



Wide crosses of durum wheat (*Triticum durum* Desf.) reveal good disease resistance, yield stability, and industrial quality across Mediterranean sites



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ABSTRACT

Durum wheat (*Triticum durum* Desf.) breeders over the past century have increased the productivity and resilience of this crop via strong selection applied to genes controlling agronomically important traits. Along this process, some of the primitive genetic diversity of this species was lost. A debate exists on whether or not some of the original primitive diversity should be re-introgress into modern germplasm in order to facilitate new improvements. Here, the possible negative effects of re-introducing primitive diversity were assessed by comparing the performances of three ICARDA elites and four commercial cultivars against seventeen durum wheat wide crosses, generated by hybridization of elites and *Triticum dicoccoides*, *T. araraticum*, and *Aegilops speltoides*. The material was grown in Lebanon, Algeria and 10 environments in Morocco. Tested under natural inoculation against *Lr14a* virulent strains of leaf rust as well as tan spot races 4 and 6, revealed that wide crosses had significantly higher levels of resistance. Further, the use of a selection index that combined selection for grain yield potential and stability revealed that 14 wide crosses performed better than any of the elites or cultivars. Finally, testing quality traits at four sites revealed that wide crosses had significantly higher grain size and protein content than the other two germplasm classes, while no significant difference could be observed for gluten strength. Only in the case of yellow pigment, an industrially important trait for durum wheat, one variety ('Tomouh') outperformed all other classes, even though wide crosses lines also achieved good scores. Hence, it was not possible to identify any negative drag in the use of wide crosses for improving durum wheat modern germplasm, with the partial exception of yellow pigment.

1. Introduction

Durum wheat (*Triticum durum* Desf., $2n = 4x = 28$, AABB) is a tetraploid cereal crop grown in a range of climatic zones varying from warm and dry to cool and wet environments (Giraldo et al., 2016). Its global acreage is estimated at 17 million hectares (ha) and the most important growing areas are situated in the Mediterranean Basin, North America, and South West Asia (Maccaferri et al., 2014). However, durum wheat is an economically important crop because of its unique rheological characteristics and the varieties of industrial end-products

that can be derived from it (Gonzalez-Segura et al., 2014). These include mostly pasta, couscous, and bourghul, but also several dishes of the tradition such as frike, gofio, and several types of flat breads.

Durum wheat growing environments are mostly located in areas subject to alternating favorable and stressed conditions (Nachit and Elouafi, 2004). Therefore, genetic improvement via breeding for tolerance to biotic and abiotic stresses remains a strategic practice to improve its productivity and stability (Rajaram and Hettel, 1994; Nsarellah et al., 2000). In the last decades, many durum wheat varieties have been developed based on field assessment for higher yield, disease

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resistance and technological seed qualities. However, the strong selection pressure imposed through genetic improvement has eroded a large part of the genetic diversity available to breeders (Jing et al., 2013). This genetic narrowing has led to a reduction in allelic plasticity, hence to a germplasm less prone to adapt to new environmental stresses, diseases and pests (Makai et al., 2016; Tanksley and McCouch, 1997). Compared with domesticated varieties, crop wild relatives and primitive wheats have been challenged in natural environments for thousands of years and maintain a much higher level of diversity (Zhang et al., 2016). Hence, interspecific hybridization between durum elite lines and wild relatives of the *Gramineae* family is a promising method to restore variability to the modern breeding germplasm (Rajaram and Hettel, 1994). Several useful traits have been identified in species related to durum wheat, for instance about half of the leaf rust genes listed in the Catalogue of Gene Symbols for Wheat (McIntosh et al., 2003) and 20 of the known genes for stem rust resistance are derived from species other than the cultivated ones (McIntosh et al., 1991; McIntosh et al., 1998; Monneveux et al., 2000). In fact, wild species have been identified as a potential source of resistance to leaf rust (Anikster et al., 2005; Cherukuri et al., 2005; Kassem et al., 2011; Lalkova et al., 2004; Marais et al., 2005) and tan spot (Tadesse et al., 2006), two diseases that cause significant losses in wheat production worldwide (Goyeau et al., 2012; Martinez et al., 2005). For scale, Singh et al. (2010) reported that yield losses in durum wheat by tan spot can exceed 50% of the production, and Herrera-Foessel et al. (2006) indicated that leaf rust can be even more devastating. Likewise, *Aegilops sharonensis*, *Triticum dicoccoides*, *A. speltoides*, *A. tauschii* have all been identified as holder of resistance to powdery mildew (Gill et al., 1985; Ji et al., 2007; Jia et al., 1996; Miranda et al., 2007), stem rust (Anikster et al., 2005; Babaiants et al., 2012; Mago et al., 2009), stripe rust (Gerechter-Amitai and Stubbs, 1970; Knaggs et al., 2000; Marais et al., 2010; Valkoun et al., 1985; Yildirim et al., 1995) and to other diseases and insect pests (Ghannoum et al., 2016; El Haddoury et al., 2005). Furthermore, it has been found that members of the *Aegilops* (*A. tauschii*, *A. umbellulata*, *A. speltoides*), *Triticum* (*T. dicoccum* and *T. dicoccoides*) and *Haynaldia* have useful traits for adaptation to drought, cold and salinity stresses (Feldman and Millet, 1993; Monneveux et al., 2000; Nachit et al., 2015; Plamenov, 2003; Trethowan and Mujeeb-Kazi, 2008; Trethowan, 2014). Also, the potential of using *T. dicoccoides* as a source of genetic variation to improve the baking quality of durum wheat was suggested (Feldman and Millet, 1993; LeClerc et al., 1918).

