Assiut Journal of Agricultural Sciences 56 (2) 2025 (1-17)
ISSN: 1110-0486 / EISSN: 2356-9840
Website: http://ajas.journals.ekb.eg/
E-mail: ajas@aun.edu.eg

(Original Article)

Genetic Analysis of Two Durum Wheat Crosses under Normal Irrigation and Water Stress Conditions

Yaser S. I. Koubisy* **and Gamal. M. M. Soliman**

Wheat Research Department, Field Crops Research Institute, Agriculture Research Center, Giza, Egypt.

*Corresponding author e-mail: dryasserkoubisy@gmail.com

DOI: 10.21608/AJAS.2025.350502.1452

Abstract

The six genetic parameters of two durum wheat hybrids, were estimated under two experimental conditions (normal irrigation, N and water stress, D). This research was accomplished at the Experimental Farm of Shandaweel Agricultural Research Station, ARC throughout 2021/2022 to 2023/2024 seasons. Additionally, it aimed to evaluate the suitability of the genetic model controlling the inheritance patterns of seven economically significant attributes in durum wheat. The scaling test revealed evidence of non-allelic interactions across all traits investigated. The significance of additive and prevalence influences varies across traits and hybrids in both standard irrigation and water stress conditions. For all examined attributes in both crosses under the two irrigation conditions, dominance effects were generally more pronounced than additive effects. Exceptions included plant height in cross 1 under water stress while heading time, spikes plant^{-1}, kernels spike^{-1} and biological yield plant^{-1} in cross 2 under normal irrigation. This indicates that, in addition to the additive genes, dominant genes have a significant influence on the inheritance of such attributes. In most traits, the dominance × dominance interaction was more prominent compared to both additive × additive and additive × dominance interactions, implying that non-allelic and dominance interactions significantly influence these traits. Thus, it is recommended to delay selection to later generations where there is higher level of homozygosity. Heterosis significantly surpassed the superior parent scores for the attributes examined in the two crosses across both irrigation treatments, except for biological yield in cross 1 in normal irrigation. In most instances, heritability in both broad and narrow senses, along with genetic advancement, varied between moderate and high levels. These findings suggest that screening within differentiating generations can be a successful approach for developing early maturing lines with high yield potential under water stress conditions.

Keywords: *Gene action, Heterosis, Heritability, Six parameters model, Triticum turgidum.*

Introduction

Wheat is the most essential staple food crop between all cereal crops in Egypt, where it was cultivated in 3.5 million feddan (1.45 million hectare); about 28% of the total agricultural cultivated land in 2022/2023 winter season (USDA-Egypt 2023). The total national wheat production was 9.5 million metric tons represent 47.5% of the total wheat domestic consumption (USDA-Egypt 2023). The gap between production and

Received: 1 January 2025/ Accepted: 3 March 2025/

consumption (52.5%) is filled by imported wheat from the international market, which cost the Egyptian government a massive amount of currency. In addition, the government of Egypt subsidizes Baladi bread to be available for everyone with proper prices, which in turn put burden on the government commitment of millions Egyptian pounds. For all these aspects, improving wheat production takes high attention from the Egyptian government for securing food. The arable land in Egypt is 8.7 million feddan (3.65 million hectares). While the cultivated land in Egypt is limited, the population is growing fast, where Egypt is one of most over-populated countries all over the world; Egypt's population exceeded 113 million in early 2022 according to Worldometers (2022), 60% increase from the early 2000s according to CAPMAS (2023). For the above-mentioned reasons, the Egyptian government's policy tends to plant wheat in the arid lands to increase the cultivated area which in turn raise the total production by which reduce the gap between production and consumption.

Durum wheat (*Triticum turgidum var.* durum) covers about 9% of the total wheat area. Modern durum wheat cultivars are high yielding. To address the gap among wheat production and consumption in Egypt, it is essential for breeders and geneticists to intensify their efforts to enhance productivity per unit area. Increasing the area under wheat cultivation can only be achieved in newly reclaimed regions, where the primary challenge is water scarcity. This scarcity is a recurring issue caused by unusually dry weather, resulting in moisture stress for crops. The intensity of water stress is influenced by several factors, such as the extent of moisture deficiency, its persistence, and its geographical distribution. Plants generally respond to water stress through three primary strategies: avoidance, escape, and resistance. While the exact physiological and genetic foundations of such processes remain unclear, plant breeders have indirectly utilized them to create drought-tolerant crop varieties. Water scarcity is a key abiotic stressor and a significant factor contributing to reduced crop yields within semi-arid farming regions (Amin-Alim, 2011). Hence, breeding initiatives must focus on creating cultivars with high yield potential that can thrive across diverse environmental stress conditions.

Generation mean analysis offers insights into the significance of additive genetic effects, non-allelic genetic interactions and dominance deviations in shaping the individuals' genotypic characteristics. This, thence, influences the average genotypic values observed in populations and generations. Generation mean analysis provides a straightforward procedure for assessing gene impacts associated with polygenic characteristics. Its primary advantage lies in its capability to evaluate epistatic interactions, including additive × dominance, additive × additive, and dominance × dominance. Genetic data gathered over several generations is considered more dependable than those obtained from a single generation. The genetic effects related to grain yield and associated traits were sufficiently explained via the additive-dominance model (Bayoumi *et al*., 2008). According to Amin (2013), the additive dominance model is not adequate for explaining the genetic transmission of mainly character examined under both normal and water stress conditions. Koubisy (2019) and Feltaous *et al.* (2024) indicated that narrow sense heritability estimates for yield and related traits in F_2 populations were generally moderate to high, both under optimal conditions and during water deficient. The current research aims are to 1) determine the genetic influence type governing yield and related attributes in two durum wheat crosses, under standard and water stress environments, 2) evaluate the heritability in broad and narrow terms, heterosis, the potency ratio, inbreeding depression, and the potential genetic improvement through selection.

Materials and Methods

The Experimental Farm of Shandaweel Agric. Res. Station, ARC., Egypt was the location where this research was performed, throughout 2021/2022, 2022/2023 and 2023/2024 growing seasons. Two crosses were made using four durum wheat (*Triticum turgidum* var. *durum*) parents, selected for their broad genetic diversity across various agronomic characteristics; Cross 1= Bani-Sweif 7 x Bani-Sweif 1 (C_1) and Cross 2= Sohag 1 x Line (C_2) (Table 1).

