Revista de Ciências Agroveterinárias
Universidade do Estado de Santa Catarina (UDESC)

Research Article

Diallel analysis of morpho-agronomic traits in durum wheat (*Triticum durum* Desf.)

Análise dialélica de características morfo-agronômicas no trigo duro (Triticum durum Desf.)

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Submission: March 19th, 2025 | Acceptance: June 27th, 2025

ABSTRACT

Durum wheat (*Triticum durum* Desf.) plays a crucial role in Algeria's agronomic sector, contributing significantly to the economy and food security. This study assesses the genetic effects and combining abilities of key agronomic traits using a 4 × 4 half-diallel mating design. The parents and their six F_1 hybrids were evaluated during the 2021–2022 growing season in a randomized complete block design with three replications at INRAA Institute (Setif, Algeria). Eight morpho-agronomic traits —plant height (PH), spike length (SL), spikes weight (SW), number of spike plant^{-1} (NS), number of grains spike^{-1} (NGS), thousand kernel weight (TKW), grain yield (GY) and above-ground biomass (BIO)—were analyzed. Combining ability was assessed using GRIFFING's Method 2, Model 1 to estimate the general combining ability (*gca*) and specific combining ability (*sca*) effects. Significant *gca* and *sca* effects were observed across all traits, confirming both additive and non-additive genetic influences. Additive gene effects predominated for PH, SL, and GY, while non-additive effects were more relevant for SW, NS, NGS, TKW, and BIO. Waha (P2) and Beni Mestina (P3) showed significant *gca* effects for PH, Achouri (P1) for SL and BIO, Beni Mestina (P3) for SW, NS, GY, and MBB (P4) for TKW, indicating their potential as good general combiners. Hybrids Achouri × Waha (H1) and Beni Mestina × MBB (H6) exhibited significant *sca* effects for PH, while Achouri × Waha (H1) also influenced SL and BIO. Additionally, Beni Mestina × MBB (H6), Achouri × MBB (H3), and Achouri × Waha (H1) exhibited notable *sca* effects for TKW, indicating complementary gene interactions. These findings provide insights into durum wheat's genetic architecture, aiding in the selection of promising parents and hybrids for breeding programs. The results emphasize the complexity of hybrid performance prediction and highlight the importance of careful parental selection to enhance yield and related traits.
KEYWORDS: *Triticum durum. gca. sca.* gene action. Heritability. Semi-arid.

RESUMO

O trigo duro (*Triticum durum* Desf.) desempenha um papel essencial na economia e segurança alimentar da Argélia. Este estudo avaliou efeitos genéticos e capacidades combinatórias de características agronômicas chave em um cruzamento dialélico parcial 4 × 4. Os genitores e seus seis híbridos F_1 foram avaliados na safra 2021–2022 em um delineamento de blocos ao acaso com três repetições no INRAA (Setif, Argélia). Foram analisadas oito características morfo-agronômicas: altura da planta (PH), comprimento da espiga (SL), peso das espigas (SW), número de espigas por planta (NS), número de grãos por espiga (NGS), peso de mil grãos (TKW), rendimento de grãos (GY) e biomassa aérea (BIO). A capacidade combinatória foi estimada pelo Método 2, Modelo 1 de GRIFFING. Efeitos significativos de capacidade geral (*cgc*) e específica (*cec*) de combinação foram observados, indicando influências genéticas aditivas e não aditivas. Efeitos aditivos predominaram para PH, SL e GY, enquanto os não aditivos foram mais relevantes para SW, NS, NGS, TKW e BIO. Os genitores Waha (P2) e Beni Mestina (P3) mostraram *cgc* significativa para PH, Achouri (P1) para SL e BIO, Beni Mestina (P3) para SW, NS e GY, e MBB (P4) para TKW. Os híbridos Achouri × Waha (H1) e Beni Mestina × MBB (H6) exibiram *cec* significativa para PH,

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enquanto Achouri × Waha (H1) também influenciou SL e BIO. Além disso, Beni Mestina × MBB (H6), Achouri × MBB (H3) e Achouri × Waha (H1) mostraram *cec* notável para TKW. Os resultados fornecem insights sobre a genética do trigo duro, auxiliando na seleção de genitores e híbridos promissores para programas de melhoramento, ressaltando a importância da escolha criteriosa de genitores para ganhos em rendimento e qualidade.
PALAVRAS-CHAVE: *Triticum durum. cgc. cec.* Ação gênica. Herdabilidade. Semiárido.

INTRODUCTION

Durum wheat (*Triticum durum* Desf.) is one of the most economically important cereal crops worldwide, playing a central role in the global food industry (OTTAIANO et al. 2022). Its hard texture distinguishes it from other wheat types, allowing it to be milled into semolina—a coarse flour used in pasta, couscous, and certain breads (BENCHELALI et al. 2022, DIMITRIOS 2023). In addition to its industrial value, durum wheat is nutritionally rich in carbohydrates, fiber, essential minerals (iron, magnesium, zinc, selenium), and B-complex and E vitamins (SHEWRY & HEY 2015, IQBAL et al. 2022, KARAKAS et al. 2021).

Adapted to dry and arid climates, durum wheat is well suited to regions with limited water availability (MARTÍNEZ-MORENO et al. 2022, BOUDIAR et al. 2025). It is mainly cultivated in the Mediterranean basin (Southern Europe, North Africa, and the Middle East), as well as in North America, Central Europe, Russia, and Argentina (BLANCO 2024, GROSSE-HEILMANN et al. 2024). Global durum wheat production reached 34.3 million tons across 13.7 million hectares worldwide, representing 6.2% of total wheat cultivation area and 4.5% of global wheat production, making it a vital component of food systems and rural economies (BLANCO 2024).