Regardless of the proven usefulness of wild relatives for trait discovery and deployment in pre-breeding, wheat breeders have often regarded to this type of crosses as a “last resource” that will inevitably require several years and multiple recurrent cycles before delivering a promising candidate for variety release (Brown and Marshall, 2015). This was mostly due to the risk indicated by several authors that undesirable linkage drag exist between useful wild traits and negative yield or quality alleles (Mondal et al., 2016). One of the exception to this breeding trend has been the ICARDA durum wheat program that broadly utilized wild relatives and landraces into their hybridization (Nachit and Elouafi, 2004). This is demonstrated by the release in 1981 of the first ICARDA mega cultivar ‘Om Rabi’, derived by the simple cross between the elite ‘Jori’ and the landrace ‘Haurani’ (Nachit, 1992). This cultivar is still cultivated today in 21 countries, mostly in the driest environments by smallholder farmers (Latican et al., 2016). Further, ‘Om Rabi’ proved to be an excellent parent, with several recent releases derived from its hybridization (Nachit et al., 2016). To further this knowledge, this article utilizes top-crosses between wild relatives of durum wheat and elite lines of the ICARDA breeding programs to assess their possible demerits for yield drags, to identify their biotic stress response, and to quantify the negative effect of wild alleles on rheological quality.

Table 1
List of 24 durum wheat genotypes used in this study and their simplified code.

Code	Type	Cross
WC1	Wide cross	Amedakul1/TdicoSyrCol//Cham1
WC2	Wide cross	Omrabi5/TdicoAlpCol//Cham1
WC3	Wide cross	Younes/TdicoAlpCol//Korifla
WC4	Wide cross	Korifla/AegSpeltoidesSyr//Amedakul
WC5	Wide cross	Amedakul1/TdicoSyrCol//Loukos
WC6	Wide cross	Korifla/AegSpeltoidesSyr//Heider
WC7	Wide cross	Omrabi5/TdicoAlpCol//Cham1
WC8	Wide cross	Korifla/AegSpeltoidesSyr//Omrabi5
WC9	Wide cross	Amedakul1/TdicoSyrCol//Cham1
WC10	Wide cross	Korifla/AegSpeltoidesSyr//Loukos
WC11	Wide cross	Korifla/AegSpeltoidesSyr//Omrabi5
WC12	Wide cross	Korifla/AegSpeltoidesSyr//Amedakul
WC13	Wide cross	Amedakul1/TdicoJCol//Cham1
WC14	Wide cross	Younes/TdicoAlpCol//Korifla
WC15	Wide cross	Heider/TAraticumMA//Omrabi5
WC16	Wide cross	Korifla/AegSpeltoidesSyr//Omrabi5
WC17	Wide cross	Korifla/AegSpeltoidesSyr//Lahn
Louiza	Cultivar	Rascon_39/Tilo1
Faraj	Cultivar	F413J.S/3/Arthur71/Lahn//Blk2/Lahn/4/Quarmal
Waha	Cultivar	Plc/Ruff//Gta/Rtte
Tomouh	Cultivar	Joric69/Hau
Icakasem1	Elite	Geromt11/lcasyr1
Secondroue	Elite	Stj3//Bcr/Lks4/3/Ter3/4/Bcr/Gro1//Mgn1
Icarnada	Elite	Src2/Azn1/3/Bcr/Gro1//Mgn1

2. Materials and methods

2.1. Plant material

Twenty-four durum wheat genotypes were selected for this study. Seventeen wide crosses (WC) F₁₂ derived by top crosses involving ICARDA parents with *T. dicoccoides*, *T. araraticum* and *A. speltoides*, were selected on the basis of leaf rust (*LR*, *Puccinia triticina*) and tan spot (*TS*, *Pyrenophora tritici-repentis*) response in one season and one environment in Morocco (data not shown). In addition, three new commercial varieties released in Morocco; ‘Tomouh’, ‘Faraj’, ‘Louiza’ and one Algerian variety ‘Waha’ (syn. ‘Cham1’) were used as checks. Finally, three elite lines were included from the ICARDA program derived by top crosses of “best-by-best” selected from the international nursery 37th IDYT on the basis of their good performances in Moroccan environmental conditions (data not shown). The full list of pedigrees is reported in Table 1.

2.2. Locations, experimental design and management practices

The genotypes were assessed in ten different agro-climatic conditions (environments) as described in Table 2, eight where located in Morocco: Sidi Allal Tazi (ALT), Jemhâa Shaim (JS), Marchouch (MCH), Melk Zhar (MKZ), Sidi el Aydi (SAD), Tessaout (TES), Laarache (LRC) and Guich (GCH), one in Lebanon: Terbol (TER), and one in Algeria: El Khroub (ELK). The experiments were run during the 2013–14 (14) and the 2014–15 (15) seasons. The experimental design used at all stations was alpha-lattice with two replications and six incomplete blocks of size four. Each entry was planted in plots of 6 rows of 5 m in length, row spacing was 0.2m, for a total sown surface of 6 m² at a seeding rate of 120 kg ha⁻¹. Agronomic practices varied based on the station, but followed the general guidelines of sowing between 15th of November and 15th of December with a base pre-sowing fertilizer application of 50 kg ha⁻¹ of N, P, and K. Planting always occurred after a fallow season, with the exception of the Lebanese site where the precedent crop was lentil. At stage 14 on Zadok’s scale (Z) herbicide was applied in a tank mixture to provide protection against both monocots and dicots. A week after herbicide application, ammonium nitrate was provided to add 36 kg ha⁻¹ of N. In MCH15, TER15 and TES15 a final

Table 2
Experimental stations used for field testing and their basic characteristics.

