



Genetic analysis of yield-related traits in F₂ diallel cross in durum wheat (*Triticum durum* Desf.)

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Abstract

The study evaluated the combining ability of four durum wheat cultivars—Achouri, Waha, Beni Mestina, and Mohamed Ben Bachir—through a 4×4 half-diallel cross design, generating six F₂ hybrid combinations. Parents and their progeny were assessed during the 2023–2024 growing season under rainfed conditions in Setif, Algeria, for eight morpho-agronomic traits including plant height (cm), spike length (cm), spike weight (g plant⁻¹), number of spikes plant⁻¹, number of grains spike⁻¹, thousand kernel weight (g), grain yield (g plant⁻¹), and aboveground biomass (g plant⁻¹). Analysis of variance revealed significant genetic variation for all traits. Both general (*gca*) and specific (*sca*) combining ability significantly influenced trait expression, indicating additive and non-additive gene actions. Additive effects controlled plant height, spike length, spikes plant⁻¹, and grains per spike, while non-additive effects prevailed for spike weight, kernel weight, grain yield, and biomass. Beni-Mestina exhibited strong positive *gca* estimates for multiple yield traits including spike weight (0.40), spikes plant⁻¹ (0.39), kernel weight (2.31), and grain yield (0.28), alongside a desirable reduction in plant height (−3.77). Achouri contributed positively to plant height (7.10), spike length (0.63), grains spike⁻¹ (4.14), and biomass (0.72). Hybrids Achouri × Mohamed Ben Bachir and Waha × Mohamed Ben Bachir showed favorable *sca* effects for kernel weight (11.54 and 6.47, respectively) and grain yield (1.45 and 1.83, respectively), with the later also improving spike weight (0.49). Superior crosses were not always derived from high-*gca* parents. These findings support strategic parent selection and generation-targeted phenotyping—early selection for additive traits and delayed selection (F₃–F₄) for non-additive traits, along with bi-parental mating within promising *sca* crosses.

Keywords: Durum wheat, combining ability, heritability, semi-arid conditions, breeding strategies.

INTRODUCTION

In recent years, durum wheat (*Triticum durum* Desf.) has gained significant attention as a vital cereal crop, primarily cultivated for its high-quality products such as pasta and couscous. This tetraploid species, characterized by its AABB genome (2n=4x=28), contributes approximately 5-8 % of total global wheat production, making it an essential staple in many regions, particularly in semi-arid environments where water scarcity and heat stress are prevalent (Fellahi *et al.*, 2024). The economic importance of durum wheat lies in its ability to thrive under challenging climatic conditions, yet it faces considerable challenges that hinder its productivity. These include limited genetic diversity, susceptibility to biotic stresses such as rusts and *Fusarium* head blight, and sensitivity to abiotic stresses like drought and heat, which collectively constrain its yield potential (Beres *et al.*, 2020). To address these challenges, innovative breeding strategies are essential for enhancing genetic gain and improving resilience in durum wheat. The low yield potential is often attributed to the scarcity of high-yielding cultivars and suboptimal agronomic practices. Consequently, breeding programs have increasingly focused on utilizing both indigenous and exotic germplasm to enhance genetic diversity and overcome yield barriers (Broccanello *et al.*, 2023). A primary objective in durum wheat breeding is to identify high-performing lines and suitable parental lines for future crosses.

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Diallel analysis provides a robust framework for investigating the genetic architecture of quantitative traits by partitioning genetic effects into additive and non-additive components (Griffing, 1956 a, b). Among various diallel approaches, Griffing's (1956 a, b) method has become predominant due to its comprehensive estimation of general and specific combining abilities across multiple experimental designs. While alternative methods exist, such as Hayman's (1954) approach (requiring absence of epistasis and maternal effects) or Gardner and Eberhart's (1966) heterosis partitioning model – Griffing's flexibility in handling different mating schemes (including reciprocal crosses and parental lines) makes it particularly valuable for breeding applications (Shamuyarira *et al.*, 2023). The general combining ability component reflects a parent's average performance across crosses, indicating additive genetic effects suitable for recurrent selection. In contrast, specific combining ability captures unique hybrid performance due to non-additive interactions, informing hybrid-breeding strategies. This differentiation enables breeders to optimize selection approaches based on trait inheritance patterns – emphasizing high-general combining ability parents for additive traits or exploiting superior specific combining ability combinations for heterosis (Griffing, 1956 a, b).