Table 1. Pedigree and breeding history of cultivars employed in both durum wheat crosses

Cross	Parent		Pedigree
Cross 1	P_1	Bani-Sweif 7	CBC509CHILE//sooty_9/RASCON_37/9/USDA595/3/D67.3/RABI//CRA/4/ALO/5/HUI/YAV_1/6/ARDENTE/7/HUI/YAV79/8/POD_9
	P_2	Bani-Sweif 1	JO"S"/AA"S"//PG"S"
Cross 2	P_1	Sohag 1	GDOVZ469/3/JO"S"//61.130/LDS
	P_2	Line	CR"S"/PLC"S"//GDOV2469/CR"S"/3/ROK"S"

Two crosses were conducted between the four wheat varieties during the first growing season (2021/2022) to produce F_1 hybrid kernels. To obtain BC_1 ($F_1 \times P_1$) and BC_2 ($F_1 \times P_2$), the F_1 generation from every cross was backcrossed with the original parents during the second growing season (2022/2023). Simultaneously, the remaining F_1 plants underwent self-pollination to generate F_2 kernels. Throughout the third growing season (2023/2024), two separate experiments were conducted, where six populations F_1, F_2, P_1, P_2, Bc_1, and Bc_2 obtained from each cross, were planted.

These experiments followed a randomized complete block design with three repetitions for every cross. Every replication comprised 13 rows: one row for each of P_1, P_2 and F_1, with 6 rows for F_2 and 2 rows for each of BC_1 and BC_2. This structure was applied to each cross, resulting in 26 rows, in addition to two border rows. Every row was 2.0 meters long, with a spacing of 30 cm and 10 cm between rows and plants, respectively.

The first experiment was conducted with standard irrigation, (N) (irrigation every 21 day) as recommended with six irrigations. The second experiment, which was under water stress (D), was deprived of irrigation following the second watering (planting irrigation and two additional watering during the growth phase), resulting in a total of three irrigations. All recommended agronomic practices for wheat production were followed. Agronomic traits were collected from 10 guarded plants for every P_1, P_2, and F_1, along with 60 F_2 plants and 20 plants from each of BC_1 and BC_2 in every replication.

The measured traits were: days to 50% heading, grain yield plant^{-1} (g), biological yield plant^{-1} (g), 100-grain kernel weight (g), plant height (cm), kernels spike^{-1} and spikes plant^{-1}.

Statistical and genetic analysis

The MSTAT-C statistical software was employed to perform the analysis of variance and compare the mean values of the traits. The existence or lack of non-allelic interactions and their types (Mather, 1949) were detected through the application of the scaling test.

$A = 2\overline{BC}_1 - \overline{P}_1 - \overline{F}_1$ $\quad V(A) = 4V(\overline{BC}_1) + V(\overline{P_1}) + V(\overline{F}_1)$

$B = 2\overline{BC}_2 - \overline{P}_2 - \overline{F}_1$ $\quad V(B) = 4V(\overline{BC}_2) + V(\overline{P}_2) + V(\overline{F_1})$

$C = 4\overline{F}_2 - 2\overline{F}_1 - \overline{P}_1 - \overline{P}_2$ $\quad V(C) = 16V(\overline{F}_2) + 4V(\overline{F}_1) + V(\overline{P}_1) + V(\overline{P}_2)$

$D = 2\overline{F}_2 - \overline{BC}_1 - \overline{BC}_2$ $\quad V(D) = 4V\overline{F}_2 + V\overline{BC}_1 + V\overline{BC}_2$

The square root of the variances corresponding to A, B, C, and D was taken to achieve their standard error (SE). The computed values of A, B, C, and D were divided by the corresponding standard errors to perform the t-test. The importance of these scales is considered to reflect presence if epistasis. The six genetic parameter model, as described by Hayman (1958) and Jinks and Jones (1958), were utilized to evaluate gene effects in the presence of epistasis.

m = mean effect= F_2

h = dominance effect = $\overline{F}_1 - 4\overline{F}_2 - 0.5\overline{P}_1 - 0.5\overline{P}_2 + 2\overline{BC}_1 + 2\overline{BC}_2$

d = additive effect = $\overline{BC}_1 - \overline{BC}_2$

i= Additive × Additive gene interaction = $2\overline{BC}_1 + 2\overline{BC}_2 - 4\overline{F}_2$

j = Additive × Dominance gene interaction = $\overline{BC}_1 - 0.5\overline{P}_1 - \overline{BC}_2 + 0.5\overline{P}$

l = Dominance × Dominance gene action = $\overline{P}_1 + \overline{P}_2 + 2\overline{F}_1 + 4\overline{F}_2 - 4\overline{BC}_1 - 4\overline{BC}_2$

The variance scores for this aspect were determined as follows:

$V_m = V(\overline{F}_2)$

$V_h = V(\overline{F}_1) + 16V(\overline{F}_2) + 0.25V(\overline{P}_1) + 0.25V(\overline{P}_2) + 4V(\overline{BC}_1) + 4V(\overline{BC}_2)$

$V_d = V(\overline{BC}_1) + V(\overline{BC}_2)$

$V_i = 4V(\overline{BC}_1) + 4V(\overline{BC}_2) + 16\overline{F}_2$

$V_j = V(\overline{BC}_1) + 0.25V(\overline{P}_1) + V(\overline{BC}_2) + 0.25V(\overline{P}_2)$

$V_j = V(\overline{BC}_1) + 0.25V(\overline{P_1}) + V(\overline{BC}_2) + 0.25V(\overline{P}_2)$

$V_l = V(\overline{P}_1) + V(\overline{P}_2) + 4V(\overline{F}_1) + 16V(\overline{F}_2) + 16V(\overline{BC}_1) + 16V(\overline{BC}_2)$

To assess the significance of the genetic attributes, a t-test was applied using the formula: ± t = effect/ (variance effect) $^{1//2}$.

Inbreeding depression was calculated as the mean percent decline in F_2 generation compared to the F_1, using the following method:

(I.D %) = $100 \times (\overline{F}_1 - \overline{F}_2 / \overline{F}_1)$

The subsequent equation was utilized to estimate the potence ratio (P): $P = (F_1 - MP) / 1/2 (P_2 – P_1)$ with MP is the mid-parent value = $1/2(P_1+ P_2)$, P_2 and P_1: the average of the higher and lower parents, respectively, and F_1 is first generation mean.

The grain yield stress tolerance index (STI) was computed based on the method outlined in Farshadfar *et al.* (2001), with $STI = Yp \times Ys /(Yp)^2 \times 100$

In which, Ys grain yield in stress conditions, Yp grain yield in normal conditions.