Code	Site	Country	Year	Experiment	Average grain yield (Kg ha ⁻¹)	Climate	Annual rainfall (mm)	Coordinates	Soil type
ALT14	Sidi Allal Tazi	Morocco	2013–2014	Yield trial	7322	Mediterranean/hot and temperate	570	34° 31' 11" N, 6° 19' 25" W	Vertisol
MKZ15	Melk Zhar	Morocco	2014–2015	Yield trial	7209	Mediterranean/hot and temperate	192	30° 2' 33" N, 9° 33' 4" W	Sandy limestone
TER15	Terbol	Lebanon	2014–2015	Yield trial	6859	Mediterranean/temperate	559	33° 48' 29" N, 35° 59' 22" W	Chromic Vertisols
TES15	Tessaout	Morocco	2014–2015	Yield trial	6646	Hot steppe	250	29° 49' 48" N, 8° 34' 48" W	Calcic Xerosols
MCH15	Marchouch	Morocco	2014–2015	Yield trial	5741	Mediterranean/warm temperate	449	33° 34' 3.1" N, 6° 38' 0.1" W	Clay vertisol
SAD15	Sidi el Aydi	Morocco	2014–2015	Yield trial	5152	Mediterranean/hot and temperate	237	33° 9' 36" N, 7° 24' 0" W	Vertisol
MCH14	Marchouch	Morocco	2013–2014	Yield trial	5052	Mediterranean/warm temperate	449	33° 34' 3.1" N, 6° 38' 0.1" W	Clay vertisol
JS15	Jemhâa Shaim	Morocco	2014–2015	Yield trial	3966	Hot steppe	270	32° 21' 0" N, 8° 51' 0" W	Calcic Cambisols
ELK15	El Khroub	Algeria	2014–2015	Yield trial	3080	Mediterranean/hot and temperate	540	36° 16' 17.1" N, 6° 41' 6.7" W	Calcic Xerosols
JS14	Jemhâa Shaim	Morocco	2013–2014	Yield trial	1749	Hot steppe	270	32° 21' 0" N, 8° 51' 0" W	Calcic Cambisols
LRC15	Larache	Morocco	2014–2015	Sick plot	–	Mediterranean/warm temperate	627	35° 10' 27.9" N, 6° 8' 50.6" W	Sandy limestone
GCH15	Guich	Morocco	2014–2015	Sick plot	–	Mediterranean/warm temperate	350	33° 58' 17.7" N, 6° 50' 59.3" W	Sandy limestone

application of urea was used to deliver additional 46 kg ha⁻¹ of N. In MKZ15, the first basal fertilization was followed by 5 split applications each of 20 kg ha⁻¹ of N via fertigation through drip pipes. Five environments were irrigated: ALT14, where two gravity irrigations of 35 mm each were provided at tillering stage (Z18) and after flowering (Z65); TES15, where four gravity irrigations of 35 mm each were provided after germination (Z10), Z18, booting (Z45), and after Z65; G-CH15, where disease pressure was increased by three consecutive overnight mist irrigations after Z65; MKZ15, where 12 irrigations of 10 mm each were provided via drip irrigation at one week interval from two weeks after Z10 to dough phase (Z89); TER15, where two sprinkle supplemental irrigation of 20 mm each were provided before Z10 and after Z65. The remaining experiments are conducted under rainfed conditions with total rainfall values and other details presented in Table 2.

2.3. Recorded traits

Leaf rust (LR) was assessed in JSH14, ALT14 and TES15, whereas tan spot (TS) was evaluated in ALT14, JSH15, LRC15 and GCH15, both under natural inoculation conditions. Leaf rust severity was estimated according to Cobb's modified scale and the four classical categories of infection type were also recorded (Stakman et al., 1962). The coefficient of infection (CI) was calculated according to Saari and Wilcoxson (1974) and Pathan and Park (2006) by multiplying disease severity by constant values of infection type. From Z79, tan spot severity was assessed using the double-digit scale (00–99) developed as a modification of Saari and Prescott's scale for assessing severity of foliar diseases of wheat (Eyal et al., 1987; Saari and Prescott, 1975). To obtain a single pathogen response overall, for each genotype the worst susceptible score obtained at any location or replication was considered. For each environment except ALT14 race-typing was done in Minnesota Saint Paul Rust Cereal Disease Laboratory and the University of Montevideo (Gamba et al., 2017), for leaf rust and tan spot, respectively.

Grain yield (GY) was recorded in ten environments: ALT14, ELK15, JSH14, JSH15, MCH14, MCH15, MKZ15, SAD15, TER15 and TES15 by harvesting the central four rows of each plot for a total surface of 4 m², weighting it on a precision scale and dividing this value by the plot surface to obtain kg ha⁻¹.

From the harvest of JSH15, MCH15, TES15 and SAD15, 200 g of seeds for each plot were analyzed for four major quality characteristics: 1000-kernel weight (TKW), grain protein content (GPC), yellow pigment index (YI), and gluten strength (SDS).

1000-kernel weight (TKW) was determined by counting five hundred randomly selected grains on a Choppin Numigral counter followed by weighting on a precision scale. Grain protein content (GPC) was measured using a Chopin Technologies Infraneo near-infrared spectroscopy (NIRs). Whole grain flour samples were obtained with a whole mill grinder (Udy-Cyclone 0.5 mm sieve). The whole flour was used to determine YI as b* value reading on a chroma meter Konica Minolta CR-400. Gluten strength was determined by the SDS (Sodium Dodecyl Sulfate) sedimentation test following a Moroccan standard method (N.M.08.1.217, 1999) equivalent to American Association for Cereal Chemistry method (AACC 56–70).

2.4. Statistical analysis

The residual maximum likelihood (ReML) method of Genstat program version 18 was used to obtain the best linear unbiased estimates (BLUEs) of genotypes across environments, considering genotypes and environments as fixed effects. With the same software, the significance of the fixed effects was assessed using the Wald test to analyze variation and assess the effect of genotype, environment and genotype by environment interaction (GxE).