The F₂ generation is particularly valuable for genetic studies, as it represents the first segregating generation where recombination and transgressive segregation occur, offering opportunities to select superior recombinants (Gupta *et al.*, 2023). Unlike the F₁ generation, which primarily exhibits heterosis, the F₂ generation reveals inheritance patterns, inbreeding depression, and gene interactions, making it a critical stage for evaluating genetic potential (Shamuyarira *et al.*, 2023). Further, the F₂ generation allows breeders to assess the stability of desirable traits before advancing selections in breeding programs (Ribeiro *et al.*, 2025).

Thus, this study aims to investigate combining ability in the F₂ generation of durum wheat using diallel analysis, with the goal of identifying promising parental lines and hybrid combinations for future breeding efforts. By enhancing our understanding of genetic variation and combining ability, this research seeks to contribute to the development of high-yielding, resilient durum wheat cultivars that can thrive in diverse environmental conditions.

MATERIALS AND METHODS

Plant materials and experimental design

The study utilized four durum wheat (*Triticum durum* Desf.) cultivars: Achouri, Waha, Beni Mestina, and Mohamed Ben Bachir. The parental genotypes were crossed in a 4 × 4 half-diallel mating design during the 2020–2021 cropping season, resulting in the production of six F₁ hybrids. These F₁ hybrids were subsequently planted during the 2021–2022 season to generate F₂ progenies.

In total, 10 genotypes, comprising the four parental lines and six F₂ hybrids, were evaluated during the 2023–2024 growing season at the experimental field of the National Agronomic Research Institute of Algeria (INRAA), Unit of Setif, a semi-arid region of Algeria. The experimental layout was established in a randomized complete block design (RCBD) with three replications under rainfed conditions. Each genotype (parents and their F₂ hybrids) was planted in three rows, with a spacing of 15 cm between plants within a row and 20 cm between rows. Standard cultural practices, including manual weeding, were employed to ensure optimal growing conditions throughout the study.

Data collection

Data collection occurred after physiological maturity, focusing on the parents and the F₂ hybrids. The traits measured included: plant height (cm), spike length (cm), spikes weight (g plant⁻¹), number of spikes plant⁻¹, number of grains spike⁻¹, thousand kernel weight (g), grain yield (g plant⁻¹) and above-ground biomass (g plant⁻¹). Measurements were recorded on a single-plant basis to ensure accuracy and reliability in the analysis of genetic parameters.

Statistical analyses

Analysis of variance (ANOVA) was conducted individually for each trait to assess the significance of genotypic effects using data from ten genotypes comprising four parents and six F₁ hybrids, following procedures described by Singh and Chaudhary (1985). Mean separation was accomplished using Fisher's Least Significant Difference test at $\alpha = 0.05$ (LSD_{0.05}).

Diallel analysis was performed for traits showing significant genetic variation among genotypes. General and specific combining ability parameters, including variance components and effects, were estimated using the fixed effects model of Griffing (1956 a) - Method 2, Model 1, as presented by Singh and Chaudhary (1985). Testing for significance of general combining ability (σ^2_{gca}) and specific combining ability (σ^2_{sca}) variance components involved comparison with their respective error terms derived from the reduced ANOVA model. Statistical evaluation of individual combining ability effects was conducted using Student's *t*-test. Decomposition of total genetic variance into additive (σ^2_A), dominance (σ^2_D), and environmental (σ^2_E) components was performed for each trait based on the relationships between general combining ability and specific combining ability variance estimates as described by Griffing (1956 b). The predictability ratio was computed according to Baker (1978). Broad-sense (h^2_{bs}) and narrow-sense (h^2_{ns}) heritability estimates were calculated from the variance components using equations provided by Acquaah (2012). Statistical and genetic analyses of the recorded morpho-agronomic traits were conducted using the Genes software package (Cruz, 2013).

RESULTS AND DISCUSSION

Analysis of variance

The analysis of variance (ANOVA) revealed significant differences among the studied genotypes for all measured traits, as summarized in **Table 1**. This indicates that the genotypes exhibit variability in their performance across the traits assessed.

Performance evaluation of parents and their F₂ hybrid combinations

For plant height, the tallest genotypes were parent Achouri at 78.97 cm and hybrid Achouri × Mohamed Ben Bachir at 76.14 cm, suggesting that the parent Achouri contributes dominant alleles for height (**Table 2**). In contrast, parents Waha and Beni Mestina exhibited more compact growth habits at 56.45 cm and 56.40 cm, respectively. This compactness could be advantageous for reducing lodging risk in semi-arid environments, where wind and rain can adversely affect taller plants (Fellahi *et al.*, 2023). The

variation in plant height highlighted the genetic diversity present in the population, offering opportunities for breeding programs targeting optimal plant architecture, which is crucial for maximizing yield potential under stress conditions.

