



RESEARCH

Genetic analysis of yield and associated traits in bread wheat crosses under deficit irrigation conditions using generation mean analysis

Muhammed G Abd-Elnaser¹ · Afaf M Tolba¹ · Yasser A El-Gabry¹

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Abstract

Drought stress severely limits bread wheat (*Triticum aestivum* L.) productivity in arid and semi-arid systems. We used generation-mean analysis on six populations derived from two contrasting crosses (Giza-171 × Var-16, Cross I; PL-10 × Var-18, Cross II) evaluated under both well-watered and water-deficit regimes. Significant genotypic variation was detected for flag leaf area, chlorophyll content, spike number, spike length, kernels per spike, 100-kernel weight, biological yield, and grain yield. Drought Sensitivity Index (DSI) analysis highlighted two different patterns of drought adaptation. In Cross I, the tolerant parent (P₁) appeared to transmit its resilience to subsequent generations. In contrast, Cross II (F₁) exhibited hybrid vigor and maintained consistency. Scaling tests and a six-parameter model indicated the involvement of both additive and non-additive (dominance and epistatic) gene actions, with their relative contributions being trait- and environment-dependent. Grain yield showed marked mid-parent heterosis under drought conditions (30.50% in Cross I and 33.07% in Cross II), accompanied by substantial inbreeding depression (up to 41.83% in Cross I), highlighting the relevance of non-additive effects. Heritability estimates indicated the presence of genetic variation for grain yield under both optimal and water-deficit conditions, with consistently high broad-sense and moderate narrow-sense heritability across both crosses. Cross I exhibited favorable additive and complementary epistatic effects under drought, suggesting that it may be amenable to recurrent selection, whereas the heterosis observed in Cross II warrants further evaluation under water-limited environments. These findings provide preliminary genetic indications that may help guide future assessments of pedigree-based and hybrid breeding approaches.

Keywords Gen-action · Heterosis · Inbreeding-depression · Heritability · Drought · *Triticum aestivum* L.

1 Introduction

Wheat (*Triticum aestivum* L.) is a strategic major crop providing essential calories and proteins to a large proportion of the global population. In Egypt, domestic wheat production remains insufficient to meet the growing national demand, creating a persistent gap between consumption and local supply that necessitates substantial imports (Gebeltová et al. 2024).

Egypt produced approximately 9.2 million metric tons (MMT) of wheat in the 2024/25 marketing year, compared with a total national consumption of 20.65 MMT. This disparity necessitated wheat imports of about 12.5 MMT to bridge the production–consumption gap, a dependency projected to persist through the 2025/26 season (USDA Foreign Agricultural Service 2024). These figures underscore the critical need to enhance wheat productivity to reduce reliance on imports under increasing water constraints. Enhancing wheat productivity is therefore crucial to strengthen food security and reduce import dependency, particularly under deficit irrigation conditions and within the limitations of scarce arable land and a rapidly increasing population.

Drought stress is one of the major limiting factors for wheat production in arid and semi-arid regions such as Egypt, where declining water availability continues to constrain irrigated agriculture (Mohie-El-Din and Moussa 2016). Projected fluctuations in Nile River flow associated

✉ Muhammed G Abd-Elnaser
Muhammedgamal@agr.asu.edu.eg
Afaf M Tolba
dr_afaftolba2011@agr.asu.edu.eg
Yasser A El-Gabry
elgabry@agr.asu.edu.eg

¹ Department of Agronomy, Faculty of Agriculture, Ain Shams University, Cairo, Egypt

with regional hydrological developments such as the Grand Ethiopian Renaissance Dam (GERD) may further intensify water shortages and threaten the sustainability of water-dependent cropping systems (Heggy et al. 2021). Consequently, breeding high-yielding, drought-tolerant cultivars has become a key priority in modern wheat improvement programs.

Grain yield is a complex quantitative trait controlled by multiple genetic and environmental factors. Generation mean analysis, as outlined by Mather and Jinks (1971), has been extensively employed to partition genetic variation into additive, dominance, and epistatic components. This approach provides valuable insight into gene action and supports the formulation of efficient selection strategies. Recent studies have demonstrated that yield-related traits under drought conditions are influenced by both additive and non-additive genetic effects, as well as genotype-by-environment interactions (Li et al. 2020), underscoring the importance of integrating classical genetic tools with contemporary breeding approaches.

Heterosis (hybrid vigor) enhances complex traits such as yield and drought tolerance when genetically divergent parents contribute favorable allelic combinations (Voss-Fels et al. 2019). In contrast, inbreeding depression resulting from increased homozygosity and the expression of deleterious recessive alleles can impair yield stability and adaptability. Understanding the relative contributions of additive, dominance, and epistatic effects is essential for designing effective breeding strategies. Additive effects contribute across a wide range of selection approaches and remain central to long-term selection response, whereas non-additive components (dominance and epistasis) can have a marked influence on the performance of particular genotype combinations, including hybrids, synthetic varieties, and multi-genotype stands. Heritability estimates, particularly narrow-sense heritability, provide useful insight into the potential response to selection and may help indicate traits with relatively greater scope for genetic improvement under both irrigated and drought-stressed conditions (Feltaous 2020; Swelam et al. 2022).

The present study aims to elucidate the genetic mechanisms governing yield-related and drought-adaptive traits in bread wheat through generation mean analysis under

contrasting irrigation regimes. By integrating parameters reflecting both gene effects and breeding potential, the research provides insights into the inheritance and expression of key traits under water stress. The findings are expected to support the development of high-yielding, drought-tolerant wheat genotypes adapted to sustainable production systems in Egypt.

2 Materials and methods

2.1 Plant material

Four bread wheat (*Triticum aestivum* L.) genotypes were used as parents in this study (Table 1). Two Egyptian genotypes, Giza-171 (a local cultivar) and PL-10 (a pure line selection), along with two genotypes obtained from the International Center for Agricultural Research in the Dry Areas (ICARDA), Egypt (Var-16 and Var-18), were selected based on their diversity in agronomic traits. The Egyptian genotypes (Giza-171 and PL-10) were included due to their promising performance under drought conditions observed in preliminary evaluations. These genotypes were used to develop two crosses: Cross I (Giza-171 × Var-16) and Cross II (PL-10 × Var-18).

2.2 Experimental site, design, and irrigation treatments

Field experiments were conducted during three consecutive growing seasons (2022/2023–2024/2025) at the Agricultural Research Station, Faculty of Agriculture, Ain Shams University, Shalakan, Kalubia Governorate, Egypt (30.191° N, 31.161° E; 15 m above sea level). The soil at the site is classified as clay loam, with particle-size distribution (0–30 cm depth) of approximately 40% sand, 24.3% silt, and 35.7% clay. Key chemical properties, averaged over the same depth, were pH 7.9, EC 0.9 dS m⁻¹, and organic matter content 1.1%.

In the first season (2022/2023), crosses were made among the four parental genotypes to produce F₁ hybrid grains. In the second season (2023/2024), F₁ plants were backcrossed to their respective parents to obtain BC₁ and BC₂ seeds, and

Table 1 Pedigree and origin of the bread wheat genotypes used as parents in Cross I and Cross II

Cross	Name	Pedigree	Origin
I	Giza-171 (P ₁)	SAKHA 93/GEMMEIZA 9 (S.6-1GZ-4GZ-1GZ-2GZ-0S)	Egypt
	Var-16 (P ₂)	MILAN/KAUZ/6/TOB/ERA/TOB/CNO67/3/PLO/4/VEE#5/5/KAUZ/7/MILAN/PAS-TOR/8/SANDALL-5	ICARDA
II	PL-10 (P ₁)	Giza157(Egypt) × Bow "S"/YD" S"/ZZ" S"(Mexico)	Egypt
	Var-18 (P ₂)	PBW343*2/KHVAKI//BAVIACORA*2/3/HEILO/4/HUBARA-3*2/SHUHA-4	ICARDA

some F_1 plants were selfed to generate the F_2 generation. In the third season (2024/2025), six populations (P_1 , P_2 , F_1 , F_2 , BC_1 , and BC_2) from both crosses were sown on 25 November 2024 under two irrigation regimes: normal irrigation and water deficit (Fig. 1).