For grain yield, GxE was partitioned by additive main effects and multiplicative interaction 2 (AMMI) model using R software (version

3.2.4) on R Studio (Nachit et al., 1992). The ‘AMMI wide adaptation index’ (AWAI) was derived from this partitioning to measures the overall stability of each entry as determined by its distance from each significant IPCs axis and it was calculated using the following formula:

$$AWAI = \sum_i s_i * |PC_i|$$

Where i is the number of significant IPCs determined by classical Gollob F-test in R Studio corresponding to 4 IPC in this specific case, s_i is the percentage of total GxE variance explained by each IPC, and PC is the actual IPC value. AWAI values close to ‘0’ are obtained for the most widely adapted and stable germplasm (Malosetti et al., 2013; Bassi and Sanchez-Garcia, 2017). In addition, a “which won where” analysis was conducted using the GEA-R (Genotype x Environment Analysis with R for Windows) version 2.0.

For quality parameters a comparison of the means was performed using the LSD test ($p < 0.05$) estimated from the ANOVA results. The broad sense heritability was estimated by the following formula (Falconer and Mackay, 1996):

$$H^2 = \frac{\sigma_g^2}{\sigma_p^2}$$

Where; σ_g^2 is the genotypic variance and σ_p^2 is the phenotypic variance.

The genotypic and phenotypic variance components were estimated based on the method suggested by Burton and Devane (1953).

$$\sigma_p^2 = \sigma_g^2 + \sigma_e^2 + \sigma_{ge}^2$$

$$\sigma_g^2 = \frac{MS_g - MS_e}{r}$$

$$\sigma_{ge}^2 = \frac{MS_{ge} - MS_e}{r}$$

Where MS_g and MS_{ge} are the mean square due to genotype and GxE interaction, MS_e is the error mean square and r is the number of replicates.

3. Results

3.1. Disease response

Two major durum wheat fungal diseases were recorded, LR and TS. The first was scored in three and TS in four environments. The highest score for LR was 80S (CI=80%) with the highest severity and the maximum virulence found in TES15 with 42% of lines falling above the set susceptibility score of 20MS corresponding to CI of 16%. In TES15 the races were determined to be durum-specific types BBBS and BBBQ, which combined provide virulence against *LrB*, *Lr14a*, and *Lr10*. In addition, race MCDS was identified on the same field but not on durum wheat, which has virulence on *Lr1*, *Lr3*, *Lr26*, *Lr17*, *LrB*, *Lr10* and *Lr14a*. The highest infection for TS in the four environments was 85 (CI = 40%) recorded in ALT14 with 54% of lines scored as susceptible, when susceptibility was set for values above 73 (CI = 21%). In ALT14 and JSH15 the tan spot race was determined to be type 5 and 6 (Gamba et al., 2017). Full details of the responses are provided in Table S1. Instead, Fig. 1 summarizes the overall response of the different types of entries. Regarding LR, 100%, 67%, and 53% susceptible entries were recorded for cultivars, elites, and wide crosses, respectively. For TS, 75%, 33% and 76% susceptible entries were recorded for cultivars, elites, and WC, respectively.

3.2. Grain yield performances

Analysis of variance was conducted for GY over ten environments to confirm statistically significant differences in genotypes, environments, and their interaction (Table 3). Significance differences ($p < 0.001$) were found for all sources of variation. The magnitude of variation was

the highest for environment (97%), then GxE (2%) and G (1%). Broad sense heritability was measured at 41% for the trait. The ten environments varied widely for water abundance and yield performances (Fig. 2), with SAD15 and ELK15 causing the maximum and minimum range of yield variation among genotypes, respectively. ALT14 was the highest yielding environment with a top yield mean of 7322 kg ha⁻¹ despite very virulent strains of LR and TS, where ‘Secondroue’ resulted as the top yielder with 9526 kg ha⁻¹. JSH14 was the most drought prone environment and therefore it had the lowest average yield with only 1749 kg ha⁻¹, and ‘Faraj’ as the best performer with 3762 kg ha⁻¹.

To partition GxE an AMMI study was conducted. In Fig. 3A the AMMI results are graphically present for the first two interaction principal component axes (IPC1 and IPC2), which combined explain 43.5% of the total GxE variation. The high yielding environments MCH14, MCH15, MKZ15, and TES15 fell into the same region and can therefore be considered as having similar effects on the genotypes. The low yielding environments JSH14, JSH15, and SAD15 and the diseased trial of ALT14 spread instead in the opposite axis direction. The two coldest environments TER15 and ELK15 identified a separate cluster. Considered together, these sites provided good contrasting agro-environmental conditions for adequate selection. From the AMMI results a stability index was derived to account for GxE stability (AWAI). The combination of AWAI and the genetic component of GY (BLUES) provides an ideal selection index to combine G and GxE effects across sites (Fig. 3B, Bassi and Sanchez-Garcia, 2017). Three wide-crosses (WC2, WC10, and WC13) resulted as the most stable and high yielding genotypes. ‘Icakasem1’ and ‘Faraj’ were the top yielders of the elites and varieties, respectively, while the elite ‘Secondroue’ and the variety ‘Tomouh’ were the most stable. In total, seven wide crosses fell above average for both BLUE and AWAI. Overall, 14 wide-crosses entries could be selected on the basis of this index before encountering an equally performing elite or variety. In addition, a GGE analysis of “which won where” (Fig. S1) was conducted to identify for each site the best entries that combined G and GxE effects. The analysis revealed seven main ‘where’, four were ‘won’ by WC (WC8, WC13, WC16, and WC14), two by cultivars (‘Louiza’ and ‘Faraj’) and one by the elite line ‘Icarnada’.