Spike-related traits showed considerable variation, with implications for grain yield potential. Parent Achouri had the longest spikes (7.48 cm), while hybrid Beni Mestina × Mohamed Ben Bachir displayed the shortest spikes at 5.35 cm. This indicates possible trade-offs between spike elongation and other yield components, which is consistent with findings that longer spikes may not always correlate with higher grain yield due to resource allocation trade-offs (Philipp *et al.*, 2018). Spike weight was highest in hybrid (7.90 g plant⁻¹), demonstrating heterotic effects for biomass allocation to spikes. Conversely, the lowest performance in this trait was observed in hybrid Achouri × Waha at 4.90 g plant⁻¹, suggesting that

Table 1. ANOVA results for yield-related traits evaluated in durum wheat genotypes

S.O.V	df	PH	SL	SW	NS	NGS	TKW	GY	BIO
Block	2	58.18	0.02	0.63	0.30	4.35	1.99	0.32	0.71
Genotypes	9	196.78**	1.17**	2.03**	0.79**	67.68**	177.05**	3.40**	6.28**
Error	18	50.49	0.03	0.31	0.18	5.16	20.04	0.38	1.14

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 kernels weight, GY: Grain yield, BIO: Aboveground biomass. **: significant 0.01 probability levels, respectively.

Table 2. Average values of yield-related traits in durum wheat

Genotypes	PH	SL	SW	NS	NGS	TKW	GY	BIO
P1	78.97 ^a	7.48 ^a	5.94 ^{bc}	2.85 ^c	38.99 ^a	38.43 ^{bc}	3.96 ^{de}	14.73 ^{bc}
H1	70.28 ^{abc}	6.54 ^b	4.90 ^d	2.80 ^c	39.23 ^a	35.29 ^c	3.33 ^{ef}	13.63 ^{cd}
H2	70.18 ^{abc}	6.39 ^b	6.48 ^b	3.36 ^{bc}	35.67 ^{ab}	35.15 ^{cd}	4.84 ^{bcd}	17.83 ^a
H3	76.14 ^a	6.49 ^b	5.98 ^{bc}	3.00 ^c	36.85 ^a	46.04 ^{ab}	5.79 ^{ab}	15.81 ^b
P2	56.45 ^d	5.68 ^d	6.57 ^b	3.36 ^{bc}	28.35 ^{cd}	40.33 ^{bc}	4.23 ^{cde}	12.70 ^d
H4	63.65 ^{bcd}	5.75 ^d	5.80 ^{bcd}	3.40 ^{bc}	32.60 ^b	42.10 ^{bc}	4.70 ^{cd}	13.70 ^{cd}
H5	70.90 ^{ab}	5.78 ^{cd}	6.65 ^b	3.44 ^{bc}	32.60 ^b	42.10 ^{bc}	6.33 ^a	14.34 ^{bcd}
P3	56.40 ^d	5.65 ^{de}	6.71 ^b	3.97 ^{ab}	25.25 ^d	50.17 ^a	5.13 ^{bc}	13.50 ^{cd}
H6	62.67 ^{bcd}	5.35 ^e	7.90 ^a	4.43 ^a	28.13 ^d	27.61 ^{de}	4.83 ^{bcd}	14.63 ^{bc}
P4	58.19 ^{cd}	6.06 ^c	5.44 ^{cd}	3.01 ^c	32.16 ^{bc}	25.49 ^e	2.80 ^f	13.92 ^{cd}
Parents mean	62.50	6.22	6.17	3.30	31.19	38.61	4.03	13.71
Hybrids mean	68.97	6.05	6.14	3.41	34.18	38.05	4.97	14.99
Overall mean	66.38	6.12	6.15	3.36	32.98	38.27	4.59	14.48
LSD _{0.05}	12.19	0.31	0.96	0.72	3.89	7.679	1.06	1.83