In Algeria, durum wheat is a strategic crop for food security and rural livelihoods. It is primarily grown under rainfed conditions in the northern regions, and to a lesser extent under irrigation in parts of the Sahara (RABTI et al. 2020, HADDAD et al. 2021, KOURAT et al. 2022, FELLAHI et al. 2024). National production has varied from 1.3 to 3.2 million tons annually, depending on weather, disease pressure, and agronomic practices (MADR-DSASI 2021, BENBELKACEM 2022). In 2020, durum wheat covered 1.5 million hectares, producing 2.6 million tons with an average yield of 1.7 t ha^{-1} (MADR-DSASI 2021), reflecting the lower productivity typical of North African countries compared to major producing regions (GROSSE-HEILMANN et al. 2024). This yield gap reflects the limitations of rainfed systems and highlights a major constraint to Algeria's cereal self-sufficiency. As a result, the country continues to import large volumes of durum wheat, with an average annual cost of around $1 billion (KOURAT et al. 2022).

To improve productivity and reduce reliance on imports, it is essential to develop durum wheat varieties with higher yield potential, better stress tolerance, and improved agronomic traits (LAALA et al. 2021, HANNACHI & FELLAHI 2023). These goals are particularly urgent in the face of climate change and increasing population demands (MANSOURI et al. 2018). In response, the Algerian government has launched several support programs—including subsidies, low-interest credit, technical assistance, and sustainable agriculture policies—to promote domestic wheat production and strengthen food security (BENBELKACEM 2022).

Breeding improved varieties is a central component of this strategy. It involves crossing genotypes with desirable traits such as high yield, stress resistance, and adaptability, followed by selection within segregating populations (FELLAHI et al. 2018, 2020, LAMARA et al. 2022, HANNACHI & FELLAHI 2023). This process is supported by close collaboration between breeders, researchers, and institutions.

Among the tools used in breeding programs, diallel mating designs are particularly valuable for dissecting the genetic architecture of complex traits. These designs involve making crosses among a set of parental lines in a complete, half, or partial diallel fashion, where each parent is crossed with the others to produce hybrid offspring. Several models can be used for diallel analysis, including GRIFFING's (1956a) method, HAYMAN's (1954) method, and mixed model approaches such as the JINKS (1954) model.

The choice of method depends on genetic assumptions, the number of parental lines, and the specific objectives of the study (SINGH & CHAUDHARY 1985). GRIFFING's method allows for the estimation of general combining ability (*gca*) and specific combining ability (*sca*), providing insights into the genetic potential of parents and their interactions. *gca* reflects additive genetic variance, the heritable component used to estimate narrow-sense heritability (h^2_{ns})—a key predictor of selection response. Higher h^2_{ns} values suggest greater expected genetic gain from selection (ACQUAAH 2012). In contrast, *sca* captures non-additive effects, such as dominance and epistasis, which affect hybrid performance but are not reliably inherited. Thus, diallel analysis helps breeders identify superior parents, understand trait inheritance, predict hybrid performance, and design effective breeding strategies (RIBEIRO et al. 2025).

Despite the importance of durum wheat in Algeria, few studies have analyzed the combining ability of local and improved genotypes using diallel designs, especially under semi-arid conditions. This represents a key gap in the knowledge required for breeding programs aiming at yield improvement. Therefore, the objective of this study was to estimate combining ability effects (*gca* and *sca*), heritability, and genetic variance components for key agro-morphological traits in durum wheat, and to identify superior parents and hybrid combinations for breeding high-yielding cultivars adapted to Algerian conditions.

MATERIALS AND METHODS

Plant material and experimental design

The plant material consisted of four durum wheat varieties and their six hybrids developed through 4 × 4 half diallel mating design (Figure 1). The parents are from diverse origins, genetically distinct and represent a wide range of desirable traits and genetic backgrounds.

Achouri (*Mrf1/Stj2//Gdr2/Mgnl1*) is an advanced breeding line, recently selected at Khroub Research station within ICARDA[1]'s nursery coming from Syria. This promising line is characterized by its agronomic performance such as the grain yield, number of spikes and plant height (EL-AREED et al. 2014).

[1] International Center for Agricultural Research in the Dry Areas.

Waha (*Plc/Ruff//Gta's/3/Rolette CM 17904*) is breeding line selected from material originating from CIMMYT[2]-ICARDA. Waha is a stable cultivar known for its adaptability to the Algerian agro-climatic conditions and its agronomic performance (NOUAR et al. 2012, RABTI et al. 2020). Waha possesses several other desirable traits such as short life cycle, medium plant stature and a high capacity for translocation of carbohydrates stored in stems to the grain (BELKHERCHOUCHE et al. 2009). It has, however, a high sensitivity to spring late frost as reported earlier by MEKHLOUF et al. (2006).

Beni Mestina (*Lahn/cham12003*) is a recently registered variety. With its combination of high yield potential, disease resistance, adaptability, and quality attributes, this variety would help meet the demand for durum wheat, supports local food security, and contributes to the economic growth of the country's agricultural industry.

Mohamed Ben Bachir commonly called MBB is a well-known durum wheat cultivar grown in Algeria. This old variety is a selection from a local land race recognized for its wide adaptability to the local agro-climatic conditions. MBB has a tall stature, characterized by its late heading and low above ground biomass partitioning and low grain yield (MEKHLOUF et al. 2006).

Controlled crosses were conducted, in a half diallel mating system, between the four parents during April 2021 by emasculating the florets of the female parent and applying pollen from the male parent. Proper isolation and labeling were maintained to ensure accurate pedigree information.

