released as a variety in many countries including Syria. The population was developed using repeated backcrossing after the first hybridization, the purpose of backcrossing was to restore fertility and reduce the size of exotic genome. An example illustrating the crossing scheme for the lines derived from *T. urartu* and *T. aegilopoides* is provided in figure 2-1.

The pedigree selection started at BC2/BC3/BC4-F2 based on morphology and disease resistance until F5 where individual plants were selected. The lines were advanced as bulk after that until F11. The pedigrees of the 67 accessions used in this study are presented in Table 2-1 while the information about each accession is provide in Annex 1. Ten checks including the recurrent parents were used in this research. The checks represent Moroccan cultivars (Marzak, Louiza and Faraj), varieties released from ICARDA breeding program (Cham1 and Gidara2) and elite lines from the current breeding pipeline at ICARDA (Icarachaz and Miki3).

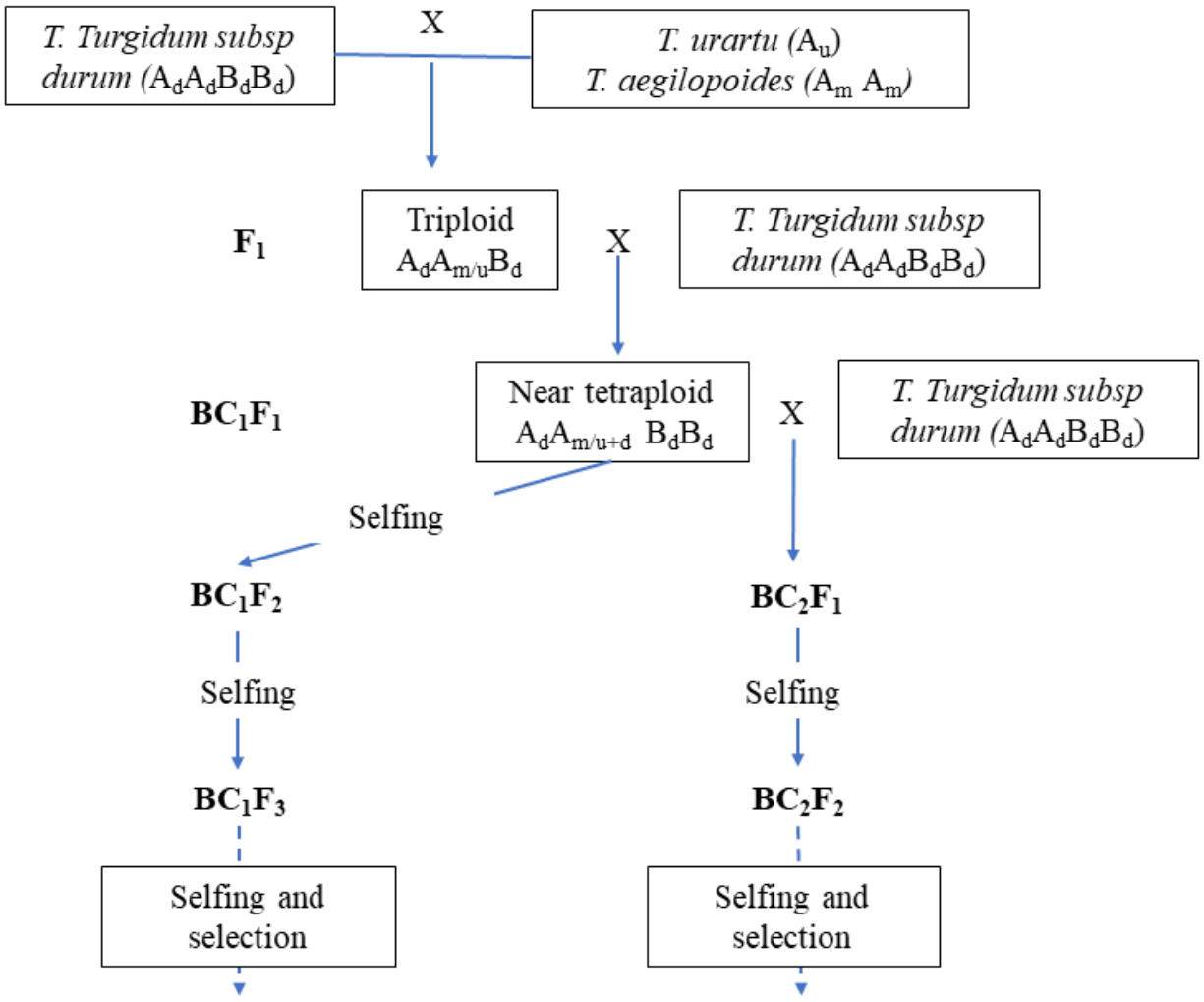

Figure2-1. Crossing scheme for the crosses and backcrosses between durum wheat and the diploid wild triticum.

Table 2-1. Pedigree and number of lines derived from each cross used in the study.

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**

2.2. Field trials and crop management

Six locations were selected for the trials establishment to represent different agro-ecological conditions (Table 2-2). Five locations in Morocco representing the Mediterranean hot and temperate types of environments while Wad Medani in Sudan is a heat prone environment. The trials were conducted under rainfed conditions except at Tessaout and Melk Zhar where two different trials were established each season. The first trial was under full irrigation representing optimal conditions, the second under rainfed or supplementary irrigation as drought stressed. The purpose was to assess yield losses under drought stress. Allal Tazi was selected as disease hotspot, especially leaf rust, to evaluate the yield under disease pressure. Marchouch is an important breeding location for ICARDA as it represents the typical semi-arid environment. It also has a high correlation with other locations in the Mediterranean region. The trials at Wad Medani were fully irrigated to avoid crop exposure to the combined effect of drought and heat.

The trials were established in an alpha-lattice incomplete block design with two replicates. Each replication was composed of eleven incomplete blocks of size seven. Alpha-lattice was selected based on its high efficiency compared to randomized complete block design (RCBD). For instance, alpha lattice can be 30% more efficient than RCBD for grain yield (Abd El-Mohsen and Abo-Hegazy, 2013). The plots were laid out in four rows of 2 meters long each, a row-to-row distance of 0.25-0.3 m and a sowing density of 300 seeds/m². *Agricolae* package (De Mendiburu, 2020)

from R software (R Core Team, 2021) was used for the randomization of each trial. Conventional tillage was used for land preparation prior to the sowing and the recommended agronomic package for each location was applied.

Table 2-2. Summary of the environments included for the evaluation of durum wheat derivatives and the purpose from each environment

Location		Coordinates	Soil type	ENV	Seasons	Treatment	Purpose	Data collected
Morocco	Allal Tazi	34°31' N 6°14' W	Vertisol	AT-17 AT-18	2016-17 2017-18	Rainfed/natural infection	Yield under Disease pressure	- Yield and its components - Leaf rust scoring
	Annoceur	33°41' N 4°51' W	Lime-clay	AN-17 AN-18	2016-17 2017-18	Rainfed	Yield in high altitude and Tan spot	- Yield and its components
	Marchouch	33°36' N 6°42' W	Clay vertisol	MCH-16 MCH-17 MCH-18	2015-16 2016-17 2017-18	Sup. Irrigation Rainfed Rainfed	Yield under semi-Arid conditions	- Yield and its components - Physiological parameters
	Melk Zhar	30°02'N 9°33'W	Sandy limestone	MZIR-16 MZRF-16	2015-16 2015-16	Full irrigation Sup. Irrigation	Yield under drought	- Yield and its components
	Tessaout	31°49′ N 7°25′ W	Calcic xerosol	TSIR-17 TSRF-17 TSIR-18 TSRF-18	2016-17 2016-17 2017-18 2017-18	Full irrigation Rainfed Full irrigation rainfed	Drought tolerance assessment	- Yield and its components - Physiological parameters
Sudan	Wad Medani	14◦24′ N 33◦31′ E	Heavy cracking montmorillonitic	WMD-17 WMD-18	2016-17 2017-18	Full irrigation	Heat tolerance assessment	- Yield and its components - Physiological parameters

2.3. Collected data

2.3.1. Phenology and agro-morphological data

Days to heading (DHE): Heading time is critical to assess wheat adaptation to specific environment, it is affected by the vernalization requirement and photoperiod. The heading was calculated starting from the day of irrigation or the first effective rains until 50% of the plot has emerged ears.

Days to maturity (DMA): Maturity is the result of different successive physiological changes in wheat. Number of days to maturity was recorded when 90% of the plants in each plot are yellow.

Grain filling period (GFP): The duration of filling is determinant of yield and grain quality. GFP was calculated as the difference between DHE and DMA.

Plant heigh (PHT): Plant height is an important trait as it is associated with susceptibility to lodging and contribute to the total biomass. Plant height was measured at physiological maturity from the ground to the top of the stem excluding the spike, it is expressed in centimetre (cm).

Number of spikes/m² (SPKM²): The number of spikes is informative about the number of effective tillers and can directly be associated with the grain yield. SPKM² was calculated on the inner rows from each plot on 0.25m² and converted to spikes/m².

Number of seeds/spike (SDSPK): The number of seeds per spike was estimated by threshing three random spikes from the inner rows and counting the number of seeds from each spike.

Thousand kernel weight (TKW): Thousand kernel weight is highly correlated with grain yield and it is influenced by environmental factors. The measurement of TKW was done by counting and weighing 500 seeds, it is expressed in grams (g).

Biological yield (BY): The total biomass was estimated by harvesting and weighing the two internal rows avoiding the borders. It was then converted to kilograms per hectare (kg/ha).

Grain yield (GY): The grain yield was measured after harvesting and threshing the two internal rows avoiding the borders. It was converted and expressed as (kg/ha).

Grain filling rate (GFR): The grain filling rate was calculated only at Wad Medani under heat stress, it was calculated as follows: GFR = [Grain yield (kg. ha^{-1})/Grain filling period (days)]

Harvest index (HI): The harvest index represents the ratio of grain yield to the total biomass and it is expressed in percentage. The harvest index was calculated as follow:

$$\boldsymbol{HI}\ (\%) = \boldsymbol{GY} * \mathbf{100}/\boldsymbol{BY}$$

2.3.2. Physiological measurements

Physiological parameters were measured to assess the physiological response of durum wheat to drought and heat stresses. They consisted of canopy temperature, chlorophyll fluorescence, chlorophyll content and the Normalized difference vegetation index. The physiological parameters were recorded in the experiments involved in drought and heat tolerance (i.e. trials established at Tessaout and Wad Medani). At Tessaout the measurements were taken on clear sunny days at heading stage between 12.00 and 2.00 p.m. At Wad Medani, the physiological parameters were measured in three growth stages every season between 1:00 p.m. and 3:00 p.m. on clear sunny days as well.

2.3.2.1. Canopy temperature (CT)

Canopy temperature is associated with the evaporative cooling and can be informative about the hydration status. CT has the advantage of being an integrative, fast, and non-destructive measurement. However, caution should be taken for the growth stage and the time of the day when CT is collected. At Tessaout, CT was measured using a thermal camera (model *FLIR T460*) and the FLIR tools software (Version 5.5.16064.1001) was used to analyze the pictures. CT was estimated from the average CT from 10 random plants in each plot and used for statistical analysis (Example in Figure 2-2). At Wad Medani, an infrared thermometer was used to measure the canopy temperature (*model Center 325*). The CT was measured on three random plants from the internal rows in each plot avoiding the borders. The average from the three plants was used for the statistical analysis.

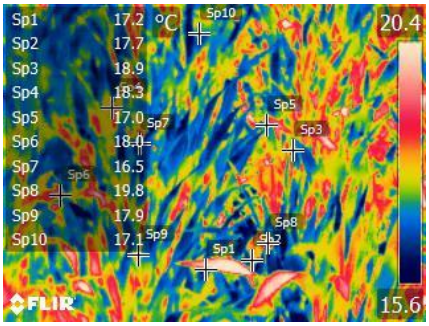

Figure 2-2. Example of the picture generated by the *FLIR T460* thermal camera and analyzed for Canopy temperature in durum wheat.

2.3.2.2. Chlorophyll fluorescence

The principle underlying chlorophyll fluorescence measurement based on the light remittance of non used energy by the chloropyll. When light is intercepted by chlorophyll molecules, it goes into one of the three pathways. It can be used for photosynthesis, the excess in energy can return as heat or reemitted as light (chlorophyll fluorescence). By measuring the reflected energy, the photosynthetic yield can be estimated allowing to inform about the photosynthetic efficiency. Fluorometer OS30p+ was used to measure the chlorophyll fluorescence, the fluorometer takes five parameters.

Initial fluorescence (F_o): It corresponds to the minimal value of fluorescence when all the captor from the PSII are oxidated. It is obtained by weak modulating light.

Maximum fluorescence (F_m): It corresponds to the maximum value of fluorescence resulting from closing all the electron acceptors (Q_A) and a complete reduction of PSII.

Variable fluorescence (F_v): It is obtained as the difference between the maximum and the initial fluorescence ($F_v=F_m-F_o$).

Maximum Quantum Efficiency (F_v/F_m): It is generally affected by the variable fluorescence, F_v/F_m is an indicator of photo-inhibition in PSII, and it is therefore the most widely used parameters from chlorophyll fluorescence.

Ratio of variable to initial fluorescence (F_v/F_o): It can also be used as a stress indicator, $Fv/Fo=(Fm-F_o)/F_o$.

The chlorophyll fluorescence was measured on the dark-adapted flag leaf of three random plants from the internal rows avoiding the borders. Only F_v/F_m was included in the analysis of variance and to assess its correlation with yield and other agronomic traits.

Chlorophyll content

Chlorophyll content is measured based on light transmittance at 650nm and 940nm. It can inform about the loss of chlorophyll resulting from stress and the loss of photosynthetic potential. Chlorophyll content was measured only under heat stress at Wad Medani during different growth stages (see Materials and Methods chapter 4). *Minolta SPAD-502* was used to collect chlorophyll content measurements, The SPAD was calibrated prior to data collecting from each replication. The measurements were collected on clean intact leaves (flag leaf or the youngest fully expanded leaf) avoiding the major veins. Chlorophyll content was measured on five random plants from the internal rows of each plot and the average was used for the statistical analysis. The readings do not represent absolute chlorophyll values, it refers to the "chlorophyll concentration index" which ranges from 0 to 99.9.

2.3.2.3. Normalized difference vegetation index (NDVI)

The normalized difference vegetation index is calculated from measuring the light reflectance in red and near infrared (NIR) regions from a spectrum. A healthy green canopy absorbs the red light and reflect the NIR light as chlorophyll absorbs blue and red light and mesophyll reflects NIR light (Pask et al., 2012).

$$NDVI= (R_{NIR}-R_{Red})/(R_{NIR}+R_{Red})$$

NDVI was measured at Wad Medani under heat stress using a *greenseeker*. NDVI readings range from 0 to 0.99 and higher values are indicator of healthier plants.

2.4. Statistical analysis

The analysis of variance (ANOVA) was performed for the collected data to assess the effect of genotypes, environments, and their interaction. ANOVA was also conducted to assess the genotypic effect within each environment. Linear mixed models were used for all variance analysis and to estimate the best linear unbiased predictions (BLUPs) and the best linear unbiased

estimations (BLUEs). The details for appropriate analysis for each objective are described in chapters three, four and five.

Chapter 3: Evaluation of durum wheat lines derived from interspecific crosses under drought and heat stress

Hafid Aberkane[1,2], Ahmed Amri[1], Bouchra Belkadi[2], Abdelkarim Filali-Maltouf[2], Zakaria Kehel[1], Izzat S. A. Tahir[3], Sara Meheesi[3], Athanasios Tsivelikas[1]

[1]International Center for Agricultural Research in the Dry Areas (ICARDA), Rabat, Morocco

[2]Plant and Microbial Biotechnology, Biodiversity and Environmental Research Center, Faculty of Sciences, Mohammed V Univ. of Rabat, Rabat, Morocco

[3]Agricultural Research Corporation (ARC), WadMedani, Sudan

3.1.Abstract

The productivity of durum wheat [*Triticum turgidum* subsp. *durum* (Desf.) vanSlageren] 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 Wad Medani, Sudan, under full irrigation combined with heat stress. The recurrent parents, along with eight 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.

3.2. Introduction

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 et al., 2000; Valkoun, Hammer, Kucerova, & Bartos, 1985) and insects (Bassi et al., 2019; Nsarellah, Amri, Nachit, El Bouhssini, & Lhaloui, 2003). Accessions of *Aegilops sharonensis* Eig, *Ae. searsii* M. Feldman & M. Kislev, *Ae. 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.

3.3.Materials and Methods

3.3.1. 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 (Annex 1). 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 3-1). 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 Annex2. Pedigree selection started at the (BC2, BC3, and BC4) F2 lines in 2002 and lasted until F5, where the lines were advanced as bulk until F11.

In addition to the pedigree and selection history (annex 1), 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 ≤ 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.

Table 3-1. 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**

3.3.2. 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′ W) in Morocco, characterized by a dry season with an average annual precipitation of 266 mm with frequent droughts, and Wad 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 Wad Medani, the trials were irrigated at an interval of 7–10 d.

Each trial was randomized as an incomplete block design (alpha-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.

3.3.3. 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 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.

3.3.4. 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:

$$H^2 = \frac{\sigma^2 g}{\sigma^2 g + \frac{\sigma^2 ge}{E} + \frac{\sigma^2 Er}{RE}}$$

where $\sigma^2 g$ is the genotypic variance, $\sigma^2 ge$ is the genotype by environment interaction, $\sigma^2 Er$ 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 SPKM2.

The heritability in each location was estimated as follows:

$$h^2 = \frac{\sigma^2 g}{\sigma^2 g + \frac{\sigma^2 e}{r}}$$

where $\sigma^2 g$ is the genotypic variance, $\sigma^2 e$ 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:

$$GY \sim Intercept + BY + DHE + GFP + SPKM2 + SDSPK + TKW + PHT$$

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:

$$DTI = \frac{Ys * Yp}{\overline{Y}^2 p}$$

where Ys is the GY under drought stress, Yp is the GY under optimal conditions (TSIR) and $\overline{Y}^2 p$ 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.

3.3.5. 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 3-1). 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.

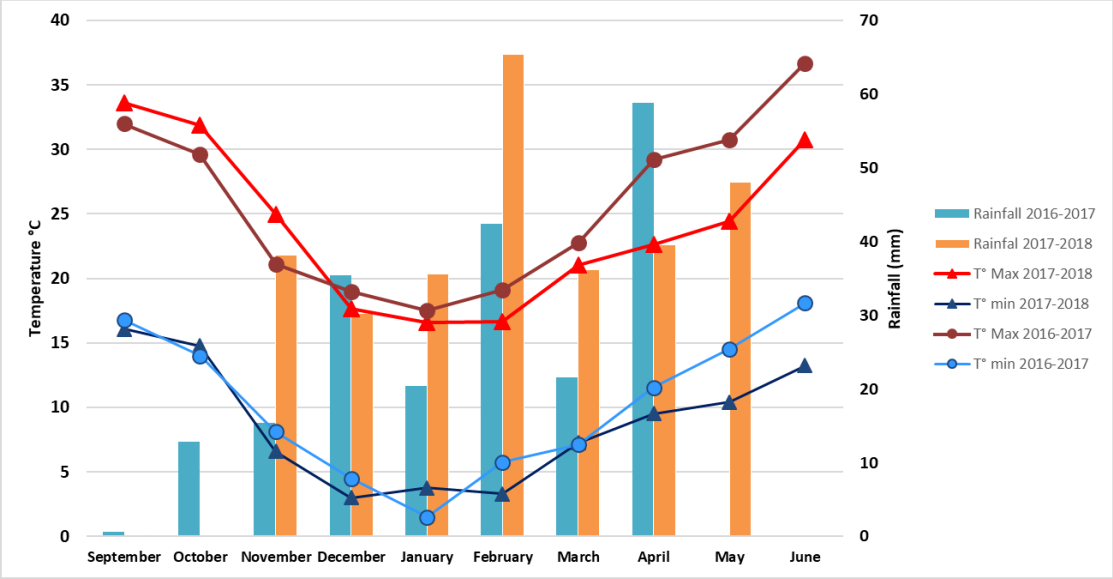

Figure 3-1. Precipitations (mm), maximum and minimum temperatures (°C) registered in Tessaout during the seasons 2016-2017 and 2017-2018

In Wad 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 3-2). 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.

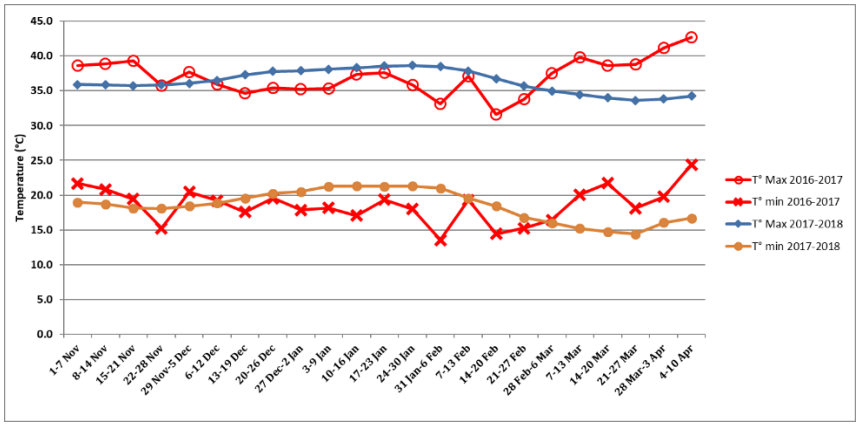

Figure 3-2. Minimum and maximum temperatures (°C) registered in Wadi Medani during the seasons 2016-2017 and 2017-2018

3.4.Results

3.4.1. Genotype × environment interaction

The combined ANVOA showed that the effect of genotypes was significant for all traits except for SPKM2, which had the lowest heritability across environments (0.40). 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 0.54 across environments.

The phenological traits (DHE and GFP) had the same heritability of 0.56, which is relatively lower in comparison with heritabilities of the other yield components such as TKW (0.74) and SDSPK (0.69) (Table 3-2).

Table 3-2. Combined analysis of variance across environments for phenology and agronomic traits of durum wheat derivatives grown at Tessaout and Wad Madi Experiment stations during 2016-2017 and 2017-2018 seasons

	Genotype variance	**Gentoype by environment variance**	**Environment variance**	**H^2**	**CV**
DF	**76**	**378**	**5**		
PHT	14.82**	17.41**	284.59**	0.70	7.3
DHE	3.21**	12.74**	308.95**	0.56	2.3
GFP	2.03**	3.35**	89.24**	0.56	6.7
SDSPK	9.73**	5.24*	20.37^{ns}	0.69	13.6
TKW	4.988**	2.72**	39.64**	0.74	11.5
HI	11.81**	13.61**	28.62*	0.70	19.1
$SPKM^2$	68.02^{ns}	5.26^{ns}	16986175.13*	0.40	16.4
BY	490327.13**	338896.9^{ns}	18985499.46**	0.54	18.4
GY	230539.29**	212157.61**	3470507.06**	0.71	23.2

PHT, plant height; DHE, days to heading; GFP, grain filling period; $SPKM^2$, number of spikes/m^2; SDSPK, number of seeds/spike; TKW, thousand kernel weight; HI, harvest index; BY, biological yield; GY, grain yield

** significant at 0.01, * significant at 0.05, ^{ns} not significant

The effect of the year on GY and other agronomic traits was important at all locations, with higher impact in the stressed environments (Figure 3-3). 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 2253 kg ha−1 in 2016–2017 to 4557 kg ha−1 in 2017–2018. Simultaneously, BY, HI, $SPKM^2$, and TKW showed higher values in the second season at TSRF (Figure 3-3). The same findings were observed in WMD as the GY increased from 1,380 kg ha−1 the first season to 2183 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 3-3). 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.

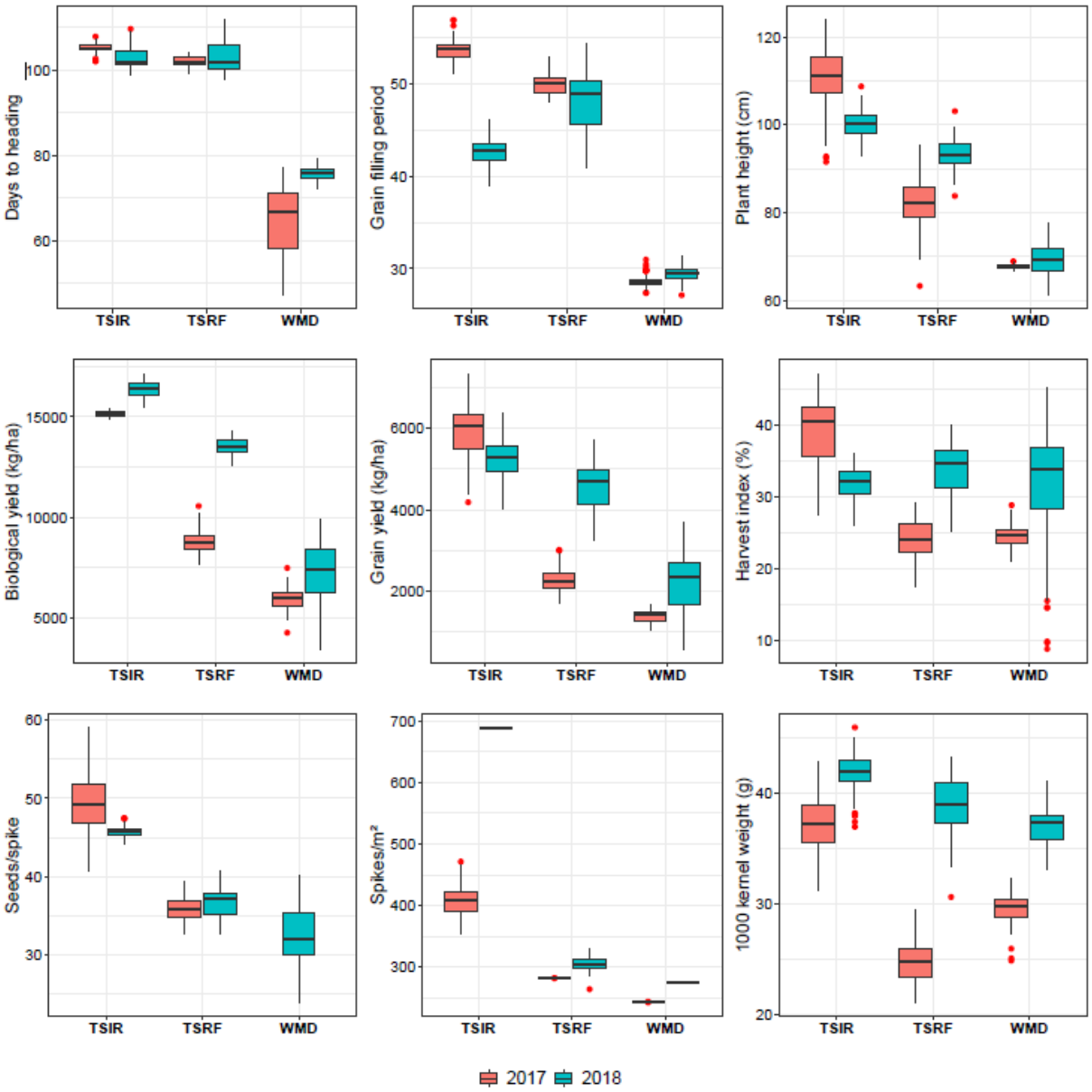

Figure 3-3. Boxplots of the best linear unbiased predictions (BLUPs) of the phenology and agronomic traits of durum wheat derivatives at Tessaout under irrigated (TSIR) and rainfed conditions (TSRF) and Wad Medani (WMD) during the 2016–2017 and 2017–2018 seasons

3.2 Screening for drought tolerance

3.4.2. 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 0.69 in TSIR to .80 in TSRF. Similarly, GFP heritability increased from .48 under optimal conditions to 0.72 under drought. On average, the

heading time was reduced by 4 days (Table 3-3), whereas PHT was reduced by 25% at TSRF. The reduction in PHT has affected the BY.

Table 3-3. Descriptive statistics and heritability across the two years of DHE, GFP, PHT and HI under optimal conditions (TSIR) and drought stress (TSRF).