Two irrigation regimes were implemented using a flood irrigation system as follows: The normal irrigation treatment received six irrigations at approximately 21-day intervals, while the water-deficit stress treatment received three irrigations, applied by withholding every alternate irrigation of the normal regime, thereby maintaining an effective interval of about 42 days between irrigations. This approach ensured uniform and consistent imposition of the intended water stress levels throughout the growing season.

Each treatment was arranged in a randomized complete block design (RCBD) with three replications for both crosses. Each replication consisted of four rows for each parent and F_1 , five rows for each backcross, and twelve rows for the F_2 generation. Rows were 2 m in length with 20 cm between rows and 10 cm between individual plants, giving approximately 20 plants per row. Hills were thinned

to one plant before the first irrigation. The dry planting method was used, following maize (*Zea mays* L.) as the preceding crop. Standard agronomic practices for wheat production, including fertilization and weed control, were uniformly applied to all plots.

2.3 Data collection

Data were recorded on an individual plant basis from 60 plants for each of P_1 , P_2 , and F_1 ; 150 plants for each of BC_1 and BC_2 ; and 300 plants for F_2 in each cross and treatment. The following traits were measured: flag leaf area (cm^2) at anthesis, calculated as leaf length $\times$ leaf width $\times$ 0.75 according to the method described by Lai and Subba (1951); chlorophyll content (SPAD units) measured on the flag leaf using a SPAD-502 chlorophyll meter; number of spikes per plant; spike length (cm) of the main stem (excluding awns); number of kernels per spike; 100-kernel weight (g); biological yield per plant (g); and grain yield per plant (g). All measurements were taken on randomly selected plants within each plot to avoid bias.

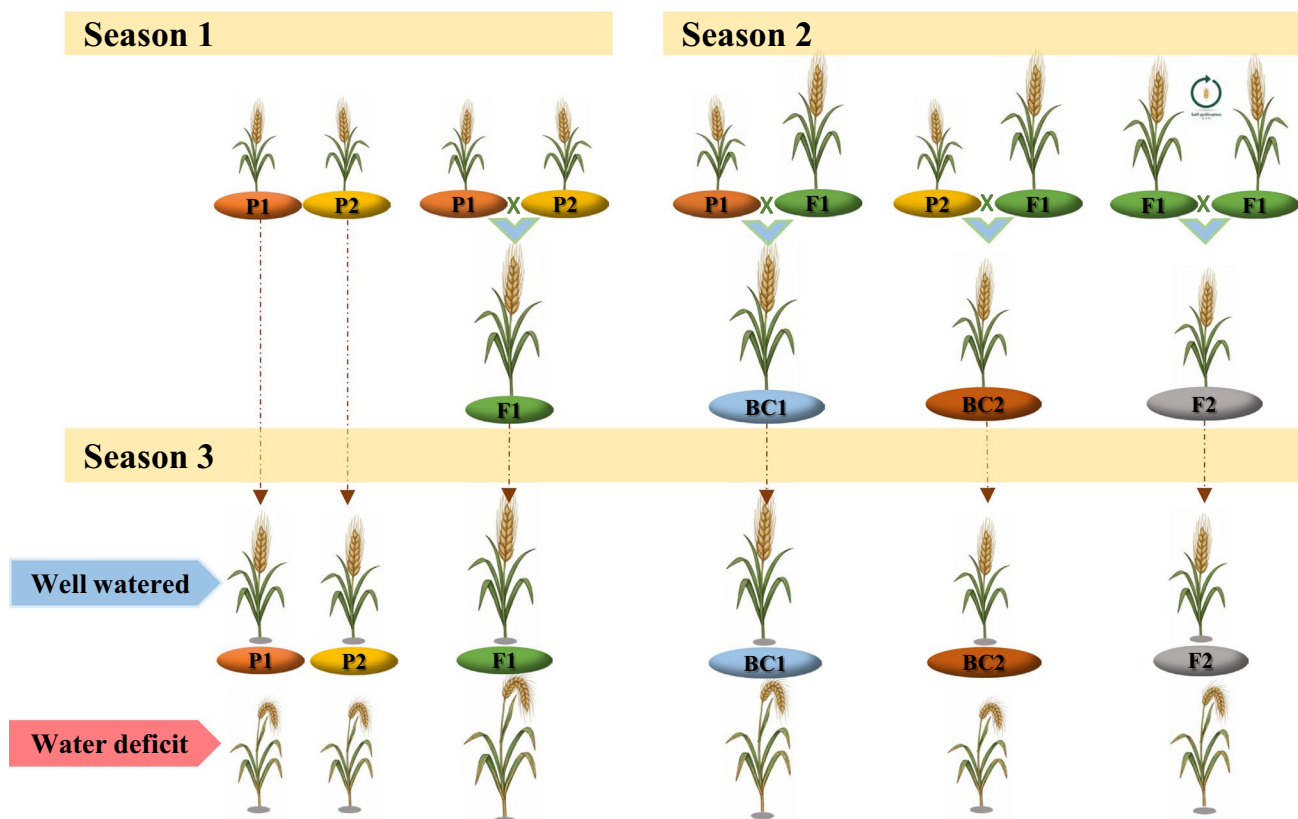


Fig. 1 Breeding scheme and evaluation of six generations derived from two wheat crosses under two environmental conditions across three growing seasons

2.4 Statistical and genetic analyses

The drought sensitivity index (DSI) was calculated to quantify the relative tolerance of each population to water deficit stress, using grain yield per plant as the selection criterion. The index was estimated according to the equation of Fischer and Maurer (1978):

$$DSI = \frac{1 - (Y_d/Y_p)}{1 - (\bar{Y}_d/\bar{Y}_p)}$$

where Y_d and Y_p represent the grain yield of a given genotype under water-deficit and well-irrigated conditions, respectively, and $\bar{Y}_d$ and $\bar{Y}_p$ denote the corresponding mean yields of all genotypes under the two conditions.

Genotypes with $DSI < 1$ were considered drought-tolerant, whereas those with $DSI > 1$ were classified as drought-sensitive.

A comprehensive genetic analysis was conducted for each trait under both irrigation conditions, separately for the two crosses. This included the estimation of mean performance, heterosis, inbreeding depression, scaling tests, a six-parameter genetic model, and heritability. Heterosis was computed as the relative percentage difference between the F_1 mean and both the mid-parent (MP) and better-parent (BP) means, following Bhatt's (1971) approach.

$$Heterosis(M.P., \%) = \left(\frac{(F_1 - M.P.)}{M.P.} \right) \times 100$$

$$Heterosis(B.P., \%) = \left(\frac{(F_1 - B.P.)}{B.P.} \right) \times 100$$

Inbreeding depression (I.D.) was estimated as:

$$I.D.(\%) = \left(\frac{(F_1 - F_2)}{F_1} \right) \times 100$$

Scaling tests (A, B, C, and D) were computed following the method of Mather and Jinks (1971) to detect non-allelic interactions (epistasis). Gene effects were estimated using the six-parameter model of Gamble (1962), where the generation means (P_1 , P_2 , F_1 , F_2 , BC_1 , BC_2) were used to calculate the mean effect (m), additive (a), dominance (d), and epistatic components (aa, ad, dd). The significance of gene effects was tested using the t-test as described by Gamble (1962).

Heritability in the broad (H^2) and narrow (h^2) senses was estimated according to Warner (1952). Broad-sense heritability was derived from the ratio of genotypic variance to phenotypic variance, while narrow-sense heritability was

based on the ratio of additive variance to total phenotypic variance in the F_2 generation. Because the Warner model assumes an additive–dominance framework without epistasis, the resulting H^2 and h^2 values should be interpreted as model-based approximations, particularly in the presence of significant non-allelic interactions detected in the scaling tests. Heritability estimates were classified as high ($> 60\%$), moderate (30–60%), and low ($< 30\%$) following the criteria of Robinson et al. (1949). All analyses were performed separately for each cross and irrigation treatment.