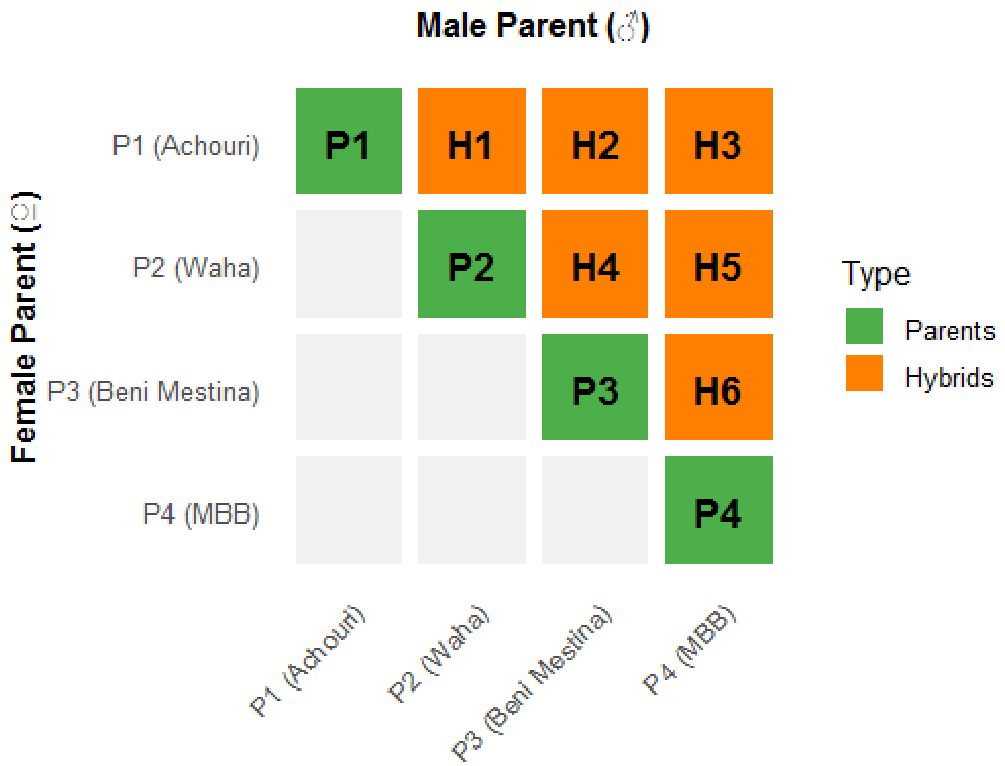

Figure 1. Half-diallel mating scheme of four wheat parents and their six F_1 hybrids.

The experiment was conducted under rainfed conditions at the experimental field

[2] International Maize and Wheat Improvement Center.

of the National Agronomic Research Institute of Algeria (INRAA), Unit of Setif (36°09′ N; 05°22′ E; 981 masl) in the northeastern semi-arid region of Algeria. The experimental plots were prepared in a suitable field site, taking into consideration soil conditions, fertilization, and weed control. The experiment was set up in December 2021 using a randomized complete block design (RCBD) with three replications. Each genotype was sown in a single 2.5 m row per replicate with 20 cm between rows and approximately 15 cm seed spacing within rows. The total rainfall from September 2021 to June 2022 was 330 mm. The soil texture at the experimental site was silty clay (44% clay, 44% silt, 12% sand) with a pH of 7.8 and 1.05% organic matter.

Data Collection and Statistical Analyses

Various morpho-agronomic traits of interest were recorded at different growth stages. These traits include plant height (PH, cm), spike length (SL, cm), spikes weight (SW, g plant^{-1}), number of spike plant^{-1} (NS, No plant^{-1}), number of grains spike^{-1} (NGS, No plant^{-1}), thousand kernel weight (TKW, g), grain yield (GY, g plant^{-1}) and above-ground biomass (BIO, g plant^{-1}). Standardized measurement protocols were followed to ensure consistency and accuracy.

Initially, one-way analysis of variance (ANOVA) for each trait was performed to determine the significance of ‘genotype’ effects based on a collected data on the ten genotypes (four parents + six hybrids) according to the procedure given by STEEL & TORRIE (1984). Sum of squares of the ‘genotype’ source of variation for measured traits were further partitioned into ‘parents’, ‘hybrids’ and the contrast ‘parents vs. hybrids’ as described by SHARMA (2006).

The comparison of means was performed using Fisher’s Least Significant Difference Test at 0.05 probability level ($LSD_{0.05}$). Traits exhibiting significant genotypic differences were subjected to combining ability analysis. Both general combining ability (*gca*) and specific combining ability (*sca*) components, including their variances and effects, were computed following GRIFFING’s Method 2, Model 1 approach (GRIFFING 1956a) as detailed by SINGH & CHAUDHARY (1985).

Statistical significance of general (σ^2_{gca}) and specific (σ^2_{sca}) combining ability variances was evaluated by comparing them with their corresponding error variances obtained from the mean-level ANOVA. Individual *gca* and *sca* effects were assessed for significance through *t*-test analysis. Partitioning of genetic variance into additive (σ^2_A), dominance (σ^2_D) and environmental (σ^2_E) components was accomplished for each measured trait following the methodology of GRIFFING (1956b) using *gca* and *sca* variance estimates.

The predictability ratio, proposed by BAKER (1978), was calculated as follows:

$$BAKER's\ ratio\ =\ 2\sigma^2_{gca}\ /\ (2\sigma^2_{gca}\ +\ \sigma^2_{sca})$$

The estimated broad-sense (h^2_{bs}) and narrow-sense (h^2_{ns}) heritability were obtained based on the above calculated variances according to the equations given by ACQUAAH (2012):

$$h^2_{bs} = \sigma^2_G\ /\ \sigma^2_P$$
$$h^2_{ns} = \sigma^2_A\ /\ \sigma^2_P$$

Where: σ^2_G and σ^2_P are the phenotypic variance is the genotypic variance, respectively. σ^2_G and σ^2_P were estimated as follows:

$$\sigma^2_G = \sigma^2_A + \sigma^2_D$$

$$\sigma_P^2 = \sigma_A^2 + \sigma_D^2 + \sigma_E^2$$

Genes software (CRUZ 2013) was used to perform the statistical and genetic data analyses of the morpho-agronomic recorded traits.

RESULTS AND DISCUSSION

Analysis of variance

The significant differences observed among the studied genotypes for all measured traits, as presented in Table 1, suggest that both parents and their hybrids exhibited substantial genetic variability.

Table 1. One-way ANOVA test for agro-morphological traits in durum wheat.