	TSIR				TSRF			
	Min	Max	Mean	h^2	Min	Max	Mean	h^2
DHE	105	106	105	0.69	96	109	102	0.81
GFP	51	56	53	0.48	45	54	50	0.72
PHT	98	121	110	0.75	73	92	83	0.72
HI	31	46	39	0.71	16	30	24	0.81

DHE, days to heading; GFP, grain filling period; PHT, plant height; HI, harvest index

The yield losses due to drought across the years was 62%; this was associated with a significant decrease in all yield components measured (Figure 3-4). Under optimal conditions, the GY ranged between 4075 and 7971 kg ha−1 with a heritability of 0.51 and an average of 5954 kg ha−1. Icarachaz was the highest yielding line at TSIR with a GY of 7971 kg ha−1, followed by the line 142064 (7491 kg ha−1) that yielded 33% higher than its recurrent parent (Haurani) at TSIR. The line 141999 (Haurani*2/*T. urartu*) yielded 7174 kg ha−1 in TSIR; this was significantly higher that the recurrent parent by 27% (Annex 3).

Under drought stress, all the lines with GY higher than 3000 kg ha−1 were derived from interspecific crosses. The highest GY in TSRF was 3628 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* (Annex 4).

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 0.61 compared to TSIR (0.51), 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 3-3). 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 distinguish genotypes, as the heritabilities were high under

both optimal conditions ($h^2 = 0.71$) and drought stress ($h^2 = 0.81$). The HI reduction due to drought was 37%.

Among yield components, SPKM2 had the lowest heritability at both TSIR (0.20) and TSRF (0.38). The mean SPKM2 decreased significantly from 408 at TSIR to 281 (31% reduction) at TSRF due to drought (Figure 3-4). The low heritability did not allow us to discriminate the most desirable genotypes for SPKM2 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 ($h^2 = 0.43$).

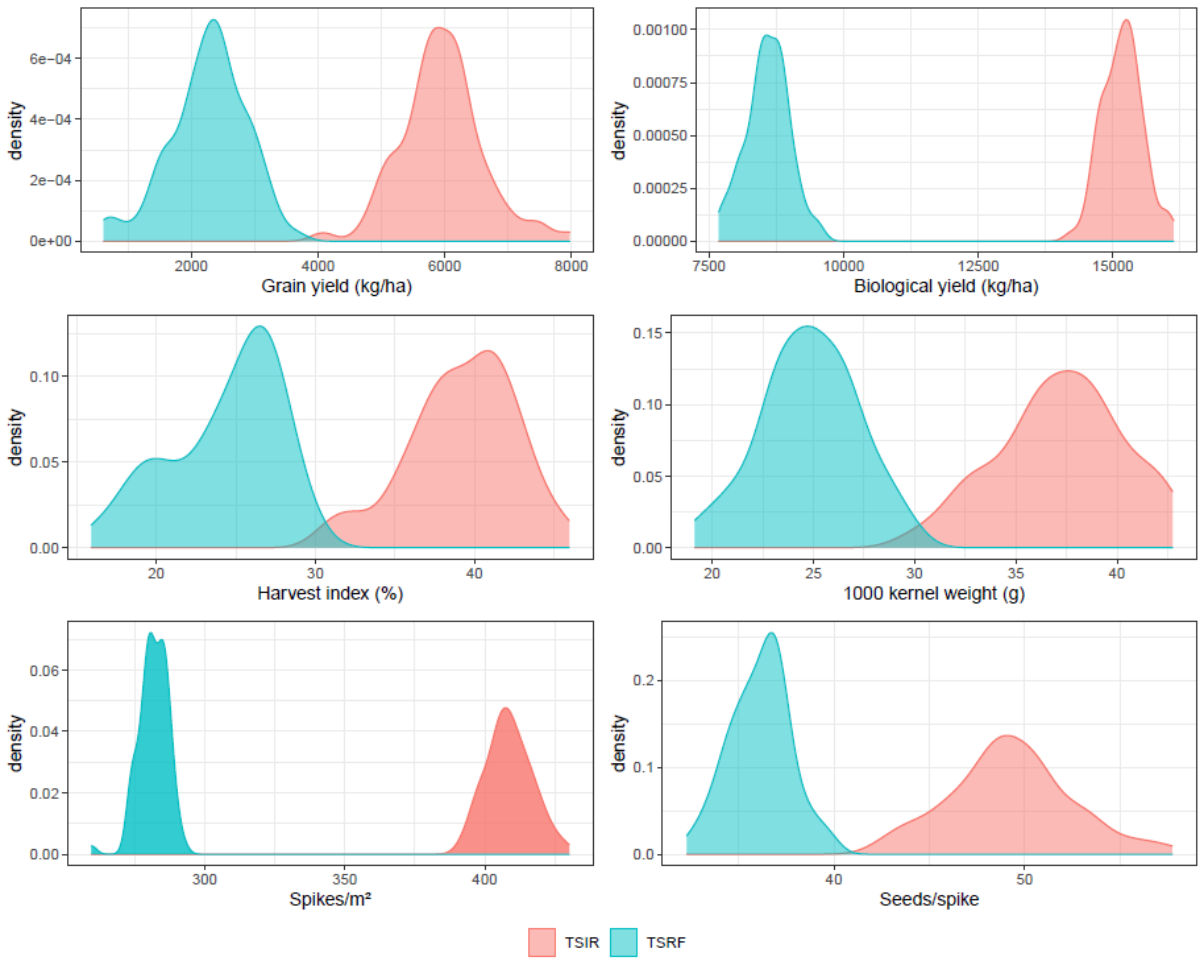

Figure 3-4. Density plots for the best linear unbiased predictions (BLUPs) of grain yield, biological yield, harvest index, 1000 kernel weight, spikes m^{-2}, and seeds $spike^{-1}$ under optimal conditions (TSIR) and drought stress (TSRF) at the Tessaout experiment station.

3.4.3. 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 3-5a). However, two interesting groups of genotypes were identified with respect to drought tolerance (Figure 3-5b). In the first group combining drought tolerance and high yield potential, the line 142013 had the second highest DTI (0.52) and yielded 6829 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; Annex 5). However, these lines did not respond positively to the favorable conditions at TSIR. (Figure 3-5).

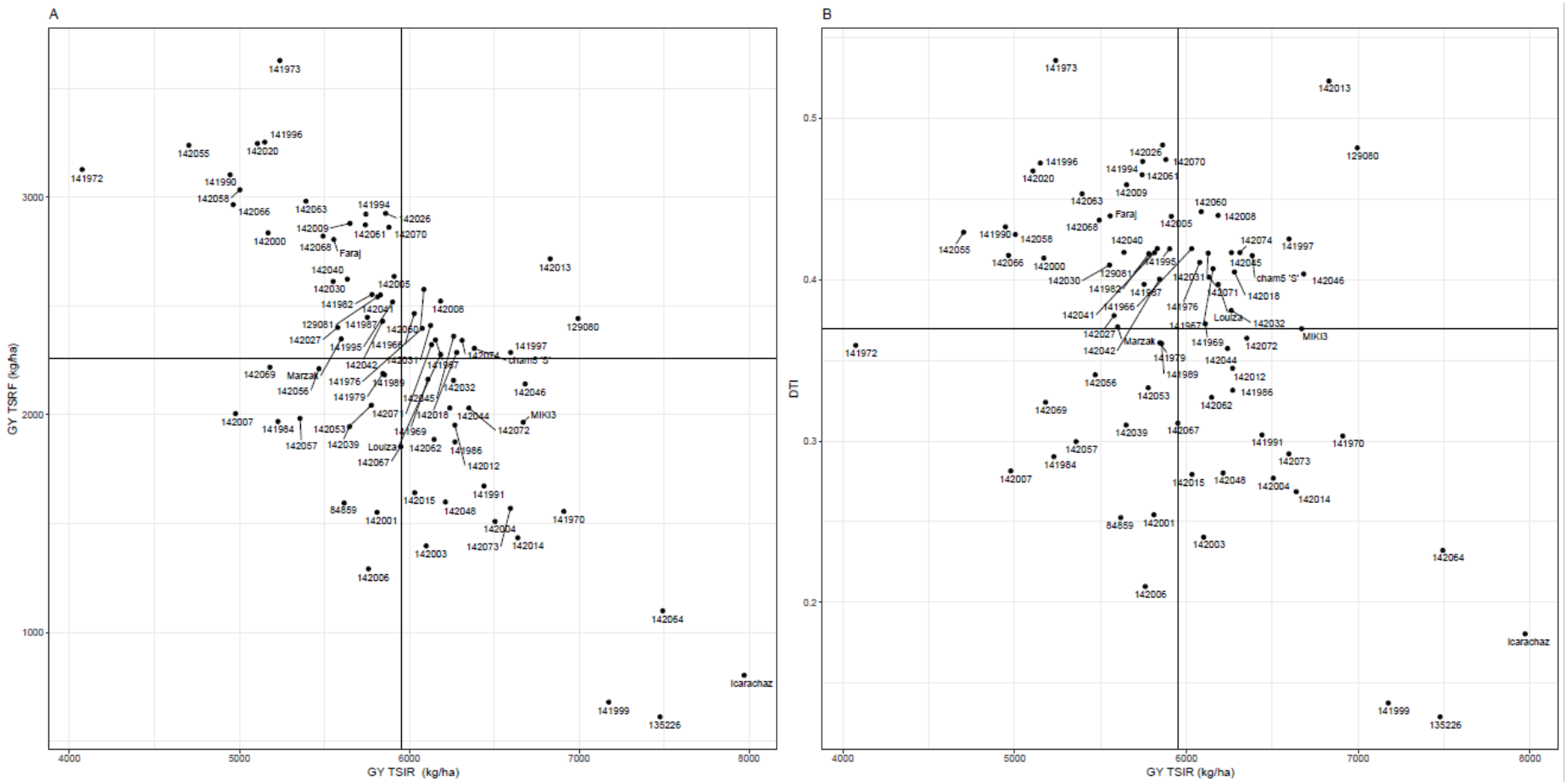

Figure 3-5. Biplot of (a) grain yield (GY) at Tessaout under irrigated (TSIR) and rainfed (TSRF) and (b) drought tolerance index (DTI) plotted against the GY at TSIR of durum wheat line.

3.4.4. 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 0.68 and 0.50, respectively (Table 3-4). 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 days only. The lines 142001 and 142015 (both derived from *T. urartu*) headed after 58 and 67 days, respectively. The line 142007, also derived from *T. urartu* , headed 13 days before its recurrent parent (Haurani) (Annex 5).

Table 3-4. Descriptive statistics for phenology and agronomic traits under heat stress at Wad Medani across the two seasons 2016-2017 and 2017-2018

	DHE	GFP	PHT	SPKM²	SDSPK	TKW	BY	GY	HI
Min	55	27	63	238	28	26.59	4271	634	17
Max	70	31	72	247	44	32.23	7276	2082	29
Mean	64	29	68	243	36	29.52	5922	1377	24
h²	0.68	0.5	0.48	0.10	0.67	0.36	0.47	0.60	0.37

DHE, days to heading; GFP, grain filling period; PHT, plant height; SPKM², number of spikes/m-²; SDSPK, number of seeds/spike; TKW, thousand kernel weight; BY, biological yield; GY, grain yield; HI, harvest index.

In terms of yield components, SPKM2 had the lowest heritability (0.10); 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 0.36 and 0.67, 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 5922 kg ha−1 at WMD with a heritability of 0.47 (Table 3-4). Louiza, Marzak, and the line 142074 were the most distinguished lines for BY; their BY was >7000 kg ha−1 (Annex 5).

The average GY in WMD was 1377 kg ha−1 with a heritability of 0.60 (Table 3-4). The maximum yield was 2082 kg ha−1, which was obtained by the line 142015 (Cham5*2/*T. urartu*) (Annex 5). 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 (Annex 5).

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 3-6). 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 (1930 and 1831 kg ha−1) with the high GY at TSIR (7476 and 7971 kg ha−1) (Figure 3-6a). 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 3-6b).

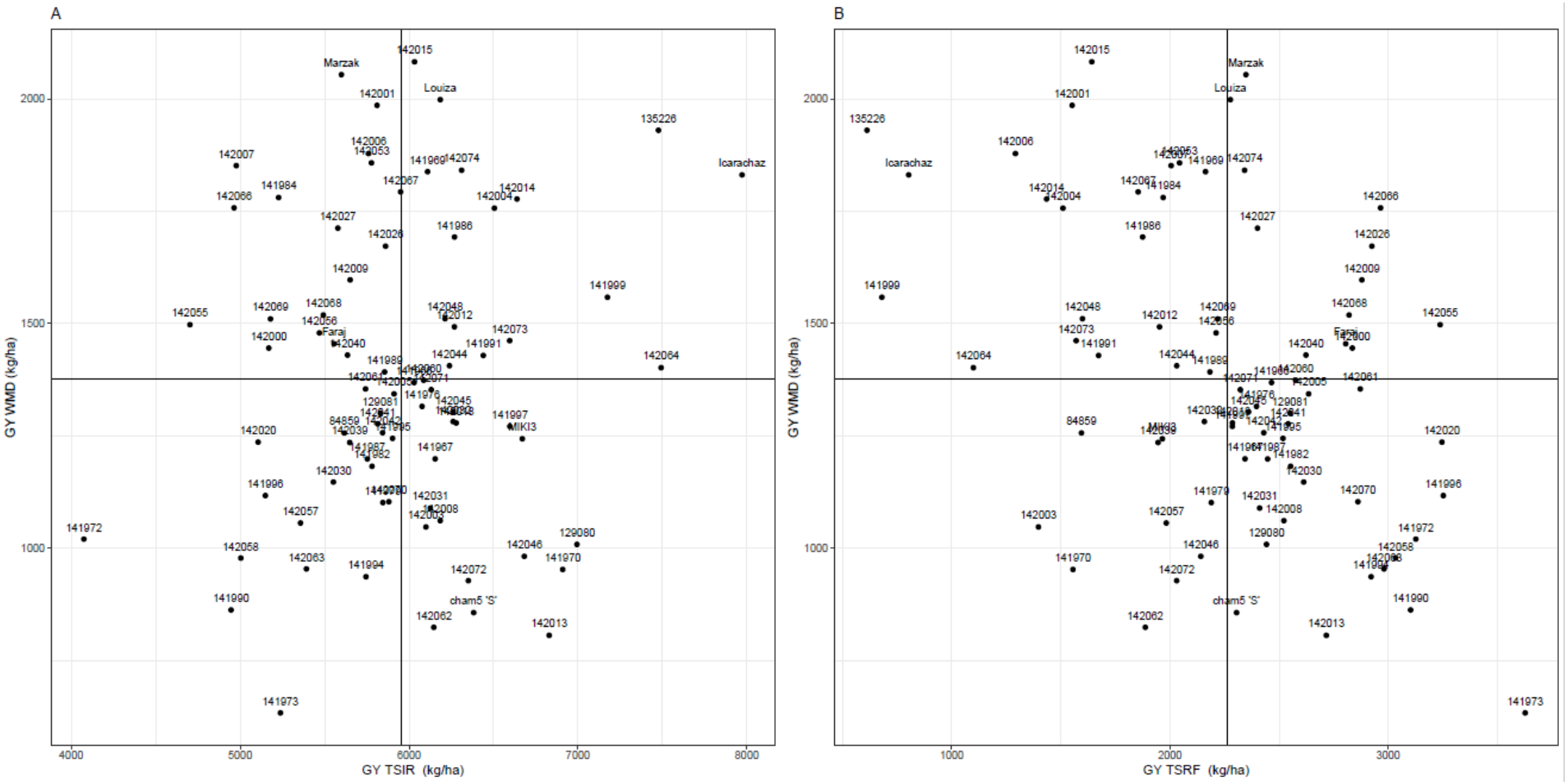

Figure 3-6. Biplot of (a) grain yield (GY) at Wad Medani (WMD) plotted against GY at Tessaout under irrigated conditions (TSIR), and (b) GY at WMD plotted against GY at Tessaout under rainfed conditions (TSRF).

3.4.5. Correlation and stepwise regression analyses results

At TSIR, GY was positively correlated to TKW (r^2 = 0.57***), HI (r^2 = 0.79***) BY (r^2 = 0.82***), and SDSPK (r^2 = 0.51***). The DHE was negatively associated with GFP (r^2 = −0.65***), TKW (r^2 = −0.38***), HI (r^2 = −0.38***), and GY (r^2 = −0.27*). Under drought stress (TSRF), an important cluster composed of interrelated traits (HI, GFP, TKW, and SDSPK) showed significant correlations with GY (Figure 3-7). Very high negative correlation was observed between DHE and GFP (r^2 = −0.93***). This later showed significant positive correlation with TKW (r^2 = 0.29*).

At WMD, GY was negatively correlated with GFP (r^2 = −0.24*), but positively correlated with HI (r^2 = 068***), TKW (0.45***), SPKM2, 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 SPKM2, 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 3-8).

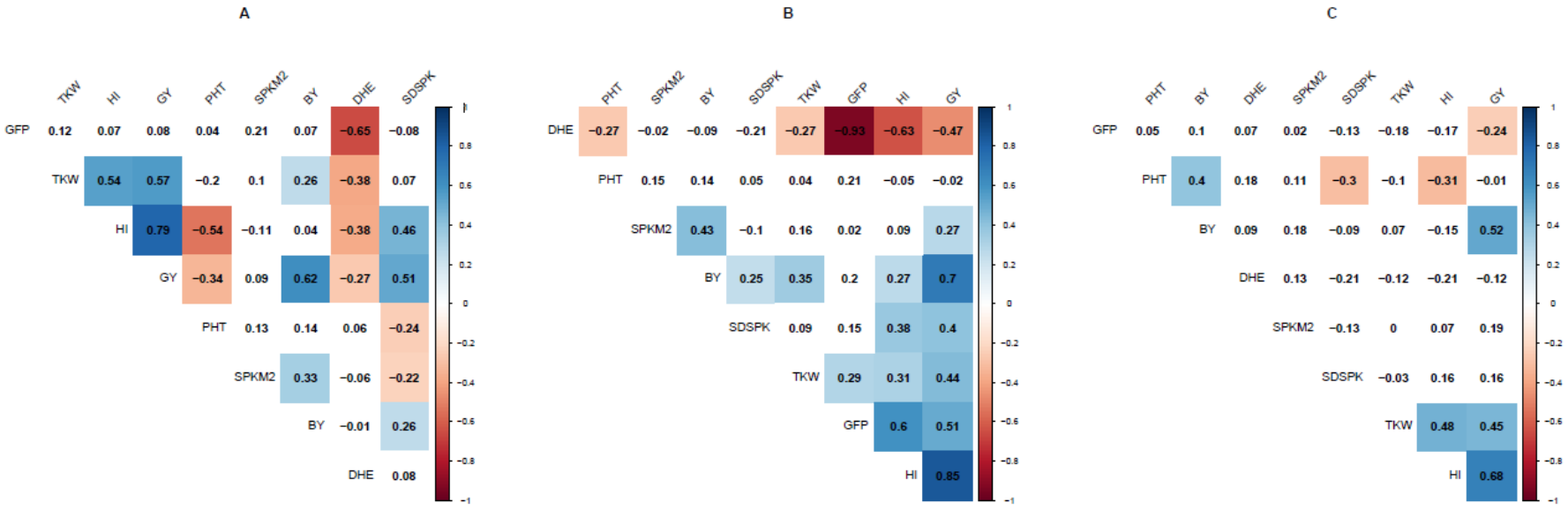

Figure 3-7. Pearson correlation coefficients between the different traits in the three environments under (a) optimal conditions, (b) drought stress, and (c) heat stress. Level of significance α = .05. GFP, grain filling period; TKW, thousand kernel weight; HI, harvest index; GY, grain yield; PHT, plant height; SPKM2, number of spikes per square meter; BY, total biomass; DHE, days to heading; SDSPK, number of seeds per spike.

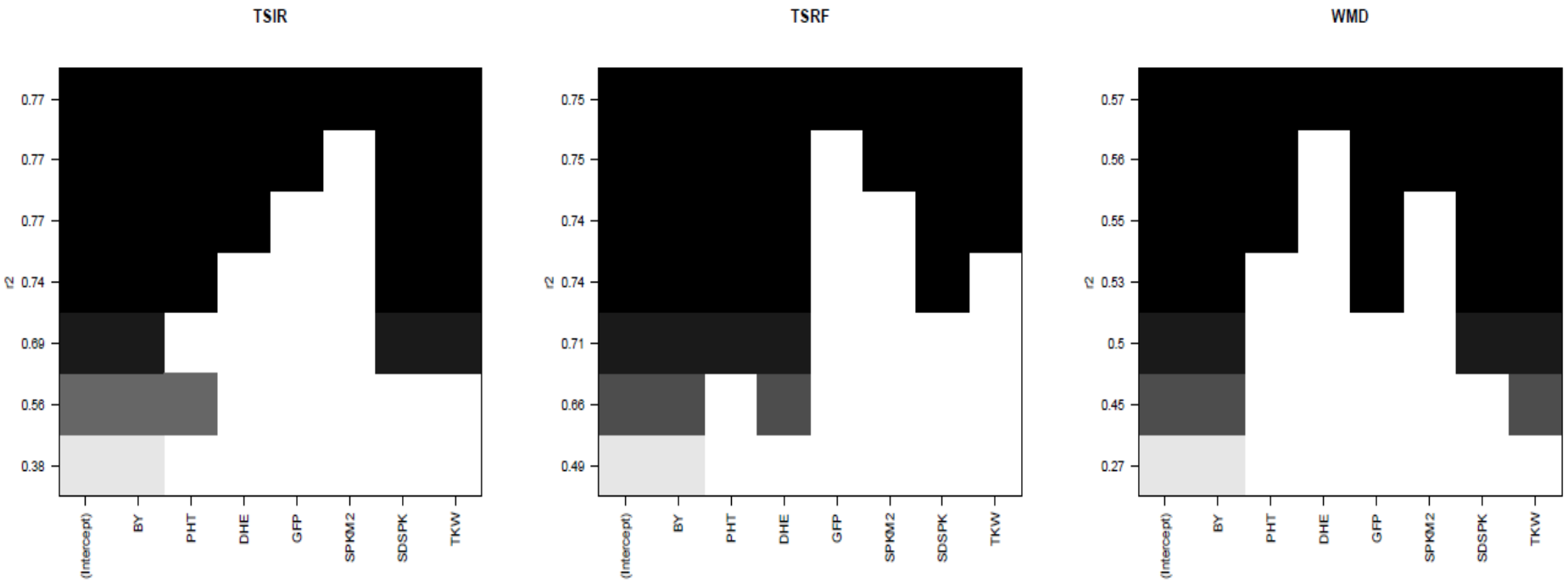

Figure 3-8. Stepwise regression for biomass, phenology, and yield components of durum wheat derivatives at Tessaout under irrigated conditions (TSIR), Tessaout under rainfed conditions (TSRF) and Wad Medani (WMD). BY, total biomass; PHT, plant height; DHE, days to heading; GFP, grain filling period; SPKM2, number of spikes per square meter; SDSPK, number of seeds per spike; TKW, thousand kernel weight

3.4.6. 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 3-9). The most interesting lines in TSRF were 141973 and 141996; they are derived from crosses with *Triticum dicoccoides* and *Aegilops speltoides*, respectively. The accession 142015 (Cham5*2/*T. urartu* ICWT 500651) had a GY of 2082 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.

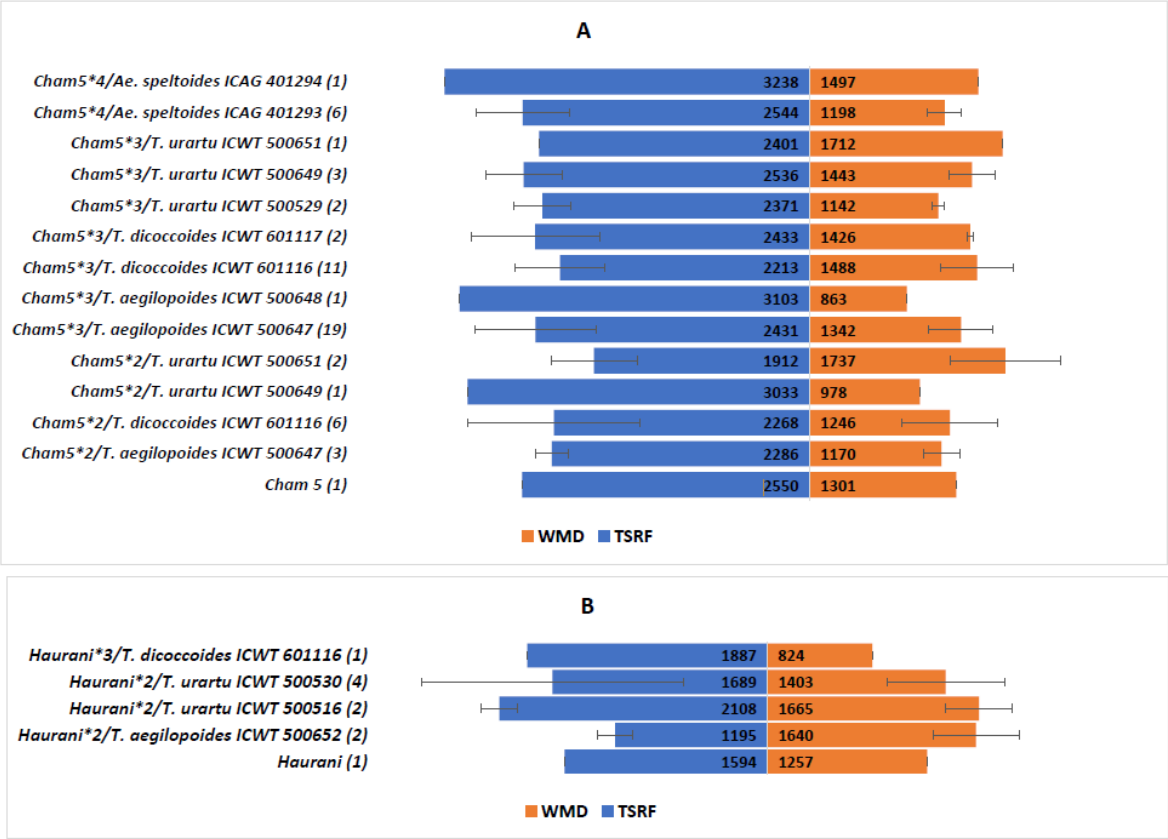

Figure 3-9. Average and standard deviation of the grain yield (GY, kg ha−1) of durum wheat derivatives lines from crosses with (a) Cham 5 and (b) Haurani by pedigree with their recurrent parents at Wad Medani (WMD) and Tessaout under rainfed conditions (TSRF). The number between parentheses represents the number of lines derived from each cross

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 3-10a), and then following the wild parents (Figure 3-10b). 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.

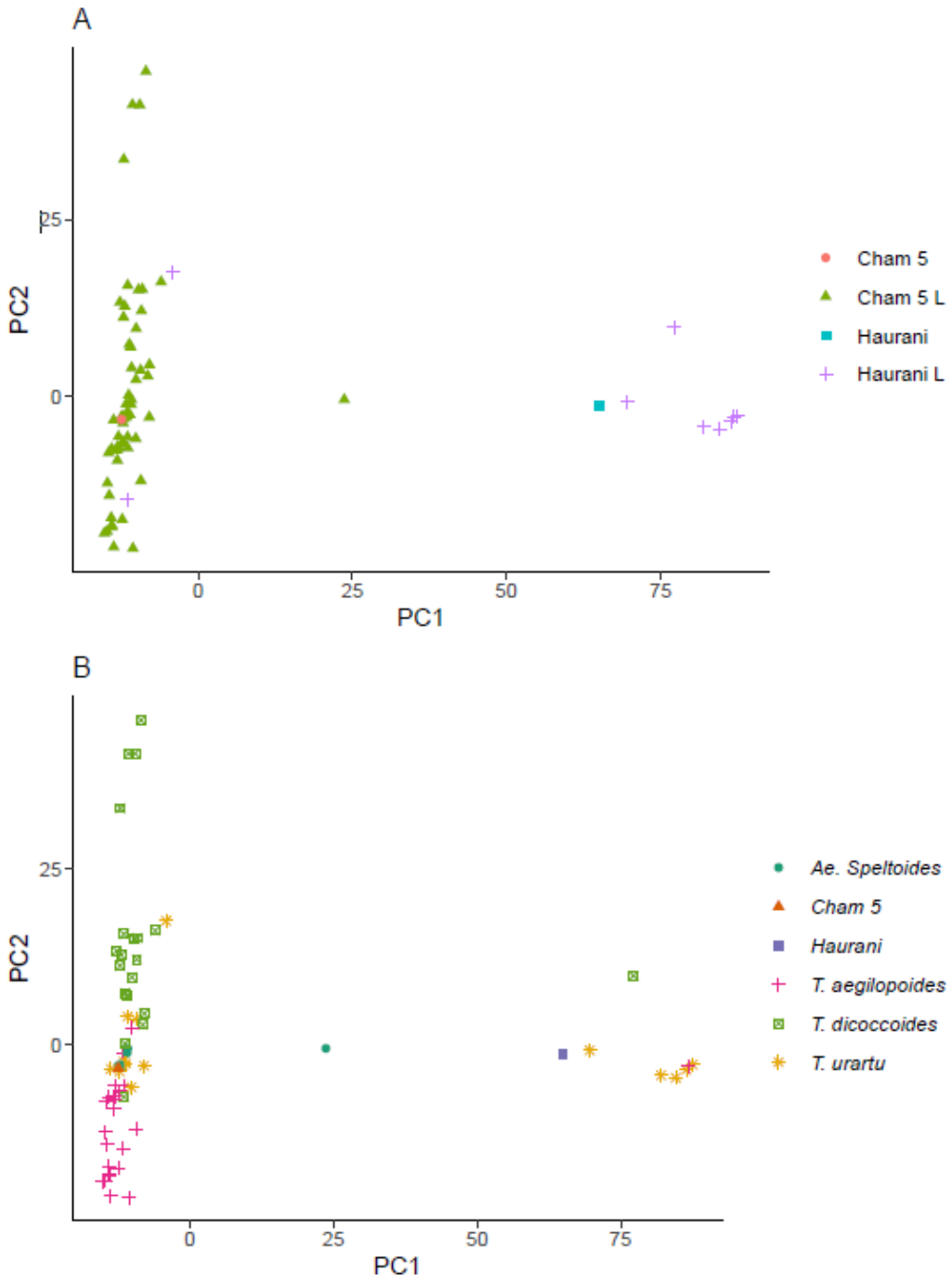

Figure 3-10. Biplot of the first two principal components (PCs) of the principal component analysis using DarTseq markers colored by (a) the cultivated parent and (b) the wild parent. Cham 5 L = lines derived from Cham 5; Haurani L = lines derived from Haurani.