3 Results and discussion

3.1 Mean performance

Flag leaf area exhibited substantial variation across generations under contrasting irrigation regimes. In Cross I, mean values ranged from 52.10 cm² (P_2) to 59.87 cm² (F_1) under normal irrigation, while drought stress reduced this range to 40.17–54.33 cm². In Cross II, F_1 plants displayed the largest flag leaf area (61.66 cm²) under optimal conditions and maintained the highest values (57.12 cm²) under water deficit (Fig. 2). The observed reduction in flag leaf area under drought stress primarily reflects restricted cell expansion and decreased turgor pressure under water-deficit conditions (Sallam et al. 2019; Sattar et al. 2020). Similar generational variation in flag leaf area was also documented in earlier generation mean analysis studies (Omran et al. 2022; Shayan et al. 2019).

Also, Fig. 2 showed that chlorophyll content exhibited noticeable variation among generations under contrasting irrigation regimes. Under normal irrigation, mean values ranged from 46.59 to 54.08 SPAD units in Cross I and from 50.25 to 55.15 SPAD units in Cross II, with F_1 plants recording the highest readings in both crosses. Drought stress decreased chlorophyll content across all generations, with ranges of 37.44–51.17 SPAD units in Cross I and 43.73–49.96 SPAD units in Cross II, which can be attributed to oxidative damage from reactive oxygen species and disruption of chlorophyll biosynthesis pathways under water-limited conditions (Nyaupane et al. 2024). Under water deficit conditions, F_1 plants retained higher chlorophyll levels relative to their parental lines, in agreement with Said and Hefny 2021.

Under normal irrigation, the number of spikes per plant values ranged from 15.18 to 18.43 spikes/plant in Cross I and from 12.97 to 18.02 spikes/plant in Cross II, with F_1 recording maximum values in both crosses. Drought stress reduced spike production across all generations, with ranges of 9.10–14.52 spikes/plant in Cross I and 8.53–12.53 spikes/plant in Cross II (Fig. 3), which can be attributed to impaired spike initiation and development resulting from reduced

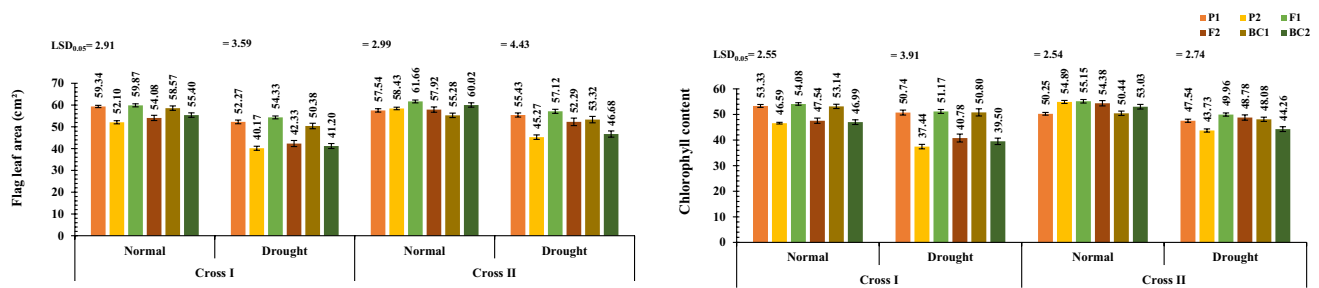


Fig. 2 Mean values and standard errors of flag leaf area and chlorophyll content evaluated in six generations of two wheat crosses under normal and drought conditions

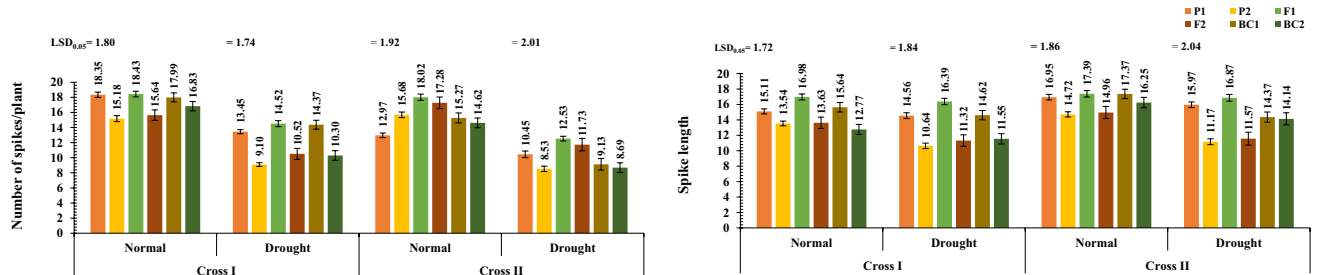


Fig. 3 Mean values and standard errors of the number of spikes per plant and spike length evaluated in six generations of two wheat crosses under normal and drought conditions

assimilate partitioning and photosynthetic activity under water-deficit conditions (Duvnjak et al. 2023; Nyaupane et al. 2024). Comparable generational responses under both irrigation regimes have been documented in previous studies of Koubisy and Soliman 2025; Swelam et al. 2022).

Spike length demonstrated variation across generations under contrasting irrigation regimes. Under well-watered conditions, values ranged from 12.77 to 16.98 cm in Cross I and from 14.72 to 17.39 cm in Cross II, with F₁ generation attaining maximum spike length in both crosses. Drought stress substantially diminished spike length across all generations, with ranges of 10.64–16.39 cm in Cross I and 11.17–16.87 cm in Cross II (Fig. 3), which can be attributed to impaired spike elongation due to limited assimilate availability and reduced photosynthetic capacity during critical developmental stages (Duvnjak et al. 2023; Nyaupane et al. 2024). Comparable results have been documented previously (Abdelgani et al. 2025; Swelam et al. 2022).

Furthermore, the kernel number per spike differed markedly among generations across both irrigation regimes. F₁ plants produced the maximum kernel number under normal irrigation in both crosses, recording 88.60 kernels/spike in Cross I and 80.77 kernels/spike in Cross II, compared to parental ranges of 74.93–83.50 and 70.38–79.83 kernels/spike, respectively. Drought stress substantially diminished kernel production, with values declining to 62.18–81.60 kernels/spike in Cross I and 63.08–75.68 kernels/spike in Cross II (Fig. 4), which reflects the sensitivity of reproductive

processes, particularly floret fertilization and grain set, to water limitation due to reduced photosynthetic activity and limited assimilate supply (Arriagada et al. 2025; Nyaupane et al. 2024). Similar results have been reported (Abdelgani et al. 2025; Swelam et al. 2022).

Similarly, hundred-kernel weight displayed notable variation among generations under both irrigation regimes. Under normal irrigation, Cross I ranged from 5.02 to 6.05 g, with BC₁ and F₁ recording the highest values (6.05 and 5.97 g, respectively), while Cross II ranged from 4.70 to 5.81 g, with F₁ and F₂ exhibiting maximum values (5.81 and 5.79 g, respectively). Drought stress reduced kernel weight across all generations, with ranges of 3.70–5.33 g in Cross I and 3.25–4.88 g in Cross II (Fig. 4), which can be attributed to impaired assimilate supply during grain filling due to reduced photosynthetic activity and accelerated leaf senescence that shorten the effective grain-filling period and restrict starch accumulation in developing kernels (Arriagada et al. 2025; Camaille et al. 2021; Ghaffar et al. 2023). Consistent results were observed (Koubisy and Soliman 2025; Said and Hefny 2021; Swelam et al. 2022).