The formulas provided by Mather and Jinks (1982) were utilized to compute the genetic components of variance, with the F2 variance determined accordingly as follows:

H (dominance variance) = $4 (V_{F2} – 1/2V_D - V_E)$

D (additive variance) = $4 V_{F2} – 2 (V_{BC1} + V_{BC2})$

E (environmental variance) = $1/3 (V_{P1} + V_{P2} + V_{F1})$

Narrow-sense ($h^2_{n.s}$) and broad-sense ($h^2_{b.s}$) heritability were calculated utilizing Warner (1952) formulas:

h2n.s = [2VF2 – (VBC1 + VBC2)]/VF2

h2b.s = [VF2 – (Vp1 + Vp2 + F1)/3]/VF2

The genetic advance was calculated based on the method described by Johnson *et al.* (1955), using a selection intensity factor of K = 5% (2.06) for all traits, as outlined below:

$G.S = K \times (\sigma^2 F_2)^{1/2} \times h^2_n.$ and $(G.S \%) = (G.S / \overline{F_2}) \times 100$

Heterosis was quantified by measuring the difference between the F1- generation and the average scores of the mid-parent or better parent, as outlined below:

Heterosis over the better-parent % (BP) = $(\overline{F_1} – \overline{BP}) /\overline{BP} \times 100$
Heterosis over mid-parent % (M.P) = $(\overline{F_1}-\overline{MP})/\overline{MP} \times 100$

Results and Discussion

Mean performance

As shown in Table 2, the averages of the seven attributes across the six populations F_1, F_2, P_1, P_2, BC_1, and BC_2 under water stress and normal irrigation conditions in the two-durum wheat crosses.

The variance analysis revealed substantial differences between the generations examined across all traits under both environmental conditions. The average F_1 scores exceeded the mid-parental values for every trait analyzed in both crosses in both of water stress and normal irrigation, except for days to 50% heading in cross 2 in both conditions.

This suggests that heterotic and dominance effects are the primary factors influencing these traits. In both crosses across the two environments, the F_1 generation surpassed the better parent for all traits studied, except for biological yield^{-1} in cross 1 in normal irrigation, suggesting the occurrence of over dominance.

Table 2. Mean performance ± standard error of P_1, P_2, F_1, F_2, BC_1 and BC_2 populations of two durum wheat crosses for the examined attributes across normal (N) and water stress (D) conditions

Trait	Cross	Environments	Generation						L.S.D 0.05
			P_1	P_2	F_1	F_2	BC_1	BC_2	
Days to 50% heading	C_1	N	98.00±0.15	89.00±0.23	104.33±0.18	97.38±0.11	102.17±0.18	102.67±0.16	2.72
		D	97.00±0.40	87.67±0.09	98.67±0.23	95.22±0.25	100.50±0.46	100.00±0.31	3.11
	C_2	N	96.33±0.23	99.67±0.09	88.33±0.23	89.56±0.16	94.97±0.29	89.67±0.28	2.66
		D	93.33±0.46	102.67±0.46	86.33±0.23	90.11±0.22	93.00±0.40	94.83±0.35	2.68
Plant height, cm.	C_1	N	101.93±0.54	100.10±0.38	105.40±0.45	101.84±0.47	101.87±0.63	101.37±0.62	4.79
		D	100.33±0.53	99.73±0.40	102.47±0.44	100.42±0.29	99.13±0.46	100.10±0.47	3.25
	C_2	N	102.33±0.57	99.60±0.63	105.40±0.63	105.31±0.35	103.87±0.55	100.77±0.59	5.36
		D	100.53±0.46	100.00±0.25	101.93±0.52	101.04±0.29	100.93±0.49	99.37±0.53	1.79
Spikes plant^{-1}	C_1	N	9.13±0.25	8.40±0.24	10.87±0.26	9.04±0.11	9.70±0.19	9.47±0.19	0.54
		D	8.60±0.21	8.80±0.23	9.40±0.22	9.01±0.12	8.57±21	8.87±0.21	0.35
	C_2	N	10.47±0.30	8.87±0.26	11.80±0.25	11.11±0.21	10.93±0.38	10.20±0.33	1.14
		D	8.67±0.20	8.47±0.19	10.07±0.16	9.60±0.12	9.07±0.26	8.57±0.17	0.38
Kernels spike^{-1}	C_1	N	40.54±0.37	41.26±0.65	43.44.57±0.47	42.90±0.46	42.81±0.59	42.47±0.65	2.85
		D	39.70±0.62	38.38±0.50	42.29±0.59	41.27±0.41	40.79±0.68	42.44±0.63	3.18
	C_2	N	42.80±0.76	44.00±0.52	47.34±0.36	42.98±0.54	41.05±0.77	43.42±0.82	4.68
		D	39.91±0.44	40.92±0.64	44.96±0.50	43.89±0.29	40.39±0.45	42.11±0.56	3.47
100-kernel weight, g	C_1	N	5.55±0.05	5.47±0.06	5.53±0.07	5.26±0.03	5.34±0.05	5.40±0.06	0.16
		D	4.80±0.04	4.82±0.06	5.29±0.07	5.09±0.03	4.96±0.06	4.99±0.05	0.17
	C_2	N	5.29±0.08	5.17±0.05	5.44±0.06	5.43±0.02	5.27±0.05	5.25±0.04	0.26
		D	4.94±0.05	4.97±0.06	5.15±0.05	5.00±0.03	4.98±0.05	4.95±0.04	0.12
Biological yield plant^{-1}, g	C_1	N	85.33±1.39	84.93±1.34	88.67±1.20	85.13±0.70	87.87±1.05	88.13±1.13	3.33
		D	81.65±1.32	78.80±0.60	84.70±0.86	82.69±0.44	80.37±0.80	79.88±0.77	5.65
	C_2	N	96.80±1.11	94.47±1.02	100.67±0.69	95.93±0.48	96.87±0.74	93.40±0.91	6.10
		D	89.73±0.83	87.53±0.87	93.47±0.64	91.20±0.49	90.77±0.87	87.67±0.85	2.49
Grain yield plant^{-1}, g	C_1	N	20.20±0.39	19.82±0.27	24.72±0.44	20.96±0.24	21.96±0.35	21.57±0.36	1.72
		D	18.87±0.37	19.28±0.29	21.29±0.34	19.93±0.29	19.08±0.61	19.63±0.33	1.27
	C_2	N	22.77±0.63	21.90±0.43	25.58±0.49	24.31±0.27	23.36±0.45	22.37±0.49	1.31
		D	19.52±0.34	19.13±0.38	21.98±0.46	20.27±0.28	19.23±0.49	18.84±0.45	1.65
STI%	C_1		93.43	93.42	86.12	95.09	86.89	91.01	
STI%	C_2		85.74	85.73	85.93	83.38	82.32	84.22	

STI= Stress tolerance index for grain yield plant^{-1}, Cross 1= (Bani-Sweif 7 × Yavaros 79), Cross 2 = (Mexical C75 × Line)

The average values for all traits in the F_2 population for all the attributes examined in both crosses were lower than those of the F_1 generation in both environments, except for days to 50% heading in cross 2 in two irrigation conditions. This highlights the significance of non-additive genetic variance components for these traits.