3.5. 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 total amount of precipitation during the cropping season. The evaluation of breeding germplasm under irrigated and non-irrigated 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 Wad 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 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 SPKM2 was reached by lines derived from *Triticum dicoccoides*, followed by those derived from crosses with *Triticum aegilopoides*. The SPKM2 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 SPKM2 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 SPKM2, 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 BC2 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.

Chapter 4: Assessment of drought and heat tolerance of durum wheat lines derived from interspecific crosses using physiological parameters and stress indices

Hafid Aberkane [1,2,*], Bouchra Belkadi [2,3], Zakaria Kehel [1], Abdelkarim Filali-Maltouf [2,3], Izzat S. A. Tahir [4], Sara Meheesi [4] and Ahmed Amri [1]

[1] International Center for Agricultural Research in the Dry Areas (ICARDA), Rabat 10000, Morocco;
Z.Kehel@cgiar.org (Z.K.); A.Amri@cgiar.org (A.A.)

[2] Plant and Microbial Biotechnology, Biodiversity and Environmental Research Center, Faculty of Sciences,
Mohammed V University of Rabat, Rabat 10000, Morocco; bbelkadi@gmail.com (B.B.); filalimaltouf@gmail.com (A.F.-M.)

[3] Laboratory of Microbiology and Molecular Biology, Faculty of Sciences, Mohammed V University of Rabat,
Rabat 10000, Morocco

[4] Agricultural Research Corporation (ARC), P.O. Box 126, Wad Medani 21111, Sudan; izzatahir@yahoo.com (I.S.A.T.); smeheesi@yahoo.com (S.M.)

***** Correspondence: h.aberkane@cgiar.org

4.1.Abstract

Drought and high temperature are the major abiotic stresses for wheat production. The present study investigated the effect of drought and chronic heat stress on physiological parameters of durum wheat lines derived from interspecific crosses and their association with yield. Seventy-seven durum wheat lines were evaluated during two seasons (2016–2017 and 2017–2018) for drought tolerance at Tessaout (Morocco) using irrigated and rainfed treatments and for heat tolerance at Wad Medani (Sudan). Five drought screening indices (alone or combined) and physiological parameters were used to assess drought and heat tolerance. Among the physiological parameters used, canopy temperature (CT) had moderate heritability and was significantly affected by both severe and moderate drought stresses. CT at early heading showed a stronger correlation with grain yield (GY) and total biomass (BY) under heat stress. The use of maximum quantum yield of PSII (Fv/Fm) for drought/heat screening was limited by the low genetic variation despite its significant correlation with yield under drought ($r^2 = 0.22$) and heat ($r^2 = 0.4$). The normalized difference vegetation index (NDVI) at vegetative stage was highly correlated with GY and BY and it showed high genotypic variation that can allow for efficient selection. The grain filling rate (GFR) was found to be highly correlated with GY and BY under heat stress. The modified stress tolerance index (MsSTI) had the highest association with GY under drought ($R^2 = 0.82$) while the mean productivity (MP) was adapted to both optimal conditions ($R^2 = 0.77$) and drought stress ($R^2 = 0.73$). The computation of a mean score index (MSI) improved the selection efficiency under drought ($R^2 = 0.92$). The results showed good potential for lines derived from wide crosses to increase variability for heat and drought adaptive physiological traits.

4.2.Introduction

Drought and heat are the major abiotic stresses affecting wheat productivity in the world. The global wheat area exposed to drought doubled between 1979 and 2006 (Li et al., 2013) and the future availability of water to meet crop requirements will be a major challenge in arid and semi-arid regions (Food and Agriculture Organization of the United Nations, 2013). Global wheat production is expected to decrease by 4.1% to 6.4% for every 1 °C increase in temperature as warming is already slowing yield gains in the majority of wheat production areas (Asseng et al., 2015; Liu et al., 2016).

These two abiotic stresses can occur at different wheat growth stages and affect several morphological, physiological, and molecular plant processes (Sultan et al., 2012; Jha et al., 2014) resulting in significant yield losses (Li et al., 2006; Sukumaran et al., 2018; El Hassouni et al., 2019; Aberkane et al., 2021a). These complex changes in addition to the high genotype by environment interaction limit the effectiveness of empirical selection for drought and heat tolerance (Araus, 2002; Sallam et al., 2019), especially under the fluctuations of Mediterranean environments (Araus, 2002). Therefore, the development of drought and heat tolerant wheat cultivars requires an integrated breeding strategy that includes screening techniques for physiological and morphological adaptive traits in addition to the molecular tools to harness diverse genetic resources (Reynolds et al., 2012; Hu and Xiong, 2014; Jha et al., 2014; van Oosten et al., 2016; Mwadzingeni et al., 2016).

For instance, canopy temperature (CT) was reported to be useful to select for water stressed environments and high correlation with grain yield (GY) was found for CT measured at anthesis halfway and grain filling stages (Pradhan et al., 2012b, 2020). CT is an integrative measurement that is correlated with other physiological mechanisms. Cooler CT was associated with root spreading in bread wheat (Pinto and Reynolds, 2015) and its association with genetic gains in hot conditions was established (Reynolds et al., 1998; Reynolds and Trethowan, 2007). CT is also influenced by the stomatal control of transpiration as stomatal closure under reduced water status results in an increase of CT (Ludlow and Muchow, 1990). The negative correlation between CT and grain yield, plant height, and heading time suggests that a cooler canopy provides yield benefits at both drought and heat stresses. These benefits are more pronounced under heat stress (Mason and Singh, 2014).

Drought and heat stresses affect the photosynthetic activity by reducing the chlorophyll content (Feng et al., 2014; Sangwan et al., 2018) and damaging the photosystem II reaction sites (Zlatev, 2009; Cowley and Luckett, 2011). Chlorophyll content measurement provides information on the health status of the leaf (Araus et al., 2008) while chlorophyll fluorescence informs about the effectiveness in using the energy absorbed by the chlorophyll to diagnose the onset of photoinhibition (Maxwell and Johnson, 2000). Both traits were reported to be valuable for wheat breeding. Chlorophyll fluorescence was found to be useful for evaluating yield performance under rainfed Mediterranean conditions when measured during grain filling period (Araus et al., 1998; Li et al., 2006). The maximum quantum yield of PSII (Fv/Fm) represents the most meaningful chlorophyll fluorescence reading (Cowley and Luckett, 2011), as it measures the efficiency of light harvesting and the conversion to chemical energy (Baker and Rosenqvist, 2004). Fv/Fm was identified as a suitable trait to screen for tolerance to high temperatures (Baker and Rosenqvist, 2004) and several quantitative trait loci (QTLs) were identified for fluorescence parameters under heat stress (Bhusal et al., 2018). Chlorophyll content showed a correlation with grain yield and thousand kernel weight under heat and drought stresses (Mohammadi et al., 2009; Cao et al., 2015) and it was found negatively correlated with the heat susceptibility index (Yang et al., 2002).

Broadening the genetic base for these physiological adaptive traits requires access to novel diversity, which can be supplied by crop wild relatives (Dempewolf et al., 2017). Screening of wheat wild relatives identified several donors for useful traits in wheat breeding (Monneveux et al., 2000). *Triticum monococcum* subsp. *aegilopides* showed more potential to improve relative water content for drought tolerance than tetraploid and hexaploid wheat species (Sultan et al., 2012). *Aegilops geniculata* and *Triticum dicoccoides* were identified as sources for chlorophyll and photosynthesis related traits to improve drought and heat tolerance (Rekika et al., 1997; Zaharieva et al., 2001). Screening under field conditions identified a higher level of heat tolerance during a vegetative stage in *Aegilops speltoides* and *Aegilops tauschii* (Waines, 1994). Nachit and Elouafi, (2004) reported several durum wheat lines generated through interspecific hybridization combining adaptation to dry conditions with high yield potential.

In addition to physiological and morphological mechanisms involved in drought tolerance, several indices were proposed to screen for drought adaptation. Fischer and Maurer, (1978) suggested the drought susceptibility index (DSI), Rosielle and Hamblin, (1981) developed the mean productivity (MP) and tolerance (TOL) while the drought tolerance index (DTI) was suggested by Fernandez

(1992). Farshadfar and Sutka, (2002) introduced a correction coefficient to DTI and proposed a modified stress tolerance index (MsSTI). All these indices consider the performance of the genotypes under optimal and stressed conditions to separate susceptible genotypes from tolerant genotypes.

These indices were used extensively to screen and select genotypes for drought tolerance (Mohammadi et al., 2010; Karimizadeh and Mohammadi, 2011; Asfaw and Blair, 2014; Gholinezhad et al., 2014). Tolerance and susceptibility indices can select genotypes with specific adaptation to drought stressed or favorable environments, and also genotypes combining high yield under both types of environments. There is some variation in the ability of these indices to select effectively suitable genotypes for dry environments, which suggests that their combination can be useful to achieve higher selection efficiency (Thiry et al., 2016). The objectives of this study are: (i) assess the heritability of some physiological traits and their association with grain yield under drought and heat stresses, (ii) examine the ability of tolerance indices and their combination to select the best genotypes for drought stress, and (iii) select pre-breeding lines from a durum wheat population derived from interspecific crosses with high yield potential and good levels of drought and tolerance.

4.3.Materials and Methods

4.3.1. Plant material and field conditions

The study was conducted with 77 lines of durum wheat (*Triticum turgidum* var. *durum*) including 67 lines derived from wide crosses, eight checks, and the two recurrent parents (Annex 1). 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*. Haurani is a locally adapted Syrian landrace with low yield potential but drought tolerant while Cham5 is a high yielding variety released in Syria from ICARDA supplied germplasm. The wild parents were selected based on the ecology of their collecting sites and their disease resistance. Repeated backcrosses followed the initial hybridization to restore fertility and break the undesirable gene linkages. The derivative lines showed high variation for agro-morphological traits and resistance to yellow and leaf rust (Valkoun, 2001).

4.3.2. Field conditions

The screening trials for drought and heat were conducted during the two seasons (2016–2017 and 2017–2018). For drought tolerance screening, the trials were conducted at the Tessaout experimental station (31°49' N, 7°25' W) in Morocco. Tessaout is characterized by frequent droughts with average annual precipitations of 266 mm. Two trials were established each season. The first trial is non stressed under full irrigation (TSIR) and the second trial is under rainfed conditions (TSRF), representing the drought stressed. Both trials were irrigated at sowing to ensure homogeneous germination and emergence. TSIR received five additional irrigations at different growth stages. The heat tolerance screening was conducted at a heat research platform at wad Medani (WMD), Sudan (14°24' N, 33°31' E, Altitude 407 m). WMD is characterized by a hot season with a temperature ranging between 18 °C and 36 °C on average. The trials were irrigated at an interval of 7 to 10 days to avoid the confounding effect of drought and heat.

Each trial was randomized in an incomplete block design (alpha-lattice) with two replications. Each replicate consisted of 11 blocks with seven genotypes in each. The plots were laid out in 4 rows of 2 m long with a sowing density of 300 seeds per m². The distance between rows was 0.30 m. The optimal agronomic practices in terms of fertilizers, weeding, and fungicides recommended for each location were applied.

4.3.3. Data collection

At Tessaout, the collected traits were grain yield (GY) and biological yield (BY) estimated from the two internal rows in each plot avoiding the border and converted to Kg/ha. Number of days to the heading (DHE) recorded when 50% of each plot reached the heading and thousand kernel weight (TKW) was estimated by counting and weighing 500 seeds. When both trials (TSIR and TSRF) were at heading, the canopy temperature (CT) was recorded using a thermal camera (FLIR T460). The pictures were analyzed with FLIR tools (Version 5.5.16064.1001) to estimate the CT of each plot. Chlorophyll fluorescence was measured on the dark adapted flag leaf of three random plants from the internal rows in each plot using Fluorometer OS30p+. CT and chlorophyll fluorescence were measured at sunny days between 12.00 and 2.00 p.m.

At WMD, the normalized difference vegetation index (NDVI), chlorophyll content (CHL), and CT were measured at the heading time and grain filling period in 2017. During the second season

(2017–2018), an additional third measurement was performed at the vegetative stage. The maximum air temperature was always higher than 35 °C at the day of measurements during both seasons (Table 4-1). CT was measured with a hand-held infrared thermometer (Center 325). Each measurement represents the average of three random readings in each plot. CHL was measured using a chlorophyll meter (Minolta SPAD-502). Each measurement represents the average of five readings performed on random plants. NDVI measurements were collected using a greenseeker following the manufacturers' instructions. At WMD, the readings of all physiological traits were taken during clear days under sunny conditions between 1:00 p.m. and 3:00 p.m. GY and BY were estimated similarly to that at Tessaout and the grain filling rate (GFR) was calculated by Pinto, (2017).

$$GFR = \frac{grain\ yield\ (Kg.ha^{-1})}{grain\ filling\ period\ (days)}$$

Table 4-1. Maximum and minimum temperatures during physiological trait records at wad Medani for the two seasons 2016–2017 and 2017–2018.

		2016–2017		2017–2018	
	Sowing Date	**18 December 2016**		**7 December 2017**	
Trait	**Stage**	**T min**	**T Max**	**T min**	**T Max**
NDVIv	Vegetative	-	-	18.8	38.5
NDVIh	Heading (ZGS 5)	16.5	38.5	21	39.2
NDVIf	Grain filling (ZGS 7)	22.5	41.7	22.5	40.5
CHLv	Vegetative	-	-	17.5	38.5
CHLh	Heading (ZGS 5)	16.5	38.5	21	39.2
CHLf	Grain filling (ZGS 7)	22.5	41.7	22.5	40.5
CTv	Vegetative	-	-	18.8	38.5
CTh	Heading (ZGS 5)	16.5	38.5	17.5	38.5
CTf	Grain filling (ZGS 7)	22.5	41.7	18.5	37

NDVIv, Normalized difference vegetation index at vegetative stage. NDVIh, NDVI at heading. NDVIf, NDVI during grain filling. CHLv, Chlorophyll content at vegetative stage. CHLh, Chlorophyll content at heading. CHLf, chlorophyll content during grain filling. CTv, canopy temperature at vegetative stage. CTh, canopy temperature at heading. CTf, canopy temperature during grain filling. T min, minimum temperature (°C). T max, maximum temperature (°C). ZGS 5, Zadoks growth scale 5. ZGS 7, Zadoks growth scale 7.

4.3.4. Statistical analysis and tolerance indices

Data from Tessaout and WMD were analyzed separately with two stages analysis for each location. Linear mixed models were used for both first and second stage analysis, with replication and block effects nested in each trial as random effects. The first stage analysis was conducted using lme4 (Bates et al., 2015) and sommer (Covarrubias-Pazaran, 2016) in R software (R Core Team, 2021).

At Tessaout, the water regime, year, and their interaction were used as fixed effects for the first stage, while the genotypes were considered as random effects. A diagonal structure variance across years and water regimes was used to compute the genotypic variance and heritability in each environment (combination of year and water regime). The broad sense heritability in each environment was computed by (Falconer and Mackay, 1996).

$$h^2 = \frac{\text{Var (G)}}{\text{Var (G)} + \frac{\text{Var (e)}}{r}}$$

where Var(G) is the genotypic variance, Var(e) is the error variance, and r is the number of replications.

The second stage analysis was performed using meta-R software (Alvarado et al., 2020) to assess the genotype by environment interaction (GxE). Both genotypes and GxE were used as random effects for this analysis. Only environments with heritability above 0.10 were included in GxE analysis. Meta-R was also used to compute the best linear unbiased estimations (BLUEs) of all traits in each environment. The BLUEs across years at each water regime were computed for GY. They were used for computing drought tolerance/susceptibility indices.

Five tolerance and susceptibility indices were computed to assess the drought impact on the yield and select tolerant genotypes (Table 4-2). The methodology suggested by Thiry et al., (2016) was then used to score the genotypes based on their ranking within the population for each index. The range of each index allowed us to define 10 groups with each representing 10% of the population. The genotypes were then scored from 1 to 10 with 10 representing the most desirable genotypes for that index. The scores' attribution provides more flexibility to test a different combination and improve the selection efficiency. The scores were used to perform and plot a hierarchical clustering analysis using the packages maptree, dendextend, gclus, and cluster (White and B. Gramacy, 2012; Galili, 2015; Hurley, 2019; Maechler et al., 2019) in R software (R Core Team, 2021).

Table 4-2. Equations and references of the drought tolerance and susceptibility indices used for drought tolerance evaluation.

Index	Equation	Reference
Drought tolerance index (DTI)	$DTI = \frac{(Yp)(Ys)}{(\overline{Yp})^2}$	(Fernandez, 1992)
Drought susceptibility index (DSI)	$DSI = \frac{1-\left(\frac{Ys}{Yp}\right)}{1-\left(\frac{\overline{Ys}}{\overline{Yp}}\right)}$	(Fischer and Maurer, 1978)
Mean productivity (MP)	$MP = \frac{Yp+Ys}{2}$	(Rosielle and Hamblin, 1981)
Tolerance (TOL)	$TOL = Yp - Ys$	(Rosielle and Hamblin, 1981)
Modifies stress tolerance index (MsSTI)	$MsSTI = \frac{(Ys)^2}{(\overline{Ys})^2} \times DTI$	(Farshadfar and Sutka, 2002)

Yp, yield under optimal conditions. *Ys*, yield under drought stress. $\overline{yp}$, Average yield under optimal conditions. $\overline{ys}$, average yield under drought stress.

At WMD, the first stage analysis was performed considering the year as a fixed effect and genotypic variance was estimated for each year similarly to Tessaout. For all traits, the year with zero or low heritability (<0.10) was excluded from the GxE analysis of variance. The BLUEs in each year were computed for all traits using Meta-R (Alvarado et al., 2020).

The Hmisc Package (Harrell and Dupont, 2020) was used to compute the phenotypic Pearson correlation coefficients among traits at Tessaout and WMD. The linear regression analysis and scatterplots were performed with ggpubr package (Kassambara, 2020).

4.4.Results

4.4.1. Climatic data

Climatic data showed the difference between the two seasons at Tessaout where the second season had more favorable growing conditions, especially during the reproductive stage. Despite the difference in heading time between TSIR and TSRF, the average maximum temperature during the reproductive stage was not different between TSIR and TSRF. In addition, the second season received more precipitations at both vegetative (167.4 mm) and reproductive (87.6 mm) stages. At WMD, the temperature was consistently high during all growth stages in both seasons. The first season was characterized by a higher maximum temperature during the vegetative stage (36.05 °C) in comparison to the second season (33.9 °C). This is also valid for the minimum temperature that averaged 18.24 °C in 2016–2017 and 16.3 °C in 2017–2018 during the vegetative stage. The

opposite was observed during the reproductive stage as the average minimum and maximum temperatures were higher during 2017–2018 (Table 4-3). No rainfall was registered at WMD during both seasons.

Table 4-3. Average minimum and maximum temperatures (°C) and precipitations (mm) at vegetative and reproductive stages during two cropping seasons (2016–2017 and 2017–2018) at Tessaout (TST) and wad Medani (WMD).

Season	Location	Vegetative Stage			Reproductive Stage		
		Min T (°C)	Max T (°C)	Prec. (mm)	Min T (°C)	Max T (°C)	Prec. (mm)
2016–2017	TST	4.4	19	118	11.96	29.75	60
	WMD	18.24	36.05	0	17.42	36.89	0
2017–2018	TST	4.55	18.04	167	9.9	24.04	87.6
	WMD	16.3	33.9	0	20	39.8	0

4.4.2. Drought screening

4.4.2.1. Analysis of variance

The application of two water regimes at Tessaout (Irrigated/Rainfed) resulted in highly significant differences in GY and other measured traits. Only Fv/Fm was less affected by the water regime. However, the year effect on this trait was higher. The interaction between the year and water regime was significant for GY and other agronomic traits, while it was not significant for CT and Fv/Fm (Table 4-4). In terms of the genotypic effect, it was consistently significant over years and trials for DHE, TKW, and GY, which was associated with high heritabilities for these traits (Table 4-4). The effect of the genotypes was significant for Fv/Fm only at TSRF-17 ($h^2 = 0.56$) and TSIR-18 ($h^2 = 0.48$) while, at TSIR-17 and TSRF-18, no genetic contribution to the variance of this trait was observed. The genotypic effect of CT was significant during the two seasons under both irrigated and rainfed conditions. The highest CT heritability was observed at TSIR-17 (0.52). Higher heritability was expressed for BY under drought stress in comparison to optimally irrigated conditions during both seasons (Table 4-4).

Table 4-4. F-statistics for the fixed effects (year and water regime (WR)) and heritabilities of traits of durum wheat lines across years and WR at Tessaout during the seasons 2016–2017 and 2017–2018.

F Statistics for Fixed Effects						
	CT	**Fv/Fm**	**DHE**	**BY**	**TKW**	**GY**
WR	28.75 ***	4.55·	39.37 ***	48.6 ***	37.57 ***	31.56 ***
Year	25.75 ***	8.34 *	5.5 *	19.94 *	54.98 ***	4.12 ns
WR: Year	0.80 ns	0.0016 ns	36.44 ***	6.89 *	13.92 *	14.33 *
Heritability						
TSIR-17	0.52 **	0 ns	0.57 **	0.10 ns	0.54 **	0.53 ***
TSRF-17	0.16 **	0.56 **	0.63 **	0.39 **	0.59 ***	0.44 ***
TSIR-18	0.31 **	0.48 *	0.82 **	0.19 ns	0.47 ***	0.48 ***
TSRF-18	0.28 **	0 ns	0.91 **	0.26 *	0.74 ***	0.66 ***

CT, canopy temperature. GY, grain yield. BY, total biomass. TKW, thousand kernel weight (g). DHE, days to heading. Fv/Fm, maximum quantum yield of PSII. WR, water regime.
. $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, ns non significant.

The genotype by environment (GxE) analysis showed a significant GxE interaction for all the measured traits except for BY. The year-to-year fluctuations for all traits, especially under the rainfed conditions, are summarized in Table 4-5. At TSRF, the mean GY doubled in the second season as it went from 2253 kg/ha to 4561 kg/ha. Similarly, TKW and BY under rainfed conditions increased by 53% and 57%, respectively, in 2018. Days to heading in 2018 ranged between 97 and 113 days. This range was wider than the first season despite similar means for both seasons. At TSIR, the effect of year on GY and other agronomic traits was less important. Only TKW showed an increase during the second season under irrigated conditions (Table 4-5).

The comparison of the performance between TSRF and TSIR showed that drought stress was more severe in the first season with an average decrease of 62% in GY, compared to only 13% reduction in the second season. This observation is also valid for TKW, which was reduced by 33% due to drought stress in 2017. Similarly, the total biomass showed 41% and 17% reductions under drought stress in 2017 and 2018, respectively.

Table 4-5. Descriptive statistics and significance of the GxE of traits collected at Tessaout during the two seasons of 2016–2017 and 2017–2018 under rainfed (TSRF) and irrigated conditions (TSIR).

Trait	Location	Year	Min	Max	Mean	SD	GxE Significance
GY	TSIR	2017	2393	8614	5955	1248	*
		2018	2572	7562	5251	1087	
	TSRF	2017	728	4157	2253	706	
		2018	2490	6330	4561	950	
BY	TSIR	2017	10,564	21,546	15,133	2315	ns
		2018	11,685	19,798	16,375	1953	
	TSRF	2017	5319	14,036	8810	1694	
		2018	9443	17,200	13,510	1654	
TKW	TSIR	2017	25.4	48.4	37.2	4.8	*
		2018	31.0	51.2	41.9	4.1	
	TSRF	2017	18.5	32.6	24.8	3.2	
		2018	28.0	45.0	38.9	3.6	
DHE	TSIR	2017	100	109	105	2	***
		2018	97	111	103	3	
	TSRF	2017	97	106	102	2	
		2018	97	113	103	4	
Fv/Fm	TSIR	2017	-	-	-	-	***
		2018	0.62	0.75	0.69	0.03	
	TSRF	2017	0.60	0.74	0.68	0.03	
		2018	-	-	-	-	

GY, grain yield. BY, total biomass. TKW, thousand kernel weight (g). DHE, days to heading. Fv/Fm, maximum quantum yield of PSII. * $p < 0.05$. *** $p < 0.001$. ns, non-significant.

For the physiological parameters, the GxE interaction was significant for both CT and Fv/Fm. However, for Fv/Fm, only two environments (TSRF-2017 and TSIR-2018) were included in the GxE analysis because no genetic variation was observed in other environments. All the genotypes had higher CT under drought stress during both seasons.

The canopy temperature was more affected by the drought during both seasons and all the genotypes had higher CT under drought stress. On average, the lines at TSIR were 3.2 and 4.6 °C cooler than at TSRF in 2017 and 2018, respectively. The first season was characterized by a higher average CT at both TSIR (23.16 °C) and TSRF (26.4 °C) in comparison to the second season where CT ranged between 18.8 °C at TSIR and 23.4 °C at TSRF (Figure 4-1).

Wider ranges of Fv/Fm were registered in the environments where heritability was high. At TSRF (2017), Fv/Fm ranged from 0.60 to 0.74 with an average of 0.68. This range was similar to what was observed under irrigated conditions in the second season (0.62–0.75) where the average was 0.69. The low heritability did not allow us to assess the genotypic response of Fv/Fm to drought stress in each season (Table 4-5).

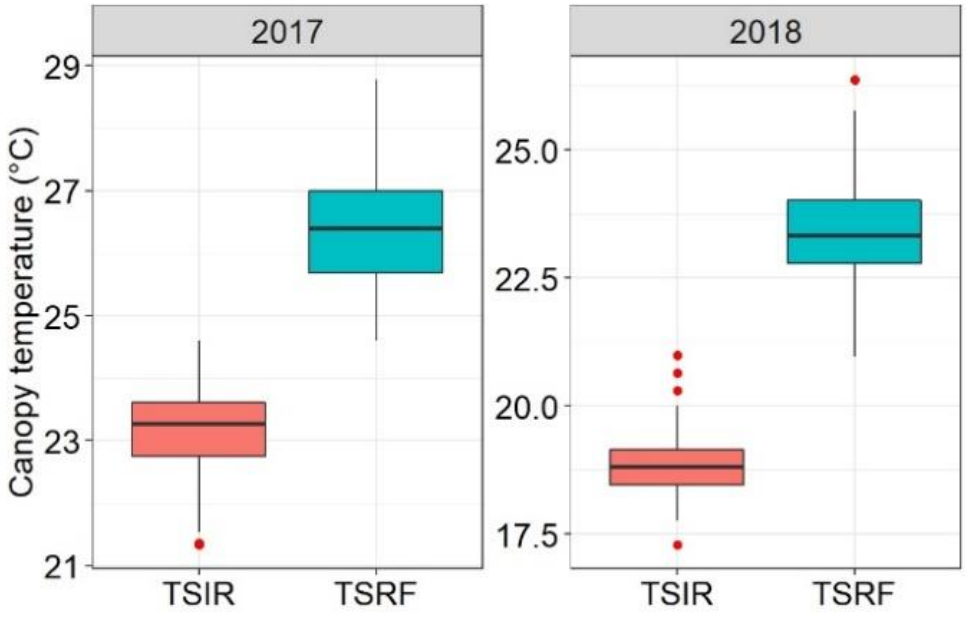

Figure 4-1. Boxplot of the canopy temperature (°C) measured at heading stage at Tessaout under irrigated (TSIR) and rainfed (TSRF) conditions during two consecutive seasons of 2016–2017 and 2017–2018.