Biological yield per plant exhibited under normal irrigation values ranged from 106.35 to 122.11 g/plant in Cross I and from 113.16 to 128.84 g/plant in Cross II, with F₁ recording maximum yield in both crosses. Drought stress reduced biological yield across all generations, with ranges of 54.32–88.21 g/plant in Cross I and 70.07–97.20 g/plant in Cross II (Fig. 5), which reflects decreased dry matter

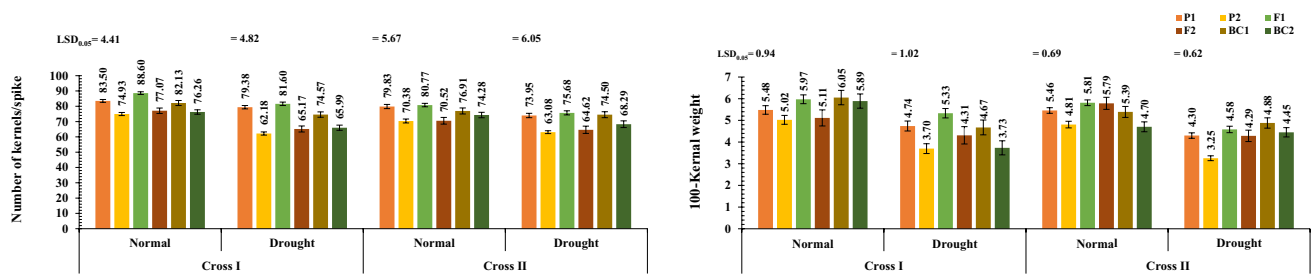


Fig. 4 Mean values and standard errors of the number of kernels per spike and 100-kernel weight evaluated in six generations of two wheat crosses under normal and drought conditions

production due to reduced leaf area, diminished photosynthetic activity, and accelerated senescence that limit assimilate accumulation during critical growth stages (Abid et al. 2018; Arriagada et al. 2025; Nyaupane et al. 2024). Similar results have been reported (Feltaous 2020; Koubisy and Soliman 2025; Said and Hefny 2021).

Under both irrigation regimes, grain yield per plant demonstrated considerable variation across generations. Under normal irrigation, values ranged from 44.88 to 56.28 g/plant in Cross I and from 43.40 to 50.47 g/plant in Cross II, with F₁ attaining maximum grain yield in both crosses. Drought stress substantially reduced grain yield across all generations, with ranges of 20.45–36.77 g/plant in Cross I and 21.30–36.56 g/plant in Cross II (Fig. 5), which reflects restricted carbon assimilation due to stomatal closure and reduced photosynthetic activity, coupled with accelerated senescence that impairs assimilate supply and translocation during the critical grain-filling period (Ghaffar et al. 2023; Nyaupane et al. 2024; Zhuang et al. 2024). Generational responses under both irrigation regimes have been documented (Koubisy and Soliman 2025; Mohamed et al. 2022; Said and Hefny 2021; Swelam et al. 2022).

Drought Sensitivity Index values from the current evaluation reflected contrasting genetic patterns of drought response among generations of the two wheat crosses. In Cross 1, drought tolerance originated mainly from P₁ (0.69) and was effectively expressed in F₁ (0.81) and BC₁ (0.95) (Said and Hefny 2021), whereas the influence of the

susceptible parent P₂ (1.26) re-emerged in F₂ (1.22) and BC₂ (1.16) (Aboud et al. 2020). In Cross 2, the F₁ (0.75) generation displayed the strongest tolerance across all populations, indicating pronounced heterosis under drought stress (Said and Hefny 2021; Koubisy and Soliman 2025), which was moderately maintained in F₂ (0.92) and BC₁ (0.81). The higher DSI of P₂ (1.41) and BC₂ (1.29) confirmed the transmission of sensitivity alleles (Aboud et al. 2020) (Fig. 6). Collectively, our results suggest that Cross 1 is a promising source of drought tolerance, while Cross 2 exhibited favorable hybrid performance under water-deficit conditions, indicating potential for further evaluation in drought-oriented breeding programs. These findings are consistent with earlier work (Swelam et al. 2022).

3.2 Heterosis and inbreeding depression

Heterosis over mid-parent for flag leaf area was highly significant and positive in both crosses, as shown in Table 2, recording 7.45% and 17.54% in Cross I and 6.34% and 13.43% in Cross II under both well-irrigated and water-deficit conditions, respectively. Better-parent heterosis was inconsistent across environments, being highly significant under normal irrigation in Cross II (5.53%) and significant under drought stress in Cross I (3.93%). Inbreeding depression was highly significant and positive in both crosses under both irrigation regimes, ranging from 6.06% to 22.08%, with the highest value observed in Cross I under drought stress,

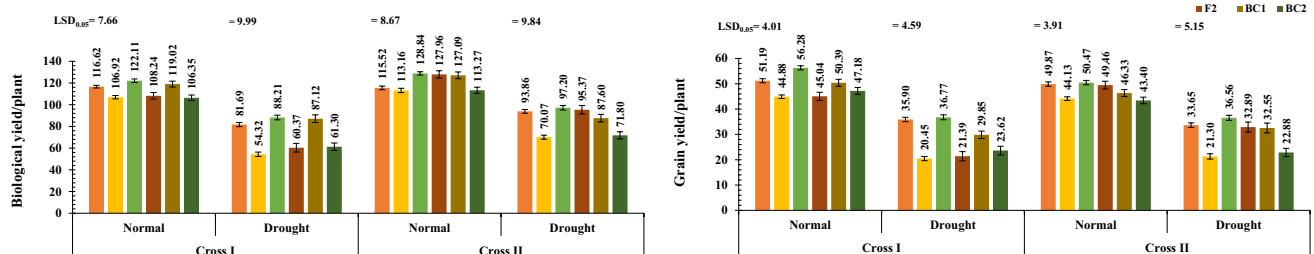


Fig. 5 Mean values and standard errors of biological yield per plant and grain yield per plant evaluated in six generations of two wheat crosses under normal and drought conditions

reflecting a substantial reduction in hybrid performance upon selfing. Similar genetic patterns for flag leaf area have been documented (Salmi et al. 2021).

Significant positive mid-parent heterosis for chlorophyll content was observed in both crosses across irrigation regimes (16.06% and 9.48% in Cross I and Cross II, respectively) relative to normal irrigation (8.25% and 4.90%, respectively). Better-parent heterosis was generally insignificant under normal irrigation but showed a highly significant positive value under drought stress in Cross II (5.08%), indicating enhanced photosynthetic capacity in hybrids under stress. Inbreeding depression was positive and highly significant in Cross I (12.10% and 20.31% under normal irrigation and drought stress, respectively), while Cross II exhibited positive but insignificant values (1.40% and 2.36%, respectively) (Table 2). Positive heterosis and inbreeding depression for chlorophyll content have been reported in wheat breeding populations (Mohamed 2014; Said and Hefny 2021).

Both crosses exhibited highly significant positive mid-parent heterosis for spike number per plant across irrigation regimes, with values ranging from 9.94% to 28.75% in Cross I and from 25.77% to 32.05% in Cross II. Better-parent heterosis was highly significant under drought stress in Cross I (7.93%) and under both irrigation regimes in Cross II (14.88% and 19.94%, respectively), reflecting superior spike production capacity in hybrids. Inbreeding depression was positive and highly significant in Cross I (15.15% and 27.55% under normal irrigation and water-deficit conditions, respectively) and positive and significant in Cross II (4.09% and 6.38%, respectively) (Table 2). Heterotic effects and inbreeding depression for spike number have been

documented in wheat breeding populations (Koubisy and Soliman 2025; Sharshar and Genedy 2020).

Cross I demonstrated highly significant positive mid-parent heterosis for spike length (18.52% and 30.09% under normal irrigation and drought stress, respectively), with better-parent heterosis also highly significant under both irrigation regimes (12.38% and 12.57%, respectively). Cross II exhibited highly significant positive mid-parent heterosis (9.81% and 24.29%, respectively), while better-parent heterosis was significant only under drought stress (5.61%), indicating enhanced spike elongation in hybrids under water-deficit conditions (Table 2). Positive heterosis for spike length has been documented in wheat breeding populations (Elmassry and El-Nahas 2018; Swelam et al. 2022). Inbreeding depression was highly significant and positive in both crosses under both irrigation regimes, reaching a maximum of 31.38% under drought stress in cross II. Similar inbreeding depression patterns have been reported by Elmassry and El-Nahas 2018.