The average scores of the BC_1 and BC_2 progenies from both crosses fluctuated in both normal and water stress conditions, with each approaching the average of the recurrent parent. These outcomes aligned with the results indicated by El-Aref *et al.* (2011), Said (2014), Koubisy (2019) and Feltaous *et al.* (2024).

The STI presented in Table 2 indicates that F_2 exhibited the highest heat tolerance value at 95.09%. It was succeeded by P_1 (93.43%), P_2 (93.42%), BC_2 (91.01%), BC_1 (86.89%), and F_1 (86.12%) in the case of cross 1. Whereas, in cross 2, the F_1 hybrid exhibited the greatest STI value (85.93%) succeeded by P_1 (85.74%), P_2 (85.73), BC_2 (84.22%), F_2 population (83.38%) and BC_1 (82.32%). The findings suggested that selecting isolating populations for grain yield improvement under water-limited conditions might be a beneficial strategy for developing high-yielding, drought-tolerant lines. Amin (2013), Koubisy (2019) and Feltaous *et al.* (2024) obtained similar findings.

Gene effects

The outcomes of the A, B, C, and D scaling assessments conducted on the two durum wheat hybrids across two environmental conditions (Table 3) highlighted the importance of these assessments for both hybrids in all conditions, except for the 100-kernel weight in hybrid 2 in water-limited conditions. The findings indicated that neither the dominance-additive model nor the occurrence of non-allelic gene interactions could sufficiently account for the inheritance of these attributes. In Cross 2, the scaling test for 100-kernel weight under water stress conditions yielded no significant findings, implying that non-allelic interactions were not present. This also reinforces that the gene action for these attributes could be effectively described through the additive-dominance model. These findings align with Amin (2013), El-Hawary (2016), Kumar *et al.* (2017), Koubisy (2019) and Feltaous *et al.* (2024).

Table 4 presents the six gene effect parameters for both wheat crosses evaluated in both environmental conditions. The average effect (m), representing the contribution of the comprehensive mean along with the locus impacts and fixed loci interactions, was revealed to be extremely notable for the attributes examined across both crosses in normal and water-stressed conditions. This suggests that such attributes follow a quantitative inheritance manner. Imren *et al.* (2016), and Koubisy (2019) acquired similar findings.

The additive gene effect (d) showed a positive, notable influence on days to 50% heading in cross 2 in standard irrigation, the spikes plant^{-1} in cross 2 in normal irrigation, and plant height in cross 2 across both environments.

This highlights the substantial role of additive gene impacts on the transmission of such attributes, implying that further enhancement could be achieved through choosing to utilize the pedigree technique. Conversely, significant or highly significant negative scores were discovered for days to 50% heading in cross 2 in water stress conditions, and kernels spike^{-1} in cross 2 in two environmental conditions and cross 1 under normal irrigation. El-Aref *et al*. (2011), Koubisy (2019), and Feltaous *et al*. (2024) all reported similar findings, noting a significant negative additive gene effect on the 1000-kernel weight.

Table 3. Scaling assessment aspects A, B, C and D of two durum wheat crosses for the examined attributes in both normal (N) and water stress (D) conditions

Cross	Environments	Scaling test			
		A	B	C	D
		Days to heading			
C_1	N	2.01**±0.43	11.68**±0.44	-6.47**±0.62	-10.08**±0.32
	D	5.33**±1.03	13.67**±0.66	-1.11±1.18	-10.06**±0.75
C_2	N	5.27**±0.67	-8.67**±0.62	-14.44**±0.84	-5.52**±0.52
	D	-6.33**±0.95	0.67±0.86	-8.22**±1.18	-7.61**±0.68
		Plant height			
C_1	N	-3.59*±1.44	-2.76*±1.40	-5.47*±2.20	0.44±1.30
	D	-4.54**±1.75	-4.07*±1.11	-19.60**±1.61	-3.00±0.88
C_2	N	-1.73±1.40	-3.47**±1.49	8.51**±2.08	6.86**±1.08
	D	-0.60±-0.96	-3.20**±1.20	-0.22±1.63	1.79*±0.84
		spikes plant^{-1}			
C_1	N	-0.60±0.52	-0.33±0.53	-3.11**±0.77	-1.09**±0.34
	D	-0.87±0.66	-1.27**±0.46	0.51±1.40	1.09±0.71
C_2	N	-0.40±0.73	-2.25**±0.73	-7.74±1.05	-2.32±0.48
	D	-0.60±0.57	-1.40**±0.43	1.13*±0.64	1.57**±0.39
		kernels spike^{-1}			
C_1	N	-1.98**±0.82	0.24±1.01	2.92±2.04	2.33*±1.07
	D	-0.41±0.93	2.21*±1.00	2.42±2.09	0.31±0.95
C_2	N	-8.05**±1.75	-4.51**±1.76	-9.57**±2.44	1.49±1.55
	D	-4.09**±1.12	-1.66±1.38	4.82**±1.72	5.29**±0.92
		100-kernel weight			
C_1	N	-0.40**±0.14	-0.20±0.13	-1.04**±0.19	-0.22*±0.09
	D	-0.17±0.13	-0.13±0.14	0.62±0.20	0.23*±0.10
C_2	N	-0.19±0.14	-0.12±0.11	0.48**±0.17	0.40**±0.08
	D	-0.12±11	0.22±0.13	-0.21±0.15	-0.06±0.08
		Biological yield plant^{-1}			
C_1	N	1.74±2.80	2.66±2.90	-7.08±4.17	-5.74**±2.09
	D	-5.61**±2.24	-3.74*±1.86	0.91±2.86	5.13**±1.42
C_2	N	-3.74**±1.87	-8.34**±2.20	-8.87**±2.74	1.60±1.52
	D	-1.67±2.03	-5.67**±2.01	0.60±2.64	3.97**±1.56
		Grain yield plant^{-1}			
C_1	N	-1.00±0.92	-1.40*±0.89	-5.62**±1.38	-1.61±0.70
	D	-2.00*±0.90	-1.31±0.80	-1.00±1.42	1.15±0.76
C_2	N	1.62*±1.00	-2.73**±0.82	1.40±2.65	2.88**±1.38
	D	-3.04**±1.13	-3.42**±1.09	-1.52±1.55	2.47**±0.88

* & ** donate significance at probability levels of 0.05 and 0.01, respectively.