PH: Plant height (cm), SL: Spike length (cm), SW: Spikes weight (g plant⁻¹), NS: Number of spike plant⁻¹ (spikes plant⁻¹), NGS: Number of grains spike⁻¹ (grains spike⁻¹), TKW: Thousand kernels weight (g), GY: Grain yield (g plant⁻¹), BIO: Aboveground biomass (g plant⁻¹). 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}). P1: Achouri, P2: Waha, P3: Beni Mestina, P4: Mohamed Ben Bachir, H1: Achouri × Waha, H2: Achouri × Beni Mestina, H3: Achouri × Mohamed Ben Bachir, H4: Waha × Beni Mestina, H5: Waha × Mohamed Ben Bachir, H6: Beni Mestina × Mohamed Ben Bachir.

not all hybrids benefit equally from heterosis. The number of spikes plant⁻¹ varied significantly, with Beni Mestina × Mohamed Ben Bachir showing the highest values (4.43 spikes plant⁻¹), suggesting genetic potential for tillering capacity. In contrast, Achouri × Waha and Achouri displayed the lowest values for this trait (2.80 and 2.85 spikes plant⁻¹), hinting at potential limitations in spike development and reproductive performance. This variation in tillering ability is crucial for adaptation to variable rainfall patterns typical of Mediterranean environments.

The number of grains per spike was high in hybrid Achouri × Waha at 39.23 grains spike⁻¹ and 39.23 grains spike⁻¹ in parent Achouri, while Beni Mestina and Beni Mestina × Mohamed Ben Bachir had lower values (25.25 grains spike⁻¹ and 28.13 grains spike⁻¹, respectively). This disparity may be due to resource allocation trade-offs between spike number and spike fertility, as previously reported in wheat studies (Philipp *et al.*, 2018). Yield components also exhibited notable differences. For thousand kernels weight, parent Beni Mestina produced the bold grains at 50.17 g, followed by hybrid Achouri × Mohamed Ben Bachir at 46.04 g, indicating their potential for improving grain quality. In contrast, Beni Mestina × Mohamed Ben Bachir (27.61 g) and Mohamed Ben Bachir (25.49 g) had lower thousand kernel weight, which may reflect genetic limitations in grain filling or shorter grain filling duration (Bai *et al.*, 2025). Grain yield was highest in hybrid Waha × Mohamed Ben Bachir at 6.33 g plant⁻¹ and Achouri × Mohamed Ben Bachir at 5.79 g plant⁻¹, surpassing parental mean (4.03 g plant⁻¹) and demonstrating positive heterosis for yield. Parent Mohamed Ben Bachir was the lowest-yielding genotype at 2.80 g plant⁻¹, reinforcing the importance of careful parental selection in hybridization

programs. Above-ground biomass followed a similar trend, with hybrids Achouri × Beni Mestina (17.83 g plant⁻¹) and Achouri × Mohamed Ben Bachir (15.81 g plant⁻¹) showed the highest accumulation, correlating with their superior grain yield. This correlation between biomass and yield is well-documented, emphasizing the need for breeding strategies that enhance both traits simultaneously.

Component of genetic variation

The diallel analysis of F₂ progenies revealed a complex genetic architecture for durum wheat traits, with both general combining ability and specific combining ability contributing to trait expression (Table 3). The highly significant general combining ability effects for plant height, spike length, number of spikes, number of grains per spike, thousand kernel weight, and above-ground biomass indicate substantial additive genetic control, while the significant specific combining ability effects for spike length, spikes weight, number of grains spike⁻¹, thousand kernel weight, grain yield and aboveground biomass demonstrate important non-additive interactions. This dual pattern of inheritance, where both additive and non-additive gene actions contribute to phenotypic variation, has been widely observed in wheat (Ribeiro *et al.*, 2025). The relative importance of these gene actions varied by trait. For plant height and number of spikes, the highly significant general combining ability with non-significant specific combining ability suggests nearly complete additive control, making these traits particularly amenable to early generation selection. Conversely, spikes weight and grain yield showed the opposite pattern (non-significant general combining ability but highly significant specific combining ability), indicating their expression depends primarily on specific gene combinations rather than average parental performance. Most traits (spike length, number grains per

Table 3. Genetic variance component analysis for yield-related traits in durum wheat