S.O.V	df	PH	SL	SW	NS	NGS	TKW	GY	BIO
Block	2	3.98	0.16	4.99	0.34	5.81	2.76	2.31	1.16
Genotypes	9	669.14**	1.62**	130.42**	38.75**	74.57**	41.18**	55.35**	461.10**
Parents (P)	3	1109.90**	1.50**	86.62^{ns}	35.76*	1.32^{ns}	40.79*	73.40**	95.90^{ns}
Hybrids (H)	5	455.22**	1.42**	78.42**	18.65**	45.74**	28.51^{ns}	23.47**	287.19**
P vs H	1	138.70^{ns}	0.98^{ns}	173.97*	49.40*	146.16**	35.22^{ns}	53.49^{ns}	808.80**
Error	18	23.61	0.09	16.01	3.29	6.69	6.79	2.79	65.94

S.O.V: Source of variation, PH: Plant height, SL: Spike length, SW: Spikes weight, NS: Number of spike plant^{-1}, NGS: Number of grains spike^{-1}, TKW: Thousand kernel weight, GY: Grain yield, BIO: Above-ground biomass. ns, * and **: non-significant and significant at 0.05 and 0.01 probability levels, respectively.

The partitioning of the analysis of variance revealed highly significant mean squares attributed to ‘genotypes’, ‘parents’ and ‘hybrids’ across most traits, indicating substantial genetic variability within the durum wheat population studied. Exceptions included thousand kernel weight (TKW) in ‘hybrids’ and spike weight (SW), number of grains per spike (NGS), and above-ground biomass (BIO) in ‘parents’, which showed non-significant variation.

The significant contrast observed between parents and hybrids for traits such as spike weight (SW), number of spikes per plant (NS), number of grains per spike (NGS) and above-ground biomass (BIO) suggests differences in trait expression between the parental lines and their hybrids. This significant contrast underscores the potential for exploiting heterosis or hybrid vigor in current durum wheat breeding program.

Such findings provide valuable insights into the genetic architecture of the traits studied and may inform breeding strategies aimed at enhancing yield and agronomic performance in durum wheat varieties. These results are in harmony with those reported by KAMARA et al. (2022) and GALAL et al. (2023).

Mean performance of parents and their F_1 hybrids

Table 2 presents a detailed analysis of the mean performance of agro-morphological traits measured in durum wheat population under study.

Notably, considerable phenotypic diversity was observed among the genotypes for each trait assessed. For instance, in terms of plant height (PH), parental line Achouri (P1) exhibited the tallest plants at 103.42 cm, while hybrid Beni Mestina × MBB (H6) displayed the shortest plants at 51.00 cm. This substantial range in plant height suggests the presence of diverse genetic backgrounds contributing to phenotypic differences within the durum wheat population.

Table 2. Mean performance of agro-morphological traits in durum wheat.

Genotypes	PH	SL	SW	NS	NGS	TKW	GY	BIO
P1	103.42[a]	8.73[a]	17.73[bcd]	9.17[c]	48.47[ab]	23.00[e]	9.21[cd]	47.82[a]
H1	74.78[cd]	8.57[ab]	15.25[cd]	7.58[c]	43.63[cd]	29.35[bcd]	8.61[cd]	27.61[cd]
H2	82.82[bc]	8.01[c]	20.04[bc]	9.42[bc]	44.92[bc]	29.61[bcd]	11.35[bc]	39.75[abc]
H3	85.44[b]	7.83[cd]	13.94[cd]	6.97[c]	35.82[f]	33.38[ab]	7.85[d]	30.83[bcd]
P2	65.11[e]	8.07[bc]	23.38[ab]	12.33[b]	49.76[a]	26.66[de]	13.34[b]	38.36[abc]
H4	68.98[de]	7.41[de]	15.32[cd]	7.50[c]	45.53[abc]	30.47[bcd]	9.06[cd]	28.67[bcd]
H5	70.20[de]	6.90[ef]	11.76[d]	7.01[c]	40.27[de]	28.23[cd]	7.24[d]	21.93[de]
P3	63.17[e]	8.80[a]	29.03[a]	15.67[a]	49.80[a]	28.10[cd]	19.24[a]	51.07[a]
H6	51.00[f]	6.77[f]	4.65[e]	2.00[d]	38.33[ef]	36.44[a]	2.90[e]	10.45[e]
P4	87.53[b]	7.28[ef]	17.87[bcd]	7.97[c]	48.86[ab]	31.91[bc]	8.44[d]	42.34[ab]
Parents mean	79.81	8.22	22.01	11.28	49.22	27.42	12.56	44.90
Hybrid mean	72.20	7.58	13.49	6.75	41.42	31.25	7.83	26.54
Overall mean	75.24	7.84	16.90	8.56	44.54	29.72	9.72	33.88
$LSD_{0.05}$	8.34	0.52	6.86	3.11	4.44	4.47	2.87	13.93

PH: Plant height, SL: Spike length, SW: Spikes weight, NS: Number of spike plant^{-1}, NGS: Number of grains spike^{-1}, TKW: Thousand kernel weight, GY: Grain yield, BIO: Above-ground biomass. Means in each column followed by similar letter (s), are not significantly different at 0.05% probability level, using Fisher's Least Significant Difference Test ($LSD_{0.05}$).

Spike length (SL), spike weight (SW) and number of spikes (NS) showed significant variability across the studied genotypes, indicating diverse spike characteristics in durum wheat. Beni Mestina (P3) stood out with the highest SL (8.80 cm), SW (29.03 g plant^{-1}), and NS (15.67 spikes plant^{-1}), suggesting superior spike attributes compared to other genotypes. Conversely, Beni Mestina × MBB (H6) displayed the lowest values for these traits (6.77 cm, 4.65 g plant^{-1}, 2.00 spikes plant^{-1}), hinting at potential limitations in spike development and reproductive performance. Moreover, the number of grains per spike (NGS) also showcased substantial diversity among genotypes.

The parent Beni Mestina (P3) exhibited the highest spike's fertility (49.80 grains spike^{-1}), indicating robust reproductive potential, whereas the hybrid Beni Mestina × MBB (H6) displayed the lowest value (35.82 grains spike^{-1}) for this trait. These findings underscore the critical importance of comprehending the genetic variability present in spike characteristics to effectively optimize grain yield and overall productivity in durum wheat breeding programs.