Table 4. Gene action types utilizing generation means ± standard error for the examined attributes of two durum wheat crosses in both normal (N) and water stress (D) conditions

Trait	Cross	Environments	Gene effect						Epistasis
			Mean (m)	Additive (d)	Dominance (h)	Additive × Additive (i)	Additive × Dominance (j)	Dominance × Dominance (L)	
Days to heading	C$_1$	**N**	97.38**±0.11	-0.50±0.24	30.83**±0.68	20.16**±0.64	-4.84**±0.28	-33.85**±1.14	D
		D	95.22**±0.25	0.50±0.55	26.44**±1.53	20.11**±1.49	-4.17*±0.59	-39.11**±2.51	D
	C$_2$	**N**	89.56**±0.16	5.30**±0.41	1.38±1.07	11.04**±1.04	6.97**±0.43	-7.64**±1.83	D
		D	90.11**±0.22	-1.83**±0.53	3.56**±1.42	15.22**±1.37	2.83**±0.62	-22.22**±2.42	D
Plant height, cm.	C$_1$	**N**	101.84**±0.47	0.50±0.89	3.50±2.67	-0.88±2.61	-0.42±0.95	7.23*±4.20	C
		D	100.42**±0.29	-0.97±0.66	-0.79±1.84	-3.22*±1.75	-1.27*±0.74	9.76**±3.08	D
	C$_2$	**N**	105.31**±0.35	2.23**±0.81	-9.28**±2.28	-13.71**±2.15	0.87±0.92	18.91**±3.85	D
		D	101.04**±0.29	1.57**±0.62	-1.91±1.79	-3.58**±1.69	1.30*±0.68	7.38**±2.98	D
Spikes plant^{-1}	C$_1$	**N**	9.04**±0.11	0.23±0.26	4.29**±0.75	2.18**±0.69	-0.14±0.32	-1.25±1.31	D
		D	9.01**±0.28	-0.30±0.23	-0.48±1.25	-1.18±1.22	-0.20±0.25	2.51*±1.54	D
	C$_2$	**N**	11.11**±0.32	0.73**±0.33	-0.54±1.45	-2.18*±1.41	0.43±0.36	3.84**±1.89	D
		D	9.60**±0.12	0.50±0.31	-1.63**±0.81	-3.13**±0.78	0.40±0.34	5.13**±1.39	D
kernels spike^{-1}	C$_1$	**N**	42.90**±0.46	-1.47**±0.55	-2.12±2.19	-4.66*±2.14	-1.11±0.60	6.40**±2.99	D
		D	41.27**±0.41	-0.65±0.48	2.63*±2.01	-0.62±1.90	-1.31**±0.54	-1.18±2.83	D
	C$_2$	**N**	42.98**±0.54	-2.37*±1.12	0.95±3.16	-2.99±3.11	-1.77±1.21	15.54**±5.12	C
		D	42.89**±0.29	-1.72**±0.72	-6.03**±1.95	-10.57**±1.85	-1.22±0.82	16.32**±3.35	D
100-kernel weight, g	C$_1$	**N**	5.26**±0.05	-0.06±0.11	0.46*±0.32	0.44**±0.31	-0.10±0.12	0.16±0.53	C
		D	5.09**±0.03	-0.03±0.07	0.04±0.21	-0.46**±0.19	-0.02±0.08	0.76**±0.36	C
	C$_2$	**N**	5.46**±0.02	0.02±0.06	-0.58**±0.17	-0.79**±0.15	-0.04±0.08	1.10**±0.30	D
		D	5.00**±0.03	0.03±0.06	0.07±0.17	-0.12±0.16	0.05±0.07	0.46*±0.29	C
Biological yield plant^{-1}, g	C$_1$	**N**	85.13**±0.70	-0.26±1.55	15.02**±4.45	11.48**±4.18	-0.46±1.83	-15.88*±7.46	D
		D	82.69**±0.44	0.49±1.11	-5.79*±3.05	-10.26**±2.83	-0.94±1.32	19.62**±5.27	D
	C$_2$	**N**	95.93**±0.48	3.47**±1.18	1.84±3.20	-3.20*±3.05	2.30±1.36	15.27**±5.45	C
		D	91.20**±0.49	3.10**±1.21	-3.11±3.25	-7.93**±3.13	2.00±1.35	15.27**±5.53	D
Grain yield plant^{-1}, g	C$_1$	**N**	20.96**±0.24	0.39±0.50	7.93**±1.48	3.22**±1.39	0.20±0.56	-0.82±2.45	D
		D	19.93**±0.29	-0.55±0.50	-0.09±1.58	-2.31±1.53	-0.34±0.55	5.61**±2.45	D
	C$_2$	**N**	24.31**±0.63	0.99*±0.55	-2.51±2.79	-5.76**±2.76	0.56±0.61	10.11**±3.45	D
		D	20.27**±0.28	0.39±0.67	-2.28*±1.83	-4.94**±1.75	0.19±0.71	11.41**±3.08	D

*p < 0.05, **p < 0.01. D = Duplicate, C = Complementary

Dominance gene action (h) was positive and important, or highly important, for days to 50% heading in both crosses under water stress, as well as in cross 1 under normal irrigation. This included the spikes plant^{-1}, kernels spike^{-1} count under water stress conditions, biological yield plant^{-1}, 100-kernel weight, and grain yield plant^{-1}, all measured under standard irrigation (Table 4).