3.3. Assessment of quality traits

Harvested grains from four stations in Morocco (MCH15, TES15, JSH15, and SAD15) were used for laboratory analysis of end-use quality traits. These four stations were selected because representing three of the four heterogeneous agro-environments as shown by the AMMI study (Fig. 3A). Four parameters were considered: TKW, GPC, gluten strength (SDS), and YI. ANOVAs for all traits showed significant differences for the genotype effect, while environment and GxE effects were significant only for GPC and TKW. The magnitude of the G effect was higher than the magnitude of the G × E interaction for all quality parameters. The heritability values were 84%, 48%, 81%, and 82% for TKW, GPC, SDS, and YI, respectively (Table 3).

The mean and best BLUE of cultivars, elites and wide crosses are summarized in Table 4. For TKW, the wide crosses were significantly superior in grain size both for maximum and average values, with WC6 having the top score of 56.5 g (full details are provided in Table S2). JSH15 provided the most ideal condition for grain size development with a mean TKW of 53.3 g and maximum value of 60.8 g (Table S3). For GPC, there was no significant difference between germplasm types as average performances, while wide crosses were significantly superior to all other genotypes with a maximum value of 16.1% recorded for WC6. TES15 was the most conducive environment for increasing protein concentration with an average GPC of 15.4%, while MCH15 was the lowest with a GPC mean of 14.2%. SDS test revealed that wide crosses and cultivars were significantly superior to the elites used in this study for both average and maximum strength. WC1, WC 2 and WC3

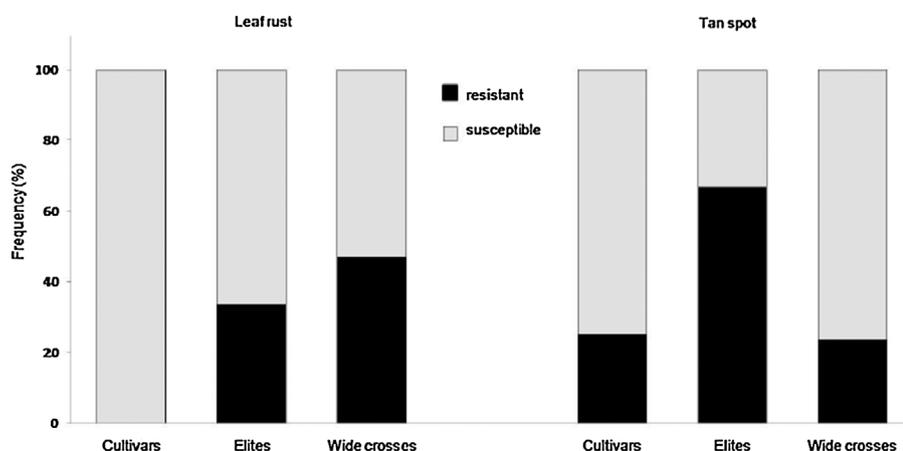


Fig. 1. Leaf rust and tan spot responses of different germplasm type assessed over several environments. Resistance was set at coefficient of infection values of 16% for LR (20MS) and 21% for TS (7-3). The most susceptible score across all environments and all replications was used to determine resistance (black bar) or susceptibility (grey bar) of each entry.

Table 3

Statistical analysis for grain yield (GY) in ten environments, sodium dodecyl sulphate sedimentation test (SDS), yellow pigment content (YPC), and 1000-kernels weight (TKW) in four environments.

Fixed term	df.	F statistic	H ²
<i>GY</i>			41%
Environment (E)	9	1263.21*	
Genotype (G)	23	15.47*	
G x E	207	21.19*	
<i>TKW</i>			84%
Environment (E)	3	9.64	
Genotype (G)	23	22.31*	
G x E	69	3.08*	
<i>GPC</i>			48%
Environment (E)	3	13.87	
Genotype (G)	23	4.96*	
G x E	68	2.66*	
<i>SDS test</i>			83%
Environment (E)	3	1.22	
Genotype (G)	23	10.7*	
G x E	68	1.07	
<i>YPC</i>			82%
Environment (E)	3	3.28	
Genotype (G)	23	13.89*	
G x E	68	1.76	

df – degree of freedom; GY – grain yield; TKW – 1000 kernels weight; GPC – grain protein content; SDS – sodium dodecyl sulphate; YPC – yellow pigment content.

* Significant at 0.001 probability level.

gave high mean of SDS volume across environments and were not significantly different from ‘Louiza’, a variety specifically grown for its good rheological characteristics. As environment source of variation was not significant for SDS, all environments performed the same for this trait. Finally, varieties were superior to the other germplasm type for the average as well as top YI score, as shown by variety ‘Tomouh’

(syn. ‘Om Rabi 3’) with b* score of 22.7, followed by ‘Louiza’, ‘Faraj’ and ‘Waha’ with b* score of 21.1, 19.5 and 19.3 respectively. Lines derived from wide crosses were not significantly different from elites as average score, but outperformed elites with top b* score of 20.2 for WC3, followed by WC2 and WC1 with b* score of 19.9 and 19.1 respectively. As for SDS, YI was not affected by the environments used for testing.