The observed diversity in spike length bears significant implications for traits such as grain yield and spike architecture, hinting at promising opportunities for targeted breeding strategies aimed at enhancing spike morphology and thereby improving yield potential in durum wheat varieties. Moreover, the variation observed in spike weight serves as a reflection of disparities in reproductive efficiency and biomass allocation, which are pivotal factors influencing grain yield in durum wheat (GUO et al. 2018).

By understanding and leveraging this variability, breeders can tailor their selection criteria and breeding efforts to prioritize genotypes with optimal spike traits for improved grain yield. Similarly, the variation in spike number holds implications for reproductive potential and ultimately grain yield, highlighting the need for careful consideration of this trait in breeding programs focused on enhancing yield and agronomic performance in durum wheat varieties.

Thousand kernel weight (TKW) varied considerably across genotypes, with hybrid Beni Mestina × MBB (H6) producing the heaviest grains at 36.44 g, while parent Beni Mestina (P3) yielded the lightest grains in spike at 23.00 g. This variation in TKW underscores the importance of grain size and weight in determining overall yield potential and grain quality in durum wheat.

Furthermore, grain yield (GY) and above-ground biomass (BIO) demonstrated a wide range of variability within the plant material under study. Beni Mestina (P3) produced the highest GY (19.24 g $plant^{-1}$) and BIO (51.07 g $plant^{-1}$), indicating superior yield potential and biomass accumulation compared to other genotypes. Conversely, hybrid Beni Mestina × MBB (H6) gave the lowest values (2.90 g $plant^{-1}$ and 10.45 g $plant^{-1}$) for these traits, suggesting potential trade-offs between yield components and biomass allocation. These findings highlight the complexity of trait interactions and the need for comprehensive breeding strategies to optimize yield and agronomic performance in durum wheat varieties.

Component of genetic variation

The analysis of variance (ANOVA) for combining ability using GRIFFING's model presented in Table 3 revealed significant insights into the genetic interactions influencing agro-morphological traits in durum wheat.

Table 3. Estimates of components of genetic variance of agro-morphological traits in durum wheat.

Components	df	PH	SL	SW	NS	NGS	TKW	GY	BIO
gca	3	1450.08**	2.88**	90.70**	31.64**	30.80*	58.43**	62.86**	233.95*
sca	6	278.73**	0.98**	150.19**	42.31**	96.51**	32.50**	51.66**	574.75**
Error	18	23.61	0.09	16.01	3.29	6.69	6.79	2.79	65.94
σ^2_{gca}		79.25	0.16	4.15	1.58	1.34	2.87	3.34	9.33
σ^2_{sca}		85.04	0.29	44.73	13.01	29.94	8.57	2.79	169.60
$\sigma^2_{gca}/\sigma^2_{sca}$		0.93	0.53	0.09	0.12	0.04	0.33	1.20	0.06
σ^2_A		158.50	0.31	8.30	3.15	2.68	5.74	6.67	18.67
σ^2_D		85.04	0.29	44.73	13.01	29.94	8.57	2.79	169.60
BAKER's ratio		0.65	0.51	0.16	0.19	0.08	0.40	0.71	0.10
h^2_{bs}		0.91	0.87	0.77	0.83	0.83	0.68	0.77	0.74
h^2_{ns}		0.59	0.44	0.12	0.16	0.07	0.27	0.54	0.07

PH: Plant height, SL: Spike length, SW: Spikes weight, NS: Number of spike $plant^{-1}$, NGS: Number of grains $spike^{-1}$, TKW: Thousand kernel weight, GY: Grain yield, BIO: Above-ground biomass. ns, * and **: non-significant and significant at 0.05 and 0.01 probability levels, respectively. *gca*: general combining ability, *sca*: specific combining ability, σ^2_{gca}: general combining ability variance, σ^2_{sca}: specific combining ability variance, σ^2_A: additive variance, σ^2_D: dominance variance, h^2_{bs}: broad-sense heritability, h^2_{ns}: narrow-sense heritability.

The mean squares due to general combining ability (*gca*) and specific combining ability (*sca*) were significant to highly significant for all traits analyzed. Significant *gca* effects reflect additive genetic effects and additive × additive interactions, representing the heritable portion of genetic variation passed from the parent to its progeny (OWUSU et al. 2020). Similarly, significant *sca* effects indicate the importance of non-additive gene action in trait expression. These findings align with previous studies by

MOHAMMADI et al. (2021), DRAGOV (2022) and GALAL et al. (2023), emphasizing the importance of both additive and non-additive gene actions in wheat inheritance.

The variances due to *sca* (σ^2_{sca}) were consistently higher in magnitude than their corresponding *gca* variances (σ^2_{gca}) for all traits, except grain yield (GY), indicating a predominant role of non-additive genetic variance in most traits. When translated into additive genetic variance (σ^2_A) and dominance genetic variance (σ^2_D), results indicated that σ^2_A values surpassed σ^2_D values for plant height (PH), spike length (SL) and grain yield (GY), indicating the preponderance of additive gene actions. Conversely, the σ^2_D values exceeded σ^2_A values for the remaining traits, signifying the significant influence of non-additive gene actions, likely attributed to dominance or various epistatic interaction effects, in governing the inheritance of yield and its component traits. This observation aligns with previous studies reporting dominance genetic variance values to exceed corresponding additive values (NAGAR et al. 2018, ES'HAGHI SHAMSABADI et al. 2019, RUBBY et al. 2023).

However, contrasting findings exist, as evidenced by studies conducted by HANNACHI et al. (2013) in durum wheat, MOHAMMADI et al. (2021) in emmer wheat, and KAMARA et al. (2022) in bread wheat, which found additive gene action predominant in most traits. These discrepancies highlight the importance of considering genetic background and environmental conditions when interpreting results across different studies.

Indeed, while the $\sigma^2_{gca}/\sigma^2_{sca}$ ratio serves as a conventional metric for evaluating gene action, its interpretation should be nuanced due to the intricate nature of gene interactions, which can be influenced by differential parental abilities to combine effectively, as well as complex gene-environment interactions. In the case of plant height (PH) and spike length (SL), although the $\sigma^2_{gca}/\sigma^2_{sca}$ ratio was below unity, indicating a greater role for non-additive gene action, the observation that the additive genetic variance (σ^2_A) exceeded the dominance genetic variance (σ^2_D) suggests a predominant influence of additive gene action on the inheritance of PH and SL.