4.4.2.2. Correlation results

The correlation results showed a cluster of GY, BY, and TKW. These traits were highly correlated to each other under both optimal and drought-stressed conditions. BY has a higher correlation with GY under rainfed conditions during both seasons while TKW was more correlated to GY under optimal conditions (Table 4-6). DHE was significantly correlated with GY only in the second season with higher correlation under drought stress ($r^2 = -0.39^{***}$) in comparison to optimal conditions ($r^2 = -0.31^{***}$). The correlation between GY and CT was not significant under any of the environments. However, it was consistently negative across years and water regimes and it was higher under drought stress. Considering only the environments where there was a genotypic effect, Fv/Fm was significantly correlated to GY at TSRF-17 ($r^2 = 0.22^{*}$) and TSIR-18 ($r^2 = 0.24^{*}$). The correlation between Fv/Fm and DHE was significantly negative at both TSIR-18 ($r^2 = -0.40^{***}$) and TSRF-17 ($r^2 = 0.41^{***}$). The correlation between BY and CT was consistently negative, but was significant only at TSIR-17 ($r^2 = -0.29^{**}$). A significant positive correlation was found between the heading time and CT at TSRF in the second season ($r^2 = 0.35^{***}$).

Table 4-6. Pearson correlation coefficients of grain yield (GY) to days to heading (DHE), thousand kernel weight (TKW), total biomass (BY), canopy temperature (CT), and Fv/Fm at Tessaout under irrigated (TSIR) and rainfed (TSRF) conditions during two consecutive seasons of 2016–2017 and 2017–2018.

		DHE	TKW	BY	CT	FV/FM
2017	**TSIR**	0.06	0.36 ***	0.67 ***	−0.03	-
	TSRF	−0.21	0.30 ***	0.82 ***	−0.12	0.22 *
2018	**TSIR**	−0.31 ***	0.56 ***	0.67 ***	−0.12	0.24 *
	TSRF	−0.39 ***	0.50 ***	0.74 ***	−0.18	-

DHE, days to heading. TKW, thousand kernel weight (g). BY, total biomass. CT, canopy temperature. Fv/Fm, maximum quantum yield of PSII. * $p < 0.05$. *** $p < 0.001$.

4.4.2.3. Drought screening indices

The drought tolerance indices had different associations to GY under optimal and drought stress conditions. Tolerance (TOL) showed no ability to select desirable genotypes for drought stress ($R^2 = 0.0038$). In addition, it was not highly correlated to GY at TSIR ($R^2 = 0.39$). In fact, some lines

within the best ranking group (10), according to TOL, were among the lowest yielding lines under both conditions (Figure 4-2). DTI and MP were more effective in the identification of drought tolerant lines. However, MP was more suitable for yield potential selection ($R^2 = 0.77$) than DTI ($R^2 = 0.58$). The drought susceptibility index (DSI) failed to distinguish between the genotypes based on the performance at TSIR ($R^2 = 0.012$) and it had a moderate ability to select superior genotypes under drought stress ($R^2 = 0.35$). The highest association to GY under drought stress was observed with MsSTI ($R^2 = 0.89$). The genotypes with scores 8, 9, and 10 were the highest yielding at TSRF. Simultaneously, the desirable lines according to MsSTI included high yielding lines under optimal conditions. This highlights the ability of this index to select for both environments.

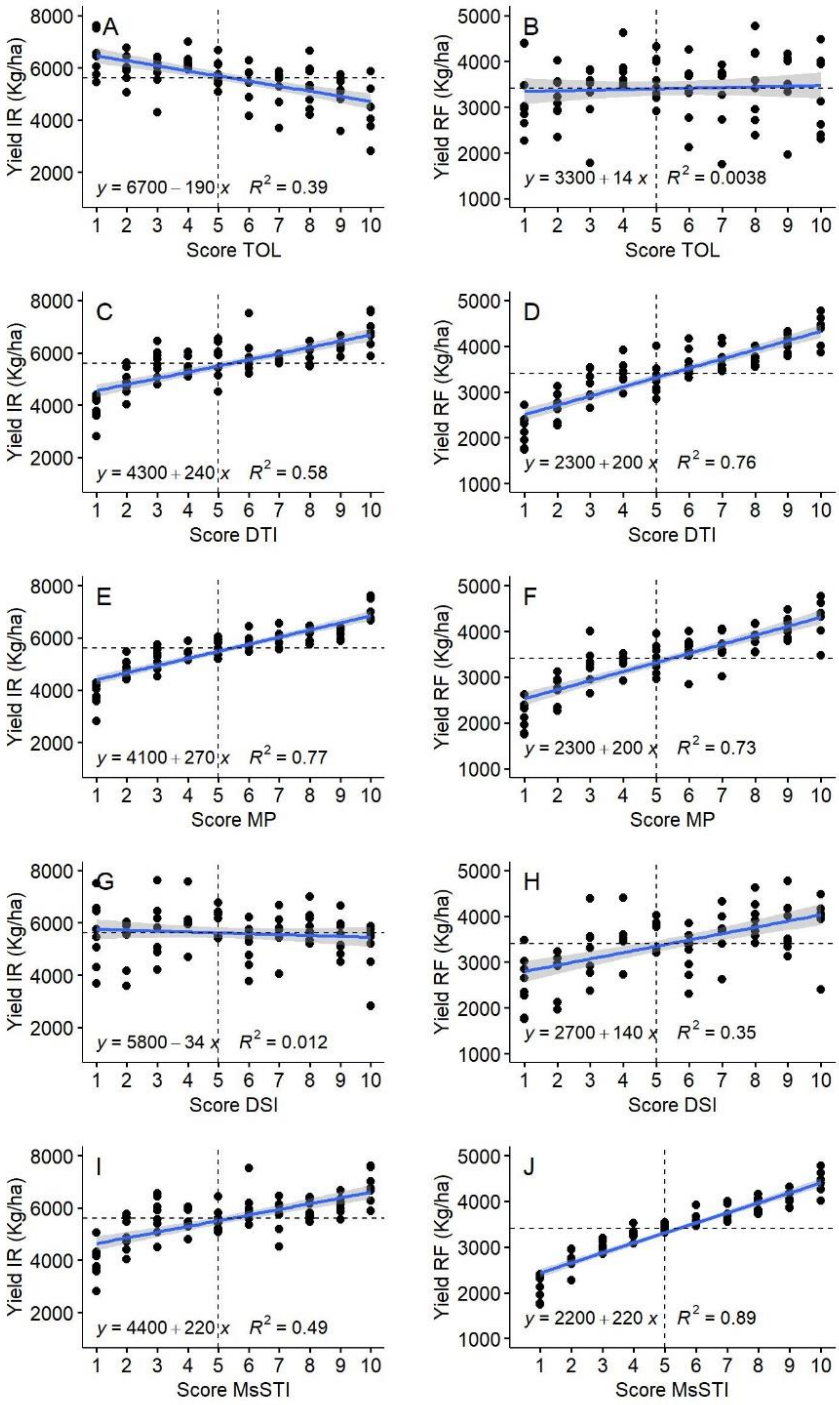

Figure 4-2. Linear regression and coefficient of determination of grain yield under irrigation (IR) and rainfed (RF) conditions at Tessaout versus the scores' indices. TOL, tolerance (A, B): DTI, drought tolerance index (C, D), MP, mean productivity (E, F), DSI, drought susceptibility index (G, H), and MsSTI, modified stress tolerance index (I, J).

In order to increase the selection efficiency for drought tolerance, a mean score index (MSI) (Thiry et al., 2016) was computed based on the indices that were effective to select good genotypes at TSRF. Therefore, TOL was excluded when calculating MSI.

$$MSI = \frac{Score\ MP + Score\ DTI + Score\ DSI + Score\ MsSTI}{4}$$

The coefficient of determination between MSI and GY at TSRF was 0.92. This association is higher than those for all indices taken individually (Figure 4-3). MSI allowed a clear distinction between the different groups of genotypes. Based on the MSI, 19 genotypes were selected as the most stable lines under drought (Annex 6). Six lines of this subset were ranked among the highest yielding at TSIR (129080, 142013,142074,141997, 142026, and Louiza). The advantage of MSI over MsSTI is the inclusion of more lines with specific adaptation to drought stress.

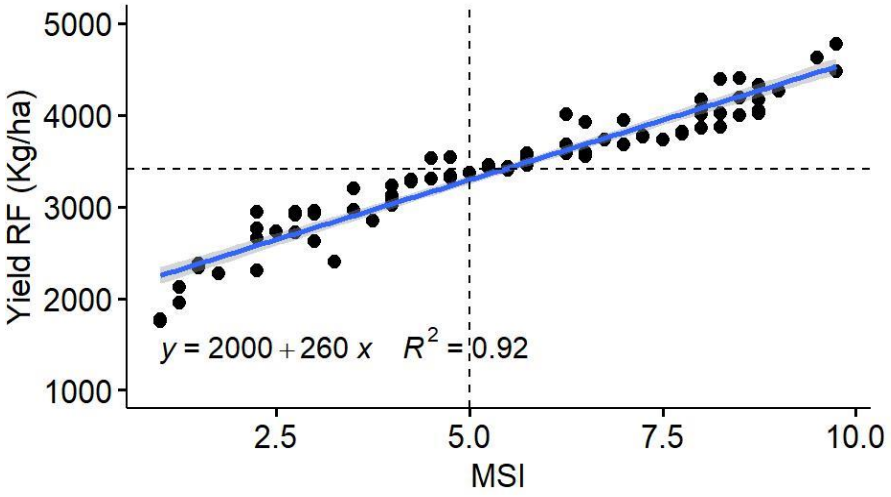

Figure 4-3. Linear regression and coefficient of determination of the mean score index (MSI) versus grain yield (kg/ha) under drought stressed conditions at Tessaout over two seasons (2016–2017 and 2017–2018).

The clustering based on the DSI, DTI, TOL, MP, and MsSTI resulted in the identification of five different groups of genotypes (Annex 7). The most desirable lines were grouped in the fourth group. They combine adaptation to drought with high yield potential (Figure 4-4). This group included four checks (Louiza, Faraj, Icarachaz, and Cham1) and 10 lines derived from interspecific crosses. The derivative lines in this group originated from crosses between Cham 5 and *Aegilops speltoides*, *Triticum dicoccoides*, *T. urartu*, and *T. aegilopoides*. The clustering confirmed that

MSI was highly effective in selecting most performant lines under drought stress. MSI combined the highest yielding lines at TSRF from the two groups (4 and 5) (Figure 4-4).

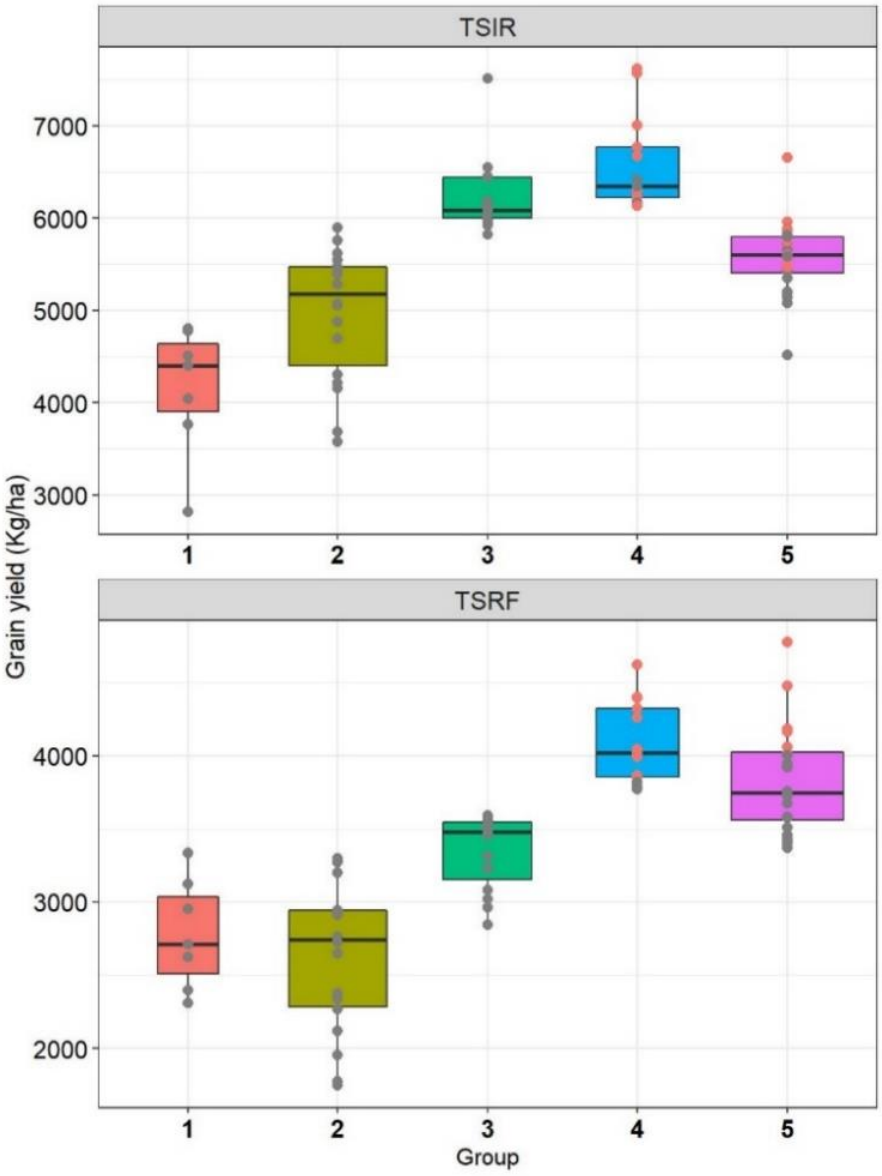

Figure 4-4. Boxplot of grain yield (kg/ha) at Tessaout under optimal conditions (TSIR) and rainfed conditions (TSRF) by cluster groups identified based on drought susceptibility/tolerance indices. A red color represents the lines selected by the mean score index (MSI).

4.4.3. Heat screening

4.4.3.1. Analysis of variance

The results of the analysis of variance showed that the year and its interaction with the genotypes were highly significant for GY, BY, and GFR. Canopy temperature at early heading (CTh) and during grain filling (CTf) were significantly affected by the season, but their interactions with the genotypes were not significant. The year and GxE effects were not computed for NDVIv, CTv, CHLv, and Fv/Fm as data was available for only one season. The lowest genotypic variance was observed in 2017 for CHLh, CHLf, and NDVIh (Table 4-7).

The heritability of most of the traits was higher in the second year and reached 0.9, 0.82, and 0.81 for GY, BY, and GFR, respectively. For the physiological parameters, higher heritability was observed for NDVIv (0.79) measured at the vegetative stage and for CHLh (0.62) in 2018. In comparison to CTf measured at grain filling, CTh had higher heritability (0.43) associated with significant differences between the genotypes in 2018. Cooler CT was observed for lines derived from both recurrent parents to *Ae. speltoides, Triticum dicoccoides*, and *Triticum aegilopides* in addition to the checks Faraj and Louiza.

The highest genetic variation for Chlorophyll content was observed in 2018 at the heading stage (CHLh) with a heritability of 0.62 and significant genotypic effect. The first season was characterized by zero heritability for both CHLh and CHLf. For NDVI, higher heritability was observed when measured at an early vegetative stage. NDVIv heritability reached 0.79 with a significant genotypic effect in 2018 while NDVIh had lower heritabilities during both seasons in comparison to other NDVI measurements. The lines derived from crosses with *T. aegilopoides*, *T. urartu*, and *T. dicoccoides* showed high variation for NDVI with high variability between the lines derived from the same cross.

Fv/Fm measured at heading stage ranged from 0.62 to 0.73 with a heritability of 0.22 in 2018. The second season was characterized by an increase in GY, BY, and GFR with their average increase by 58%, 20%, and 55%, respectively. Simultaneously, CTh and CTf had wider ranges with a decrease on average (Table 4-7).

Table 4-7. Heritability and significance of genotypes, year, and their interaction on agronomic and physiological traits collected under continuous heat stress at wad Medani during two seasons: 2016–2017 and 2017–2018.

Trait	Year	Range	Average	h^2	Year Significance	Gx Year Significance
GY	2017	230–2334	1381	0.31·	***	***
	2018	230–3930	2184	0.90 **		
BY	2017	2334–9589	5939	0.53 *	***	***
	2018	1602–10,606	7156	0.82 *		
GFR	2017	12.5–90.7	49.4	0.11 ns	***	***
	2018	10.5–134.9	76.8	0.81 ***		
CTv	2017	-	-	-	-	-
	2018	26.7–32.7	29.3	0.29 ns		
CTh	2017	26.7–30.8	29.1	0.14 ns	***	ns
	2018	23.7–31.6	26.9	0.43 *		
CTf	2017	28.2–33.1	31.1	0.27 **	**	ns
	2018	22.4–32	25.9	0.32 ns		
CHLv	2017	-	-	-	ns	-
	2018	39.8–62.6	54.1	0.29		
CHLh	2017	42.7–58.9	50.9	0	ns	-
	2018	48.2–65.2	56.3	0.62 **		
CHLf	2017	32.5–58.8	46.9	0	ns	-
	2018	39.7–62.9	52.2	0.43 *		
NDVIv	2017	-	-	-	-	-
	2018	0.31–0.69	0.50	0.79 *		
NDVIh	2017	0.41–0.79	0.56	0	ns	-
	2018	0.31–0.73	0.50	0.07		
NDVIf	2017	0.30–0.70	0.50	0.35 ns	ns	*
	2018	0.36–0.74	0.58	0.34 ns		
Fv/Fm	2017	-	-	-	-	-
	2018	0.62–0.73	0.67	0.22 ns		

GY, grain yield. BY, total biomass. GFR, grain filling rate. CTv, canopy temperature at vegetative stage. CTh, canopy temperature at heading. CTf, canopy temperature during grain filling. CHLv, Chlorophyll content at vegetative stage. CHLh, Chlorophyll content at heading. CHLf, chlorophyll content during grain filling. NDVIv, Normalized difference vegetation index at vegetative stage. NDVIh, NDVI at heading. NDVIf, NDVI during grain filling. Fv/Fm, maximum quantum yield of PSII collected at heading. $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

4.4.3.2. Association of physiological traits to grain yield and total biomass

Canopy temperature measured at different stages did not show a significant association with GY during 2017. However, during the second season, a significant negative association was observed between GY and both CTv and CTf. The strongest correlation was observed with the first measurement (CTv, R = −0.35) and it decreased with the second (CTh, R = −0.26) and the third (CTf, R = −0.22) measurements (Figure 4-5). Cooler canopy was consistently associated with higher biomass during both seasons. The highest association to BY was observed with CTh in the second season (R = −0.62). The lines 142072, 142068, and the check Faraj maintained a cooler temperature during all the reproductive stages (CTh and CTf) combined with high biomass. In addition, the line 142068 was among the highest yielding genotypes in 2018 with a GY of 3317 kg/ha.

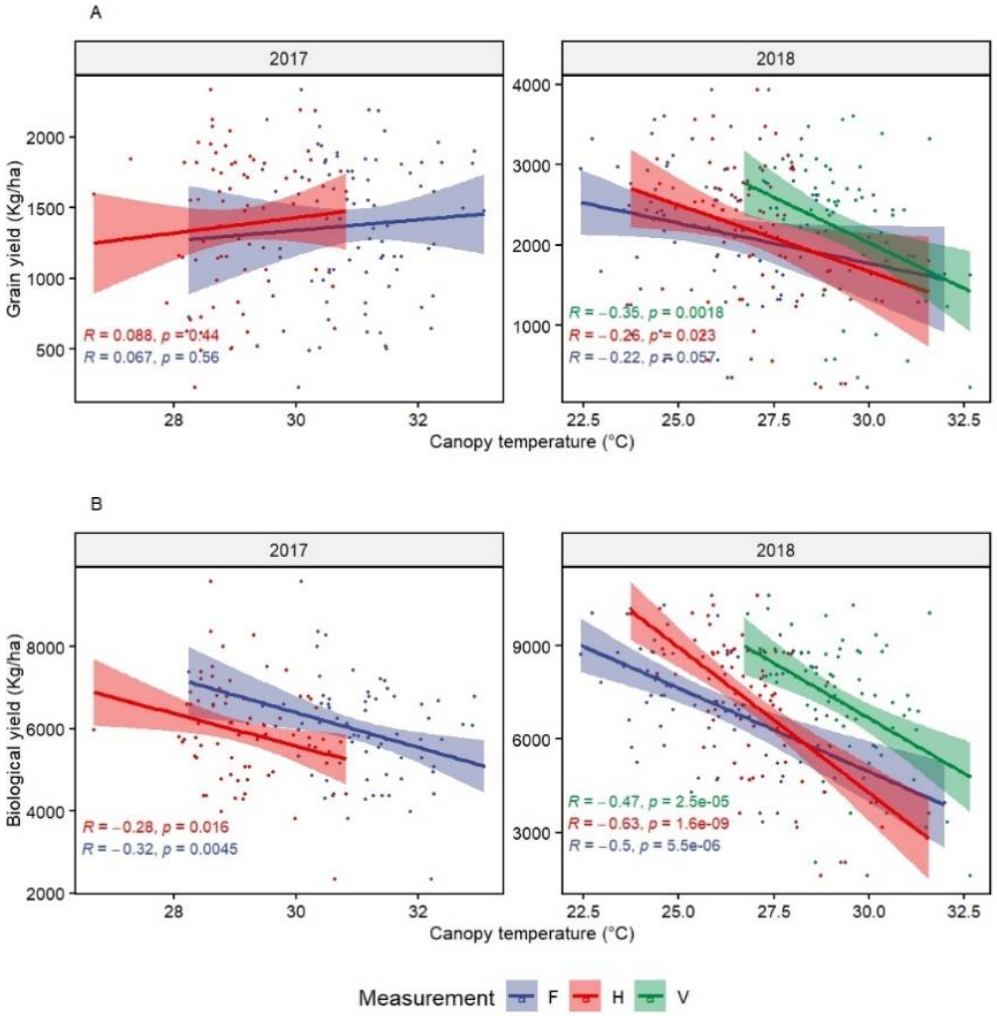

Figure 4-5. Linear regression and the Pearson correlation coefficient of canopy temperature measured at vegetative stage (V), heading (H), and grain filling (F) versus grain yield (A) and biological yield (B) under continuous heat stress at wad Medani for two seasons (2016–2017 and 2017–2018).

NDVIv had the highest correlation with BY in 2018 (R = 0.75) and GY (R = 0.32). This association decreased during the cycle and was not significant during grain filling. In 2017, the correlation between BY and NDVI was not significant for all the three measurements (Figure 4-6). In 2017, NDVIh and NDVIf correlated negatively with GY. It is also important to mention that some winter/facultative genotypes headed very late and produced a very low yield.

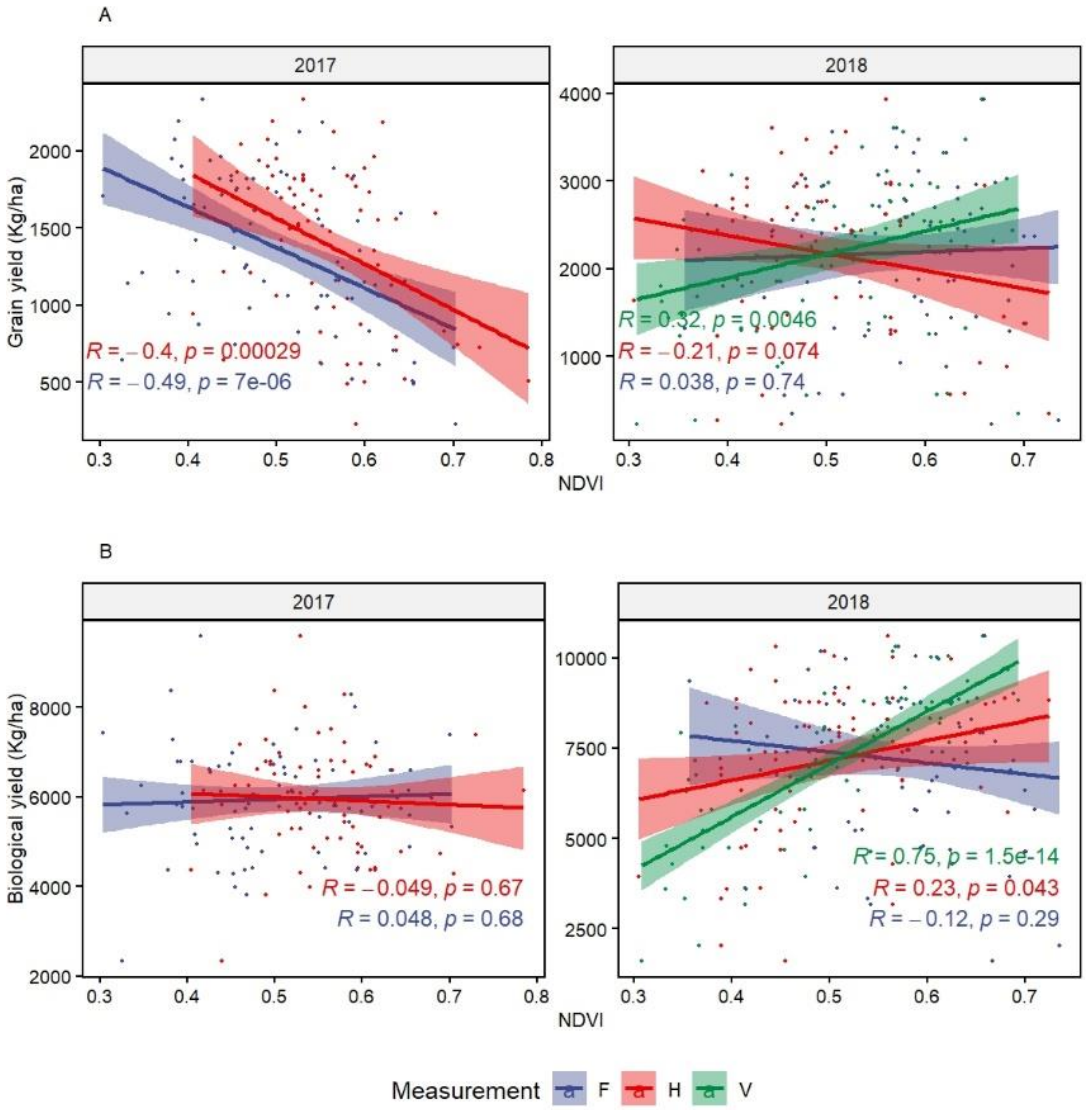

Figure 4-6. Linear regression and the Pearson correlation coefficient of normalized difference vegetation index (NDVI) measured at vegetative stage (V), heading (H), and grain filling (F) versus grain yield (A) and biological yield (B) under continuous heat stress during two seasons (2016–2017 and 2017–2018).

Chlorophyll content did not correlate significantly with GY and BY. Despite the higher correlation value between CHL and BY in comparison to GY, it was not significant (Figure 4-7). No difference was observed with regard to the time of measurement under continuous heat stress for CHL. The highest association with grain yield was obtained with GFR in 2018 (R = 0.93) and this correlation decreased to 0.56 in 2017. Fv/Fm collected at heading showed a significant correlation with GY (R = 0.4) in 2018 (Figure 4-8).