At the same time, significant negative impacts were observed on plant height in cross 2 in normal irrigation, spikes plant^{-1} in cross 2 in water stress, kernels spike^{-1} in cross 2 in water stress, 100-kernel weight in cross 2 in normal irrigation, biological yield plant^{-1} in cross 1 under water stress, and grain yield plant^{-1} in cross 2 in water stress conditions. The findings highlight the significant role of dominant gene impacts on these attributes' transmission. The negative effect associated with prevalence suggests that the alleles causing lower scores in these attributes were controlling over those that control higher values. Amin (2013), Koubisy (2019), and Feltaous *et al.* (2024) observed a negative effect on 100-kernel weight during water stress. Alternatively, considerable dominance and additive gene impacts were important in the genetic transmission of days to 50% heading in cross 2 in water deficit conditions, plant height in cross 2 in normal irrigation, kernels spike^{-1} in cross 2 in water deficit. The impact of dominance gene effects surpassed that of additive effects, suggesting that both dominance and additive genetic influences were crucial in the genetic transmission of these attributes. In addition, choosing for preferred traits might be done in the initial generations, but it would prove more efficient in later generations when the influence of dominant traits weakens. The findings were consistent with those reported by El-Aref *et al.* (2011), Zaazaa *et al.* (2012), Koubisy (2019), and Feltaous *et al.* (2024).

The epistatic gene impacts of the additive x additive (i) type (Table 4) were both positive and substantial or remarkably substantial for various traits.

These included days to heading in both crosses and environments, spikes plant^{-1} in cross 1 in standard irrigation, 100-kernel weight in cross 1 in standard irrigation, along with biological and grain yields plant^{-1} in cross 1 in standard irrigation. It could be beneficial to report that these characteristics have genes that are increasing and that selection for enhancement may be effective. These outcomes align with the conclusions drawn by Moussa (2010), Kumar *et al.* (2017), and Koubisy (2019).

Negative and substantial or remarkably substantial additive × additive gene impact was noted for plant height in both crosses in standard irrigation, in addition to cross 2 under water stress. Additionally, spikes plant^{-1} in cross 2 showed important effects in both environments, kernels spike^{-1} in cross 1 in normal irrigation and cross 2 in water stress, 100-kernel weight in cross 1 in water stress and cross 2 under normal irrigation, biological yield plant^{-1} in both crosses in water stress and cross 2 in normal irrigation and grain yield plant^{-1} in the two crosses in water stress and cross 2 in normal irrigation.

The findings revealed the spread of alleles among the parents. Consequently, selection is ineffective in the early segregating generations, as no additive genetic effect can be established in these attributes. Amin (2013), Koubisy (2019), and Feltaous *et al.* (2024) acquired similar findings. Negative additive × additive gene interactions were noted for plant height, grain yield plant^{-1}, biomass, and spikes plant^{-1} (Akhtar and Chowdhry, 2006).

The data in Table 4 regarding epistatic gene impacts and the additive x dominance (j) interaction showed varying values, all of which were positive and either important or very important. These effects were noted for days to 50% heading in cross 2 across both environments and for plant height in cross 2 in water default conditions. To minimize the impact of additive × dominance epistasis, which is prone to separate in subsequent generations, it is recommended to postpone chosen until later generations, where homozygosity is higher, and additive and additive × additive variances become more dominant. The findings align with those indicated by Koubisy (2019) and Feltaous *et al.* (2024). Negative and notably significant values for days to 50% heading were observed in cross 1 across both environments, plant height in cross 1 in water stress and kernels spike^{-1} in cross 1 in water stress conditions.

The findings demonstrated that the genetic transmission of these attributes was influenced by the duplicative impact of epistatic genes.

The dominance × dominance (l) gene interactions (Table 4) were substantial and positive for plant height in both crosses in the two environments, spikes plant^{-1} in the two crosses in water stress and cross 2 in normal irrigation, kernels spike^{-1} in both crosses in normal irrigation and cross 2 in water stress, 100-kernel weight in both crosses in water stress and cross 2 in normal irrigation, biological yield plant^{-1} in both crosses in water stress and cross 2 in normal irrigation and grain yield plant^{-1} in the two crosses in water stress and cross 2 in normal irrigation conditions. These findings validated the significance of dominance × dominance genetic interactions in the inheritance of these traits, suggesting that selection will likely be more efficient in later generations. Substantial or notable negative dominance × dominance (l) gene interactions were observed for days to 50% heading in both crosses in the two environments, in addition to biological yield plant^{-1} in cross 1 under standard irrigation. These interactions suggest a diminishing impact on the expression of these characteristics. These outcomes align with those presented by Hamam (2014), Abd El-Rady (2018), and Feltaous *et al.* (2024).

This form of epistasis was described as duplicate epistasis when the signs were different and as complementary when the effects of dominance (h) and dominance × dominance (l) genes shared similar sign.

The findings (Table 4) revealed that duplicate epistasis predominated across all attributes examined in both environments and crosses, aside from plant height in cross 1 with normal irrigation, the kernels spike^{-1} in both crosses with water stress, and biological yield plant^{-1} in cross 2 in standard irrigation, where complementary epistasis was more prominent.

These results suggest that duplicate epistasis exerted a more significant role than complementary epistasis for most of the traits. Given that non-additive effects outweighed additive effects for most of the traits examined, it is advisable to focus on intensive selection in subsequent generations to enhance these traits.

The potential to obtain desirable segregates during inter-mating in early segregating generations necessitates the disruption of unfavorable linkages. This can be achieved by employing recurrent selection to manage these crosses, facilitating swift genetic advancement. The findings align with those presented by Saint Pierre *et al.* (2010), Amin (2013), Koubisy (2019), and Feltaous *et al.* (2024).

Inbreeding depression, potence ratio and heterosis

Table 5 displays the values for inbreeding depression percentages, heterosis compared to mid-parents and better parent, as well as the potence ratio. Positive notable or very remarkable heterosis over better parent and mid-parent values were noted for the examined characters in both crosses within both environments, excluding plant height in the two crosses in water stress, spikes plant^{-1} in both crosses in water stress and cross 2 in normal irrigation, biological yield plant^{-1} in both crosses under standard irrigation, 100- kernel weight in the two crosses under both conditions, kernels spike^{-1} in cross 2 under two irrigation and grain yield plant^{-1} in both crosses in normal irrigation. The findings align with those reported by El-Hawary (2016), Abd El-Rady (2018), Koubisy (2019), and Salous *et al* (2023). The values of parent heterosis for grain yield plant^{-1} were notably positive and very significant in both crosses, signifying the crosses potential as promising candidates for hybrid wheat development in the breeding program.