Highly significant positive mid-parent heterosis for kernel number per spike was observed in both crosses across irrigation regimes, with values of 11.85% and 15.28% in Cross I and 7.53% and 10.46% in Cross II under well-watered and water-limited conditions, respectively. Better-parent heterosis was highly significant under normal irrigation (6.11%) and significant at the 5% level under drought stress (2.79%) in Cross I, while it remained insignificant in Cross II (Table 2). Positive heterosis for kernel number per spike has been documented in wheat breeding populations (Koubisy and Soliman 2025; Swelam et al. 2022). Inbreeding depression was highly significant and positive in both crosses under both irrigation regimes, ranging from 12.69% to 20.14%,

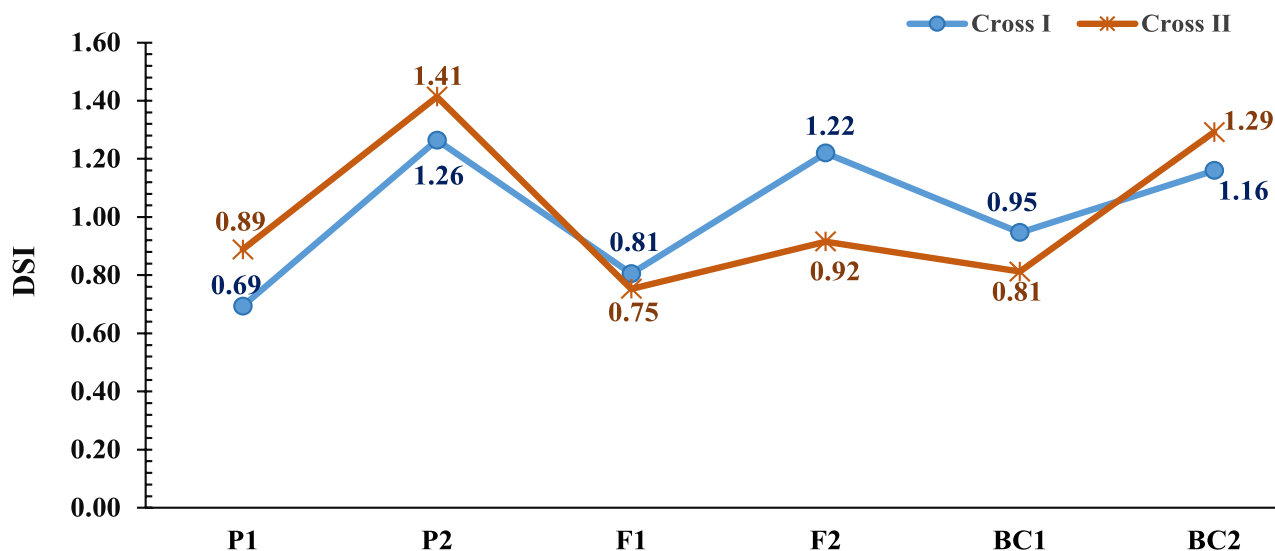


Fig.6 Drought Sensitivity Index (DSI) values of six generations from two bread wheat crosses under well-watered and drought stress conditions; lower DSI denotes greater drought tolerance

Table 2 Heterosis and inbreeding depression (I.D) for the studied traits of Cross I (G-171 × Var-16) and Cross II (PL-10 × Var-18) under normal (N) and drought (D) irrigation conditions

Traits	Treat	Heterosis %				I.D. %	
		Cross I		Cross II		Cross I	Cross II
		Mid-parent	Better Parent	Mid-parent	Better Parent		
Flag leaf area		7.45**	0.89	6.34**	5.53**	9.67**	6.06**
		17.54**	3.93*	13.43**	3.04	22.08**	8.45**
Chlorophyll Content		8.25**	1.42	4.90**	0.47	12.10**	1.40
		16.06**	0.85	9.48**	5.08**	20.31**	2.36
No. of spikes/plant		9.94**	0.45	25.77**	14.88**	15.15**	4.09*
		28.75**	7.93**	32.05**	19.94**	27.55**	6.38*
Spike length		18.52**	12.38**	9.81**	2.58	19.69**	13.95**
		30.09**	12.57**	24.29**	5.61*	30.90**	31.38**
No. of Kernels/spike		11.85**	6.11**	7.53**	1.17	13.02**	12.69**
		15.28**	2.79*	10.46**	2.34	20.14**	14.61**
100-kernel weight		13.74**	9.00*	13.28**	6.54**	14.40**	0.46
		26.35**	12.45**	21.36**	6.59*	19.14**	6.47*
Biological yield/plant		9.25**	4.71**	12.68**	11.53**	11.36**	0.68
		29.71**	7.98**	18.59**	3.57	31.56**	1.88
Grain yield/plant		17.17**	9.95**	7.38**	1.20	19.98**	1.99
		30.50**	2.42	33.07**	8.66**	41.83**	10.05**

*, ** denote significance at 0.05 and 0.01 probability levels, respectively

with higher values under drought stress in cross II. Similar inbreeding depression patterns have been reported (Koubisy and Soliman 2025; Sharshar and Genedy 2020).

Significant positive mid-parent heterosis for 100-kernel weight was observed across irrigation regimes in both crosses, with values of 13.74% and 26.35% in Cross I and 13.28% and 21.36% in Cross II under well-watered and water-deficit conditions, respectively. Better-parent heterosis was consistently significant or highly significant in both crosses under both irrigation regimes, ranging from 6.54% to 12.45%. Previous studies have documented heterosis for 100-kernel weight (Koubisy and Soliman 2025; Said and Hefny 2021; Swelam et al. 2022). Inbreeding depression was highly significant and positive in Cross I (14.40% and 19.14% under normal irrigation and drought stress, respectively), while Cross II exhibited an insignificant value under normal irrigation (0.46%) but significant depression under drought stress (6.47%) (Table 2). Comparable findings have been reported by (Elmassry and El-Nahas 2018; Koubisy and Soliman 2025).

Mid-parent heterosis for biological yield per plant was highly significant and positive in both crosses, recording 9.25% and 29.71% in Cross I and 12.68% and 18.59% in Cross II under two irrigation environments, normal and stressed, respectively. Better-parent heterosis was highly significant in Cross I under both irrigation regimes (4.71% and 7.98%, respectively) and in Cross II under well-watered (11.53%) conditions, indicating superior biomass production

in hybrids (Table 2). Heterotic improvements in biological yield have been documented (Feltaous 2020; Koubisy and Soliman 2025; Said and Hefny 2021). Inbreeding depression was positive and highly significant in Cross I (11.36% and 31.56% under normal irrigation and drought stress, respectively), while Cross II exhibited positive but insignificant values (0.68% and 1.88%, respectively). Comparable patterns have been reported by Koubisy and Soliman 2025.

Grain yield per plant, the ultimate breeding objective integrating all yield components, exhibited highly significant positive mid-parent heterosis in both crosses under both irrigation regimes, with values of 17.17% and 30.50% in Cross I and 7.38% and 33.07% in Cross II under full and deficit-irrigation regimes, respectively. Better-parent heterosis was highly significant in Cross I under normal irrigation (9.95%) and in Cross II under drought stress (8.66%), reflecting superior genetic potential in specific hybrid × environment combinations (Table 2). The observed heterosis for grain yield under drought stress suggests that hybrid vigor could be a relevant factor in these specific genetic backgrounds (Koubisy and Soliman 2025; Mohamed et al. 2022; Swelam et al. 2022). Inbreeding depression was highly significant and positive in Cross I under both irrigation regimes (19.98% and 41.83%, respectively), with a pronounced reduction observed under drought stress, while Cross II exhibited insignificant depression under normal irrigation (1.99%) but highly significant reduction under stress (10.05%), indicating differential genetic architecture

between crosses. These patterns are consistent with established reports (Koubisy and Soliman 2025; Sharshar and Genedy 2020).