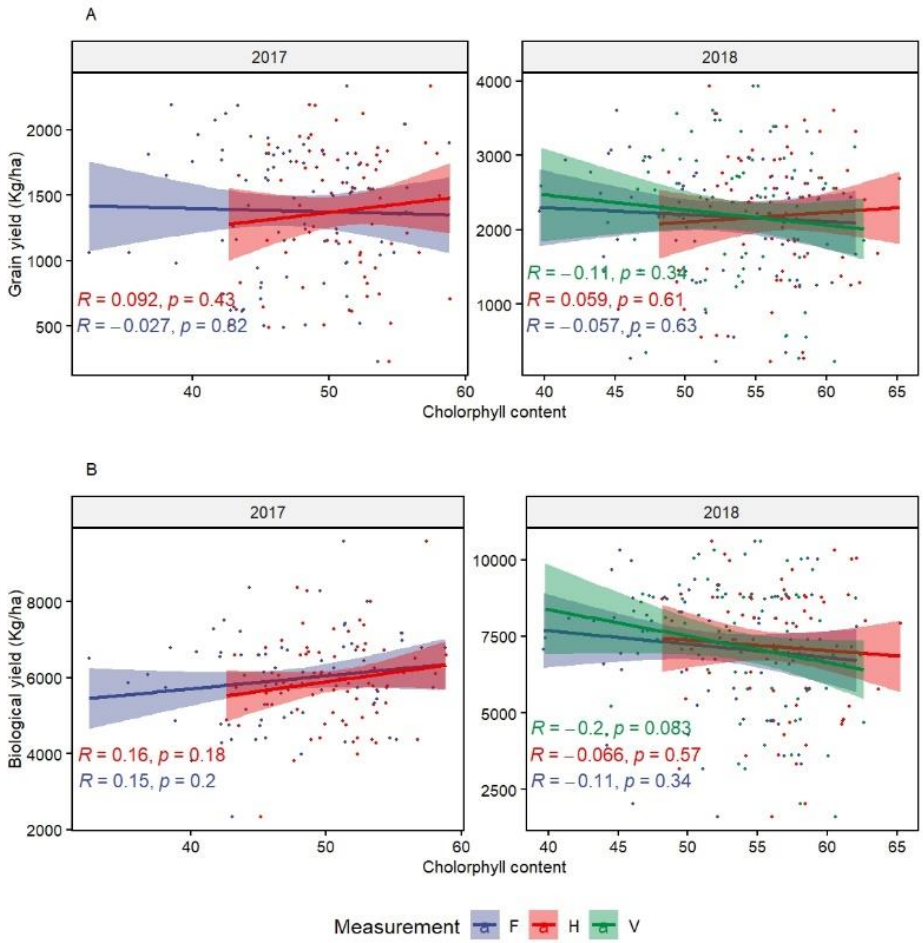

Figure 4-7. Linear regression and the Pearson correlation coefficient of chlorophyll content measured at vegetative stage (V), heading (H), and grain filling (F) versus grain yield (A) and biological yield (B) under continuous heat stress for two seasons (2016–2017 and 2017–2018).

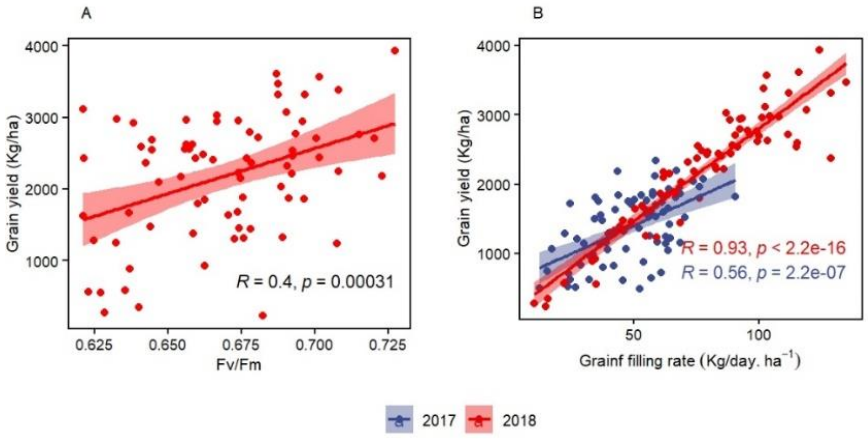

Figure 4-8. Linear regression and the Pearson correlation coefficient of maximum quantum yield of PSII (Fv/Fm) (**A**) and grain filling rate (**B**) versus grain yield under continuous heat stress for two seasons (2016–2017 and 2017–2018).

4.5. Discussion

At Tessaout, the drought penalty on the yield varied with the season rainfall and was more severe in the first season, reflecting the unpredictable climate in which wheat is exposed to in the Mediterranean region. Under these conditions, varieties, which are drought tolerant and having high yield potential under more favorable conditions, are needed to ensure higher and more stable yields. The maximum temperature at WMD was consistently above 30 °C throughout the crop cycle, confirming the choice of this site as a research platform for heat tolerance breeding.

The results showed the potential to exploit the genotypic variation for CT to select for drought and heat tolerance. CT was more useful under heat than drought stress, as it is significantly correlated with both GY and BY and it had moderate heritability. The CT correlations with other traits under drought were not significant. However, it can be considered a secondary physiological trait to increase the probability of additive gene action for drought adaptation, as suggested by Reynolds et al., (2006). Previous studies have reported an advantage of the CT measurement during grain filling for both genetic variations and correlations to GY under drought (Karimizadeh and Mohammadi, 2011; Abdipur et al., 2013). In fact, grain filling is the most vulnerable stage to drought stress (Sehgal et al., 2018), which can allow to identify tolerant from susceptible genotypes.

Taking into consideration the balance between high genotypic variation and strong association to GY and BY, the present results suggest that early heading stage is suitable to use CT for heat tolerance screening. CTv can also be recommended because of its high association to GY and BY, which could be explained by the fact that, under continuous heat stress, heat damage increases through the cycle and genotypes that can avoid early thermal shock will accumulate less damage in later stages. Lines with higher biomass had cooler CT during all stages, which is important, as BY explained the highest variation in GY at WMD (Aberkane et al., 2021a). Cooler CT and higher BY are associated with deeper root systems and root spreading, contributing to avoidance of heat stress as reported by previous studies (Reynolds et al., 1998; Mullan and Reynolds, 2010; Pinto and Reynolds, 2015). The importance of CT in heat tolerance was confirmed by many studies, which also identified several marker-trait associations and QTLs for canopy temperature under heat stress (Pinto et al., 2010; Bennett et al., 2012; Mondal et al., 2015; Pradhan et al., 2020). Some of these QTLs had pleiotropic effects on grain yield and other related traits.

For chlorophyll fluorescence parameters, the correlation between Fv/Fm and GY under rainfed conditions at Tessaout and at WMD was significant, which suggests Fv/Fm as an effective selection criteria for both drought and heat tolerance. However, low and inconsistent heritability could be the major limitation for Fv/Fm to select in early generations. Low (Araus et al., 1998) to moderate (Kumar et al., 2012) heritabilities were reported for Fv/Fm under drought stress with significant correlation to GY. However, high heritability was found at anthesis for terminal heat stress (Bhusal et al., 2018) and under controlled (heat stressed) conditions at seedling stage (Azam et al., 2015). Drought was reported to damage the PSII and decrease Fv/Fm (Sayar et al., 2008; Zlatev, 2009; Abid et al., 2016). In the present study, the limited genetic variation for Fv/Fm did not allow us to compare TSIR and TSRF during the same season in order to assess this damage. Chlorophyll fluorescence showed more potential to be used for heat than drought screening as the correlation with GY was higher at WMD. In addition, the Fv/Fm range at WMD was lower than what is reported for healthy plants (Narayan et al., 2012), confirming the effect of continuous heat stress on Fv/Fm (Yang et al., 2002).

CHL showed high genetic variation at the heading stage. However, it did not correlate significantly with GY and the other traits. This could mean that chlorophyll content is not a determinant of the photosynthetic rate. In fact, Akter and Rafiqul Islam, (2017) reported that several processes are involved in the determination of photosynthetic rate under heat stress. Despite the confirmed heat effect in reducing CHL (Ristic et al., 2007; Pradhan et al., 2012a; Cao et al., 2015), selection using CHL under chronic heat stress should be used with caution. High chlorophyl is associated with stay green (Vijayalakshmi et al., 2010; Sangwan et al., 2018), which could expose the plants to more stress during reproductive stage, leading to yield penalty.

The measurement of NDVI during the vegetative stage showed the possibility to identify and select heat tolerant genotypes. Measurements performed at later stages (NDVIh and NDVIf) did not present any advantage and NDVIf was the least effective in terms of correlation with all other major traits. The significant correlation of NDVIv with CTv and BY suggests the possibility to select lines integrating multiple tolerance mechanisms in early growth stages. Similar findings were reported for NDVI at the vegetative stage by Pinto et al., (2010) who identified several QTLs on A and B genomes. This supports the choice of using durum wheat direct progenitors (donors of A and B genome) from the primary gene pool to improve abiotic stress tolerance with polygenic

inheritance, as suggested by Valkoun, (2001). Pradhan et al., (2020) also found a positive association between NDVI at heading and grain yield. They also identified several marker-trait associations (MTAs) under heat stress. It is, however, important to consider germplasm with similar phenology when collecting NDVI and avoid very late and winter/facultative genotypes in the analysis.

GFR can be recommended as efficient screening criteria for heat tolerance. It had the highest correlation to GY during both seasons. GFR can be easily computed for large breeding populations with accurate recording of anthesis and maturity time. The correlation of GFR and BY could be associated with the importance of assimilates availability to improve efficient translocation toward the grains. The usefulness of GFR is also derived from its ability to determine the final grain weight, which is a major yield component with high genetic plasticity (Calderini and Reynolds, 2000; Wu et al., 2018; Baillot et al., 2018). Knowing that BY and thousand kernel weight explained together more than 40% of GY variation under the same conditions of the present study at WMD (Aberkane et al., 2021a), GFR can increase the selection efficiency under chronic heat stress. A high filling rate can also compensate for the reduction of spike fertility and filling period, which are, in turn, reduced by heat stress (Farooq et al., 2011; Pradhan et al., 2012a; Sukumaran et al., 2018). In addition, the contribution of GFR to grain yield was reported to be more important than filling duration under terminal heat stress (Dias and Lidon, 2009).

The drought tolerance and susceptibility indices showed different accuracies to select drought-adapted genotypes based on the groups identified by Fernandez, (1992). The susceptibility indices (TOL and DSI) were less effective than tolerance indices (DTI, MP, and MsSTI) to select suitable lines for drought stress. According to Mohammadi et al., (2010), MP and DTI can be used alternatively as they were correlated with each other and, therefore, selected the same genotypes. Using the scores, the present results showed that DTI is more efficient under drought stress while MP included some lines with moderate performance under drought stress. Selection based on MP is privileged in regions where drought stress occurs at equal frequencies as favorable conditions (Rosielle and Hamblin, 1981), which is the case in the Mediterranean region. The level and duration of drought stress could be responsible for various results of correlation among indices. This explains the identification of different best suitable indices in multiple studies. For example, Farshadfar et al., (2012) suggested that DTI and TOL had the same selection ability while

Gholinezhad et al., (2014) identified MsSTI, MP, and DTI as the most efficient screening indices under moderate and severe drought stress. In another study by Farshadfar et al., (2013), TOL and DTI were clustered in different groups and MsSTI was identified as an efficient selection index. These differences show that the ideal index to use could be environment-specific depending on the stage, duration, and severity of drought stress. Therefore, combining different indices provides breeders with the ability to increase the selection efficiency depending on the targeted environment. Thiry et al., (2016) computed MSI based on the scores of five indices (DSI, TOL, MP, GMP, and STI), which resulted in a determination coefficient of 0.98 with GY under heat stress. In the present study, MSI was computed including only the effective indices at Tessaout (MP, DTI, DSI, and MsSTI). The efficiency of MSI is shown in the coefficient of determination with GY at TSRF (0.92). MSI selected efficiently the genotypes with a high yield under both optimal and stressed conditions. Therefore, the use of scores and adapted MSI can be recommended as a flexible tool to use the drought tolerance/susceptibility indices.

The results also showed the potential of crop wild relatives to increase genetic variation for the physiological traits involved in heat and drought tolerance. For instance, the line 142001 (Haurani*2/*T. urartu*) can be a source for cooler CT during the vegetative stage and higher CHL under heat. This line was previously recommended for its earliness at WMD (Aberkane et al., 2021a), which means that it can combine both escaping and avoidance mechanisms to continuous heat stress. Under drought stress, several lines derived from *T. urartu*, *T. aegilopides*, and *T. dicoccoides* were characterized by cooler CT. An improvement in yield under terminal drought stress was also reported with lines derived from crosses with *T. dicoccoides* (Nachit and Elouafi, 2004). By selecting wild parents originating from heat and drought-prone environments, the expected derived lines can lead to drought and heat tolerant germplasm. Therefore, for further selection of wild parental germplasm, the aridity index can be an important factor. Peleg et al., (2005) also reported the potential of *Triticum dicoccoides* collected from hot and/or dry environments to improve drought tolerance in durum wheat. This supports use of wild relatives, mainly from the primary gene pool, for drought and heat tolerance breeding.

4.6. Conclusion

High genetic variation was found for yield and physiological traits in the population derived from interspecific hybridization. This means that harnessing CWR from the primary and secondary gene

pool can widen the genetic base for wheat breeders to cope with the adverse effects due to climate change. It can supply sources of physiological traits involved in continuous heat avoidance mechanisms, such as NDVI and CT. These traits can contribute to yield genetic gains through additive gene action. CWR, especially from the primary gene pool, can also contribute directly to yield improvement under drought stress without affecting the yield potential. The combination of different drought tolerance/susceptibility indices showed the potential to increase the selection efficiency of superior genotypes.

Chapter 5: Contribution of wild relatives to durum wheat yield stability across contrasted environments

Hafid Aberkane[1,2], Ahmed Amri[1], Bouchra Belkadi[2], Abdelkarim Filali-Maltouf[2], Jan Valkoun[3] and Zakaria Kehel[1]

[1]International Center for Agricultural Research in the Dry Areas (ICARDA), Rabat, Morocco

[2]Plant and Microbial Biotechnology, Biodiversity and Environmental Research Center, Faculty of Sciences, Mohammed V Univ. of Rabat, Rabat, Morocco

[3] Former head of Genetic Resources Unit, ICARDA, 15000 Praha, Czech Republic

5.1. Abstract

Durum wheat is mostly grown under Mediterranean type of environments mainly characterized by unpredictable rainfall amount and distribution, heat stress and prevalence of major diseases and pests, all to be exasperated with climate change. Pre-breeding efforts transgressing adaptive genes from wild relatives need to be strengthened to overcome these abiotic and biotic challenges. In this study, we evaluated yield stability of 67 lines issued from interspecific crosses of Cham5 and Haurani with *Triticum dicoccoides, T. agilopoides, T. urartu,* and *Aegilops speltoides* grown under 15 contrasted rainfed and irrigated environments in Morocco, heat prone conditions in Sudan. Stability analysis was assessed using parametric (univariate and multivariate) and non-parametric approaches. The combined analysis of variance showed a highly significant effects of genotypes, environments, and genotype by environment interaction (GEI). The environments varied in yield (1370-6468 kg/ha), heritability (0.08-0.9), and in their contribution to the GEI. Several lines derived from the four wild parents combined between productivity and stability, which makes them suitable for the unpredictable climatic conditions. A significant advantage in yield and stability was observed in Haurani derivatives compared to their recurrent parent. Furthermore, no yield penalty was observed in many of Cham5 derivatives, they had improved yield under unfavourable environments while maintaining the high yield potential from the recurrent parent (e.g. 142026 and 142074). It was found that limited number of backcrosses can produce high yielding/stable germplasm while increasing diversity in breeding pipeline. Comparing different stability approaches showed that some of them can be used interchangeably, others can be complementary to combine broad adaption with higher yield.

5.2. Introduction

Durum wheat (*Triticum turgidum* subsp. *durum* (Desf.)) is an important cereal cultivated worldwide with an annual production of 40 million tons (Beres et al., 2020). Durum wheat importance is related to its grain characteristics which make it suitable to develop various products namely, pasta, couscous, and burghul among others (Sissons, 2008). Most of the area cultivated with durum wheat is in the Mediterranean region which covers 60% of the world production (Lidon et al., 2014).

Durum wheat is generally grown under rainfed conditions of the semi-arid regions where it is exposed to several biotic and abiotic stresses (Able and Sissons, 2014; Beres et al., 2020). For instance, Hessian fly (*Mayetiola destructor*), a major pest for wheat in North America and the temperate Mediterranean drylands, can cause significant yield losses reaching more than 30% in Morocco (Lhaloui et al., 1992; Bassi et al., 2019). Diseases such as leaf rust, stem rust and root rot are important in west Asia and north Africa (Rajaram et al., 1992). Their economic impact was documented (Marasas et al., 2003; Herrera-Foessel et al., 2006) and new and more virulent strains of leaf rust and stripe rust are emerging in Europe especially in France and Spain (Ordoñez and Kolmer, 2007; Vergara-Diaz et al., 2015). In terms of abiotic stresses, drought and high temperatures decreased wheat yield trends worldwide and their frequency is expected to increase under climate change effects (Li et al., 2009; Lobell et al., 2011; Asseng et al., 2015).

These stresses, in addition to different crop management practices, increase the genotype by environment interaction (GEI) and affect yield stability (Turner et al., 2014; Zhang et al., 2019; Padovan, 2020). Change in climatic conditions accounted for 70% of the year to year variations in GEI and crossover interaction GEI for wheat yields between 1985 and 2017 (Xiong et al., 2020). The crossover interaction Implies changes in ranking of genotypes and reduces the selection efficiency for superior and stable genotypes, low stability was in fact recognized as an important factor for the gap between potential and actual yield (De Vita et al., 2010; Cattivelli et al., 2014; Mohammadi and Amri, 2016). Breeding stable genotypes with high yield potential becomes therefore essential for a sustainable production of durum wheat under variable environments (Cattivelli et al., 2008).

Coping with high variations in the environment requires germplasm with high plasticity which can be supplied by crop wild relatives (Mickelbart et al., 2015; Arnold et al., 2019). Durum wheat has

a rich gene pool that was used extensively in breeding for yield, pest and disease resistance as well as end use quality (Hajjar and Hodgkin, 2007; Mondal et al., 2016). *Triticum dicoccoides* was identified as a source of resistance to leaf rust, stripe rust and improved concentration of protein, zinc and iron (Anikster et al., 2005; Marais et al., 2005b; Peleg et al., 2008; Suneja et al., 2019). Resistance to leaf rust, stripe rust, stem rust, powdery mildew and wheat blast was introgressed from several *Aegilops* and wild *Triticum* species from the primary, secondary, and tertiary wheat gene pool (*Triticum monococcum* subsp. *Aegilopoides*, *Triticum urartu*, *Aegilops speltoides*, *Aegilops sharonensis*, *Aegilops kotschyi*, *Aegilops tauschii and Aegilops ventricosa)* (Vikal et al., 2004; Tanguy et al., 2005; Marais et al., 2005a; Hovhannisyan et al., 2011; Rouse et al., 2011; Millet et al., 2014; Cruz et al., 2016). Hessian fly resistance was identified in *Aegilops tauschii, Aegilops geniculata, Aegilops ventricosa, Aegilops cylindrica, Aegilops neglecta* and *Triticum araraticum* (El Bouhssini et al., 1998; Nsarellah et al., 2003). Drought adaptive traits were identified in *Triticum dicoccoides* and *Aegilops tauschii* (Gororo et al., 2001; Suneja et al., 2019) and tolerance to high temperature was be found in *Aegilops geniculata*, *Aegilops speltoides* and *Aegilops longissima* (Pradhan et al., 2012b). The mobilization of these traits into cultivated gene pool through pre-breeding can improve wheat productivity, resilience, and diversity simultaneously (Nachit and Elouafi, 2004; Dreisigacker et al., 2008).

In addition to harnessing diversity, several statistical approaches were suggested to account for the GEI and select stable genotypes. The regression coefficient (Bi) and the squared deviation from regression (S^2di) (Finlay and Wilkinson, 1963; Eberhart and Russell, 1966) were used widely to measure the phenotypic stability. Wricke ecovalence (Wi^2) (Wricke, 1962) and stability variance (σ_i^2) (Shukla, 1972) were suggested to select based on the contribution of each genotype to the GEI. These two approaches are equivalent for ranking of genotypes (Becker and Leon, 1988). Francis and Kannenberg (1978) recommended the coefficient of variation (CV) while the environment variance (EV) was proposed by Roemer (1917) (cited by (Becker and Leon, 1988) to select genotypes with low variance as stable. The genotypic superiority (Pi) (Lin and Binns, 1988) uses the mean squared distance between each genotype and the maximum response in each environment as stability measure. These approaches rely on absolute data and on the assumption of normal distribution and homogeneity of the variance. Non-parametric stability approaches are suggested based on the ranking of genotypes with no assumptions related to data distribution. Four non-parametric indices were recommended by Huehn (1979) and Nassar and Huhn, (1987). S_{i1} is

the mean of absolute rank difference over environment, S_{i2} is the variance of the ranks, S_{i3} is the sum of absolute deviations and S_{i6} is the relative sum of squares of rank for genotype.

The additive main effects and multiplicative interaction (AMMI) (Zobel et al., 1988; Gauch, 1988) is a multivariate model that was used extensively to analyze multi-environment trials with complex GEI structure. Several stability indices were derived from the AMMI model using the interaction principal components (Sneller et al., 1997; Purchase et al., 2000; Zali et al., 2012). Recently, Olivoto et al., (2019) suggested the weighted average of absolute scores (WAAS) as a multivariate analysis using mixed models. The derived superiority index (WAASY) offers the flexibility to balance between the stability and productivity based on the population and the objective of the selection.

This research was conducted to study the contribution of wheat wild relatives to yield stability under different environments characterized by drought, heat, disease pressure and under optimal conditions. Different stability approaches were used to characterize both the germplasm stability and the relationship between the testing environments.

5.3. Materials and Methods

5.3.1. Plant material

The tested germplasm is composed of 67 lines of backcrossing populations derived from interspecific crosses of two durum wheat cultivars (Haurani and Cham5) with four wild wheat progenitors: 29 lines are derived from hybridization with the tetraploid progenitor (T*riticum turgidum subsp. dicoccoides* (Syn *Triticum dicoccoides*) and 47 lines from crosses with the three diploid ancestors *Triticum monococcum* subsp. *aegilopoides* (Syn *Triticum aegilopoides*), *Triticum urartu* and *Aegilops speltoides*. Table 5-1 provides a summary of number of lines derived from each cross with the number of backcrosses and the detailed list with DOIs is given in Annex 1. The two recurrent parents and eight checks including released varieties and ICARDA elite lines were included in the trials and represented 13% of the total nursery.

Table 5-1. Pedigree and number of derivative lines from each cross

Pedigree/Name	Wild parent genome	# of lines
Cham5*2/*T. dicoccoides* IG 118178	A^uA^uBB	6
Cham5*3/*T. dicoccoides* IG 118178	A^uA^uBB	11
Haurani*2/*T. urartu* IG 45489	A^uA^u	4
Cham5*3/*T. urartu* IG 45488	A^uA^u	2
Cham5*3/*T. aegilopoides* IG 118180	A^mA^m	19
Cham5*2/*T. urartu* IG 118184	A^uA^u	2
Cham5*3/*T. aegilopoides* IG 118181	A^mA^m	1
Cham5*4/*Ae. speltoides* IG 47843	SS (BB)	6
Cham5*2/*T. aegilopoides* IG 118180	A^mA^m	3
Cham5*3/*T. dicoccoides* IG 118179	A^uA^uBB	2
*Haurani*2/T. aegilopoides* IG 118185	A^mA^m	2
Haurani*2/*T. urartu* IG 45475	A^uA^u	2
Cham5*3/*T. urartu* IG 118182	A^uA^u	3
Cham5*3/*T. urartu* IG 118184	A^uA^u	1
Cham5*4/*Ae. speltoides* IG 47844	SS (BB)	1
Cham5*2/*T. urartu* IG 118182	A^uA^u	1
Haurani*3/*T. dicoccoides* IG 118178	A^uA^uBB	1
Checks and recurrent parents	-	8
Recurrent parents	-	2

IG, the accession number of the wild parent at ICARDA genebank

5.3.2. Testing environments and experimental design

The trials were conducted in 15 environments representing six locations during different seasons between 2015 and 2018. Five locations were in Morocco representing the Mediterranean hot and temperate type of environments while Wad Medani in Sudan represented the hot and irrigated environment (Table 5-2). At Tessaout and Melk Zhar, two trials were planted in the same season with different water regimes, one under full irrigation (FIR) and the second under rainfed (RFD) or supplemental irrigation (SIR). The purpose was to assess yield losses and effects of late drought by comparing the two treatments/environments. All the other trials were conducted under rainfed conditions except for Marchouch during 2015-2016 season which received a supplementary irrigation during vegetative stage. The trials were randomized in an incomplete block design (alpha-lattice) with two replications and a block size of seven. Each plot consisted of four rows of two meters length, a between row distance of 0.25-0.30m and a sowing density of 300 seeds/m². The recommended agronomic package for each environment was applied. At maturity, the grain

yield (GY) was estimated by harvesting and weighing the two internal rows avoiding the borders and then converted to kg/ha.

Table 5-2. Testing location, seasons, and codes for the testing environments of durum wheat derivatives

Location	Country	Long	Lat	Season	ENV	Treatment
Allal Tazi	MAR	34°31'N	6°14'W	2016-17	AT-17	RFD
				2017-18	AT-18	RFD
Annoceur	MAR	33°41'N	4°51'W	2016-17	AN-17	RFD
				2017-18	AN-18	RFD
Marchouch	MAR	33°36'N	6°42'W	2015-16	MCH-16	SIR
				2016-17	MCH-17	RFD
				2017-18	MCH-18	RFD
Melk Zher	MAR	30°02'N	9°33'W	2015-16	MZIR16	FIR
				2015-16	MZRF16	SIR
Tessaout	MAR	31°49′ N	7°25′ W	2016-17	TSIR-17	FIR
				2016-17	TSRF-17	RFD
				2017-18	TSIR-18	FIR
				2017-18	TSRF-18	RFD
Wad Medani	SDN	14◦24′ N	33◦31′ E	2016-17	WMD-17	FIR
				2017-18	WMD-18	FIR

RFD, Rainfed conditions; SIR; supplementary irrigation; FIR, Full irrigation

5.3.3. Data analysis

5.3.3.1. Analysis of variance and genotype by environment interaction

In order to investigate the genotype by environment interaction (GEI) and estimate the variance components, linear mixed model and Additive Main Effects and Multiplicative Interaction Model (AMMI) (Zobel et al., 1988; Gauch, 1988) were used for the analysis of variance. The mixed model was fitted using *sommer* package (Covarrubias-Pazaran, 2016) in R version 4.0.4 (R Core Team, 2021) with the environment as fixed effects, the genotypes and GEI as random effects. Diagonal structure of variance was used to account for the heterogenous residuals variance between environments and therefore estimated the genetic and residual variance in each environment. Similarly, the effects of replication and block were considered heterogenous and estimated in each environment as random effects. The genotypic effects allowed to compute the best linear unbiased prediction (BLUP) for each genotype. *Metan* package (Olivoto and Lúcio, 2020) was used to perform the AMMI model and the results were used to compute stability

parameters based on the interaction principal components from AMMI. The best linear unbiased estimations (BLUEs) in each environment were computed using *Meta-R* software (Alvarado et al., 2020). The BLUEs were used to run a genotype and genotype by environment interaction model (GGE) (Yan et al., 2000) using *GGEBiplots* package (Dumble, 2017). GGE model was used to assess the representativeness and discrimination of each environment. Meta-R was also used to estimate the genetic correlation (ρ_g) between environments for grain yield following the equation from Cooper and DeLacy, (1994).

$$\rho_{gij} = \frac{\rho_{pij}}{\sqrt{h_i h_j}}$$

Where, ρ_{gij} is the genetic correlation, ρ_{pij} is the phenotypic correlation between the environments *i* and *j*, h_i and h_j are the broad sense heritabilities in environment *i* and *j*, respectively.