S.O.V	df	PH	SL	SW	NS	NGS	TKW	GY	BIO
<i>gca</i>	3	427.25**	3.28**	1.69	1.57**	160.62**	146.56**	0.69	7.96**
<i>sca</i>	6	81.55	0.11*	2.20**	0.39	21.22**	192.30**	4.76***	5.45**
<i>Error</i>	18	50.49	0.03	0.31	0.17	5.16	20.04	0.38	1.14
σ^2_{gca}		20.93	0.18	0.08	0.08	8.64	7.03	0.02	0.38
σ^2_{sca}		10.35	0.03	0.63	0.07	5.35	57.42	1.46	1.44
$\sigma^2_{gca}/\sigma^2_{sca}$		2.02	6.00	0.12	1.14	1.62	0.12	0.014	0.26
σ^2_A		41.86	0.36	0.16	0.16	17.28	14.06	0.04	0.76
σ^2_D		10.35	0.03	0.63	0.07	5.35	57.42	1.46	1.44
<i>Baker's ratio</i>		0.80	0.92	0.20	0.70	0.76	0.20	0.03	0.35
h^2_{bs}		0.51	0.93	0.72	0.58	0.81	0.78	0.80	0.66
h^2_{ns}		0.41	0.86	0.15	0.40	0.62	0.15	0.02	0.23

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 kernels weight, GY: Grain yield, BIO: Above-ground biomass. * 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.

spike, aboveground biomass) exhibited both significant general combining ability and specific combining ability effects, revealing a mixed inheritance pattern where additive effects provide a base level of performance that can be enhanced through specific combinations showing heterosis. However, thousand kernels weight showed a distinct pattern where the mean square due to specific combining ability substantially exceeded that of general combining ability, indicating dominance of non-additive gene action for this trait despite both components being statistically significant. This agrees with Al-Naggar *et al.* (2017), who found similar complex inheritance patterns in wheat F_2 populations, with kernel weight often showing stronger non-additive than additive control in early generations.

The $\sigma^2_{gca}/\sigma^2_{sca}$ ratio provided further insight into these genetic architectures. Traits with ratio >1 (plant height, spike length, number of spikes plant $^{-1}$, number of grains spike $^{-1}$) are predominantly additively controlled, while those with ratios <1 (spikes weight, thousand kernels weight, grain yield, aboveground biomass) showed stronger non-additive effects. In the literature, gene action in early segregating generations can vary considerably. It may be predominantly additive or non-additive depending on the specific trait, the genetic material involved, and external factors such as crop management practices and environmental conditions (Singh *et al.*, 2023; Al-Naggar *et al.*, 2017; Shamuyarira *et al.*, 2023; Ribeiro *et al.*, 2025). Collectively, these studies report that phenological and morphological traits tend to exhibit higher additive variance, whereas yield components more frequently display non-additive control. Baker's ratio reinforced these patterns, with higher values (>0.5) for traits showing additive predominance and lower values (<0.5) for traits dominated by non-additive effects.

The heritability patterns corroborated the combining ability results, showing consistent genetic control across traits. While broad-sense heritability (h^2_{bs}) remained high for most traits, narrow-sense heritability (h^2_{ns}) revealed a crucial distinction: morphological traits like plant height and spike length retained substantial additive variance, whereas yield components including grain yield and kernel weight showed predominantly non-additive inheritance. This genetic architecture suggests that simple selection would effectively improve morphological features. However, optimizing yield potential will require more complex breeding strategies that specifically target non-additive genetic effects, as recommended by Tadesse *et al.* (2019) for wheat improvement programs.

Estimates of general combining ability and specific combining ability effects

General combining ability effects

The estimates of general combining ability effects for the eight evaluated traits are presented in **Table 4**. Contrasting general combining ability effects were observed for plant height, a trait often targeted for reduced stature

to enhance lodging resistance and resource allocation (Shamuyarira *et al.*, 2023). The parent Achouri contributed significantly to increased plant stature (7.10), whereas Beni Mestina showed a significant negative effect (−3.77), making it promising for reducing height in future breeding efforts. This divergence suggests variability in allelic contribution to height regulation, with Beni Mestina potentially carrying alleles favorable for reduced height without compromising yield potential.