3.3 Types of gene action

The scaling test (A, B, C, and D) revealed that, for both wheat crosses under normal and drought conditions, at least one scale was significant for every studied trait, indicating that the simple additive–dominance model is insufficient to explain the observed inheritance patterns. Accordingly, the six-parameter Mather–Jinks model is interpreted here as an approximation, since its estimates may be influenced by higher-order epistasis or unaccounted genotype $\times$ environment interactions. These results confirm the involvement of non-allelic gene interactions in the genetic control of these traits, consistent with previous findings in wheat (Elmassry and El-Nahas 2018; Mohamed et al. 2022; Swelam et al. 2022).

Gene action analysis for flag leaf area revealed differences in genetic effects across crosses and irrigation regimes. In Cross I, additive (a), dominance (d), and additive $\times$ additive (aa) effects were positive and significant or highly significant under both normal irrigation and drought stress. In Cross II under normal irrigation, additive (a) and additive $\times$ dominance (ad) effects were negative and highly significant, whereas under drought stress, positive and highly significant additive (a) and dominance $\times$ dominance (dd) effects were detected (Table 3). These patterns indicate cross- and environment-specific variation in significant gene effects, with Cross I showing consistent additive and additive $\times$ additive epistasis, while Cross II displayed context-dependent digenic interactions, particularly under water-deficit conditions, consistent with a previous report (Salmi et al. 2021).

Gene-action analysis of chlorophyll content revealed contrasting genetic architectures across crosses and environments. In Cross I, additive (a) and dominance (d) effects, along with additive $\times$ additive (aa) and additive $\times$ dominance (ad) epistatic interactions, were positive and significant or highly significant under both normal and drought conditions. In Cross II under well-irrigated conditions, negative and significant additive (a) and additive $\times$ additive (aa) effects were observed, while dominance $\times$ dominance (dd) epistasis was positive and highly significant. Under drought stress in Cross II, additive effects (a) became positive and highly significant, whereas additive $\times$ additive (aa) remained negative and significant, and dominance $\times$ dominance (dd) was positive and significant, with changes in the direction and significance of some parameters (Table 3). These results demonstrate cross- and environment-specific regulation of chlorophyll content, with dominance $\times$ dominance epistasis showing consistent significance in Cross II, particularly under water-deficit conditions, consistent with a previous report (Said and Hefny 2021).

Gene effect analysis for the number of spikes per plant revealed distinct genetic patterns across wheat crosses and environments. In Cross I, positive and highly significant dominance (d) estimates were detected under both irrigation regimes, along with positive and significant additive $\times$ additive (aa) and, under drought stress, additive $\times$ dominance (ad) interactions. In Cross II, dominance $\times$ dominance (dd) epistasis consistently showed positive and highly significant estimates under both irrigation regimes, while additive $\times$ additive (aa) interactions were negative and highly significant (Table 3). These patterns indicate cross- and environment-specific differences in gene effects, consistent with earlier research (Koubisy and Soliman 2025; Swelam et al. 2022).

Gene-action analysis of spike length indicated differences in the direction and statistical significance of gene-effect estimates across crosses and irrigation regimes. In Cross I, additive effects were positive and highly significant under both normal and drought conditions, with dominance and additive $\times$ additive interactions also reaching significance under drought stress. Additive $\times$ dominance was significant only under normal irrigation. In Cross II, additive $\times$ additive and dominance effects were highly significant under drought stress, while additive $\times$ dominance showed a negative and significant estimate under drought (Table 3). These patterns point to cross- and environment-specific differences in gene action, consistent with previous findings (Elmassry and El-Nahas 2018; Swelam et al. 2022).

Patterns of gene effects for the number of kernels per spike varied between crosses. In Cross I, additive effects were positive and highly significant under both irrigation regimes, while dominance effects were significant and positive under well-irrigated conditions and highly significant under stress. Additive $\times$ additive epistasis was also positive and significant under drought. In Cross II, both dominance and additive $\times$ additive interactions reached significance in both environments, whereas additive effects were significant only under drought stress. Dominance $\times$ dominance estimates were negative or non-significant across environments (Table 3). These patterns indicate that multiple gene-effect components contribute to kernel number in a cross- and environment-dependent manner, consistent with earlier studies of Mohamed et al. 2022; Sharshar and Genedy 2020; Swelam et al. 2022.

Gene effect analysis for 100-kernel weight varied across crosses and irrigation environments. In Cross I under normal conditions, dominance and additive $\times$ additive interactions were positive and significant, whereas dominance $\times$ dominance epistasis showed a significant negative estimate. Under drought stress in Cross I, only additive effects remained significant, indicating that significance patterns shifted under water limitation. In Cross II, additive effects and dominance $\times$ dominance epistasis were positive and significant

Table 3 Gene action components and scaling test results for the studied traits (T) in two wheat crosses (C) under normal and drought stress conditions

C	T	Scaling test				Gene action					
		A	B	C	D	m	a	d	aa	ad	dd
Flag leaf area											
I	N	−2.06	−1.17	−14.86**	−5.82*	54.08**	3.18*	15.78**	11.63*	−0.44	−8.40
	D	−5.83*	−12.09**	−31.77**	−6.92*	42.33**	9.18**	21.96**	13.85*	3.13	4.07
II	N	−8.64**	−0.04	−7.60	0.54	57.92**	−4.75**	2.59	−1.08	−4.30**	9.77
	D	−5.91	−9.03**	−5.79	4.58	52.29**	6.64**	−2.39	−9.15	1.56	24.09**
Chlorophyll Content											
I	N	−1.12	−6.69**	−17.93**	−5.06*	47.54**	6.15**	14.24**	10.11*	2.78*	−2.30
	D	−0.30	−9.60**	−27.40**	−8.75*	40.78**	11.30**	24.57**	17.49*	4.65*	−7.59
II	N	−4.51*	−3.99	2.08	5.29*	54.38**	−2.58*	−8.00	−10.58*	−0.26	19.08**
	D	−1.34	−5.17*	3.94	5.23*	48.78**	3.83**	−6.13	−10.45*	1.92	16.96*
No. of spikes/plant											
I	N	−0.80	0.05	−7.84**	−3.55*	15.64**	1.16	8.76**	7.09*	−0.42	−6.35
	D	0.78	−3.02*	−9.52**	−3.64*	10.52**	4.07**	10.52**	7.28*	1.90*	−5.04
II	N	−0.44	−4.46**	4.44	4.67**	17.28**	0.65	−5.64	−9.33**	2.01*	14.23**
	D	−4.72**	−3.69**	2.88	5.65**	11.73**	0.45	−8.25*	−11.29**	−0.51	19.70**
Spike length											
I	N	−0.80	−4.98**	−8.07**	−1.14	13.63**	2.88**	4.94	2.29	2.09*	3.49
	D	−1.71	−3.92**	−12.67**	−3.52*	11.32**	3.06**	10.84**	7.05*	1.10	−1.42
II	N	0.40	0.39	−6.60*	−3.69*	14.96**	1.12	8.94*	7.39*	0.00	−8.17
	D	−4.10**	0.24	−14.58**	−5.36**	11.57**	0.23	14.02**	10.72**	−2.17*	−6.86
No. of Kernels/spike											
I	N	−7.85*	−11.01**	−27.37**	−4.25	77.07**	5.87**	17.89*	8.51	1.58	10.35
	D	−11.85**	−11.80**	−44.10**	−10.23*	65.17**	8.57**	31.27**	20.45*	−0.03	3.19
II	N	−6.79	−2.59	−29.67**	−10.15*	70.52**	2.63	25.95*	20.29*	−2.10	−10.92
	D	−0.63	−2.19	−29.91**	−13.54*	64.62**	6.21*	34.25**	27.08*	0.78	−24.25
100-kernel weight											
I	N	0.65	0.78	−2.00	−1.72*	5.11**	0.16	4.16*	3.43*	−0.06	−4.87*
	D	−0.72	−1.56*	−1.86	0.21	4.31**	0.94*	0.69	−0.43	0.42	2.71
II	N	−0.49	−1.21*	1.26	1.48*	5.79**	0.69*	−2.28	−2.96*	0.36	4.66**
	D	0.88	1.06*	0.43	−0.76	4.29**	0.43	2.32	1.51	−0.09	−3.45*
Biological yield/plant											
I	N	−0.69	−16.33**	−34.81**	−8.90	108.24**	12.67**	28.14*	17.79	7.82*	−0.78
	D	4.35	−19.92**	−70.96**	−27.69**	60.37**	25.82**	75.58**	55.38**	12.14*	−39.80
II	N	9.82	−15.46*	25.48	15.56*	127.96**	13.82**	−16.63	−31.13*	12.64**	36.77
	D	−15.86*	−23.68**	23.16	31.35**	95.37**	15.80**	−47.46*	−62.69**	3.91	102.23**
Grain yield/plant											
I	N	−6.70*	−6.81*	−28.48**	−7.49*	45.04**	3.21	23.22**	14.97*	0.05	−1.47
	D	−12.97**	−9.98**	−44.33**	−10.69*	21.39**	6.23**	29.97**	21.38*	−1.49	1.57
II	N	−7.67*	−7.80**	2.91	9.19*	49.46**	2.93	−14.91*	−18.38*	0.06	33.85**
	D	−5.11	−12.11**	3.48*	10.35	32.89**	9.67**	−11.61	−20.70*	3.50	37.92**