Therefore, while additive gene effects primarily govern the genetic control of these morphological traits, the presence of some degree of dominance gene action also contributes to their expression. A BAKER's ratio above 0.5 for plant height (PH), spike length (SL) and grain yield (GY) further confirms the substantial influence of additive gene action on shaping these traits.

Conversely, traits with BAKER's ratio near zero suggests a greater importance of *sca* estimates, indicating the predominance of non-additive gene action. Consequently, relying solely on *gca* values for predicting hybrid performance would be ineffective. This implies that genetic improvements for these traits would be more effective through hybridization followed by selection in subsequent generations, where genes are fully fixed and expressed, dominance is dispersed, and undesirable linkages are broken (ESTAKHR & HEIDARI 2012).

Broad-sense (h^2_{bs}) and narrow-sense (h^2_{ns}) heritability estimates provides valuable insights into the genetic control of qualitatively and quantitatively inherited traits. By understanding the relative contributions of additive and non-additive genetic effects to trait inheritance, breeders can develop more effective breeding strategies to enhance yield, quality and agronomic performance in wheat varieties (ACQUAAH 2012).

In this study, h^2_{bs} values ranged from 0.68 for thousand kernel weight (TKW) to 0.91 for plant height (PH). High h^2_{bs} estimates observed for all traits indicate that a significant portion of trait variation is attributable to genetic factors. These findings imply that there is substantial genetic variability underlying these traits, providing breeders with opportunities for effective selection and improvement through breeding programs.

Traits with high h^2_{bs} values are likely to respond well to selection, leading to more predictable improvements in subsequent generations. Narrow-sense heritability (h^2_{ns}) varied between 0.07 for number of grains per spike (NGS) and above-ground biomass (BIO, and 0.59 for plant height (PH).

The varying degrees of h^2_{ns} across traits highlight the relative contributions of additive genetic effects to trait inheritance. Selection for traits such as PH, SL and GY with intermediate h^2_{ns} values is likely to result in more predictable and heritable improvements over generations, making them ideal targets for breeding programs aimed at enhancing yield and agronomic performance in durum wheat varieties.

Conversely, traits including SW, NS, NGS, TKW and BIO with low h^2_{ns} values may be influenced to a greater extent by non-additive genetic effects or by environmental factors. Selection for these traits may result in less predictable outcomes across generations, as their expression is influenced by a combination of genetic and environmental factors (ES'HAGHI SHAMSABADI et al. 2019).

Estimates of *gca* and *sca* effects

General combining ability (gca) effects

Table 4 presents a comprehensive overview of the estimates of general combining ability (*gca*) effects for the four parents across various measured traits in durum wheat. The highly significant positive values of *gca* effects are typically desirable for most traits, indicating superior performance in hybrid combinations. However, for plant height (PH), negative values would be favorable from a breeder's perspective, as shorter plants are often preferred (FELLAHI et al. 2023). In this study, no single parent exhibited significant *gca* effects in the desired direction across all assessed traits, highlighting the need for careful selection and breeding strategies to achieve desired trait combinations.

Both positive and negative *gca* effects were observed for plant height (PH), reflecting the differential contributions of parents depending on breeding objectives. Achouri (P1) exhibited a highly significant positive *gca* effect (12.28**), indicating its strong contribution to increased plant height in its hybrids —a trait that may be desirable in contexts where greater biomass is targeted. In contrast, Waha (P2) and Beni Mestina (P3) displayed significant negative *gca* effects (−5.34** and −7.21**, respectively), making them effective choices in breeding programs aiming to reduce plant height, a common strategy for improving lodging resistance and yield stability. In terms of spike length (SL), Achouri (P1) demonstrated a significant positive *gca* effect (0.45**), supporting its use as a general combiner for this trait, since its hybrids tended to have longer spikes. This contrasts with MBB (P4), which showed a significant negative *gca* effect (−0.52**), indicating a potential limitation in this trait. Beni Mestina

(P3) recorded a significant positive *gca* effect (2.26*) for spikes weight (SW), implying its potential to contribute positively to this yield component. In contrast, MBB (P4) exhibited a significant negative *gca* effect (−3.07**), indicating its limited utility for improving spike weight.

Table 4. Estimates of general combining ability (*gca*) for the four parents for the measured traits.

Parents	PH	SL	SW	NS	NGS	TKW	GY	BIO
P1	12.28**	0.45**	0.03^{ns}	-0.08^{ns}	-0.23^{ns}	−1.71**	-0.40^{ns}	4.07*
P2	−5.34**	-0.03^{ns}	0.77^{ns}	0.66^{ns}	1.04^{ns}	-1.20^{ns}	0.50^{ns}	-2.41^{ns}
P3	−7.85**	0.10^{ns}	2.26*	1.24**	0.95^{ns}	0.69^{ns}	2.19**	1.93^{ns}
P4	0.91^{ns}	−0.52**	−3.07**	−1.82**	−1.76**	2.22**	−2.29**	−3.59*
SE (g_i)	0.99	0.06	0.82	0.37	0.53	0.53	0.34	1.66
SE ($g_i - g_j$)	1.62	0.10	1.33	0.60	0.86	0.87	0.56	2.71

PH: Plant height, SL: Spike length, SW: Spikes weight, NS: Number of spike plant^{-1}, NGS: Number of grains spike^{-1}, TKW: Thousand kernel weight, GY: Grain yield, BIO: Above-ground biomass. ns, * and **: non-significant and significant at 0.05 and 0.01 probability levels, respectively.

For the number of spikes (NS), Beni Mestina (P3) also showed a significant positive *gca* effect (1.24**), suggesting its suitability for increasing tillering capacity — an important yield determinant. Conversely, MBB (P4) displayed a significant negative *gca* effect. For number of grains per spike (NGS), MBB (P4) was the only parent to exhibit a significant *gca* effect (−1.76**), albeit in an undesirable direction. This indicates that the remaining parents had a limited ability to influence this trait positively, emphasizing the need to select superior parental combinations for improving grain number. Interestingly, MBB (P4) emerged as a strong general combiner for grain size, as evidenced by its significant and positive *gca* effect (2.22**) for thousand kernel weight (TKW).