In terms of spike length, only Achouri exhibited a significantly positive general combining ability effect (0.63), indicating its value as a donor for enhancing spike architecture. The remaining parents showed small but significant negative effects, suggesting potential dilution of spike elongation capacity when involved in crosses. For spikes weight, Beni Mestina showed the highest positive general combining ability effect (0.40), while Achouri had a negative effect (−0.32), indicating a trade-off between spike length and spike weight contributions. When evaluating number of spikes plant $^{-1}$, Beni Mestina demonstrated superior combining ability with a significant positive general combining ability effect (0.39), suggesting enhanced tillering capacity. In contrast, Achouri recorded a negative effect (−0.32), indicating lower spike production in its progenies. For number of grains per spike, Achouri was the only parent to exhibit a significantly positive general combining ability effect (4.14), while Beni Mestina contributed negatively (−3.00), representing yield component compensation where improvements in one component may be offset by reductions in another. Regarding thousand kernel weight, Beni Mestina demonstrated a significant positive general combining ability effect (2.31), indicating potential for improving grain size, while Mohamed Ben Bachir showed a strongly negative effect (−4.10). The trade-off between grain weight and grain number reflects the overlapping phases determining these major yield components (Vicentin *et al.*, 2024). For grain yield, Beni Mestina exhibited a modest yet significant positive general combining ability effect (0.28), highlighting the cumulative impact of favorable traits such as spike number and grain weight. Finally, for above-ground biomass, Achouri demonstrated a significantly positive general combining ability effect (0.72), suggesting strong vegetative growth capacity, while Waha had a significant negative effect (−0.89), which may limit biomass accumulation and indirectly affect yield.

The general combining ability analysis revealed that no single parent combined favorable effects for all traits, emphasizing the polygenic nature of yield and the need for strategic parent selection in wheat breeding. Beni Mestina emerged as a promising general combiner for several key agronomic traits including spike weight, spike number, kernel weight, yield, and its negative effect for plant height makes it valuable for developing semi-dwarf varieties. Conversely, Achouri showed advantages in biomass, spike length, and grain number, making it a

Table 4. General combining ability (gca) effects for yield-related traits in parental genotypes of durum wheat

Parents	PH	SL	SW	NS	NGS	TKW	GY	BIO
P1	7.10**	0.63**	-0.32*	-0.32**	4.14**	0.33	-0.18	0.72**
P2	-2.36	-0.19**	-0.12	-0.08	-0.63	1.47	-0.03	-0.89**
P3	-3.77*	-0.30**	0.40**	0.39**	-3.00**	2.31*	0.28*	0.12
P4	-0.97	-0.14**	0.04	0.01	-0.50	-4.10**	-0.07	0.04
SE (g _i)	1.45	0.04	0.11	0.09	0.46	0.91	0.13	0.22
SE (g _i - g _j)	2.37	0.06	0.19	0.14	0.76	1.49	0.21	0.36

PH: Plant height, SL: Spike length, SW: Spikes weight, NS: Number of spike plant⁻¹, NGS: Number of grains spike⁻¹, TKW: Thousand kernels weight, GY: Grain yield, BIO: Aboveground biomass. * and **: significant at 0.05 and 0.01 probability levels, respectively. P1: Achouri, P2: Waha, P3: Beni Mestina, P4: Mohamed Ben Bachir.

complementary parent in strategic breeding combinations. These complementary *general combining ability* profiles suggest that effective breeding strategies should exploit the unique strengths of each parent through targeted crossing schemes rather than relying on a single superior parent. The observed *general combining ability* patterns align with established quantitative genetics principles, where complex trait inheritance requires comprehensive evaluation of combining ability effects across multiple traits and environments.

Specific combining ability effects

Analysis of specific combining ability effects revealed significant variation among hybrid combinations for different traits (**Table 5**). For plant height, only Waha × Mohamed Ben Bachir demonstrated a significant positive specific combining ability effect (7.85), indicating this combination produces taller plants than expected from parental general combining ability effects. This suggests favorable dominance interactions for height in this specific cross, though increased height may be undesirable for lodging resistance.

Spike architecture traits showed contrasting patterns among hybrids. Waha × Beni Mestina exhibited a significant positive specific combining ability effect for spike length (0.17), while Beni Mestina × Mohamed Ben Bachir showed a significant negative effect (-0.33). For spike weight, Waha × Mohamed Ben Bachir and Beni Mestina × Mohamed Ben Bachir displayed significant positive specific combining ability effects (0.49 and 1.22, respectively), suggesting enhanced grain filling capacity in these combinations. Conversely, Achouri × Waha and Waha × Beni Mestina showed significant negative specific combining ability effects (-0.90 and -0.72, respectively), indicating poor combining ability for spike weight.