5.3.3.2. Analysis of stability

The BLUPs computed from the linear mixed model were the first stability parameter used for the ranking of genotypes. The stability indices derived from the AMMI model were sums of the absolute values of the IPCA scores (Sneller et al., 1997) and AMMI stability value (ASV) (Purchase et al., 2000). SIPC and ASV were computed according to the equations (1) and (2), respectively.

$$(1)\ \text{SIPC}=\sum_{k=1}^{P} |\lambda_k^{0.5} \alpha_{ik}|$$

Where P is the number of IPCs retained via the F-test, λk is the eigenvalue of the kth IPC and αik is the genotype principal component score.

$$(2)\ ASV = \sqrt{[\frac{SSIPC1}{SSIPC2}(IPC1)]^2 + (IPC2)^2}$$

Where SSIPC1 and SSIPC2 are the sum of squares of the first and second IPC, respectively. IPC1 and IPC2 are the scores of the genotypes in the first and second IPC, respectively. The weighted average of absolute scores (WAAS) (Olivoto et al., 2019) was estimated following the equation 3. A superiority index (WAASY) is derived from rescaling the yield and WAAS to balance between

productivity and stability (Olivoto et al., 2019), in the present study yield and stability were given the same weight (50/50) (Equation 4).

$$(3)\ WAAS = \frac{\sum_{k=1}^{p} |\mathrm{IPCA}_{ik} \times EP_k|}{\sum_{k=1}^{p} EP_k}$$

Where, PCA_{ik} is the score of the ith genotype in the kth IPCA, and EP_k is the amount of the variance explained by the *kth* IPCA.

$$(4)\ WAASY = \frac{(rG_i \times \theta_Y) + (rW_i \times \theta_S)}{\theta_Y + \theta_S}$$

where rG_i and rW_i are the rescaled values for GY and WAAS, Θ_Y and Θ_S are the weights for grain yield and stability assumed to be 50 for each in this study.

The rest of stability parameters were computed using the BLUEs from each environment. *Agrostab* package (Cheshkova, 2019) was used for the estimation of the regression coefficient (Bi), squared deviation from the regression (S^2di) (Eberhart and Russell, 1966), Environment variance (EV) (Roemer, 1917) and the coefficient of variation (Francis and Kannenberg, 1978). *Metan* package was used to compute, Shukla stability variance (σ_i^2) (Shukla, 1972), Geometric adaptability index (GAI) (Mohammadi and Amri, 2008) and the Superiority index (Pi) (Lin and Binns, 1988).

Four non-parametric stability indices (Huehn, 1979; Nassar and Huhn, 1987) were also estimated using *Metan*, S_{i1} is the mean of absolute rank difference over environment, S_{i2} is the variance of the ranks, S_{i3} is the sum of absolute deviations and S_{i6} is the relative sum of squares of rank for genotype. The Pearson correlation coefficients between the stability indices was computed using *Hmisc* package (Harrell and Dupont, 2020) and plotted using *corrplot* (Wei and Simko, 2017).

5.4. Results

5.4.1. Analysis of variance

The analysis of variance from the linear mixed model and AMMI showed a highly significant effect of the environment, genotypes, and their interaction (probability <0.001) (Tables 5-3 and 5-4). The highest proportion of variance was explained by the environment (66.93%) followed by the GEI (18.74%) while the genotypes accounted for 8.39% of the variance (Table 5-4). The diagonal structure of the error in the mixed model validated the assumption of residual heterogeneity between the environments (Table 5-3). Therefore, accounting for the heterogeneity

of error variance would increase the precision of genotypic variance estimation and thus the BLUPs across environments and their precision. The first seven interaction principal components (IPCs) from AMMI model were significant and explained 80.6% of the GEI. The variance explained by the first two IPCs was relatively low as they accounted only for 38.8% of the GEI. The first IPC captured 22.6% of the variance while the second (IPC2) was responsible for 16.2%, which highlights the complexity of the interaction patterns.

Table 5-3. Combined analysis of variance from the linear mixed model of durum wheat lines derived from interspecific crosses and the checks grown in contrasted environments in Morocco and Sudan.

Source of variation	DF	Variance component
ENV Mean Sq (f)	14	536126241***
Genotypic variance (r)	-	221131***
GE interaction variance (r)	-	213091***
AN-17 residuals (r)	-	264403
AN-18 residuals (r)	-	314508
AT-17 residuals (r)	-	466464
AT-18 residuals (r)	-	722924
MCH-16 residuals (r)	-	1268491
MCH-17 residuals (r)	-	332655
MCH-18 residuals (r)	-	2107375
MZIR-16 residuals (r)	-	2075582
MZRF-16 residuals (r)	-	795924
TSIR-17 residuals (r)	-	1469300
TSIR-18 residuals (r)	-	1269044
TSRF-17 residuals (r)	-	404398
TSRF-18 residuals (r)	-	566288
WMD-17 residuals (r)	-	297060
WMD-18 residuals (r)	-	203483

f, Fixed effects ; r, Random effects, ***, significant at $p<0.001$

AN, Annoceur; AT, Allal Tazi; MCH, Marchouch; MZIR, Melk Zher Irrigated; MZRF, Melk Zher Rainfed; TSIR, Tessaout Irrigated; TSRF, Tessaout Rainfed; WMD, Wad Medani; the numbers after the dash 16, 17 and 18 represent the cropping seasons 2015-2016, 2016-2017 and 2017-2018, respectively.

Table 5-4. Analysis of variance and significant interaction components from the AMMI model of durum wheat lines derived from interspecific crosses and the checks grown in contrasted environments in Morocco and Sudan

Source	DF	Mean Sq	% TSS	GEI Proportion (%)	Accumulated
ENV	14	383602598***	66.93	-	-
REP(ENV)	15	10556057***	1.973	-	-
BLOCK(REP*ENV)	300	1055308***	3.94	-	-
GEN	76	8857688***	8.39	-	-
GEN: ENV	1061	1417790***	18.74	-	-
Residuals	808	716543	-		
PC1	89	3871018	-	22.6	22.6
PC2	87	2840469	-	16.2	38.8
PC3	85	2148503	-	12	50.7
PC4	83	1854171	-	10.1	60.8
PC5	81	1343685	-	7.1	68
PC6	79	1361599	-	7	75
PC7	77	1111644	-	5.6	80.6

ENV, Environment; REP, Replication, GEN, Genotypes

***, significant at $p<0.001$

5.4.2. Characterization of the testing environments

5.4.2.1. Climatic data

The testing locations in Morocco represent typical Mediterranean semi-arid and temperate environments while Wad Medani in Sudan represents the dry hot irrigated environments. The maximum temperature at Wad Medani was consistently above 30°C and no rainfall was registered during both cropping seasons. In Morocco, the rainfall distribution seems to be as important as the total amount of rainfall to determine the type of environments. For instance, Marchouch and Annoceur locations received almost the double amount of rainfall (514 and 611 mm, respectively) in 2018 compared the 2017 (Table 5-5). In terms of rainfall distribution, MCH-17 was exposed to a severe drought during vegetative stage while drought was sharper during reproductive stage at MCH-17 and TSRF-17. Melk Zher was characterized by a dry season as the total rainfall registered was 85.5 mm, drip irrigation was applied to differentiate between fully irrigated and drought stressed environments. The trials in Melk Zher were irrigated where MZIR-16 and MZRF-16 received, between irrigation and rainfall, a total of 411mm and 127 mm, respectively. In terms of temperature, Annoceur and Marchouch are characterized by a cooler winter in comparison to other

locations, while the higher temperatures are observed during the reproductive stages in all the locations.

Table 5-5. Precipitation (mm), maximum, minimum, and average temperature in the 15 testing environments

ENV	Treatment	Max T	Min T	Mean T	Prec (mm)
AT-17	RFD	-	-	-	592
AT-18	RFD	-	-	-	-
AN-17	RFD	23.87	7.14	15.05	306
AN-18	RFD	26.66	1	12.69	611
MCH-16	SIR	25.24	10	14	204.8
MCH-17	RFD	32.2	3.63	15.96	275.9
MCH-18	RFD	26.54	2.68	14.38	514.6
MZIR-16	FIR	24.63	10.86	17.75	85.8
MZRF-16	SIR				
TSIR-17	FIR	25.76	10.19	17.98	207
TSRF-17	RFD				
TSIR-18	FIR	26.17	10.31	18.24	294
TSRF-18	RFD				
WMD-17	FIR	37	18	27	0
WMD-18	FIR	37.3	18.6	27.9	0

Max T, Average maximum temperature (°C) ; Min T, Average minimum temperature (°C) ; Mean T, Average temperature (°C) ; Prec (mm), precipitation in millimeters (mm); RFD, Rainfed conditions; SIR, Supplemental irrigation; FIR, Full irrigation.
AN, Annoceur; AT, Allal Tazi; MCH, Marchouch; MZIR, Melk Zher Irrigated; MZRF, Melk Zher Rainfed; TSIR, Tessaout Irrigated; TSRF, Tessaout Rainfed; WMD, Wad Medani; the numbers after the dash 16, 17 and 18 represent the cropping seasons 2015-2016, 2016-2017 and 2017-2018, respectively.

5.4.2.2. Environment characterization for yield

The average yield over all environments was 3387 kg/ha, six environments had yield above this average while nine were unfavourable and had lower yields (Figure 5-1). The highest mean yield was registered at MCH-18 (6468 kg/ha) followed by TSIR-17 (5955 kg/ha) and TSIR-18 (5251 kg/ha). The lowest yield was under heat stress at WMD-17 (1370 kg/ha), followed yields at AT-17 (1751 kg/ha), AN-17 (2149kg/ha), and WMD-18 (2183kg/ha). The yield at MCH-18 reflected the favourable season in comparison to MCH-17 where the average yield was 2533 kg. The supplemental irrigation at MCH-16 resulted in favourable conditions and yield of 3993kg/ha. The contrasts between fully irrigated and rainfed trials at Tessaout and Melk Zher were high as shown by the yield reduction between irrigated and rainfed conditions (Figure 5-1). On average the yield

at MZIR-16 was 73% higher than MZRF-16 while TSIR-17 had an average yield 164% higher than TSRF-17. The broad sense heritability ranged between 0.08 at AN-17 and 0.90 at WMD-18 and it was moderate in the rest of environments (Figure 5-1). Significant genotypic effect was observed in 12 environments and only three had non-significant effect of the genotypes (AN-17, AN-18, and WMD-17).

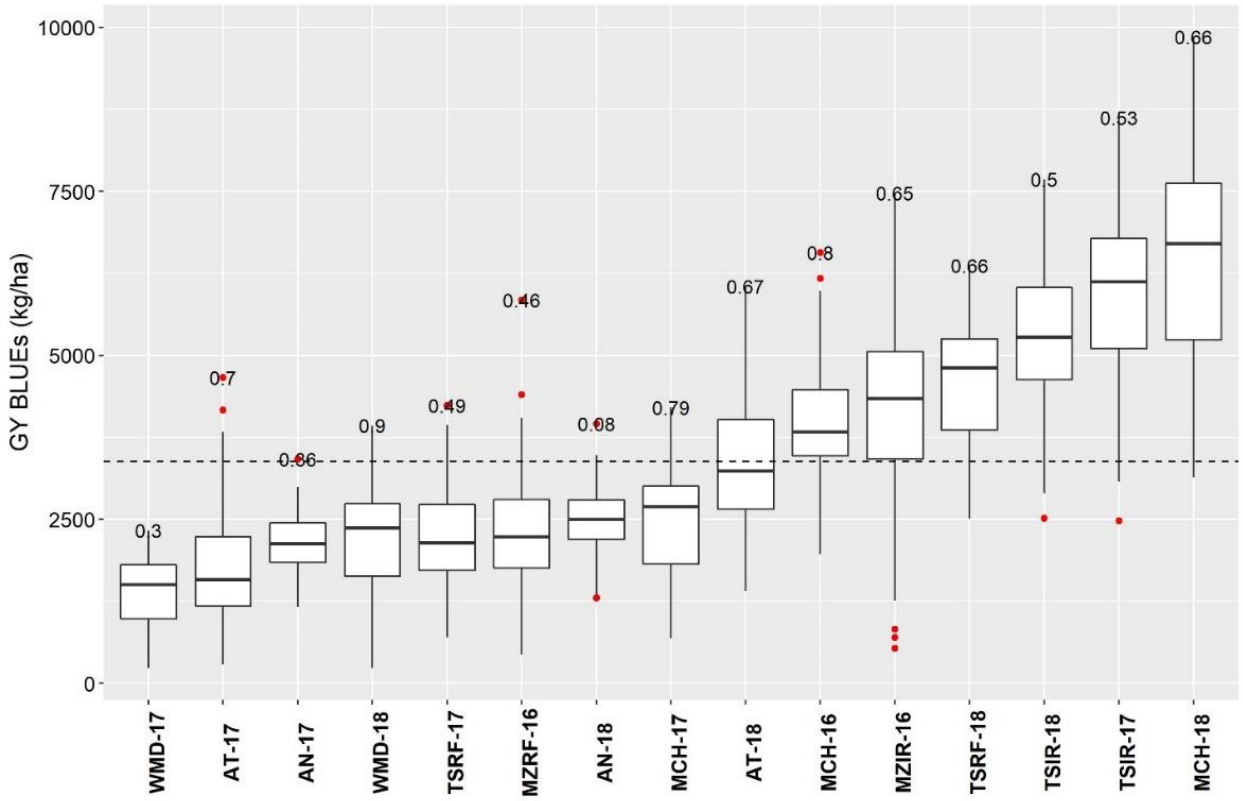

Fig 5-1. Boxplot of best linear unbiased estimations (BLUEs) and heritability for grain yield (GY) of durum wheat genotypes in the 15 environments included in the stability analysis.

The dashed horizontal line represents the grand mean across all environments. The number above each boxplot represent the heritability in that environment.

5.4.2.3. Association between the environments

The genetic correlation, providing a view of the interaction between different pairs of environments, ranged between -0.15 (MZRF-16 and TSIR-18) and 0.97 (TSIR-17 and MCH-18) (Figure 5-2). MCH-18 was highly correlated with both favourable (TSIR-17, MZIR-16) and unfavourable environments (TSRF-17 and AN-17) indicating lower GEI of MCH-18 with many other environments (Figure 5-2). It was followed by TSIR-17 and TSRF-18 in terms of correlations

with other environments. AT-17 and WMD-17 had the lowest association with the rest of environments (Figure 5-2), the correlation between AT-17 and TSRF-17 was null indicating a full interaction. WMD-17 had high interaction with most of the environments, it was correlated only with AT-18, WMD-18, and TSRF-18. WMD-18 was correlated only to TSRF-17 (r^2=0.65) and TSRF-18 (r^2=0.56). AN-18 was dropped from the analysis due to its low heritability. The genetic correlation results were corroborated by the GGE biplot for the association between environments. GGE biplot confirmed the high discrimination ability of MCH-18, TSIR-18, and MZIR-16. MCH-18 had the advantage of efficiently representing most of the other environments compared to TSIR-18 and MZIR-16. Low yielding environments such as WMD-17, AN-17 and AN-18 showed low discrimination ability for the genotypes (Figure 5-3).

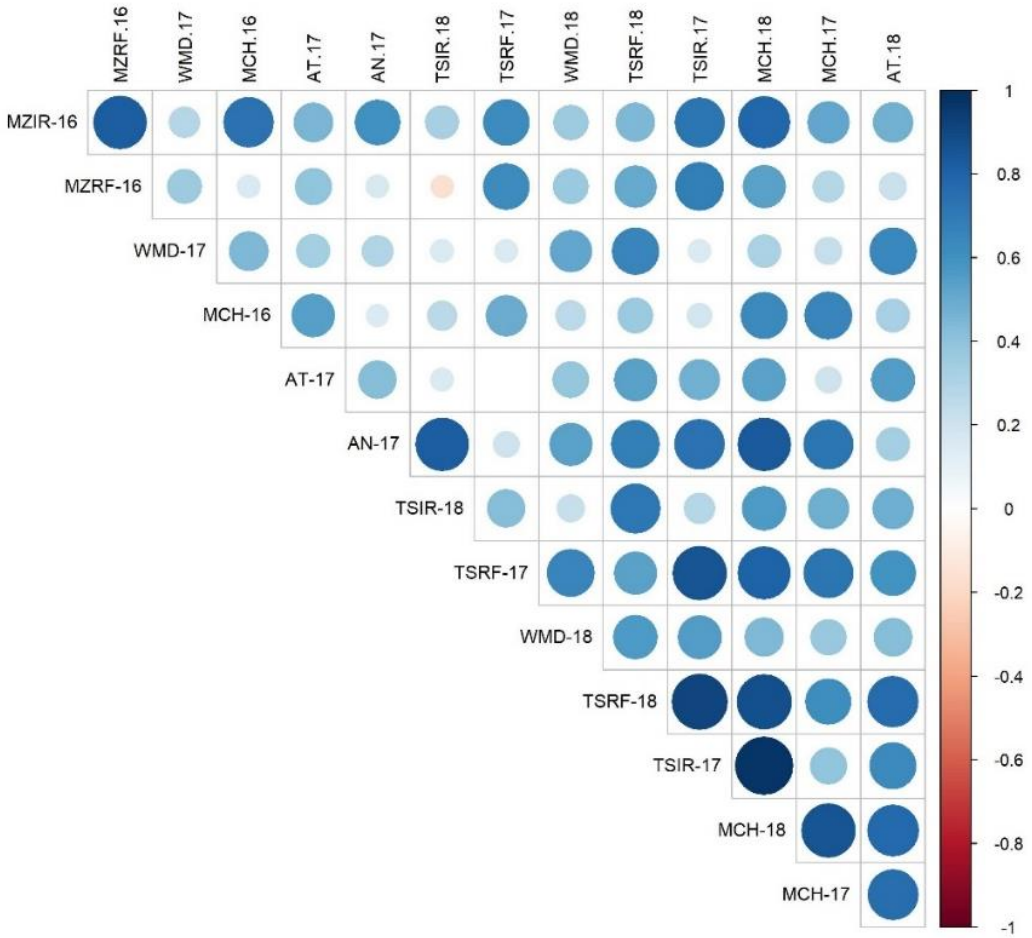

Figure 5-2. Estimated pairwise genetic correlation between 14 environments of grain yield of durum what tested genotypes. The color and size of the circles represent the direction and strength of the correlation between environments

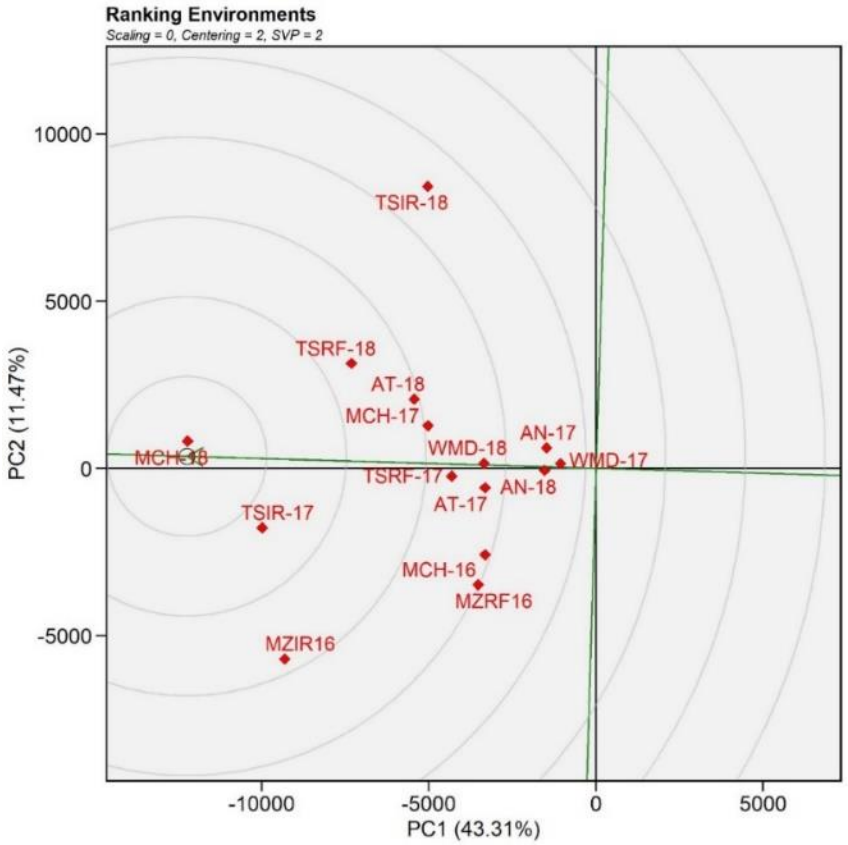

Figure 5-3. Genotype and genotype by environment (GGE) biplot of the representativeness and discrimination ability of the 15 testing environments for durum wheat tested genotypes.

5.4.3. Yield stability assessment

5.4.3.1. Parametric stability indices

More than 50% of the tested lines had BLUPs for yield above average, the check Marzak had the highest yield (2854 kg/ha) while the line 142003 had the lowest yield (1274 kg/ha). Four other checks (129080, Icarachaz, Louiza and Faraj), the recurrent parent Cham5 and four of its derivatives were also among the highest yielding lines (Table 5-6). The recurrent parent Haurani had the second lowest BLUP (1290 kg/ha), the highest yielding of its derivatives was 142001 (Haurani*2/*T. urartu*) with a yield 58% higher than its recurrent parent. The range of BLUPs suggests that the tested germplasm have high variation for yield. Therefore, the BLUPs should be taken into consideration for the interpretation of the other stability parameters in order to balance between productivity and stability.

According to the joint regression, the ideal genotype would have a regression coefficient (Bi~1) combined with low squared deviation (S^2di) and high BLUPs. However, these three conditions could be met only for few lines having average yield performance (Figure 5-4). Some lines such as Icarachaz, 129080, and 142074 (Cham5*3/*T. dicoccoides*) combined higher yields with high Bi. In addition, Icarachaz was regarded as unstable according to S^2di as it had high variance (Table 5-6). Therefore, these lines can be considered as specifically adapted to favourable environments. Plotting Bi versus BLUPs identified an interesting group of lines combining high productivity and high stability (Figure 5-4). This group included three checks (Marzak, Louiza and Faraj), the recurrent parent Cham5 and three of its derivatives. Marzak combined the highest yield (2952kg/ha) with a regression coefficient of 0.96 which makes it the most desirable genotype. The two derivatives 142009 and 142061 had yield of 2699 and 2597 kg/ha paired with regression coefficients of 1.09 and 1.05, respectively. They are derived from the same three backcrosses of Cham5 with *T. aegilopoides*. The derivative line 142005 (Cham5*4/*Ae. speltoides*) combined a yield of 2677 kg/ha with Bi of 1.13. The landrace Haurani and its derivatives showed specific adaptation to unfavourable environments, they had low yields paired with low regression coefficient. The line 141972 (Haurani*2/*T. urartu*) had the lowest Bi (0.41) and was ranked 72 according to the BLUPs. Two Haurani derivative lines showed a significant yield improvement compared to their recurrent parent. One of these two derivatives (142001) was ranked the most stable according to S^2di. Since lower S^2di is associated with more predictable performance, adding the yield suggested that the lines 141995, 141966, 142071 and 142070 are desirable (Table 5-6, Figure 5-4). S^2di did not succeed to select genotypes combining high yields with broad adaptation. For instance, the lines 142003 and 142062 were ranked high according to S^2di, but their BLUPs and Bi suggested they were poorly adapted to all environments.

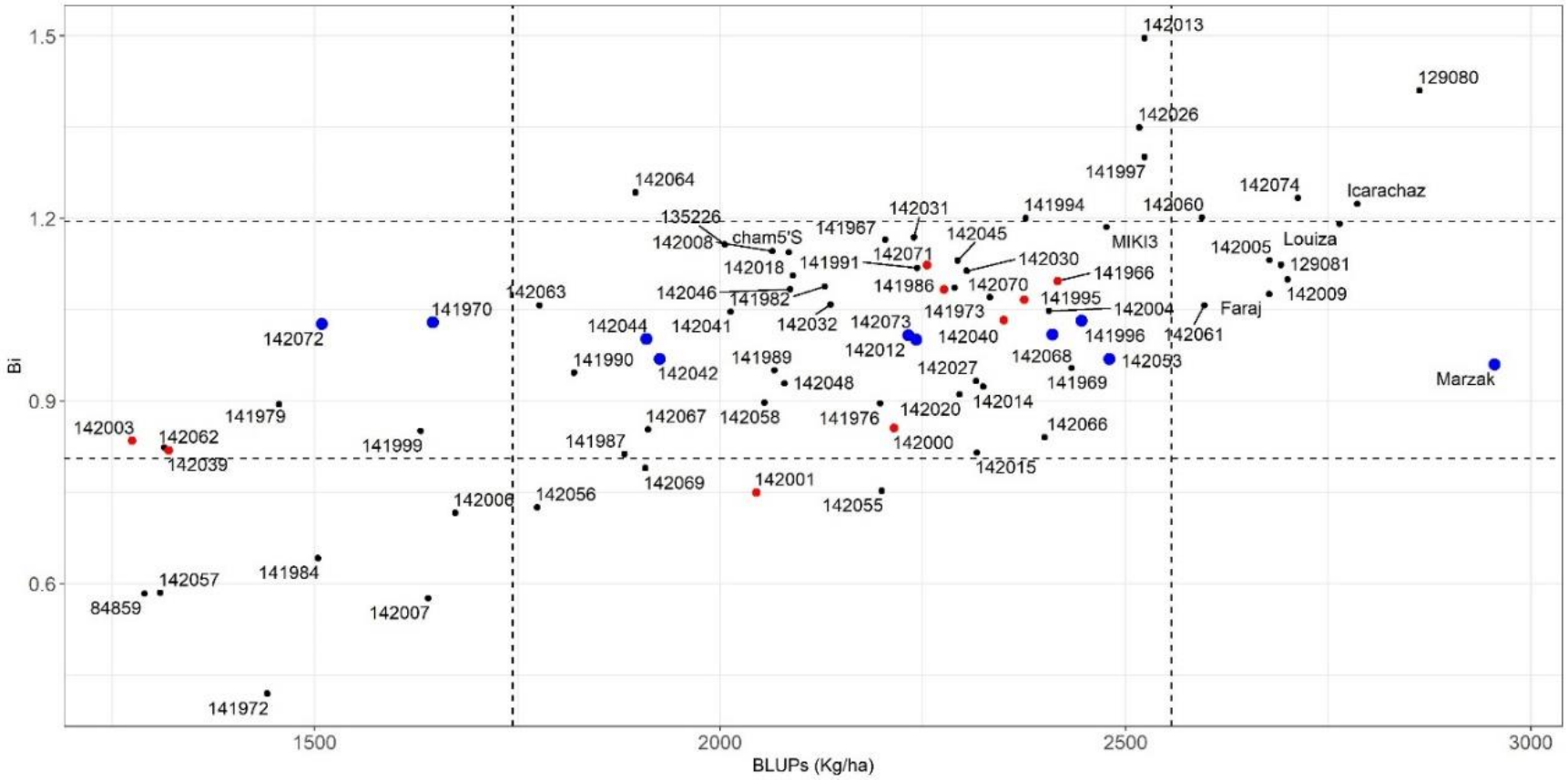

Figure 5-4. Plot of Best linear unbiased predictions (BLUPs) for grain yield plotted against the regression coefficient (Bi). Vertical and horizontal lines represent the mean± 1 SD of BLUPs and Bi, respectively. Blue color represents the first ranked lines according to Bi, red color represents the first ranked lines according to the squared deviation from the regression (S^2di)

The CV showed high efficiency to be used for negative selection to discard the low yielding unstable genotypes (Figure 5-5). Some lines such as 141979 and 142062 and 142039 were among the lowest yielding and had high CV (67%, 65% and 60%, respectively), which confirmed their poor adaptation to all environments. Marzak was ranked fifth with a CV of 42% while the first ranked line 142015 (Cham5*2/*T. urartu*) combined a CV of 38% with a BLUP of 2316 kg/ha. The two lines 142001 and 141792 had yields below average coupled with respective CVs of 40% and 41%. These two lines, derived from the same cross of Haurani and *T. urartu* with two backcrosses, were also selected as stable using EV. However, EV showed more affinity to select for the biological concept of stability than CV. Eight of best ten lines selected using EV had yields below average and only two were above average (142015 and 142055). High yielding lines like Icarachaz (3rd BLUP) and 129080 (2nd BLUP) were considered as instable, they were ranked 70 and 72 for EV, respectively (Table 5-6).