4. Discussion

The aim of this work was to assess the negative aspects associated with the utilization of wide crosses in breeding for superior durum varieties, in terms of grain yield, yield stability, and grain quality. In fact, several authors have reported that the main problem in using wide crosses is the transfer of undesirable genes from the wild. Some genes introgressed from wild relatives have been associated with negative linkage drag and therefore have not been widely deployed in breeding (Baum et al., 1992; Francl, 1992; Mondal et al., 2016; Wulff and Moscou, 2014). For testing this, four CGIAR varieties cultivated in Morocco were selected as checks. ‘Waha’ (syn: Cham1) is an old cultivar still largely cultivated in Algeria with high yield stability, good yellow pigment, early maturing, but susceptible to the new races of leaf rust. ‘Tomouh’ (syn: ‘Om Rabi 3’) is also an old cultivar that occupies approximately 10% (Latican et al., 2016) of the growing area of Morocco, mostly suitable for dry conditions, with medium-tall stature, large yellow grains, resistant to TS, but susceptible to LR. ‘Louiza’ is a recent release of 2011 that has not yet encountered large adoption. It was primarily released for its good yellow pigment and good gluten strength, but it is also susceptible to most fungal diseases. ‘Faraj’ is a release of 2007 that is gaining appreciation by Moroccan farmers thanks to its very high yield potential, resistance to Hessian fly (*Mayetiola destructor* Say.), average resistant to all major diseases, medium gluten strength and yellow pigment. In addition, three elite

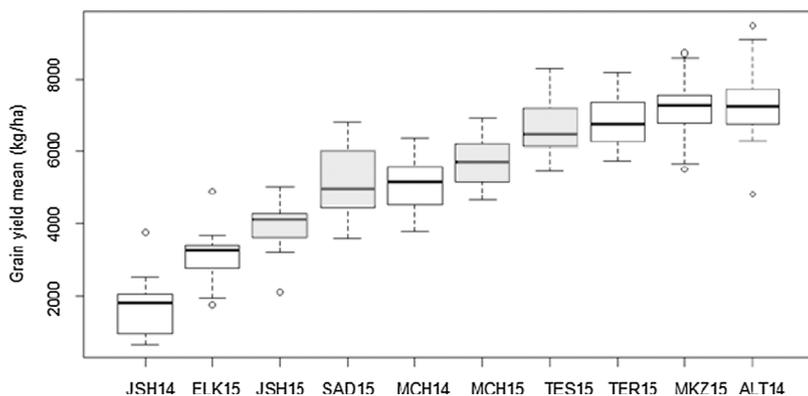


Fig. 2. Box plot of grain yield performances across environments. The medians are indicated by black line inside the boxes. The box borders indicate upper and lower quartiles, the caps indicate 90th and 10th percentiles, and the circles indicate observations below and above those percentiles. Boxes colored in grey represent environments used for end-use quality analysis.

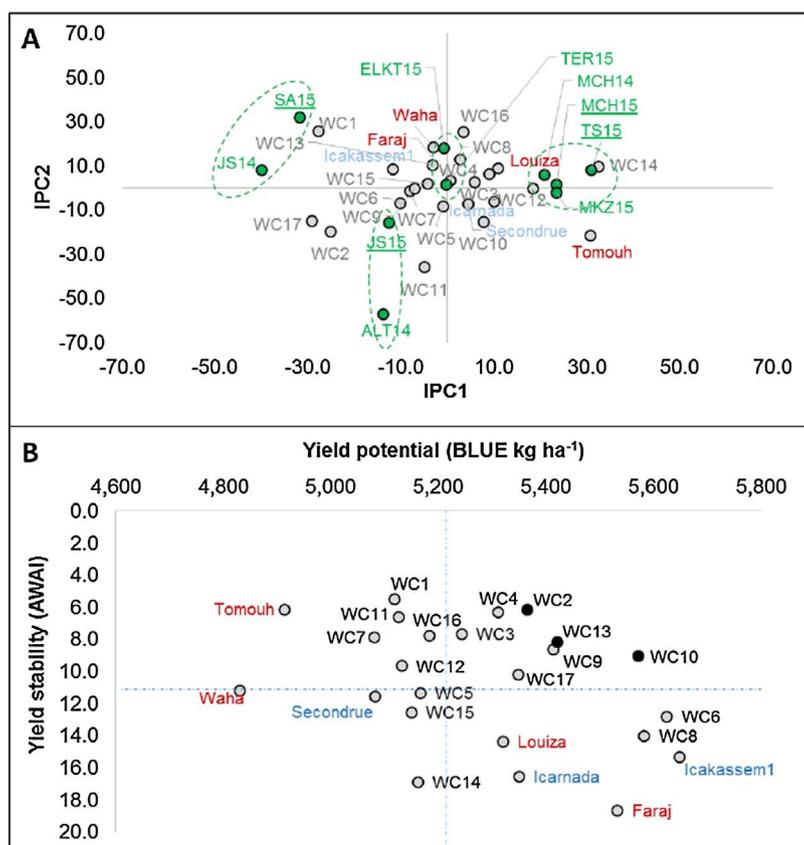


Fig. 3. Dissection of the G×E component of grain yield and its use for selecting top genotypes. (A) AMMI biplot showing the main two IPC (interaction principal components) axis effects of both genotypes and environments on grain yield. (B) Stability and yield potential measured as AMMI wide adaptation index (AWAI) vs. BLUE, best entries are in the top right corner. Green color was used to identify environments, underline to show the sites used for end-use quality analysis, and dashed circles to indicate visually similar environments. Grey color was used to mark the wide crosses (WC), blue was used for elites, and red to color code varieties. A lighter shade was used for WC and elites in Fig. 3A to allow better visualization of the environments. Dashed blue lines indicate the average of each axis. The best three genotypes above averages are indicated in Fig. 3B as solid black circles. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

lines from the ICARDA international durum nurseries were selected on the basis of one year performances at the main research station of Marchouch in season 2012-13 (data not shown). This diverse breeding germplasm was placed in competition with 17 lines derived from top crosses involving several wild species (Table 1) to old ICARDA cultivars. These included ‘Cham 1’ (syn. ‘Waha’), ‘Cham 3’ (syn. ‘Korifla’), ‘Cham 5’ (syn. ‘Om Rabi’), ‘Younes’, ‘Amedakul’, ‘Loukos’, ‘Heider’, and ‘Lahn’. Conversely, all these parental lines have been released as cultivars due to their excellent wide adaptation, moderate to high yield potential, and moderate industrial quality. The Cham series, ‘Younes’ and ‘Loukos’ are all susceptible to the new races of leaf rust, and moderately susceptible to TS. Data are not available for the other parental lines concerning their performances against the most recent races of LR and TS. Therefore, the top crosses tested here are the result of combining these useful traits from cultivars with a portion of the wild genome. In particular, 25% of the wild genome, 25% of the first crossed variety, and 50% of the top crossed variety. These 17 lines were selected from a larger set of 72 genotypes also on the basis of one year selection for yield at the main ICARDA station of Marchouch in 2012-13 (data not shown).