A, B, C, and D represent the scaling tests; m is the mean effect; a is the additive gene effect; d is the dominance gene effect; aa, ad, and dd denote additive $\times$ additive, additive $\times$ dominance, and dominance $\times$ dominance epistatic effects, respectively. *, ** indicate significance at the 0.05 and 0.01 probability levels, respectively

or highly significant under normal irrigation, with the latter showing a highly significant positive estimate. However, under stress conditions in Cross II, dominance $\times$ dominance

interactions became negative and significant, reflecting a change in direction of this interaction between environments. These results illustrate environment-dependent differences

in the significance and direction of gene-effect estimates in both crosses (Table 3), consistent with previous reports (Koubisy and Soliman 2025; Sharshar and Genedy 2020; Swelam et al. 2022).

Biological yield per plant showed environment-dependent genetic effects that differed across crosses. In Cross I, additive (highly significant) and dominance (significant) effects were positive under normal irrigation, with significant additive $\times$ dominance interactions. Under drought stress, additive, dominance, and additive $\times$ additive effects all became positive and highly significant, alongside significant additive $\times$ dominance interactions. In Cross II, additive effects were consistently positive and highly significant across environments. Under normal irrigation, additive $\times$ additive interactions were negative and significant, while additive $\times$ dominance interactions were positive and highly significant. Under drought stress, dominance became negative and significant, additive $\times$ additive epistasis intensified negatively (highly significant), and dominance $\times$ dominance interactions emerged as positive and highly significant (Table 3). These results indicate that the direction and statistical significance of gene-effect estimates differ between crosses and environments, consistent with previous findings (Amiri et al. 2024; Koubisy and Soliman 2025).

Grain yield per plant showed environmentally dependent variation in gene-effect estimates across the two crosses. In Cross I under normal irrigation, dominance showed a positive and highly significant estimate, and additive $\times$ additive interactions were also positive and significant, while other estimates were not significant. Under drought stress, both additive and dominance effects became positive and highly significant, with additive $\times$ additive epistasis also showing positive and significant estimates. In Cross II, dominance and additive $\times$ additive effects were negative and significant under normal conditions, while dominance $\times$ dominance epistasis was positive and highly significant. Under drought, positive and highly significant additive and dominance $\times$ dominance effects were observed, while additive $\times$ additive interactions remained negative and significant (Table 3). These results indicate differences in the direction and statistical significance of gene-effect estimates between crosses and environments, with repeated significance of additive and dominance effects in Cross I, alongside the repeated significance of dominance $\times$ dominance epistasis in Cross II, consistent with earlier studies (Koubisy and Soliman 2025; Mohamed et al. 2022; Swelam et al. 2022).

3.4 Heritability estimates

Heritability estimates for flag leaf area revealed moderate to high values across both crosses and environments. In Cross I, broad-sense heritability was high under both normal irrigation (70.75%) and drought stress (64.97%),

while narrow-sense heritability was moderate (55.85% and 53.29%, respectively). Similarly, in Cross II, broad-sense heritability remained high under normal (69.37%) and stress (68.25%) conditions, with moderate narrow-sense heritability (58.99% and 52.97%, respectively). The substantial narrow-sense heritability (52.97%–58.99%) across both irrigation regimes indicates that additive genetic variance is likely an important component in controlling flag leaf area (Table 4). The consistency of heritability estimates across environments underscores the trait's considerable genetic basis and its suitability as a selection criterion in breeding programs targeting drought tolerance (Omrani et al. 2022; Shayan et al. 2019).

Chlorophyll content exhibited moderate to high heritability across both crosses and environments. In Cross I, broad-sense heritability was high under both normal irrigation (78.19%) and drought stress (68.69%), while narrow-sense heritability was moderate (51.69% and 54.67%, respectively). Similarly, in Cross II, broad-sense heritability remained high under normal (65.81%) and stress (63.98%) conditions, with moderate narrow-sense heritability (55.51% and 51.22%, respectively). The moderate narrow-sense heritability (51.22%–55.51%) across both irrigation regimes indicates an additive genetic contribution to chlorophyll content (Table 4). The consistency of heritability estimates across environments suggests that the trait has a meaningful genetic basis and supports its potential as a physiological marker for photosynthetic efficiency and drought adaptation in wheat breeding programs, consistent with previous findings of Said and Hefny 2021.

The number of spikes per plant showed moderately to highly heritable variation across both crosses and environments. In Cross I, broad-sense heritability was high under both normal irrigation (71.35%) and drought stress (81.59%), while narrow-sense heritability was moderate (48.33% and 56.67%, respectively). Similarly, in Cross II, broad-sense heritability remained high under normal (77.41%) and stress (79.68%) conditions, while narrow-sense heritability was moderate (52.19% and 56.31%, respectively). The moderate narrow-sense heritability across both irrigation regimes indicates meaningful additive genetic variance underlying spike number (Table 4). The consistency of heritability estimates across environments indicates that the trait has a meaningful genetic basis and suggests its potential as a selection criterion for improving tillering capacity and grain yield performance in drought-prone environments, similar to findings reported in wheat breeding studies (Koubisy and Soliman 2025; Mohamed et al. 2022; Swelam et al. 2022).

Broad-sense heritability for spike length exceeded 60% in both crosses under all environmental conditions. In Cross I, heritability estimates were 77.70% under normal irrigation and 73.11% under drought stress, while narrow-sense heritability was moderate (48.77% and 52.94%, respectively).