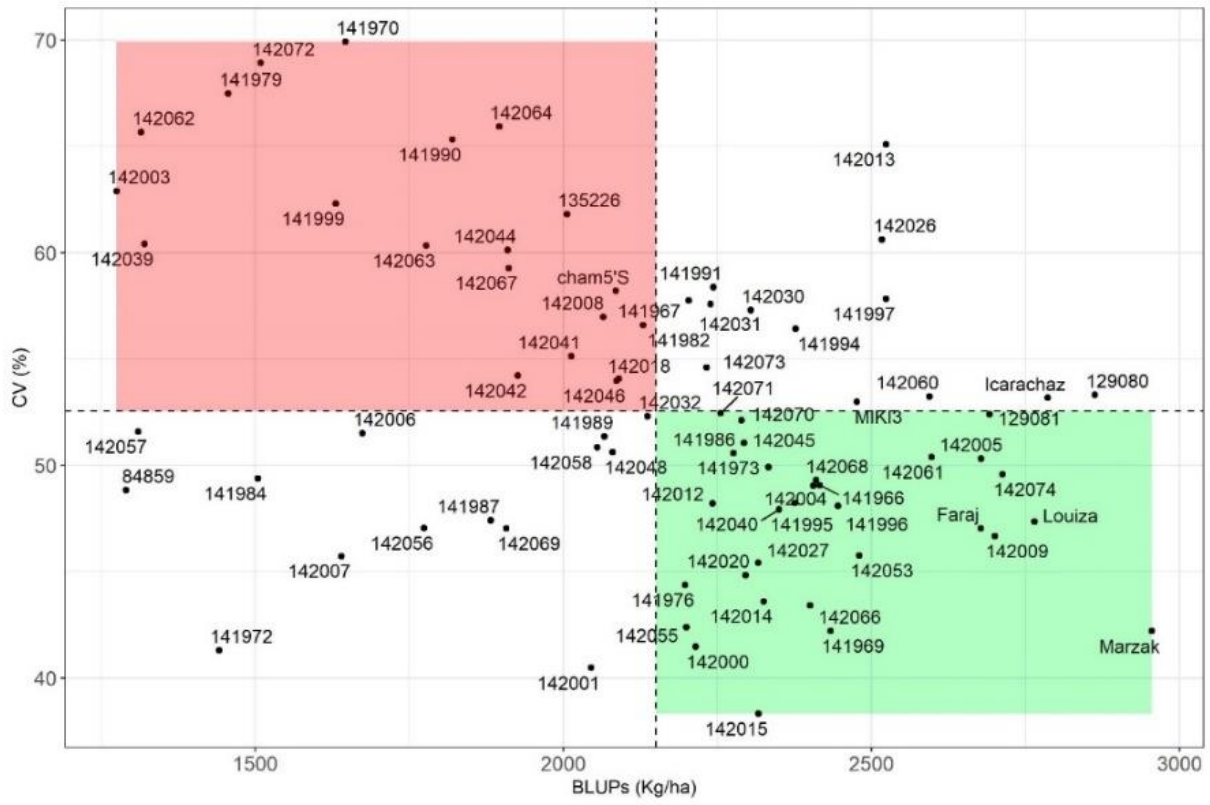

Figure 5-5. Plot of Best linear unbiased predictions (BLUPs) for grain yield plotted against Francis and kannenberg (1978) coefficient of variation (CV). Red area highlights the undesirable genotypes, green area highlights the stable and desirable genotypes. Vertical and horizontal dashed lines represent the mean of BLUPs and CV, respectively.

The selection intensity of Shukla stability variance (σ_i^2) was centred around the genotypes having an average yield performance coupled with low variance. The accession 141995 (Cham5*4/*Ae. speltoides*) was ranked first, followed by the lines 141966 and 142000 which are derived from Cham5 crossed to *T. dicoccoides* with two and three backcrosses, respectively. Shukla variance attributed lower stability to the genotypes with high and low yields such as Icarachaz and 141972 (Table 5-6).

The superiority index (Pi) and the geometric adaptation index (GAI) selected similar genotypes for stability. Nine genotypes were included in the best ten lines using both GAI and Pi, among which five checks, the recurrent parent Cham5 and four of its derivatives. The stable derivatives were issued from crosses with *T. aegilopoides* (142009 and 142060), *T. dicoccoides* (142074) and *Aegilops speltoides* (142005). Pi and GAI tended to select genotypes with high yield potential, as most of the low yielding genotypes were regarded as unstable (Table 5-6).

By giving the same weight to productivity and stability, the superiority index from weighed average of absolute scores (WAASY) balanced between productivity and general adaptation for the ranking of genotypes (Table 5-6). The lines 141986 (Cham5*3/*T. dicoccoides*) and 142045 (Cham5*3/*T. urartu*) were the most stable followed by Louiza and the line 141966. WAASY included also the two highest yielding checks Marzak and 129080 within the most stable genotypes. Interestingly, derivatives from crosses/backcrosses of Cham5 with the four wild species (*Ae. speltoides, T. urartu, T. aegilopoides and T. dicoccoides*) had superior stability/productivity compared to the recurrent parent. It was also noticeable that the same crosses resulted in genotypes with contrasted performance for yield and stability, this was the case for the lines 141984 and 142074 both derived from Cham5*3/*T. dicoccoides* (Table 5-6).

Table 5-6. Ranking of the best ten stable and the least stable genotypes of durum wheat genotypes using parametric stability indices.

					Desirable					
Rank	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
Pi	129080	129081	142005	Marzak	MIKI3	Faraj	Icarachaz	142060	142074	142009
EV	141972	84859	141984	142007	142057	142001	142056	142015	142055	142039
GAI	Marzak	129080	129081	142005	Faraj	Louiza	Icarachaz	142009	142074	142060
σ_i^2	141995	141966	142000	141986	142071	142048	142027	142039	142045	142040
BLUPs	Marzak	129080	Icarachaz	Louiza	142074	142009	129081	142005	Faraj	142061
Bi	142012	142044	142073	142068	142072	141970	142042	Marzak	142053	141996
S^2di	142001	142000	141995	141966	142071	142039	142003	141986	142040	142069
CV	142015	142001	141972	142000	Marzak	141969	142055	142066	142014	141976
WAASY	141986	142045	Louiza	141966	142009	142027	141995	Marzak	142040	129080
ASV	142045	142063	142032	142040	141986	142046	142027	142012	141989	142053
SIPC	142008	142071	142001	142068	142015	141995	141966	142032	141986	142040
					Undesirable					
Rank	**68**	**69**	**70**	**71**	**72**	**73**	**74**	**75**	**76**	**77**
Pi	142067	142007	142072	142003	142062	142039	142057	141984	84859	141972
EV	142005	141994	142064	142060	129081	Icarachaz	141997	129080	142026	142013
GAI	141972	142057	142039	142072	142062	142003	84859	141999	141970	141979
σ_i^2	142005	142061	141990	142007	142026	129081	142067	141972	Icarachaz	142013
BLUPs	141999	142072	141984	141979	141972	142039	142062	142057	84859	142003
Bi	142056	141997	141984	142013	142007	142001	129080	142057	84859	141972
S^2di	142064	142026	142044	142073	141999	Icarachaz	141990	142061	129081	142067
CV	135226	141999	142003	142013	141990	142062	142064	141979	142072	141970
WAASY	141970	141984	142062	141999	141979	142057	84859	142067	142007	141972
ASV	129080	142060	142056	142013	142005	141984	142007	129081	141972	142067
SIPC	129081	142026	Marzak	142064	141991	142007	142013	142067	142061	Icarachaz

Pi, Superiority index; EV, Environment variance; GAI, Geometric adaptability index; σ_i^2, Shukla variance; BLUPs, Best linear unbiased predictions; Bi, Regression coefficients; S^2di, Squared deviation from the regression; CV, coefficient of variation; WAASY, superioriy index from the weighed average of absolute scores; ASV, AMMI stability value; SIPC, sums of the absolute values of the IPCA scores.

5.4.3.2. Non-parametric stability indices

Despite the differences in the ranking of genotypes between the four non-parametric stability parameters, there was convergence for some lines identified as stable by all of them. S_{i1}, S_{i2}, S_{i3} and S_{i6} ranked the line 142053 (Cham5*2/*T. dicoccoides*) among the most stable, and the lines 141995 and 141966 were selected based on three of these parameters (S_{i2}, S_{i3} and S_{i6}) (Table 5-7). Si3 and Si6 selected similar lines for stability while Si6 had more affinity for the selection of high yielding genotypes (129080, 142053, Marzak). The lines selected by S_{i1} and S_{i2} could have low and high yields, this resulted in lower ability to differentiate superior from poorly adapted genotypes based on these indices (Table 5-7).

5.4.3.3. AMMI derived stability

The two stability parameters derived from the AMMI model privileged the average performance lines with low contribution to GEI (Figure 5-6). The most stable lines with low SIPC were 142008 (Cham5*3/*T. dicoccoides*), 142071 and 142001 both derived from *T. urartu* crossed with Cham5 and Haurani. The lines 142045 (Cham5*3/*T. urartu*), 142063 (Cham5*3/*T. dicoccoides*) and 142032 (Cham5*3/*T. aegilopoides*) had the lowest contribution to GEI according to ASV and therefore were the most stable. The inclusion of BLUPs with SIPC and ASV resulted in the identification of desirable lines with high yield potential (Figure 5-6). The checks Louiza and the derivative lines 142074, 142009, 142060 can be recommended for combining stability with high productivity. ASV and SIPC showed some difference for the highest yielding lines, Marzak and 129080 were ranked differently by the two parameters.

Table 5-7. Ranking of the best ten stable and the least ten stable durum wheat genotypes identified using four non-parametric stability indices.

					Desirable					
Rank	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
S_{i1}	141984	142044	142053	cham5'S	142056	142067	142071	141976	142055	141969
S_{i2}	141966	141995	142000	142071	141986	141996	142048	142069	142053	142018
S_{i3}	141995	142009	129080	Marzak	142039	Faraj	141996	142053	142060	142005
S_{i6}	129080	Marzak	142053	142009	141995	142060	Faraj	142005	141996	141966
					Undesirable					
Rank	**68**	**69**	**70**	**71**	**72**	**73**	**74**	**75**	**76**	**77**
S_{i1}	142040	Icarachaz	Marzak	142008	142045	142063	142068	141972	141990	142032
S_{i2}	142007	142066	129081	141984	141990	142026	Icarachaz	141972	142067	142013
S_{i3}	142063	142006	141984	142064	142057	142067	142062	142072	142007	141972
S_{i6}	142003	141990	84859	142067	142057	142072	142062	142007	141972	141984

$S_{i1,}$ Mean of absolute rank difference over environment; S_{i2}, Variance of the ranks; S_{i3}, Sum of absolute deviations; S_{i6}, Relative sum of squares of rank for genotype.

Figure 5-6. Biplot of the best linear unbiased predictions (BLUPs) for grain yield versus the AMMI stability value (ASV) stability (A) and sum of the absolute value of the IPC scores (SIPC) (B) of tested durum genotpes. Vertical dashed line represents the average of BLUPs while the horizontal dashed lines represents the average of ASV (A) and SIPC (B).

5.4.3.4. Association of the stability indices

The correlation between stability parameters ranged from r^2= -0.95 (BLUPs and Pi) and r^2=0.94 (BLUPs and GAI; EV and Bi) and formed two major groups of parameters. The first groups included the variance parameters (S^2di and σi^2), the two AMMI derived stability indices in addition to the non-parametric index S_{i2} (Figure 5-7). ASV showed moderate correlation with the other parameters of this cluster, it ranged from 0.46 with S_{i2} and 0.76 with σi^2. Having the same interpretation, the parameters in this group would select similar lines for stability. The second group was formed by BLUPs, WAASY, GAI, Bi and EV, all these indices were strongly correlated with the BLUPs. However, considering the interpretation of different parameters, the lines selected by EV will have low yields. Strong positive correlation was found between Pi, S_{i3} and S_{i6}. These parameters were negatively associated with the second cluster and showed low to moderate correlation with the first group of parameters (Figure 5-7). WAASY was significantly correlated with all the other parameters except with S_{i1} which itself did not correlate with any other parameter.

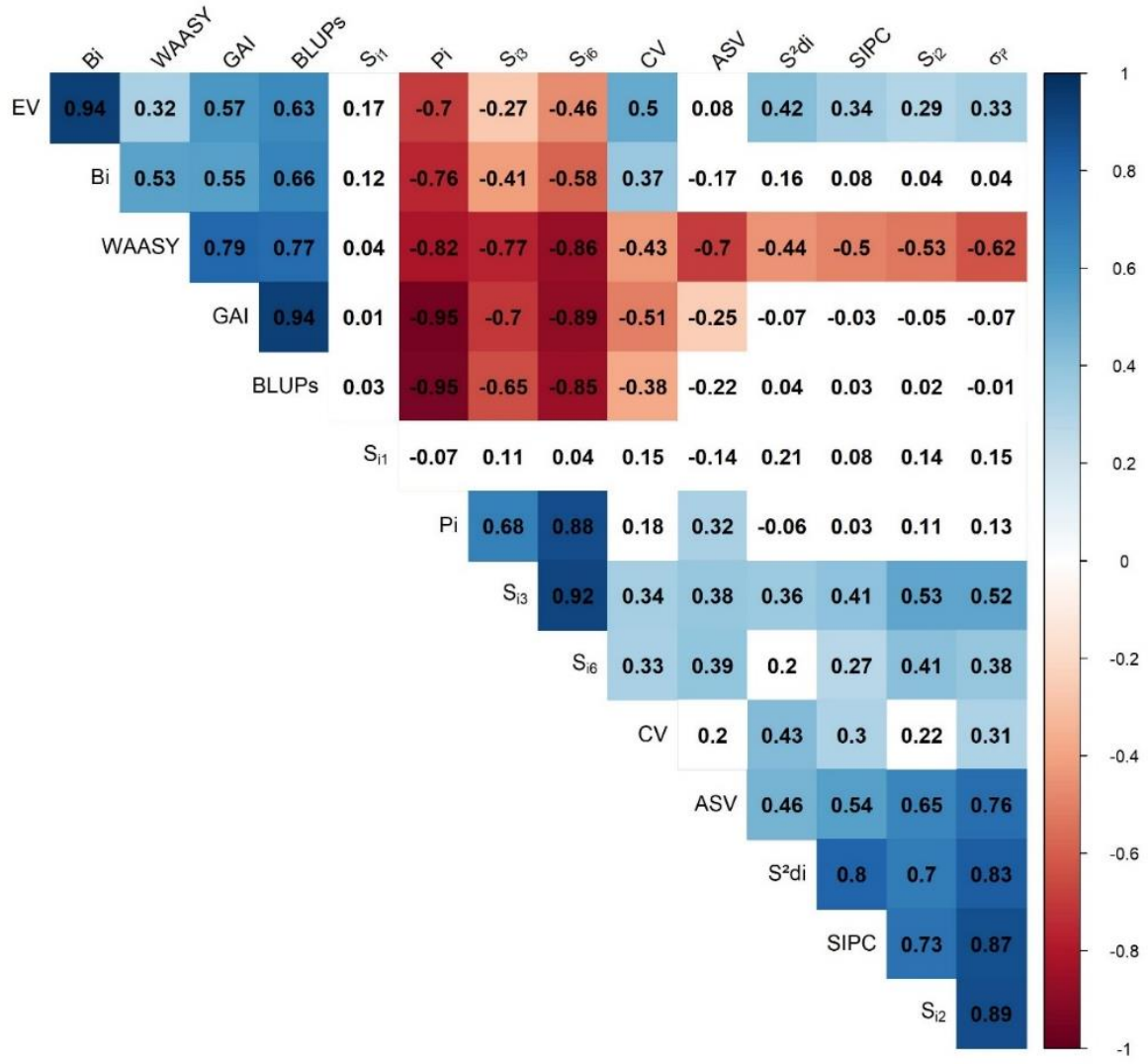

Figure 5-7. Pearson coefficient correlation between parametric and non-parametric stability parameters for 77 durum wheat lines across 15 environments.

Pi, Superiority index; EV, Environment variance; GAI, Geometric adaptability index; σ_i^2, Shukla variance; BLUPs, Best linear unbiased predictions; Bi, Regression coefficients; S^2di, Squared deviation from the regression; CV, coefficient of variation; WAASY, superiority index from the weighted average of absolute scores; ASV, AMMI stability value; SIPC, sums of the absolute values of the IPCA scores, $S_{i1,}$ Mean of absolute rank difference over environment; S_{i2}, Variance of the ranks; S_{i3}, Sum of absolute deviations; S_{i6}, Relative sum of squares of rank for genotype.

5.5. Discussion

5.5.1. Dissection of the genotype by environment interaction

The analysis of variance showed the complexity of the GEI and the crossover interaction, meaning that genotypes responded differently to the changes in environment. High GEI is common in multi-environment trials (Ceccarelli and Erskine, 1994; Mohammadi and Amri, 2008, 2016; Oliveira et al., 2020) which reduces the selection accuracy and genetic gains (Xiong et al., 2020). The dissection of the GEI and proper characterization of the environments and germplasm is therefore essential to improve the genetic gains (de Leon et al., 2016). In this study, the genetic correlation allowed to understand the relation between pairs of environments and their interaction. The low contribution of Marchouch to the GEI showed its suitability for efficient selection of superior genotypes for other environments. Despite the climatic differences between the years, the same superior genotypes can be selected for the three seasons and also for other locations. The crossover interaction due to year effects was more pronounced in the other locations, these effects were mainly associated with the total and distribution of rainfall and temperature for rainfed trials. These findings confirm previously reported effects of weather conditions on the GEI in durum wheat in the Mediterranean basin (Lidon et al., 2014; Ferrise et al., 2015; Chairi et al., 2020). Annoceur was characterized by low heritability during both seasons, and it was among the locations where low genetic gain for durum wheat was achieved (Bassi and Nachit, 2019a). The testing environments exposed durum wheat to favourable conditions, drought, and heat stresses in addition to the disease pressure, mainly leaf rust, at Allal Tazi and tan spot at Annoceur. In addition, the contrasted environments at Tessaout and Melk Zher showed their effectiveness to select for drought tolerance (Aberkane et al., 2021a). The genetic correlation showed that some genotypes can be selected simultaneously for drought and heat tolerance. This approach of using different environments was reported to be useful to select simultaneously for productivity and tolerance to major biotic and abiotic stresses (Nachit and Elouafi, 2004).

5.5.2. Considerations for the use of wheat wild relatives

Much of the progress in durum wheat breeding and genetic gains were achieved at the cost of reduction in genetic diversity (Bassi and Nachit, 2019b). At the same time, maintaining the level of genetic gains requires a diverse gene pool for the breeders to select for the adaptive traits (Hao et al., 2020). In this view, the use of CWR is strategic, it allows to increase simultaneously several traits while recovering the lost diversity (Warburton et al., 2006). In

this context, the present study investigated the potential contribution of wild relatives to yield stability in durum wheat. The choice of wild parents from the primary gene pool was of high importance as several barriers are associated with the use of species from the secondary and tertiary gene pool (Kameswara Rao et al., 2003; Kishii, 2019). The primary gene pool allows higher frequency of recombination which can be useful for quantitative traits (Valkoun, 2001). Interestingly, the performance of the derivative lines from the four wild parents was not affected by the number of backcrosses, which suggest the possibility to maintain a certain level of diversity while using these species by reducing the backcrossing. Instead, more care should be paid for the selection scheme and intensity to reduce the frequency of undesirable linkages. Our results showed that the same crosses with *T. dicoccoides* and *T. aegilopoides* produced lines outperforming the recurrent parents but also lines with very low yields. El Haddad et al., (2021) reported that no linkage drag on agronomic performance was associated with the use of wild relatives in durum wheat. In case of bread wheat, the adoption of an appropriate selection strategy resulted in the elimination of unfavourable traits and the release of high yielding and stable varieties from synthetic hexaploid derived lines (Li et al., 2014). This is where pre-breeding becomes crucial in the process of gene introgression from CWR. Pre-breeding should retain the favourable alleles while returning the background of the elite parent through reasonable top crossing (Hao et al., 2020).

5.5.3. Impact of wild relatives on yield potential

The use of two contrasting recurrent parents, the landrace Haurani with low yield potential and high tolerance to drought, and Cham 5, a high yielding cultivar released in several countries, was useful. Haurani derivatives showed an important advantage for both yield and stability, they overpassed their recurrent parent in most of the environments. For instance, the line 142001 derived from *T. urartu* had significantly higher BLUPs associated with higher stability according to both Bi and S^2di. The same line showed yield increase under drought stress with earliness and cooler canopy under heat stress (Aberkane et al., 2021a; b). Under favourable conditions, some Haurani derivatives (142064 for example) can yield twice as the recurrent parent which indicate a high contribution to yield potential. In case of Cham5 which is high yielding, the expected contribution of wild relatives can be more pronounced under stressed environments. The top yielding lines under drought stress at TSRF-17 were Cham5 derivatives crossed with the four wild parents. In fact, the line 142026 (Cham5*3/*T. urartu*) outyielded Cham5 under optimal conditions (TSIR-17) and was subject to lower yield losses due to drought. Similarly to our results, a significant increase in yield and stability was also reported

using *T. dicoccoides* and *T. monococcum* under drought and terminal stress (Nachit and Elouafi, 2004). The value of CWR in Cham5 derivatives was even greater under heat stress during both seasons. The contribution to heat tolerance was observed at the level of yield and its components (*T. dicoccoides* and *T. urartu*), phenology (*T. urartu*) and physiological response (*T. aegilopoides, T. urartu, and T. dicoccoides*) (Khanna-Chopra and Viswanathan, 1999; Ullah et al., 2018; Aberkane et al., 2021a; b). The results from MCH-18 which was the most favourable environment were interesting, Cham5 had the highest yield followed by four of its derivatives with yield above 9 tones/ha. This finding showed that the use of CWR from the primary gene pool does not always come with penalty on yield. These findings confirm that the increase in yield from crosses with wild relatives is mainly attributed, but not restricted, to the improvement of resistance/tolerance to biotic and abiotic stresses (Hajjar and Hodgkin, 2007; Mondal et al., 2016).

5.5.4. Stability of the durum wheat derivatives

Our study used different stability approaches to select stable genotypes for both biological (static) and agronomic (dynamic) stability. It was not surprising that most of the checks had high agronomic stability, especially that Cham1 (syn. 129080), Cham5 (syn. 129081), Louiza and Marzak have wide adaptation combined with moderate to high yield potential. When balancing between productivity and stability, several lines derived from crosses with *T. aegilopoides, T. dicoccoides, T. urartu* and *Ae. speltoides* are identified. For example, the lines 141995 (Cham5*4/*Ae. speltoides*) and 141966 (Cham5*2/*T. dicoccoides*) had yields above average, lower variance (σ_i^2) and deviation from regression (S^2di). In addition, they were highly stable according to SIPC, WAASY and the non-parametric indices (S_{i2}, S_{i3} and S_{i6}). These lines are desirable under unpredictable weather conditions, they can maintain average performance during poor seasons and respond positively to favourable conditions. The line 142074 (Cham5*3/*T. dicoccoides*) can also be recommended for its dynamic stability as it was highly ranked for Pi, BLUPs, GAI, S_{i6} and it had average stability for WAASY. These findings are in line with the reported contribution of *T. dicoccoides* and *Ae. speltoides* to yield stability while conserving high yield potential (Zaïm et al., 2017; El Haddad et al., 2021). Simmonds et al., (2008) reported the release of a bread wheat variety derived from a cross with *T. dicoccoides*, which exhibited high stability under different environments and cultural practices. The contribution of CWR to yield stability can be the result of the simultaneous improvement of yield and components under unfavourable environments (Farooq, 2004; Peleg et al., 2005; Reynolds et al., 2009; Lopes and Reynolds, 2011; Peng et al., 2013; Djanaguiraman et al.,

2019; Kuzmanović et al., 2021). Our results showed that the use of wild relatives can supply lines with wide adaptation, specific adaptation to unfavourable and favourable environments.

5.5.5. Association between different stability parameters

Selection from multi-environment trials is an important component for plant breeders, the adoption of appropriate statistical analysis is crucial to improve the selection accuracy. The use of linear mixed model provided a significant advantage as it allowed to account for the heterogeneity of the variance between environments. The advantage of mixed models in increasing the prediction accuracy was reported in other studies (Friesen et al., 2016; Olivoto et al., 2019). Interestingly, BLUPs did not correlate significantly with the SIPC and ASV from the AMMI model. The reason behind this is that these indices select lines with low contribution to GEI, which will privilege lines with average yield performance. This explains also why SIPC and ASV were clustered with the S^2di and σ_i^2 and confirms the association previously reported by Sneller et al., (1997). The negative correlation between CV and BLUPs was useful, it allowed to eliminate the less stable lines combining low yield potential with high variation. The value of the regression coefficient to select for agronomic stability is confirmed by its correlation with Pi, BLUPs and GAI. Different and sometimes opposite correlations between the stability statistics were reported by other studies (Mohammadi and Amri, 2008, 2016; Mehari et al., 2014; Temesgen et al., 2015; Fasahat, 2015), these correlations varied based on the population structures and environments characteristics. In this view, flexible stability statistics such as the superiority index WAASY can be more useful. The weights of productivity and stability can be adjuster depending the yield, size of the population and the environments to select superior genotypes.

5.6. Conclusion

The backcrossing population provided a view on the behaviour of different lines derived from similar crosses regarding linkage drag. It was concluded that it is possible to develop diverse adapted high yielding germplasm using CWR. This can be achieved by deploying the proper selection schemes at the pre-breeding level. WAASY can be recommended as a flexible stability index to select for stable and highly productive germplasm.

General discussion

In a context where global warming and drought waves are challenging future food security (Ainsworth and Ort, 2010), the identification of drought/heat tolerant and stable genotypes is vital for durum wheat improvement. The present results demonstrated the effects of these stresses on phenology, physiology, grain yield and its components. By the identification of traits that can be improved using wild relatives, the potential candidate lines were selected for crossing with elite lines.

Change in the environment was the major challenge to the agronomic performance of durum wheat. Fluctuations in the amount and distribution of precipitation caused a significant yield variation across the years and locations in Morocco. While some years were favourable, others were characterized by severe or moderate droughts. Heat stress at Wad Medani resulted in a significant yield reduction and change in phenology compared to other locations. These changes increased the genotype by environment interaction as shown in the stability analysis. This high genotype by environment interaction reduces the selection efficiency, especially with the changes in ranking of genotypes between environments (Crossa, 1990; Xiong et al., 2020).

Under these uncertain environments, breeding for stable and highly productive varieties is challenging. It requires strategic use of diversity, advanced molecular techniques for fast gene introgression, appropriate phenotyping and statistical approaches to increase selection efficiency (Reynolds et al., 2012; Mondal et al., 2016). In this view, selecting durum wheat derivatives for the study was of high importance. These wild species evolved during thousands of years in a wide range of environments, they were exposed to different climatic scenarios where they developed their resilience (Nevo and Chen, 2010). The study provided a view on the contribution of pre-breeding in mobilizing the diversity from CWR into adapted background. It also assessed the possibility to widen the genetic base for some traits where there is a genetic bottleneck in breeding populations.

The contrasted performance of lines from the same crosses illustrated the importance of pre-breeding in the process of using wild relatives. The purpose of pre-breeding is not only to increase diversity, but also to characterize the germplasm and maintain the high agronomic performance in breeder's collection (Dempewolf et al., 2017). The results showed also that the choice of the recurrent parent is highly crucial in pre-breeding. This was observed in the comparison of the lines using genotypic data, the distribution was affected by the recurrent parent more than the wild. This distribution is also explained by the backcrossing, which is

necessary to reduce the effects of genetic drag when using wild relatives. It is important to take into consideration that crossing ability is an important criterion driving the use of some parents over others. This explains why some recurrent parents are used more than others in the development of germplasm from wild relatives (Kishii, 2019). Therefore, crossing ability studies can improve pre-breeding by selecting high yielding parents which can be crossed easily with wild species.

Under drought stress, breeding for early lines with high biomass and spike productivity can improve yield. Several lines derived from *T. aegilopoides, T. urartu and Ae. speltoides* were identified as a source to widen genetic base for seed number per spike. The importance of improving this trait is derived from its high plasticity, which can be exploited to improve yield under drought stress (Vahamidis et al., 2019). In addition, *Triticum dicoccoides* showed the potential to improve the number of effective tillers under drought especially that high tillering capacity is correlated with the biomass. In other words, wild relatives can improve the availability of assimilates and increase the spike productivity under drought stress. Including wild relatives in such a strategy was recommended by Reynolds et al., (2017) to improve genetic gains in bread wheat.

Direct contribution to yield under drought is also possible, this was observed in several lines derived from the four wild parents in this study. In fact, some lines combined drought tolerance with high yield under non-stressed conditions. This type of germplasm is more adapted to the Mediterranean conditions, where the year to year fluctuations are significant (Araus et al., 2003). When the mean score index (MSI) was used to select for drought tolerance, the most desirable lines were derived from interspecific crosses, mostly from *Triticum dicoccoides*. These findings confirmed the importance *Triticum dicoccoides* in improving drought tolerance (Peleg et al., 2005).

In terms of physiological traits under drought, the low heritability can be a limitation for deploying and selection for chlorophyll fluorescence (Fv/Fm). Selection for canopy temperature can be useful as it is highly affected by drought. There was acceptable heritability for CT which suggest high genetic control of this trait. In fact, the genetic basis for CT were reported to be associated with deeper rooting system under drought stress (Pinto and Reynolds, 2015).