Inbreeding depression, indicated by a decline in the functionality of the F_2 generation compared to the F_1 generation, is displayed in (Table 5). The outcomes indicated notable or very significant positive inbreeding depression effects across all examined attributes in both normal and water deficit conditions, except for plant height in cross 2 in both environments. These outcomes are anticipated, as the manifestation of heterosis in the F_1 generation will decrease in the F_2 generation because of self-fertilization and the onset of homozygosity. These findings align closely with those indicated by Said (2014), and Busa *et al* (2022).

The potency ratio (Table 5) indicates the occurrence of excessive dominance in both crosses in all studied traits across both irrigations, with values surpassing one. Abd El-Rady (2018) Koubisy (2019), and Feltaous *et al.* (2024), acquired similar outcomes.

Genetic attributes of variance

The genetic variance attributes, including dominance (H) and additive (D) gene impacts presented in Table 5, indicate that the dominance variance for days to 50% heading in cross 2 in normal irrigation was greater than the additive variance, spikes plant^{-1} in both crosses in normal irrigation and cross 2 in water stress, plant height in cross 2 under water stress, kernels spike^{-1} in cross 2 in water deficit conditions, 100-kernel weight in cross 1 in water stress and grain yield plant^{-1} in cross 1 in water deficit. This suggests that the effect of dominant genes has a crucial influence in the inheritance of these attributes, and that chosen could be successful in subsequent generations as they segregate. In contrast, additive gene impacts had a more significant role in the genetic control of the other attributes, highlighting the potential of chosen in the early segregating generations to develop lines with elevated grain production under delayed planting, which suggests heat stress tolerance. These findings were consistent with those reported by El-Aref *et al.* (2011), Koubisy (2019), and Feltaous *et al.* (2024).

Table 5. Heterosis, potence ratio (P.R%), inbreeding depression (I.D%), components of variation, heritability percentage in narrow (h^2n) and broad (h^2b) senses and expected genetic advance (G.S) of two durum wheat crosses for seven examined attributes in both normal (N) and water stress (D) conditions

Trait	Cross	environments	Heterosis (%)		I.D %	P.R %	Components of variation			$H/D^{1/2}$	Heritability		G.S%
			M.P	B.P			H	D	E		h^2b	h^2n	
Days to heading	**C_1**	**N**	11.39**	6.46**	6.66**	2.46	1.15	1.46	1.07	0.89	48.64	34.93	1.07
		D	6.86**	1.72**	3.49**	1.36	7.64	20.13	2.22	0.62	84.35	70.89	5.78
	C_2	**N**	-9.68**	-11.37**	-1.38**	5.80	11.32	3.94	1.15	1.70	80.68	33.11	1.86
		D	-11.90**	-15.91**	-4.38**	2.50	4.97	9.07	4.83	0.74	54.47	42.75	13.18
Plant height	**C_1**	**N**	4.34**	3.40**	3.38**	4.79	4.09	66.22	6.40	0.25	84.22	81.69	10.52
		D	2.44	2.13**	2.00**	8.12	1.74	24.37	6.39	0.27	66.38	64.09	5.73
	C_2	**N**	4.39**	3.00**	0.08	3.24	0.49	33.42	11.28	0.12	59.88	59.45	6.17
		D	1.66	1.39**	0.87	6.25	29.39	10.89	5.49	1.64	69.98	29.79	2.60
Spikes plant^{-1}	**C_1**	**N**	24.02*	19.06**	16.84**	5.77	0.56	0.18	1.91	1.76	10.75	4.21	1.40
		D	8.05	6.82**	4.14**	7.00	2.51	2.55	1.37	0.99	58.09	38.94	16.10
	C_2	**N**	16.07	12.74**	5.84**	5.44	13.18	8.60	2.20	1.24	77.51	43.88	25.47
		D	17.51	16.15**	4.64**	15.00	5.96	1.47	1.01	2.01	68.74	22.71	10.77
kernels spike^{-1}	**C_1**	**N**	6.21**	5.28**	1.24**	7.06	1.84	59.70	7.86	0.18	79.41	78.20	23.20
		D	8.32*	6.52**	2.41**	4.92	14.49	49.03	9.86	0.54	74.06	64.53	19.85
	C_2	**N**	9.07	7.59**	9.21**	6.58	5.42	107.64	9.65	0.22	85.12	83.03	32.04
		D	11.25	9.87**	2.37**	9.00	14.20	13.57	8.58	1.02	54.62	35.86	10.32
100-kernel weight	**C_1**	**N**	0.82	0.55**	4.88**	3.00	0.01	0.06	0.11	0.38	21.43	20.00	2.93
		D	10.08	9.82**	3.82**	42.76	0.13	0.12	0.10	1.03	47.40	31.07	5.61
	C_2	**N**	3.99	2.82**	0.76**	3.52	0.01	0.02	0.12	0.74	19.34	16.67	2.20
		D	3.90	3.51**	2.90**	10.36	0.07	0.14	0.06	0.69	57.89	46.67	10.45
Biological yield plant^{-1}	**C_1**	**N**	4.16	3.91	3.99**	17.70	13.12	66.84	51.90	0.55	41.42	37.72	10.59
		D	5.58*	3.74**	2.37**	3.15	3.47	29.93	28.34	0.34	35.84	33.88	5.62
	C_2	**N**	5.27	4.00**	4.71**	4.32	12.21	44.26	27.53	0.53	47.78	41.99	6.55
		D	5.45*	4.16**	2.43**	4.39	61.46	41.39	18.49	1.22	66.10	37.94	6.33
Grain yield plant^{-1}	**C_1**	**N**	23.54	22.38**	15.21**	24.79	3.19	10.64	4.19	0.44	59.33	51.60	16.28
		D	11.62*	10.44**	6.38**	10.89	26.04	17.63	3.39	1.22	81.88	47.10	21.06
	C_2	**N**	14.52	12.33**	4.97**	7.44	8.29	12.54	8.16	0.81	50.57	38.00	13.08
		D	13.76*	12.60**	7.78**	13.34	14.89	19.49	4.73	0.87	73.99	53.55	23.21

*$p < 0.05$, **$p < 0.01$. B.P= Heterosis over better parent, M.P= Heterosis over mid parents.