4.1. Wide crosses provide disease resistance

This germplasm was challenged with virulent races of LR at three stations. The naturally occurring races in Morocco carry virulence for *Lr14a*, a gene of great importance for resistance in durum wheat around the World (Terracciano et al., 2013). Further, all races were of the durum type with virulence on *Lr72*, a peculiar gene that distorts the spectrum of virulence on the bread wheat differential set but causes heavy infection on durum wheat (Loladze et al., 2014). Only one variety (‘Faraj’) and one elite (‘Icarmada’) were resistant at all sites against these races, while almost half of the wide crosses lines were immune to the disease. Tan spot diversity in Morocco is wide, with four naturally occurring races (Gamba et al., 2017), probably a result of the lack of cultural rotation in favor of wheat monoculture. In the stations used for testing two of the races were present, providing a broad spectrum of virulence. Elite lines were selected against probably the same races of tan spot the season before this experiment, and it is therefore not surprising that more than 60% of the challenged elites showed good levels of resistance, contrary to wide crosses reaching less than 25% of resistant lines. Among the varieties only ‘Faraj’ showed acceptable response against TS. Overall, the wide crosses showed higher levels of resistance to LR but relatively low resistance to TS. A

Table 4
Average and maximum values of rheological quality traits for varieties, elites and wide crosses across four environments: MCH15, TES15, JSH15, and SAD15.

Germplasm	1000-Kernel weight (g)		Grain protein content (%)		SDS sedimentation test (ml)		Yellow index (b*)	
	Average	Max	Average	Max	Average	Max	Average	Max
Varieties	44.8c	47.5b	14.9a	15.6b	35.4a	46.8a	20.7a	22.7a
Elites	47.3b	48.4b	14.7a	14.9c	24.6b	29.6b	17.4b	18.2c
Wide cross	51.9a	56.6a	15.0a	16.1a	34.4a	44.0a	18.3b	20.2b
Grand Mean	50.1		14.9		33.3		18.6	
LSD	2.3		0.6		5.9		1.0	

total of three lines from wide crosses were simultaneously resistant to TS and LR (WC5, WC7 and WC16), which were derived from crosses with *T. dicoccoides*, *A. speltoides* for both disease, while *T. araraticum* crosses showed good response against LR alone. This is in line with what is reported in the literature to date, since wild relatives and primitive wheats have often been declared as good sources of disease resistance traits (Hadzhiivanova et al., 2012; King, 2015; Mondal et al., 2016; Zhang et al., 2016). Breeding for durable and race non-specific disease resistance requires enlargement of the genetic base using diverse sources of resistance for the different diseases (Zhang et al., 2016), and the material presented here can help in this direction.

4.2. Wide crosses maintain good yield performances

Moderate heritability was obtained for grain yield, a result not dissimilar to what presented by other authors when very diverse environments were used for testing (Bilgin et al., 2010; Karimizadeh et al., 2012; Rashidi, 2011). In fact, the largest part of variation for GY was observed for the environment. Stations average yields varied significantly from 1749 to 7322 kg ha⁻¹, with diverse rainfall, irrigation, soils, management practices, diseases, and temperatures patterns. The AMMI model (Fig. 3A) showed a clear differentiation among the sites used. The group of MCH15, MCH14, MKZ15, and TES15 were similar, probably due to the fact that these stations were able to achieve high yield potential and they had better management practices compared to the other stations. ALT14 is the top yielding environment and should therefore be grouped by AMMI with the other high yielding ones, but it also had some of the most virulent disease races and for this reason its effect on genotypes might be different. Similarly, TER15 was a high yielding site, which instead grouped by AMMI with ELK15, probably due to their similarities in terms of cold winter temperatures, since both stations are located above 800 m from sea level.

In terms of means across environments, the best performing genotype was 'Icakasem1' with an average GY of 5648 kg ha⁻¹. A significant GxE pattern was identified and used to dissect production stability via an AWAI index (Malosetti et al., 2013). A selection index was deployed (Bassi and Sanchez-Garcia, 2017) to combine the genetic (G) factor of GY (BLUE) and the GxE component (AWAI). WC2, WC10, and WC13 were identified as the top yielders and most stable entries. In addition, a "which won where" study also indicated that WC tend to have higher specific adaptation in terms of G plus GxE with four victorious entries over two cultivars and one elite. Line WC13 was identified by both AWAI and "which won where" analysis and should therefore be considered as an ideal candidate for further studies.