The response of durum wheat to chronic heat stress was an important component of the present study. The first finding was that the growth cycle is significantly reduced at Wad Medani and

all other traits were affected. Lines derived from *Triticum aegilopoides* (e.g. 142014), *Triticum dicoccoides* (e.g. 142074) and *Triticum urartu* (e.g. 142015) were among the highest yielding under heat stress. Many lines out yielded their recurrent parent under heat stress showing the contribution of CWR to yield gains under heat. In addition to total biomass, improving TKW and SDSPK can increase the yield under heat stress. *Triticum urartu* can be a source to improve TKW, especially that this trait was not largely exploited to improve yield under heat stress as reported by Lopes et al., (2012). It was also found that higher grain filling rate is more useful than grain filling period as a selection criteria. Increasing the grain filling duration can have yield penalty as it exposes the plant to more severe heat at the end of the cycle.

The physiological screening under heat was informative about the genetic variation in canopy temperature, chlorophyll content and NDVI. CT and NDVI can be used starting from early growth stages as they showed high heritability combined with significant correlation with yield and biomass. Chlorophyll content can be deployed during reproductive stage where the highest variation was observed. It was interesting that some lines derived from wild species combined adaptive physiological traits with earliness, higher biomass, and ultimately higher yields. These lines had both escaping and avoidance mechanisms for heat tolerance.

By supplying adaptive traits under stressed environments, CWR can limit the yield reductions and contribute to yield stability of durum wheat. The stability analysis revealed that using wild relatives could improve adaptation to stressed environments without affecting yield potential. This is supported by the high yielding lines (e.g. 142009, 142005, 142074) which had higher yields than many checks. These findings are similar to other studies on durum wheat where many CWR resulted in high yielding, stable and disease resistant lines (Zaïm et al., 2017; El Haddad et al., 2021).

Combining different stability indices showed that while some of them can be used interchangeably, others can be complementary to combine between wide adaptation and high productivity. The adoption of linear mixed models to account for the heterogeneity of the variance was efficient in selecting high yielding and stable lines. This was confirmed by the correlation as the BLUPs were correlated with dynamic (e.g. GAI, Pi, Bi) but also static stability parameters (e.g EV). WAAS and WAASY showed their effectiveness as a flexible stability parameter that can be adjusted based on the heterogeneity of the population and environments.

The study did not observe differences regarding the number of backcrosses for performance under drought, heat or for yield stability. These findings concluded that the number of backcrossing can be reduced when using direct wheat progenitors. It is therefore possible to develop diverse and performant germplasm while maintaining high level of diversity in the population. Therefore, several advantages can be deduced from using primary gene pool species. The crosses are easy to succeed, there is possibility to improve traits controlled by multiple genes and the time to produce desirable lines can be reduced by improved selection schemes after restoring fertility (Valkoun, 2001).

Considering that less than 10% of the available CWR collections was used for breeding (Reynolds et al., 2009), more efforts should be deployed to mobilize genes from these species into the cultivated wheat. Global initiatives such as the one initiated by the global crop diversity trust are important (Kilian et al., 2021), they allow to fill the gaps in the collections and also strengthen pre-breeding to utilize these CWR.

Conclusions and perspectives

By assessing the response of durum wheat derivatives under different environments, the changing climatic conditions is confirmed as an important challenge for durum wheat breeding. Taking into consideration the yield losses observed under drought and heat, adding to it the expanding area exposed to these two stresses, more efforts should be deployed in the breeding programs to maintain/increase the genetic gains in the Mediterranean region.

Several lines from this study were identified for tolerance to drought/heat and yield stability. With a limited number of crosses, high variation was observed for several traits illustrating the allelic diversity in CWR. This confirms that CWR are an important reservoir of useful traits for durum wheat improvement under a changing climate. The study concluded that using CWR should not be restricted to disease and pest resistance. There is also a high potential to improve quantitative traits (e.g. drought/heat tolerance, yield), especially with species from the primary gene pool.

It is however important to recognize that developing germplasm from crosses with CWR is laborious, time consuming and expensive. The exploitation of the diversity available in CWR will require a complementary strategy between optimizing ex-situ collections and pre-breeding to harness the use of CWR. Collecting is necessary because there is high level of duplication in CWR between and within different genebanks. It is therefore essential to identify the gaps in the "global collection" and join efforts to fill these gaps. The strategy should also be "anticipative" and identify the gaps for the traits needed to cope with future challenges of climate change.

Pre-breeding projects must be linked to genebank collections, otherwise CWR will remain underutilized. Pre-breeding should also address the medium-term and long-term challenges associated with climate change. For this purpose, several approaches can be used for targeted crosses to mobilize useful genes from CWR. In one hand, exploiting the geographic distribution in designing the crosses can be useful to prepare germplasm for different scenarios. Especially that plants co-evolve with a wide range of abiotic/biotic stresses in different environments.

On the other hand, exploiting new genotyping technics can identify genetically unique accessions from exotic germplasm. Special collections can be developed from the most diverse accessions and then cross them with elite lines. By using new/diverse accessions for the crosses, novel combination of alleles can be created to overcome the genetic bottleneck for

several traits. Advanced cytogenetic technics and chromosome engineering are also crucial in the manipulation of wild genomes to reduce the linkage drag effects, especially when using genetically distant species.

This research used germplasm that is publicly available at ICARDA genebank, therefore the generated data from the study can be beneficial for different users. The desirable lines can be directly shared with national/international researchers as donors for the useful traits. Breeders can therefore cost-effectively access pre-breeding germplasm, especially from difficult crosses. This highlight the dynamic role of the genebank in conserving both raw germplasm (CWR) and the adapted germplasm derived from pre-breeding (durum wheat derivatives).

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Appendix

Annex 1: List of genotypes used in the study with their accession number, DOIs, pedigree and selection history.

ENTRY/Acc Number	Pedigree/Name	DOI	Remarks	Selection history
84859	Haurani	10.18730/842V5	Parent	-
129080	Cham 1	10.18730/983J3	Check	-
129081	Cham 5	10.18730/983K4	Parent	-
135226	Gidara 2	10.18730/9DS33	Check	-
141966	Cham5*2/*T. dicoccoides* ICWT 601116	10.18730/9NBGV		2002:10294-3; 2003:20652
141967	Cham5*2/*T. dicoccoides* ICWT 601116	10.18730/9NBJX		2002:10294-5; 2003:20654
141969	Cham5*3/*T. dicoccoides* ICWT 601116	10.18730/9NBN*		2002:10317-1; 2003:20776
141970	Cham5*2/*T. dicoccoides* ICWT 601116	10.18730/9NBQ$		2002:10312-2; 2003:20750
141972	Haurani*2/*T. urartu* ICWT 500530	10.18730/9NBV1		2002:10309-5; 2003:20736
141973	Cham5*2/*T. dicoccoides* ICWT 601116	10.18730/9NBW2		2002:10294-4; 2003:20653
141976	Cham5*3/*T. dicoccoides* ICWT 601116	10.18730/9NC39		2002:10284-1; 2003:20595
141979	Cham5*3/*T. urartu* ICWT 500529	10.18730/9NC7D		2002:10352-4; 2003:20972
141982	Cham5*3/*T. urartu* ICWT 500529	10.18730/9NCDK		2002:10352-5; 2003:20973
141984	Cham5*3/*T. dicoccoides* ICWT 601116	10.18730/9NCHQ		2002:10292-4; 2003:20642
141986	Cham5*3/*T. dicoccoides* ICWT 601116	10.18730/9NCNV		2002:10317-2; 2003:20777
141987	Cham5*3/*T. aegilopoides* ICWT 500647	10.18730/9NCPW		2002:10334-3; 2003:20872
141989	Cham5*2/*T. urartu* ICWT 500651	10.18730/9NCSZ		2002:10299-2; 2003:20678
141990	Cham5*3/*T. aegilopoides* ICWT 500648	10.18730/9NCV~		2002:10286-4; 2003:20609
141991	Cham5*3/*T. dicoccoides* ICWT 601116	10.18730/9NCX=		2002:10319-2; 2003:20788
141994	Cham5*3/*T. aegilopoides* ICWT 500647	10.18730/9ND34		2002:10351-4; 2003:20966
141995	Cham5*4/*Ae. speltoides* ICAG 401293	10.18730/9ND56		2002:10356-2; 2003:20992
141996	Cham5*4/*Ae. speltoides* ICAG 401293	10.18730/9ND78		2002:10353-3; 2003:20976
141997	Cham5*2/*T. aegilopoides* ICWT 500647	10.18730/9ND9A		2002:10295-4; 2003:20658

141999	Haurani*2/*T. urartu* ICWT 500530	10.18730/9NDBC		2002:10280-1; 2003:20573
142000	Cham5*3/*T. dicoccoides* ICWT 601117	10.18730/9NDCD		2002:10324-4; 2003:20818
142001	Haurani*2/*T. urartu* ICWT 500530	10.18730/9NDEF		2002:10333-3; 2003:20866
142003	Haurani*2/*T. urartu* ICWT 500530	10.18730/9NDJK		2002:10309-3; 2003:20734
142004	Cham5*3/*T. aegilopoides* ICWT 500647	10.18730/9NDKM		2002:10314-5; 2003:20764
142005	Cham5*4/*Ae. speltoides* ICAG 401293	10.18730/9NDNP		2002:10354-4; 2003:20983
142006	Haurani*2/*T. aegilopoides* ICWT 500652	10.18730/9NDPQ		2002:10327-1; 2003:20831
142007	Haurani*2/*T. urartu* ICWT 500516	10.18730/9NDQR		2002:10306-5; 2003:20720
142008	Cham5*3/*T. dicoccoides* ICWT 601116	10.18730/9NDTV		2002:10319-5; 2003:20791
142009	Cham5*3/*T. aegilopoides* ICWT 500647	10.18730/9NDVW		2002:10340-5; 2003:20907
142012	Cham5*3/*T. aegilopoides* ICWT 500647	10.18730/9NE0~		2002:10340-1; 2003:20903
142013	Cham5*3/*T. aegilopoides* ICWT 500647	10.18730/9NE2=		2002:10348-2; 2003:20948
142014	Cham5*3/*T. aegilopoides* ICWT 500647	10.18730/9NE40		2002:10339-2; 2003:20898
142015	Cham5*2/*T. urartu* ICWT 500651	10.18730/9NE62		2002:10299-5; 2003:20681
142018	Cham5*4/*Ae. speltoides* ICAG 401293	10.18730/9NEB7		2002:10358-1; 2003:21002
142020	Cham5*3/*T. aegilopoides* ICWT 500647	10.18730/9NEEA		2002:10334-4; 2003:20873
142026	Cham5*3/*T. urartu* ICWT 500649	10.18730/9NESN		2002:10301-4; 2003:20691
142027	Cham5*3/*T. urartu* ICWT 500651	10.18730/9NEVQ		2002:10287-3; 2003:20613
142030	Cham5*3/*T. aegilopoides* ICWT 500647	10.18730/9NF1X		2002:10334-5; 2003:20874
142031	Cham5*3/*T. aegilopoides* ICWT 500647	10.18730/9NF2Y		2002:10335-1; 2003:20875
142032	Cham5*3/*T. aegilopoides* ICWT 500647	10.18730/9NF4*		2002:10337-5; 2003:20890
142039	Cham5*3/*T. dicoccoides* ICWT 601116	10.18730/9NFH8		2002:10323-4; 2003:20812
142040	Cham5*3/*T. dicoccoides* ICWT 601116	10.18730/9NFJ9		2002:10323-4; 2003:20756
142041	Cham5*4/*Ae. speltoides* ICAG 401293	10.18730/9NFMB		2002:10358-4; 2003:21005
142042	Cham5*2/*T. aegilopoides* ICWT 500647	10.18730/9NFPD		2002:10295-2; 2003:20656
142044	Cham5*3/*T. dicoccoides* ICWT 601117	10.18730/9NFSG		2002:10325-5; 2003:20824
142045	Cham5*3/*T. urartu* ICWT 500649	10.18730/9NFVJ		2002:10301-5; 2003:20692
142046	Cham5*2/*T. aegilopoides* ICWT 500647	10.18730/9NFXM		2002:10367-3; 2003:21053
142048	Cham5*3/*T. aegilopoides* ICWT 500647	10.18730/9NG0Q		2002:10342-2; 2003:20915

142053	Cham5*2/*T. dicoccoides* ICWT 601116	10.18730/9NGA~		2002:10364-5; 2003:21039
142055	Cham5*4/*Ae. speltoides* ICAG 401294	10.18730/9NGDU		2002:10361-3; 2003:21020
142056	Haurani*2/*T. urartu* ICWT 500516	10.18730/9NGG2		2002:10306-4; 2003:20719
142057	Cham5*3/*T. aegilopoides* ICWT 500647	10.18730/9NGJ4		2002:10347-5; 2003:20945
142058	Cham5*2/*T. urartu* ICWT 500649	10.18730/9NGK5		2002:10302-2; 2003:20695
142060	Cham5*3/*T. aegilopoides* ICWT 500647	10.18730/9NGRA		2002:10346-4; 2003:20939
142061	Cham5*3/*T. aegilopoides* ICWT 500647	10.18730/9NGSB		2002:10351-2; 2003:20964
142062	Haurani*3/*T. dicoccoides* ICWT 601116	10.18730/9NGVD		2002:10279-5; 2003:20571
142063	Cham5*3/*T. dicoccoides* ICWT 601116	10.18730/9NGWE		2002:10321-3; 2003:20800
142064	Haurani*2/*T. aegilopoides* ICWT 500652	10.18730/9NGZH		2002:10327-2; 2003:20832
142066	Cham5*3/*T. aegilopoides* ICWT 500647	10.18730/9NH3N		2002:10348-3; 2003:20949
142067	Cham5*3/*T. dicoccoides* ICWT 601116	10.18730/9NH5Q		2002:10323-3; 2003:20811
142068	Cham5*3/*T. aegilopoides* ICWT 500647	10.18730/9NH7S		2002:10342-3; 2003:20817
142069	Cham5*3/*T. aegilopoides* ICWT 500647	10.18730/9NH8T		2002:10315-2; 2003:20766
142070	Cham5*3/*T. aegilopoides* ICWT 500647	10.18730/9NHAW		2002:10315-5; 2003:20769
142071	Cham5*3/*T. urartu* ICWT 500649	10.18730/9NHCY		2002:10288-4; 2003:20620
142072	Cham5*4/*Ae. speltoides* ICAG 401293	10.18730/9NHDZ		2002:10353-5; 2003:20978
142073	Cham5*2/*T. dicoccoides* ICWT 601116	10.18730/9NHE*		2002:10312-4; 2003:20752
142074	Cham5*3/*T. dicoccoides* ICWT 601116	10.18730/9NHG$		2002:10282-5; 2003:20588
cham5 'S'	-	-	Check	-
Faraj	F413J.S/3/Arthur71/Lahn//Blk2/Lahn/4/Quarmal	-	Check	Year of registration 2007
Icarachaz	Stj3//Bcr/Lks4/3/Ter3	-	Check	Elite line
Louiza	Rascon_39/Tilo1	-	Check	Year of registration 2011
Marzak	-	-	Check	Year of registration 1984
MIKI3	Stj3//Bcr/Lks4	-	Check	Elite line

Annex 2: List of the wild parents used in the development of durum wheat derivatives with their origins.

Accession number	crop No	ORI	Taxon	DOI
45475	500516	LBN	*Triticum urartu*	10.18730/6ZCY*
45488	500529	SYR	*Triticum urartu*	10.18730/6ZDB8
45489	500530	LBN	*Triticum urartu*	10.18730/6ZDC9
47843	401293	SYR	*Aegilops speltoides*	10.18730/70T93
47844	401294	SYR	*Aegilops speltoides*	10.18730/70TA4
118178	601116	SYR	*Triticum turgidum subsp. dicoccoides*	10.18730/8YYPX
118179	601117	SYR	*Triticum turgidum subsp. dicoccoides*	10.18730/8YYQY
118180	500647	SYR	*Triticum monococcum* subsp. *aegilopoides*	10.18730/8YYRZ
118181	500648	SYR	*Triticum monococcum* subsp. *aegilopoides*	10.18730/8YYS*
118182	500649	SYR	*Triticum urartu*	10.18730/8YYT~
118184	500651	SYR	*Triticum urartu*	10.18730/8YYW=
118185	500652	SYR	*Triticum monococcum* subsp. *aegilopoides*	10.18730/8YYXU

Annex 3: Best linear unbiased predictions of agronomic traits of durum wheat derivative lines and checks at Tessaout under irrigated conditions

ENTRY	PHT	SDSPK	TKW	BY	GY
Icarachaz	104	51	42.3	15987	7971
142064	112	53	37.7	16129	7492
135226	103	48	39.2	15431	7476
141999	111	44	35.7	15621	7174
129080	101	52	40.1	15573	6994
141970	119	44	42.6	15342	6910
142013	113	57	38.4	15603	6829
142046	118	58	39.8	15645	6682
MIKI3	98	49	36.5	14815	6670
142014	114	55	39.5	15388	6639
141997	100	49	41.3	15137	6596
142073	106	42	35.6	14988	6596
142004	118	45	32.9	15623	6505
141991	109	47	39.5	15134	6439
cham5	112	46	36.7	15138	6382
142072	119	51	38.6	15715	6351
142074	109	46	40.3	15032	6311
142018	108	53	40.3	15493	6279
141986	109	49	36.6	15200	6269
142012	110	50	41.3	15416	6268
142045	119	48	38.7	15981	6261
142032	110	51	37.7	15351	6261
142044	109	53	38.3	15065	6239
142048	112	48	38.1	14634	6213
Louiza	100	49	41.7	15222	6185
142008	108	53	42.0	15561	6184
141967	111	50	42.7	14900	6154
142062	116	48	36.0	15184	6146
142071	115	51	42.4	15427	6131
142031	106	51	37.7	15257	6126
141969	110	49	37.0	15399	6109
142003	115	45	39.6	14763	6100
142060	108	51	38.5	15634	6086
141976	116	49	33.9	15942	6077
142015	110	50	33.1	14900	6032
141966	105	53	38.9	14911	6030
142067	109	50	34.7	15347	5950
142005	111	55	33.0	15294	5911
141995	111	47	37.7	14797	5902
142070	108	46	38.9	15140	5880
142026	111	49	32.8	15309	5861

141989	112	50	37.1	14722	5855
141979	109	52	35.3	15118	5845
142042	118	45	36.9	15341	5843
129081	109	46	35.9	15372	5830
142041	107	53	35.8	14854	5814
142001	110	49	33.8	14762	5810
141982	111	49	30.5	15346	5781
142053	114	49	33.9	15186	5777
142006	115	53	29.8	14821	5760
141987	112	49	35.2	15630	5753
141994	106	50	36.4	15283	5745
142061	109	56	35.6	15351	5742
142009	109	50	39.1	15462	5651
142039	109	51	33.1	14705	5648
142040	103	48	36.7	15312	5636
84859	111	43	41.2	15099	5617
Marzak	103	52	42.6	15108	5599
142027	113	47	41.2	15007	5579
Faraj	100	49	40.3	14688	5556
142030	115	50	37.6	14784	5552
142068	106	48	38.7	14764	5492
142056	117	47	36.2	14786	5469
142063	107	50	31.4	15258	5392
142057	114	48	32.2	15042	5357
141973	106	48	37.0	15028	5238
141984	122	54	34.5	15242	5227
142069	114	44	38.6	14226	5179
142000	112	47	37.6	15066	5169
141996	103	46	35.1	14599	5149
142020	117	48	38.0	15376	5106
142058	105	51	32.0	14972	5004
142007	107	48	32.1	14693	4977
142066	111	46	36.6	15003	4964
141990	116	48	38.8	15161	4946
142055	111	52	35.1	14559	4702
141972	108	43	36.3	14474	4075
LSD (p=0.05)	10	8	5.2	1450	1184

Annex 4: Best linear unbiased predictions of agronomic traits of durum wheat derivative lines and checks at Tessaout under rainfed conditions

ENTRY	PHT	SDSPK	TKW	BY	GY
141973	77	37	26.22	8846	3628
141996	81	40	26.02	8595	3253
142020	84	37	23.55	8852	3246
142055	81	34	27.72	8467	3238
141972	82	35	23.67	8373	3127
141990	92	36	24.78	8740	3103
142058	80	35	25.24	8100	3033
142063	82	37	26.51	9348	2981
142066	84	37	23.01	8873	2965
142026	88	37	29.84	9477	2925
141994	84	35	25.30	8496	2922
142009	83	36	21.82	9149	2879
142061	82	35	28.33	8758	2872
142070	80	39	26.38	8694	2861
142000	86	39	26.66	8718	2836
142068	88	36	25.57	8827	2821
Faraj	75	38	24.70	8858	2805
142013	83	36	27.35	8842	2716
142005	79	33	27.11	8613	2635
142040	80	37	24.69	8695	2623
142030	86	37	27.48	8366	2613
142060	83	36	26.69	9000	2576
141982	81	36	29.64	8263	2553
129081	77	34	28.09	8834	2550
142041	84	33	25.41	8700	2542
142008	81	34	19.93	8599	2522
141995	85	37	26.29	8583	2518
141966	79	36	24.57	8539	2465
141987	81	37	24.48	8782	2448
129080	75	37	24.59	9192	2442
142042	87	38	26.63	8691	2430
142031	83	36	24.89	8889	2411
142027	84	36	23.36	8460	2401
141976	88	37	26.42	8547	2397
142045	89	37	25.90	9117	2360
Marzak	76	36	24.33	8827	2348
141967	83	38	21.03	8423	2344
142074	82	36	24.72	9047	2342
142071	88	37	25.21	9179	2322
cham5	82	37	27.05	8363	2305
142018	84	34	23.69	8808	2286

141997	77	36	21.87	8424	2286
Louiza	76	35	22.90	8915	2277
142069	86	37	19.35	7993	2218
142056	85	34	28.42	9017	2211
141979	79	33	26.32	8223	2189
141989	81	38	24.47	8108	2183
141969	83	37	24.77	8897	2163
142032	87	34	24.77	8276	2158
142046	83	32	23.79	8521	2141
142053	84	35	25.60	8282	2044
142044	83	36	20.95	8568	2031
142072	86	35	23.15	8845	2031
142007	73	35	23.21	8485	2005
142057	82	35	28.53	7903	1983
141984	87	35	20.74	8789	1969
MIKI3	75	35	26.67	8556	1965
142012	88	35	23.19	8953	1952
142039	82	36	25.28	8098	1946
142062	86	37	29.07	8356	1887
141986	86	37	23.74	8666	1875
142067	86	37	23.83	8449	1854
141991	82	38	20.75	7676	1673
142015	85	37	25.51	8039	1642
142048	79	35	19.13	8475	1599
84859	80	34	22.88	8104	1594
142073	81	39	24.23	7832	1570
141970	92	37	23.03	9084	1556
142001	85	37	22.53	8326	1552
142004	85	37	27.03	8526	1510
142014	88	34	22.70	8493	1435
142003	78	36	22.94	7739	1397
142006	83	34	26.39	7767	1292
142064	84	37	23.55	9542	1099
Icarachaz	81	36	22.49	8395	803
141999	82	39	28.64	8053	680
135226	73	40	21.76	8035	612
LSD (p=0.05)	5	7	3.94	1382	933

Annex 5: Best linear unbiased predictions of agronomic traits of durum wheat derivative lines and checks at Wad Medani

ENTRY	PHT	DHE	SDSPK	TKW	BY	GY
142015	68	67	38	30.9	5743	2082
Marzak	68	60	36	29.2	7108	2054
Louiza	68	60	44	30.0	7276	1998
142001	70	58	34	30.2	6497	1986
135226	67	67	33	30.3	5891	1930
142006	69	70	29	31.1	5567	1878
142053	65	64	36	30.5	6478	1858
142007	69	57	37	31.3	5811	1851
142074	66	66	41	29.3	7090	1841
141969	65	67	33	30.4	6543	1838
Icarachaz	67	58	39	30.5	5996	1831
142067	71	66	35	30.0	6046	1793
141984	69	63	37	30.6	5720	1780
142014	68	62	32	30.9	6438	1777
142066	67	66	36	31.4	6174	1757
142004	68	59	37	31.6	5774	1757
142027	68	66	39	29.6	6015	1712
141986	66	67	30	29.4	5851	1693
142026	69	65	38	31.1	6286	1672
142009	69	62	38	29.9	6178	1597
141999	69	67	28	28.0	5899	1559
142068	67	69	42	28.6	6441	1519
142048	68	65	35	31.2	5343	1511
142069	68	67	36	28.7	5783	1510
142055	68	66	35	29.6	6116	1497
142012	69	63	35	28.5	6310	1493
142056	70	65	35	29.6	5712	1479
142073	67	67	38	32.2	5733	1462
Faraj	67	69	32	31.2	6914	1455
142000	69	67	35	31.3	6409	1446
142040	68	61	41	28.8	6344	1430
141991	68	68	35	30.8	5803	1429
142044	65	59	35	28.1	5303	1406
142064	70	66	30	28.1	6264	1402
141989	68	66	41	28.7	5610	1392
142060	66	61	40	28.6	5647	1374
141966	67	65	34	29.7	5404	1369
142061	69	66	35	27.1	5835	1355
142071	66	68	36	28.9	6098	1353
142005	67	66	35	31.1	5682	1344
141976	67	59	32	30.2	5729	1316

142045	67	65	36	28.9	5537	1304
129081	68	61	38	29.5	6302	1301
142032	67	63	44	29.3	5732	1282
142018	68	66	33	28.4	6029	1279
142041	65	66	34	30.7	5454	1277
141997	70	64	40	28.2	6577	1271
142042	72	66	35	28.7	6240	1257
84859	68	68	44	28.0	5899	1257
141995	65	63	41	29.6	5714	1245
MIKI3	66	60	43	29.5	5634	1244
142020	68	67	40	30.2	6056	1236
142039	68	64	35	30.5	5068	1235
141967	67	63	38	28.7	5541	1199
141987	66	69	37	29.6	5551	1199
141982	65	64	42	28.2	5612	1182
142030	67	64	31	28.3	5761	1147
141996	69	62	38	28.6	5778	1117
142070	66	62	36	28.4	5724	1104
141979	66	66	41	30.0	5174	1102
142031	64	64	32	30.2	5191	1089
142008	67	67	36	29.5	5680	1061
142057	70	67	33	26.6	5985	1056
142003	72	69	36	28.4	5610	1047
141972	68	68	40	29.8	5235	1020
129080	66	60	31	30.5	5864	1009
142046	67	62	32	28.4	5918	982
142058	63	57	34	31.5	4271	978
142063	66	68	34	30.0	5525	954
141970	66	65	40	26.8	5529	953
141994	67	62	38	29.4	5092	937
142072	71	65	32	30.2	6829	928
141990	67	69	34	28.0	6499	863
cham5 'S'	66	61	42	27.9	5697	857
142062	71	66	29	27.0	6652	824
142013	70	63	35	29.2	6289	806
141973	66	64	40	29.4	5897	634
LSD(p=0.05)	5	10	9	3.9	1602	639

Annex 6: List of selected durum wheat derivative lines and checks based on Mean Score Index (MSI) for drought tolerance

ENTRY	TSIR_GY	TSRF_GY	S_TOL	S_MP	S_DTI	S_DSI	S_MsSTI	MSI
142074	7002	4623	4	10	10	8	10	9.5
141973	5859	4168	8	8	9	9	9	8.75
141969	6333	3863	4	9	10	5	9	8.25
141966	6223	3852	4	8	9	6	9	8
142026	6659	4773	8	10	10	9	10	9.75
141996	5475	4005	9	6	8	10	8	8
142005	6128	3993	5	9	9	7	9	8.5
142009	5874	4478	10	9	10	10	10	9.75
142013	7567	4401	1	10	10	4	10	8.5
142061	6283	4261	6	9	9	8	10	9
142070	5963	4184	8	9	7	9	9	8.5
142068	5605	4060	9	7	7	10	8	8
142060	6172	4047	5	9	9	8	9	8.75
141997	6766	4016	2	10	10	5	10	8.75
142020	5559	4012	9	7	8	9	9	8.25
129080	7618	4392	1	10	10	3	10	8.25
Louiza	6671	4323	5	10	9	7	9	8.75
Marzak	5749	4163	9	8	6	10	8	8

Annex 7: Dendrogram of the groups of durum wheat genotypes identified based on the clusters using the drought tolerance/susceptibility indices.