Conversely, Achouri (P1) exhibited the highest negative *gca* effect (−1.71**) for this yield-contributing trait. For grain yield (GY), *gca* effects varied considerably across parents. Beni Mestina (P3) showed a significant positive *gca* effect (2.19**), while MBB (P4) displayed a significant negative *gca* effect (−2.29**), indicating differential contributions of these parents in GY of their hybrids. Finally, Achouri (P1) demonstrated significant positive *gca* effect (4.07*) for above-ground biomass (BIO), reinforcing its potential as a parent contributing to biomass accumulation. Conversely, MBB (P4) showed significant negative *gca* effect (−3.59*), suggesting its hybrids may have lower biomass production, which could impact overall plant vigor and productivity.

Overall, the *gca* effects observed across parents in this study underscored their differential contributions to various traits in hybrid combinations, emphasizing the necessity of considering parental genetic backgrounds in durum wheat breeding programs. These results are consistent with previous findings in the literature, where both positive and negative significant *gca* effects for yield and yield-related traits have been reported (NAGAR et al. 2018, MOHAMMADI et al. 2021, KAMARA et al. 2022, MEZZOMO et al. 2022, SAINI et al. 2023). This highlights the complexity of trait inheritance and the importance of understanding the genetic basis of trait expression in breeding efforts aimed at improving durum wheat varieties.

Specific combining ability (sca) effects

Table 5 provides insightful estimates of specific combining ability (*sca*) effects for six hybrid combinations across various agronomic traits in durum wheat. Notably, no hybrid combinations displayed significant *sca* effects in the desired direction for all measured traits. Nonetheless, certain hybrids exhibited noteworthy and favorable *sca* effects for multiple traits, highlighting their potential for targeted breeding programs. For plant height (PH), hybrid Waha × Beni Mestina (H4) demonstrated a significant positive *sca* effect (6.92**), indicating its tendency to produce taller plants. In contrast, Beni Mestina × MBB (H6) and Achouri × Waha (H1) exhibited significant negative *sca* effects (−17.31** and −7.40**, respectively) for PH, suggesting their potential to generate shorter plants.

Table 5. Estimates of specific combining ability (*sca*) for the six hybrids for the measured traits.

Hybrids	PH	SL	SW	NS	NGS	TKW	GY	BIO
H1	−7.40**	0.31*	-2.45^{ns}	-1.55^{ns}	-1.72^{ns}	2.54*	-1.22^{ns}	−7.93*
H2	3.15^{ns}	−0.38**	0.84^{ns}	-0.30^{ns}	-0.33^{ns}	0.91^{ns}	-0.17^{ns}	-0.14^{ns}
H3	-2.99^{ns}	0.06^{ns}	0.07^{ns}	0.31^{ns}	−6.73**	3.16**	0.81^{ns}	-3.53^{ns}
H4	6.92**	−0.50**	−4.61**	−2.96**	-1.00^{ns}	1.26^{ns}	−3.36**	-4.73^{ns}
H5	-0.62^{ns}	−0.38**	-2.84^{ns}	-0.40^{ns}	−3.5**	−2.50*	-0.69^{ns}	-5.95^{ns}
H6	−17.31**	−0.65**	−11.45**	−5.99**	−5.40**	3.82**	−6.72**	−21.78**
SE (s_{ii})	1.77	0.11	1.46	0.66	0.94	0.95	0.83	2.97
SE (s_{ij})	2.40	0.15	1.98	0.90	1.28	1.29	0.61	4.01
SE ($s_{ii} - s_{jj}$)	2.29	0.14	1.89	0.85	1.22	1.23	0.79	3.83
SE ($s_{ij} - s_{ik}$)	3.62	0.23	2.98	1.35	1.93	1.94	1.25	6.05
SE ($s_{ij} - s_{kl}$)	3.24	0.20	2.67	1.21	1.72	1.74	1.11	5.41

PH: Plant height, SL: Spike length, SW: Spikes weight, NS: Number of spike plant^{-1}, NGS: Number of grains spike^{-1}, TKW: Thousand kernel weight, GY: Grain yield, BIO: Above-ground biomass. ns, * and **: non-significant and significant at 0.05 and 0.01 probability levels, respectively.

Regarding spike length (SL), significant negative *sca* effects were observed for Achouri × Beni Mestina (H2) (−0.38**), Waha × Beni Mestina (H4) (−0.50**), Waha × MBB (H5) (−0.38**), and Beni Mestina × MBB (H6) (−0.65**), indicating that these crosses may produce shorter spikes than their parental lines. Conversely, Achouri × Waha (H1) exhibited a significant positive *sca* effect (0.31*), suggesting a tendency toward increased spike length. Additionally, crosses Beni Mestina × MBB (H6) and Waha × Beni Mestina (H4) showed significant negative *sca* effects for spikes weight (SW) per plant (−11.45** and −4.61**, respectively) and number of spikes (NS) (−5.99** and −2.96**, respectively), indicating a decrease in tillering capacity and their potential to produce hybrids with lighter spikes.

None of the hybrids displayed significant positive *sca* effects for SW and NS, emphasizing the need to select alternative parental combinations for improving this trait. For the number of grains per spike (NGS), Beni Mestina × MBB (H6) recorded a highly significant negative *sca* effect (−5.40**), while Waha × MBB (H5) also exhibited a negative effect (−3.50**). Achouri × MBB (H3) showed the most substantial reduction (−6.73**), suggesting potential constraints in grain formation in these hybrids. Thousand kernel weight (TKW), a crucial yield component, displayed significant positive *sca* effects (3.82**, 3.16** and 2.54*) in Beni Mestina × MBB (H6), Achouri ×

MBB (H3) and Achouri × Waha (H1), producing larger grains. Conversely, Waha × MBB (H5) exhibited a significant negative *sca* effect (−2.50*), suggesting a potential reduction in grain size.