Table 4 Broad-sense (H^2) and narrow-sense (h^2) heritability estimates for agronomic traits in two wheat crosses under well-irrigated (N) and drought conditions (D)

Traits	Treatments	Cross I		Cross II	
		H^2	h^2	H^2	h^2
Flag leaf area	N	70.75	55.85	69.37	58.99
	D	64.97	53.29	68.25	52.97
Chlorophyll Content	N	78.19	51.69	65.81	55.51
	D	68.69	54.67	63.98	51.22
No. of spikes/plant	N	71.35	48.33	77.41	52.19
	D	81.59	56.67	79.68	56.31
Spike length	N	77.70	48.77	77.20	63.97
	D	73.11	52.94	77.79	49.03
No. of Kernels/spike	N	72.42	49.90	66.87	56.26
	D	69.59	46.37	72.51	51.36
100-kernel weight	N	70.27	40.54	75.17	48.42
	D	68.65	61.70	75.87	52.13
Biological yield/plant	N	75.65	48.66	73.39	39.64
	D	73.90	46.69	76.44	51.03
Grain yield/plant	N	76.59	52.16	72.56	50.10
	D	75.91	46.45	75.72	42.29

Similarly, in Cross II, broad-sense heritability remained high under normal (77.20%) and stress (77.79%) conditions, with narrow-sense heritability declining from high (63.97%) under normal irrigation to moderate (49.03%) under drought stress. The moderate to high narrow-sense heritability values (48.77%–63.97%) across environments reflect a meaningful additive genetic contribution, particularly in Cross II under normal irrigation (Table 4). The consistency of heritability estimates across irrigation regimes indicates that the trait has a meaningful genetic basis, supporting findings from drought tolerance investigations (Amiri et al. 2024; Elmassry and El-Nahas 2018; Swelam et al. 2022).

The number of kernels per spike exhibited moderate to high values with meaningful additive genetic contributions across both crosses and environments. In Cross I, broad-sense heritability was high under both normal irrigation (72.42%) and drought stress (69.59%), while narrow-sense heritability was moderate (49.90% and 46.37%, respectively). In Cross II, broad-sense heritability remained high under both normal (66.87%) and stress (72.51%) conditions, with moderate narrow-sense heritability declining from 56.26% to 51.36%. The moderate narrow-sense heritability (46.37%–56.26%) across both irrigation regimes reflects meaningful additive genetic variance underlying kernel number per spike (Table 4). The consistency of heritability estimates across environments indicates that the trait has a meaningful genetic basis and suggests potential responsiveness to selection, making it a valuable indirect selection criterion for grain yield improvement under both optimal

and water-deficit conditions. The present findings align well with earlier reports on wheat breeding (Amiri et al. 2024; Koubisy and Soliman 2025; Swelam et al. 2022).

100-kernel weight demonstrated contrasting patterns of heritability across environmental conditions (Table 4). In Cross I, broad-sense heritability was high under both normal irrigation (70.27%) and drought stress (68.65%), while narrow-sense heritability was moderate (40.54%) under normal conditions but increased to high (61.70%) under drought stress. Similarly, in Cross II, broad-sense heritability remained high under both normal (75.17%) and stress (75.87%) conditions, with moderate narrow-sense heritability (48.42% and 52.13%, respectively). The narrow-sense heritability (40.54%–61.70%) across both irrigation regimes reflects meaningful additive genetic variance underlying kernel weight, particularly the substantial increase in Cross I under water-limited conditions (Table 4). The consistency of high broad-sense heritability coupled with variable narrow-sense heritability indicates that the trait has a meaningful genetic basis and is responsive to environmental conditions. The enhanced additive control under water-deficit conditions suggests that 100-kernel weight has potential value as an indirect selection criterion for improving grain yield in drought-prone wheat breeding programs, consistent with observations in wheat breeding studies (Koubisy and Soliman 2025; Swelam et al. 2022).

Biological yield per plant revealed contrasting genetic architectures across crosses and environments. In Cross I, broad-sense heritability was high under both normal irrigation (75.65%) and drought stress (73.90%), while narrow-sense heritability was moderate (48.66% and 46.69%, respectively). Similarly, in Cross II, broad-sense heritability remained high under both normal (73.39%) and stress (76.44%) conditions, with moderate narrow-sense heritability increasing from 39.64% under normal irrigation to moderate (51.03%) under drought stress (Table 4). The clear difference between broad- and narrow-sense heritability in Cross I suggests the involvement of non-additive genetic effects, whereas the elevated narrow-sense heritability in Cross II under stress indicates enhanced additive variance and more predictable inheritance patterns. The differential narrow-sense heritability values (39.64%–51.03%) across crosses and environments indicate variation in additive genetic contributions to biomass accumulation. These findings underscore biological yield as a trait with cross-specific genetic architectures, highlighting the importance of population-tailored selection strategies for biomass improvement in water-limited environments, as reported in earlier investigations on this trait (Koubisy and Soliman 2025; Said and Hefny 2021).

Grain yield per plant demonstrated a meaningful genetic basis across both crosses and environments, with substantial additive variance underlying yield potential. In Cross I, broad-sense heritability was high under both normal irrigation (76.59%) and drought stress (75.91%), while

narrow-sense heritability was moderate, declining from 52.16% under normal irrigation to moderate (46.45%) under stress. In Cross II, broad-sense heritability remained high under both normal (72.56%) and stress (75.72%) conditions, with moderate narrow-sense heritability declining from 50.10% to 42.29% (Table 4). The moderate narrow-sense heritability (42.29%–52.16%) across irrigation regimes reflects the combined influence of additive and non-additive genetic effects, with the consistent moderate values under stress suggesting that genetic improvement remains possible even under water-limited conditions. These findings support the relevance of this trait for yield enhancement and stability in drought-prone wheat breeding programs, as reported in earlier investigations on grain yield genetics (Koubisy and Soliman 2025; Mohamed et al. 2022; Swelam et al. 2022).

Across traits and environments, qualitative consistencies were observed between heterosis responses, gene-action estimates, and heritability patterns. Traits showing notable mid-parent heterosis under drought, particularly grain yield and biological yield in both crosses, and spike number in Cross I, were generally those with significant non-additive gene effects (d, aa, or dd) in the generation-mean analysis. This correspondence suggests that heterosis expression tends to align with non-additive components in these genetic backgrounds. Conversely, traits that exhibited relatively higher narrow-sense heritability under drought stress, such as 100-kernel weight and chlorophyll content in Cross I, also showed more consistent additive contributions alongside moderate heterosis. These patterns are qualitative rather than quantitative, but they illustrate how additive and non-additive effects may correspond with heterosis and inheritance behavior across environments.

4 Conclusion

This study elucidated the genetic architecture governing yield-related and drought-adaptive traits in bread wheat across contrasting irrigation regimes using generation mean analysis. DSI analysis indicated inherited drought tolerance in Cross I and heterotic adaptability in Cross II, highlighting complementary genetic pathways relevant to drought resilience. Both additive and non-additive gene effects contributed to trait expression, with dominance and additive $\times$ additive interactions showing significant roles that varied by trait and cross under water-deficit conditions. Positive heterotic responses and moderate inbreeding depression across key yield components underscored the importance of maintaining genetic diversity and the potential relevance of hybrid vigor under stress. The moderate narrow-sense heritability estimates, coupled with high broad-sense heritability, suggest that selection targeting additive effects may contribute

to improving drought resilience, although further evaluation is needed. Future integration of genomic data could further accelerate genetic gains through marker-assisted approaches. Collectively, these results contribute to a genetic framework for understanding the inheritance of drought-responsive traits in wheat, with potential relevance to breeding considerations. Classical quantitative analyses demonstrated meaningful genetic variation and additive effects for key traits under both optimal and water-limited conditions. The integration of future genomic data with these quantitative findings may improve breeding efficiency and support the development of high-yielding, drought-resilient wheat cultivars. This integrated approach may be relevant for both pedigree-based and hybrid breeding strategies, with potential implications for improving wheat performance in water-limited environments such as Egypt.

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Author Contribution M.A. performed all field operations, including hybridization during the first and second growing seasons, and data collection under normal and drought conditions in the third season. He also conducted the statistical analyses, interpreted the results, and wrote the first draft of the manuscript. A.T. supervised the research, contributed to the experimental design, and made frequent field visits throughout the three growing seasons to closely monitor the experiments. She also provided comments and suggestions that improved the manuscript. Y.G. contributed to the experimental design, supervised the research, reviewed the field results and statistical analyses, and provided critical revisions that improved the final version of the manuscript. All authors read and approved the final manuscript.

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Data availability All data supporting this study are available from the corresponding author upon reasonable request.

Declarations

Competing interests The authors declare no competing interests.

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