The best performing entries were derived by top crosses with *T. dicoccoides* and *A. speltoides*, while *T. araraticum* crosses did not perform quite as well for GY as shown for disease resistance. As reported by previous studies, wild emmer germplasm harbors a rich allelic pool, which can be exploited through breeding (Dong et al., 2009; Wang et al., 2008; Nachit and Elouafi 2004; Habash et al., 2009). Merchuk-Ovnat et al. (2016) had also demonstrated that introgression of wild emmer QTLs can enhance productivity and yield stability across environments in wheat. In addition, the top 14 yielding and stable entries in the study presented here were all wide crosses, suggesting a strong potential to use the wild gene pool for improving agronomic performances, accepting that adequate selection pressure is provided during the selection cycles. This result is not in line with the majority of the available literatures (Dempewolf et al., 2017; Mondal et al., 2016; Nevo and Chen, 2010; Peng et al., 2011; Wulff et al., 2014) that seems to suggest that wide crosses tend to reduce agronomic performances. Here, simple top crosses followed by targeted field selection did not appear to provide any negative effect, rather delivered substantial genetic gain in productivity. An additional good supporting case for the use of wide crosses in wheat breeding for GY is the success obtained by using synthetics and durum by bread wheat crosses to derive new varieties, as shown by the CIMMYT breeding program (Jafarzadeh

et al., 2016; Ratteya et al., 2011).

4.3. Wide crosses do not limit end-use industrial quality

Another important trait targeted by durum wheat breeders is the good industrial transformation performance of the grains. The durum food industry is very careful in purchasing only grains of varieties that guarantee high semolina yields, protein content above 13%, good gluten strength, and high yellow pigment. Farmers have become extremely interested in these characteristics that ensure premium prices at the time of sale, obliging breeders to often prefer them over other mere agronomic characteristics (Nardi, 2016). For that reason, the material was tested for TKW, a good proxy for semolina yield, GPC, SDS to determine gluten strength, and YI in four environments of Morocco. It was found that only two traits (TKW and GPC) depended partially on environmental factors and GxE effect, while SDS and YI were entirely genetically controlled. This is in line with other authors (Nachit et al., 1995; Donatella et al., 2014; Martre et al., 2015; Nazco et al., 2014; Noha et al., 2016) that have come to the same conclusion, also suggesting that GPC was negatively correlated to GY. However, in TES15 both GY and GPC were very high thanks to good management and favorable environmental conditions, indicating that good agronomy can partially break the negative interaction between GPC and GY (Blanco et al., 2011).

Heritabilities were high for all quality traits, meaning that genetic improvement for industrial quality is possible. The only exception is GPC, for which management practices are as important as genetic factors (Nachit et al., 1995; Blanco et al., 2011). In terms of TKW, WC derived from *A. speltoides* resulted in larger kernels, outperforming all other germplasm types. Also for GPC, top crosses with *A. speltoides*, *T. dicoccoides*, and *T. araraticum* provided the highest protein rate. Since *T. araraticum* derivatives did not achieve high GY, it is possible that the high GPC is a result of the negative linkage with productivity. On the other hand, *A. speltoides* and *T. dicoccoides* types were among the best performer, meaning that rather the negative linkage between GY and GPC was broken through breeding, or that these lines responded better to good agronomic practices. Regardless, Levy and Feldman (1989) identified emmer accessions with GPC as high as 24%, compared to about 12% for durum varieties. It is therefore a useful endeavor to seek genetic improvement for this trait among emmer entries. In terms of SDS, there was no significant difference between varieties and WC, meaning that the use of wild relatives did not negatively affect this trait. Varieties performed outstanding for yellow pigment, a critical characteristic considered at the moment of durum wheat variety registration. In particular, 'Tomouh' (syn. 'Om Rabi 6') was the top entry for yellow color. Nevertheless, *T. dicoccoides* derivatives had also good scores for this trait. In fact, several WC scored as high as the remaining three released varieties assessed here (Table S3). Interestingly, no previous selection for yellow pigment was operated throughout the breeding cycle of the WC presented here, meaning that it might be possible to further improve this trait via crosses with wild relatives, if adequate priority is given to it. Previous studies have shown that higher levels of carotenoid pigments are often accumulated by primitive and wild relatives, landraces, and synthetic hexaploids (Zhai et al., 2016). For instance, ancient wheat species einkorn (*Triticum monococcum* var. *monococcum*), Khorasan (*T. turgidum* var. *turanicum*) and durum wheat was shown to contain higher levels of lutein (5.4–7.4 µg g⁻¹) compared to common wheat (1.9 µg g⁻¹) (Hidalgo et al., 2006). However, most authors continue to suggest that the use of wild relatives in wheat breeding often result in poor end-use quality (Farooq and Siddique, 2017; Mondal et al., 2016; Wulff and Moscou, 2014). Considering the results obtained for the germplasm tested here, it was not possible to sustain this claim. Rather, several genetically superior entries could be identified among WC for TKW and GPC, gluten strength was the same for all germplasm types, and acceptable levels of yellow pigment were also identified among WC entries.

5. Conclusion

Several authors have indicated that wheat breeders should rely on crosses with wild relatives only when no other options remains available, because it would inevitably result in a linkage drag of negative alleles for GY or industrial quality (Baum et al., 1992; Curwen-McAdams and Jones, 2017; Dempewolf et al., 2017; Mondal et al., 2016). Here, an experiment was set up to test this hypothesis in durum wheat. The results for all tested traits disagreed with those conclusions, with just a possible exception for yellow pigment, for which one variety was superior to all other germplasm tested. Considering that all WC included here were derived by simple top cross of three wild relative species with old ICARDA varieties, it is hard to justify these results as a unique exception to the general concept that wide crosses are a certain source of negative linkage drags. Rather, it appears that in durum wheat breeding the use of wild relatives through top crossing results in clear genetic gain for all traits of interest. Furthermore, greater variability may yet be found for other traits that were not considered here or by exploiting different wild entries. These findings support good potential outcomes for those breeders and pre-breeders that attempt to introgress novel diversity in durum wheat, including the conscious targeting of complex multi-genic traits that were previously considered as negatively affected.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.fcr.2017.09.007>.

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