For grain yield (GY), none of the hybrids displayed significant positive *sca* effect (3.43*). In contrast, Beni Mestina × MBB (H6) and Waha × Beni Mestina (H4) exhibited significant negative *sca* effects (−6.72** and −3.36**, respectively), suggesting lower yield potential. The results highlight the challenge of obtaining hybrids that simultaneously improve multiple yield-contributing traits. Above-ground biomass (BIO) showed a significant negative *sca* effect in Beni Mestina × MBB (H6) (−21.78**), indicating reduced biomass accumulation in this cross. Achouri × Waha (H1) also exhibited a significant negative *sca* (−7.93*). Further underscoring the variation in biomass production among hybrids. The remaining cross combinations did not exhibit a significant deviation from their parents in terms of BIO, highlighting the variability in genetic interactions affecting above-ground biomass accumulation among hybrids.

Overall, the observed *sca* effects reflect the complex genetic interactions shaping morpho-agronomic traits in durum wheat hybrids and provide valuable insights for future breeding endeavors. These findings resonate with previous research, which has similarly documented positive and negative significant *sca* effects in wheat hybrid combinations, particularly concerning various yield-contributing traits (KAMARA et al. 2022, MEZZOMO et al. 2022, GALAL et al. 2023, SAINI et al. 2023).

Progeny selection stands as a critical phase in the field of plant breeding, where the choices regarding parental lines profoundly shape its success. Central to this process is the assessment of combining ability, a valuable tool for evaluating the genetic potential of both parent lines and the hybrids they produce (FASAHAT et al. 2016). Consequently, the level of combining ability emerges as a crucial criterion in parental selection for hybridization, directly influencing the quality of the resulting progeny.

Our results indicate the presence of a direct correlation between *gca* effects and parental performance. This suggests that *gca* effects can serve as a reliable predictor of overall performance across the measured traits. Moreover, we observed a significant association between specific combining ability (*sca*) effects and hybrid performance, suggesting that the performance *per se* of hybrids can be more accurately forecasted based on their *sca* effects. Interestingly, for certain traits, parents demonstrating high *gca* effects yielded hybrids with lower *sca* effects, while those with low *gca* effects produced hybrids with important *sca* effects.

This underlines the intricate dynamics between parental *gca* and the resulting crosses' *sca*, which are essential for enhancing breeding efficiency based on combining abilities (LIU et al. 2021). Our findings challenge the notion of a clear relationship between the *gca* effects of parents and the *sca* effects of the single crosses. The performance of hybrids appeared largely independent of the mean performance of the parents involved, suggesting that high *gca* values of parents may not guarantee high *sca* effects of their crosses.

Therefore, relying solely on specific combining ability tests for parent selection may not be advisable. Our study, akin to findings by ZHANG et al. (2017), HAN et al. (2018) and LIU et al. (2021) who reported a lack of fixed correlation between *gca* and *sca*. Nonetheless, it's important to note that other studies, such as YU et al. (2020) and SCHWARZWÄLDER et al. (2022), suggest that parental *gca* could still serve as a dependable predictor of hybrid performance *per se*.

CONCLUSION

This study assessed the genetic effects and combining abilities in durum wheat using a 4 × 4 half-diallel mating design. Additive gene action predominantly governed plant height (PH), spike length (SL), and grain yield (GY), whereas non-additive gene action influenced yield-related traits including spike weight (SW), number of spikes (NS), number of grains per spike (NGS), thousand-kernel weight (TKW), and biomass (BIO).

These results suggest that additive traits can be targeted through conventional selection and pedigree breeding methods, while non-additive traits require hybrid development or recurrent selection strategies to exploit heterosis. The *gca* effects significantly varied among parents, with Waha (P2) and Beni Mestina (P3) favoring shorter plant height, while Achouri (P1) promoted taller plants, longer spikes and enhanced biomass accumulation.

Beni Mestina (P3) emerged as a strong combiner for yield-related traits, particularly SW, NS, GY), whereas MBB (P4) showed a positive influence on grain size (TKW) but negatively impacted other traits. For *sca* effects, Waha × Beni Mestina (H4) produced taller plants, while Beni Mestina × MBB (H6) and Achouri × Waha (H1) favored shorter plants. Achouri × Waha (H1) also had a tendency toward increased spike length and accumulated biomass. Beni Mestina × MBB (H6), Achouri × MBB (H3) and Achouri × Waha (H1) promoted larger grains, but most hybrids exhibited negative *sca* effects for key yield traits, posing breeding challenges for simultaneous improvement of these components. While *gca* effects reliably predict parental performance, *sca* effects provided insights into hybrid vigor, revealing the complex genetic interactions shaping hybrid performance.

The weak *gca*-*sca* correlation suggests that hybrid performance cannot be inferred solely from parental performance, emphasizing the need for careful selection in durum wheat breeding. Future research should explore molecular markers and multi-environment trials to further dissect these genetic interactions and optimize breeding strategies.

NOTES

AUTHOR CONTRIBUTIONS

Conceptualization, methodology, and formal analysis**, Bentouati I., Hannachi A., Fellahi Z. and Mekhlouf A.**; software and validation**, Fellahi Z. and Hannachi A.**; investigation**, Bentouati I. and Hannachi A.**; resources and data curation**, Bentouati I. and Hannachi A.**; writing-original draft preparation**, Bentouati I., Hannachi A. and Fellahi Z.**; writing-review and editing**, Hannachi A. and Fellahi Z.**; visualization**, Bentouati I., Hannachi A., Fellahi Z. and Mekhlouf A.**; supervision, **Mekhlouf A. and Hannachi A.**; project administration, **Mekhlouf A. and Hannachi A.** All authors have read and agreed to the published version of the manuscript.

FUNDING

This work was not supported by any funding agency.

INSTITUTIONAL REVIEW BOARD STATEMENT

Not applicable for studies not involving humans or animals.

INFORMED CONSENT STATEMENT

Not applicable because this study did not involve humans.

DATA AVAILABILITY STATEMENT

The data can be made available under request.

ACKNOWLEDGEMENTS

There are no acknowledgements.

CONFLICTS OF INTEREST

The authors declare no conflict of interest.

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