For tillering capacity, only Beni Mestina × Mohamed Ben Bachir recorded a significant positive specific combining ability effect for number of spikes plant⁻¹ (0.67), suggesting favorable gene interactions for tiller production. Regarding grain number per spike, Achouri × Waha and Waha × Beni Mestina exhibited significant

positive specific combining ability effects (2.74 and 3.25, respectively), indicating enhanced spike fertility through complementary gene action. Thousand-kernel weight displayed the most pronounced specific combining ability effects, with Achouri × Mohamed Ben Bachir and Waha × Mohamed Ben Bachir showing large positive effects (11.54 and 6.47, respectively). These combinations suggest favorable dominance or epistatic interactions for grain filling. Conversely, three hybrids (Achouri × Waha, Achouri × Beni Mestina, Beni Mestina × Mohamed Ben Bachir) exhibited significant negative specific combining ability effects (-4.78, -5.76 and -8.86, respectively), indicating poor combining ability for grain weight despite potentially favorable individual parent contributions.

For grain yield, Achouri × Mohamed Ben Bachir and Waha × Mohamed Ben Bachir displayed significant positive specific combining ability effects (1.45 and 1.83, respectively), while Achouri × Waha showed a significant negative effect (-1.06). These patterns largely reflect the cumulative effects of individual yield components, with Achouri × Mohamed Ben Bachir and Waha × Mohamed Ben Bachir benefiting from favorable specific combining ability effects for thousand kernels weight. Aboveground biomass showed a significant positive specific combining ability effect only in Achouri × Beni Mestina (2.50), indicating enhanced vegetative growth through specific gene interactions. The remaining crosses showed non-significant deviations from expected parental performance.

The specific combining ability analysis revealed that no hybrid combination displayed consistently favorable effects across all traits, emphasizing the complexity of genetic interactions in determining hybrid performance. The magnitude and direction of specific combining ability effects varied considerably among trait-hybrid combinations, reflecting the intricate nature of gene interactions and the challenge of simultaneously improving multiple yield-related traits through hybridization. Nonetheless, specific crosses such as Achouri × Mohamed Ben Bachir and Waha × Mohamed Ben Bachir showed promising specific combining ability profiles for

Table 5. Specific combining ability (sca) effects for yield-related traits in F₂ hybrids of durum wheat

Hybrids	PH	SL	SW	NS	NGS	TKW	GY	BIO
H1	-0.84	-0.02	-0.90**	-0.16	2.74**	-4.78**	-1.06**	-0.68
H2	0.46	-0.06	0.17	-0.06	1.55	-5.76**	0.15	2.50**
H3	3.62	-0.12	0.03	-0.05	0.23	11.54**	1.45**	0.57
H4	3.40	0.17*	-0.72**	-0.27	3.25**	-0.06	-0.15	-0.02
H5	7.85**	-0.01	0.49*	0.14	0.75	6.47**	1.83**	0.71
H6	1.03	-0.33**	1.22**	0.67**	-1.35	-8.86**	0.03	-0.01
SE (s _{ii})	2.59	0.07	0.20	0.15	0.83	1.64	0.23	0.39
SE (s _{ij})	3.51	0.09	0.27	0.21	1.12	2.21	0.31	0.53
SE (s _{ii} - s _{ij})	3.35	0.08	0.26	0.20	1.07	2.11	0.29	0.50
SE (s _{ij} - s _{ik})	5.30	0.13	0.41	0.31	1.69	3.34	0.46	0.80
SE (s _{ij} - s _{kl})	4.74	0.12	0.37	0.28	1.52	2.99	0.41	0.71

PH: Plant height, SL: Spike length, SW: Spikes weight, NS: Number of spike plant⁻¹, NGS: Number of grains spike⁻¹, TKW: Thousand kernels weight, GY: Grain yield, BIO: Aboveground biomass. * and **: significant at 0.05 and 0.01 probability levels, respectively. H1: Achouri × Waha, H2: Achouri × Beni Mestina, H3: Achouri × Mohamed Ben Bachir, H4: Waha × Beni Mestina, H5: Waha × Mohamed Ben Bachir, H6: Beni Mestina × Mohamed Ben Bachir.

key traits like thousand kernels weight and grain yield, making them suitable candidates for further evaluation in breeding programs targeting yield enhancement and quality improvement in durum wheat.

These results highlight the need to evaluate both general and specific combining ability in breeding programs. While general combining ability identifies good parents, specific combining ability reveals promising hybrid combinations and the role of non-additive effects, which, though partially diluted in F₂ due to segregation, can still guide the selection of superior recombinant lines (Acquaah, 2012).