In most traits, the average degree of dominance $(H/D)^{0.5}$ listed in Table 5 was below one, with the exception of days to 50% heading in cross 2 in standard irrigation, plant height in cross 2 in water stress, spikes plant^{-1} in the two crosses in normal irrigation and cross 2 in water stress, kernels spike^{-1} in cross 2 in water deficit conditions, 100- kernel weight in cross 1 under water stress, biological yield plant^{-1} in cross 2 in water stress and grain yield plant^{-1} in cross 1 in water stress conditions. These findings support the influence of partial dominance gene effects in governing these attributes, suggesting that choosing for these characteristics could yield better results in the early generations. The other traits, exhibiting a degree of prevalence greater than one, suggest that gene effects of over dominance are influencing these traits. Therefore, choosing to improve them must be postponed to subsequent generations. The findings suggest that both additive and non-additive gene impacts influence the genetic mechanisms governing these characteristics in both conditions. Abd El-Rady (2018), Koubisy (2019), Attri *et al* (2021), and Feltaous *et al.* (2024) drew a similar conclusion.

Heritability in broad and narrow-senses and genetic advance

Table 5 presents the heritability estimates, both in broad and narrow senses, along with the genetic improvement. For all the characteristics examined in the two crosses, the broad-sense heritability values ranged from moderate to high across both environments, excluding spikes^{-1} plant in cross 1 in normal irrigation, 100-kernel weight in normal irrigation in both crosses. They ranged from 35.84% for biological yield plant^{-1} in cross 1 in water stress conditions to 85.12% for kernels spike^{-1} in cross 2 in normal irrigation. This suggests that most of the phenotypic variation stemmed from genetic factors, and there is possibility for enhancing these attributes through selective breeding.

The genetic predominance of these characteristics was demonstrated by the differentiation between h^2b and h^2n. According to Robinson *et al.* (1949), heritability levels are classified as high (60% or greater), moderate (30–60%), and low (below 30%). Heritability values in the narrow sense ranged from moderate to high across most attributes, except for plant height in cross 2 in water stress, spikes plant^{-1} in cross 1 in normal irrigation and cross 2 in water stress and 100-kernel weight in the two crosses in normal irrigation. The findings suggest that these characteristics were significantly influenced by both additive and non-additive genetic effects, with a notable level of heritable variation observed. Conversely, selecting for traits with low estimates of narrow-sense heritability may prove challenging due to the disruptive impact of environmental factors. These outcomes align closely with the observations indicated by El-Sayed and El-Shaawawy (2006), Koubisy (2019) and Feltaous *et al.* (2024).

As stated by Johnson *et al.* (1955), genetic progress expressed as a percentage of the mean is classified as high (>20%), moderate (10-20%) and low (<10%). According to this, the predicted genetic improvement (G.S) as a percentage of the F_2 mean (Table 5) varied from moderate to high in both crosses across irrigation treatments. However, for heading duration, it was lower in both crosses in standard irrigation and in cross 1 in water-stress conditions, plant height in both crosses under water stress and cross 2 in normal irrigation, spikes plant^{-1} in cross 1 in normal irrigation, 100-kernel weight in normal irrigation in both crosses and cross 1 in water stress and biological yield plant^{-1} in the two crosses in water stress conditions and cross 2 in normal irrigation. This suggests the potential for choosing high-yielding genotypes during the early generations. Conversely, traits with low expected genetic advance appear to be influenced by environmental factors and the supremacy of gene action within their inheritance systems. Comparable findings were observed by Koubisy (2019) and Feltaous *et al*. (2024).

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التحليل الوراثي لهجينين من قمح الديورم تحت ظروف الري العادي والاجهاد المائي

ياسر سيد ابراهيم قبيصي*، جمال محمد محمد سليمان

قسم بحوث القمح، معهد بحوث المحاصيل الحقلية، مركز البحوث الزراعية، الجيزة، مصر.

الملخص

أجريت هذه الدراسة بمحطة بحوث شندويل خلال ثلاثة مواسم زراعية 2022/2021 حتى 2024/2023 بغرض دراسة طبيعة الفعل الجيني ونظام التحكم الوراثي والموديل الوراثي الملائم والتنبؤ بالتراكيب الوراثية المبشرة في الأجيال الانعزالية والتي تفوق حدود الآباء الداخلة في التهجين وذلك لسبع صفات اقتصادية لهجينين من قمح الديورم تحت ظروف الري العادي والإجهاد المائي باستخدام موديل العشائر الست لتقدير المقاييس الوراثية ونوع فعل الجين المتحكم في وراثة صفة المحصول ومكوناته وبعض الصفات الأخرى.

أظهرت نتائج تحليل اختبار المقياس وضوح تأثير التفاعلات غير الأليلية في معظم الصفات ماعدا صفة عدد أيام حتى طرد السنابل في الهجين الثاني تحت ظروف الري العادي، وطول النبات في الهجين الأول تحت ظروف الاجهاد المائي، (عدد السنابل للنبات، عدد حبوب السنبلة والمحصول البيولوجي) في الهجين الثاني تحت ظروف الري العادي.

اختلفت الأهمية النسبية لتأثير كل من الفعل الوراثي المضيف والسيادي تبعا للصفات والهجن تحت ظروف الري العادي الاجهاد المائي.

كان التأثير السيادي بصفة عامة أكبر من التأثير المضيف لجميع الصفات المدروسة فيما عدا (عدد الأيام حتى طرد السنابل، عدد حبوب السنبلة والمحصول البيولوجي) في الهجين الثاني تحت ظروف الري العادي، طول النبات في الهجين الأول تحت ظروف الاجهاد المائي مؤكدا على الأهمية الأكبر للتأثير السيادي للجينات في وراثة هذه الصفات بجانب التأثير المضيف. وكان المكون السيادي × السيادي ذو تأثير أكبر من تأثير كل من المضيف × المضيف والمضيف × السيادي في معظم الصفات موضحا الدور الأكبر للتأثير السيادي والتفاعلات غير الأليلية، لذلك من المفضل تأخير الانتخاب حتى الأجيال الانعزالية المتأخرة لزيادة الأصالة الوراثية. كانت تقديرات قوة الهجين بالمقارنة بالأب الأفضل عالية المعنوية وموجبة لكل الصفات المدروسة فيما عدا المحصول البيولوجي للنبات في الهجين الاول تحت ظروف الري العادي. تباينت قيم كلاً من درجة التوريث بالمعنى الواسع والضيق وكذلك التحسين الوراثي المتوقع من متوسطة لمرتفعة في معظم الحالات. وفي ضوء هذه النتائج يمكن الاستفادة من هذه الهجن لاستنباط سلالات قمح مبكرة النضج عالية المحصول تحت ظروف الإجهاد المائي.

الكلمات المفتاحية: *التهجين، القمح، الوراثة، عمل الجينات، نموذج المعايير الستة*