Relationship between combining ability and hybrid performance

High general combining ability effects primarily result from additive gene effects or additive × additive interaction effects (Griffing, 1956 a), making general combining ability particularly valuable for breeding programs. The results demonstrate that general combining ability rank for most traits (Table 4) correlates strongly with parental performance (Table 2), suggesting that general combining ability effects serve as reliable predictors of overall *per se* performance across measured traits. The parents Achouri and Beni Mestina showed exceptional combining ability and should be utilized extensively in hybridization programs to accelerate genetic improvement.

The estimates of specific combining ability revealed that the crosses exhibiting consistently positive specific combining ability (Table 5) also demonstrated superior performance, excluding plant height and spike length (Table 2). For most traits, performance showed highly significant positive correlations with specific combining ability, confirming that specific combining ability can reliably predict hybrid performance and that selecting

crosses with high specific combining ability values facilitates the development of excellent hybrids with strong developmental potential. A particularly noteworthy finding emerged from the specific combining ability analysis: some of the best hybrid combinations resulted from crossing parents with contrasting general combining ability effects. This pattern demonstrates that superior hybrid combinations can arise not only from “good” × “good” general combining ability combinators but also from “good” × “poor” and “poor” × “poor” combinations. The results obtained in crosses with significant positive specific combining ability effects involving “good” × “poor” general combinators include Achouri × Waha for number of grains per spike, Achouri × Beni Mestina for biomass, and Beni Mestina × Mohamed Ben Bachir for spike weight and number of spikes. Similarly, “poor” × “poor” combinations showed positive specific combining ability effects, such as Achouri × Mohamed Ben Bachir for thousand kernel weight and grain yield, Waha × Beni Mestina for spike length and number of grains per spike, and Waha × Mohamed Ben Bachir for spike weight, thousand kernels weight, and grain yield. These unexpected combining patterns likely result from non-allelic interactions and genetic diversity manifested through numerous heterozygous loci in parents involved in cross combinations. Consequently, predicting F₂ progeny performance based solely on parental general combining ability effects proves unreliable.

In self-pollinated crops such as wheat, specific combining ability is generally less relevant for direct exploitation (e.g., in hybrid seed production), but it remains crucial for identifying crosses that may yield transgressive segregants in advanced generations (Gupta *et al.*, 2023). Although dominance and epistatic effects represented by specific combining ability are not directly fixable, additive × additive interaction components can become stable

in homozygous lines through selection. As emphasized by Jinks and Jones (1958), hybrid superiority may not necessarily indicate the ability to produce transgressive segregants; rather, specific combining ability provides more satisfactory criteria for predicting the potential of crosses to generate superior segregating generations. Therefore, breeders should prioritize early-generation selection for additively controlled traits while allowing non-additive traits to segregate and stabilize before selection, as recommended in delayed selection strategies (e.g., F₃–F₄ generations). Additionally, bi-parental mating among selected individuals within promising cross combinations, such as the high-specific combining ability crosses identified in this study (Achouri × Mohamed Ben Bachir for grain yield and Waha × Mohamed Ben Bachir for multiple traits), could enhance the probability of capturing superior recombinations and developing transgressive segregants with exceptional performance.

This diallel analysis of durum wheat F₂ progenies under semi-arid conditions demonstrated that additive gene action governed spike fertility (number of grains per spike) and tillering capacity (number of spikes plant⁻¹), while non-additive effects primarily influenced yield-related traits (grain yield, kernel weight, spike weight, and biomass). Beni Mestina stood out as the best general combiner for yield traits and plant height reduction, whereas Achouri exhibited favorable alleles for spike length, grain number per spike, and biomass production. Notably, the crosses Achouri × Mohamed Ben Bachir and Waha × Mohamed Ben Bachir showed significant specific combining ability effects, revealing transgressive segregation potential for isolating superior recombinants in advanced generations. The significant positive correlations between specific combining ability effects and hybrid performance for most traits (except spike length) confirmed that specific combining ability serves as a reliable predictor of cross potential, even in unexpected “good” × “poor” and “poor” × “poor” combinations. Consequently, breeding strategies should incorporate early-generation selection for additively controlled traits while implementing delayed selection approaches (F₃–F₄ generations) to optimize genetic gains for non-additive traits. Furthermore, bi-parental mating among selected individuals within high-specific combining ability crosses could enhance the probability of capturing superior gene combinations. These insights provide a roadmap for breeding programs to enhance genetic gains in durum wheat, combining strategic parental selection with generation-targeted phenotyping to improve productivity in semi-arid regions.

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