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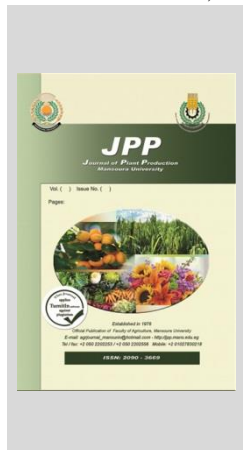
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Allelic and Non-Allelic Interaction of some Quantitative Traits in Rice under Water Deficit Conditions

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ABSTRACT

This study was carried out at the Experimental Farm of Sakha Rice Research Station, Kafr El-Sheikh, Egypt, during the 2021, 2022, and 2023 growing seasons. The objective was to evaluate heterosis, inbreeding depression, allelic and non-allelic interactions, and genetic advance for root, physiological, and yield-related traits in rice using a six-population approach: P₁, P₂, F₁, F₂, BC₁, and BC₂. Two rice crosses, Sakha106 × Nerica7 (CI) and Giza177 × GZ 10848-1-2-2-1 (Giza183) (CII), were investigated. Field trials were conducted in a randomized complete block design with three replications. The results revealed highly significant and positive heterosis, as a deviation from both mid-parent and better-parent values, for most traits under both irrigation conditions. Most traits displayed incomplete dominance to over-dominance. Both additive and dominance genetic effects played important roles in trait control, with additive × additive, additive × dominance, and dominance × dominance interactions also contributing to the genetic regulation of most traits, with a few exceptions. High values of Broad-sense heritability and predicted genetic advance were estimated for most traits in the studied crosses. However, narrow-sense heritability was generally moderate to low in most traits of both crosses. Based on these findings, Giza 177 × GZ 10848-1-2-2-1 (Giza183) is recommended for cultivation under water deficit conditions for most of the studied traits.

KeyWords: rice, water deficit, allelic and non-allelic interaction, heterosis and genetic advance.

INTRODUCTION

Rice (*Oryza sativa* L.) is a major cereal crop and a crucial source of nutrition, playing an essential role in global food security (Kondhia *et al.*, 2015). It supplies around 23% of global per capita energy intake and 16% of protein (Ye *et al.*, 2000). Rice cultivation spans over 160 million hectares worldwide, yielding approximately 740 million tons annually (Kumar *et al.*, 2019).

Drought is a major abiotic stress that limits rice production worldwide, affecting about 30% of rice-growing areas with moisture stress and water shortages. Annually, drought results in the loss of roughly 18 million tons of rice, valued at \$650 million, in both rainfed and irrigated regions (Pandey *et al.*, 2005, Hassan, 2013). Developing drought-tolerant rice varieties has thus become a priority in breeding programs, especially in Egypt, where the River Nile's irrigation water is limited. Key plant responses to drought include leaf rolling and early senescence (Anjum *et al.*, 2017). To identify drought-tolerant varieties, studies (Mishra and Panda, 2017, Hussain *et al.*, 2018) have examined traits such as flag leaf area, leaf area index, leaf relative water content, and leaf pigment content. Root traits are critical for improving yield under drought conditions, as root system architecture affects crop performance in low-water environments. Root dry weight and length are useful indicators for predicting rice yield during drought (Comas *et al.*, 2013, Hassan *et al.*, 2023). Various root responses are observed under water stress, such as increased abscisic acid in roots, which is associated with enhanced root length under drought (Manivannan *et al.*, 2007). Generally, rice cultivars with deep, extensive root systems are more drought-resistant (Mishra *et al.*, 2019, Kim

et al., 2020). Key root traits for drought resilience in rice include deep roots, thick roots, prolific branching, and a high root-to-shoot ratio (Kim *et al.*, 2020). These root morpho-physiological traits significantly influence shoot growth and grain yield under drought conditions (Kim *et al.*, 2020). Morphological adaptations to drought include longer, thicker roots, waxy or thick leaves, reduced epidermal cell density, delayed leaf senescence, and increased green leaf area (Hao *et al.*, 2018, Sahebi *et al.*, 2018, Melandri *et al.*, 2020).

Heterosis refers to the phenomenon where an F₁ hybrid, produced by crossing two genetically distinct individuals, exhibits enhanced traits compared to either parent or the average of the two. Additionally, assessing genetic variance, heritability in both broad and narrow senses, genetic gain, and the nature of gene action is crucial, as these factors influence the selection of the most effective breeding method.

The study aimed to evaluate heterosis, dominance levels, genetic variance, heritability, genetic advance, and both allelic and non-allelic interactions for traits related to root, physiological, and yield components in rice under water deficit (WD) and normal (N) conditions, and to apply breeding and selection methods to identify drought-tolerant rice populations.

MATERIALS AND METHODS

The study was conducted at the Experimental Farm of the Rice Research Department in Sakha, Kafr El-Sheikh, Egypt, over three growing seasons (2021–2023) to investigate the inheritance of specific root, vegetative, and yield traits in rice under water deficit (WD) conditions. Traits evaluated included root length (RL cm), root volume (RV cm³), number

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of roots/plant (NRP), root/shoot ratio (RSR), leaf rolling (LR), flag leaf area (FLA cm²), relative water content (RWC), chlorophyll content (Cc), days to 50 % heading (NDH days), plant height (PH cm), panicle length (PL cm), number of panicles/plant (NPP), number of filled grains/panicle (NFP), 1000-grain weight (TGW g), sterility % (SP) and grain yield/plant (GYP g). Based on previous studies, four rice varieties were selected and crossed to produce F₁ hybrids from two crosses: Sakha106 × Nerica7 (CI) and Giza177 × GZ 10848-1-2-2-1 (Giza183) (CII). The six populations (P₁, P₂, F₁, F₂, BC₁, and BC₂) for two crosses were used in this study.

In 2021, four rice varieties were planted at the Sakha Rice Research Station over three successive planting dates with ten-day intervals to synchronize flowering times. Thirty-day-old seedlings were transplanted into 5-meter-long rows, and hybridization was performed during flowering using the method proposed by Jodon (1938) and modified by Butany (1961), yielding two F₁ crosses.

In 2022, both parent and F₁ plants were grown under standard conditions, with repeated hybridization to produce additional F₁ seeds. Some F₁ plants self-pollinated to produce F₂ seeds, while others were backcrossed with parent plants to produce BC₁ and BC₂ seeds.

In the 2023 season, seeds from all generations of each cross (P₁, P₂, F₁, F₂, BC₁, and BC₂) were grown under normal and water-deficit conditions. Twelve entries (including four parents, two F₁, two F₂, two BC₁, and two BC₂ populations) were arranged in a randomized complete block design (RCBD) with three replications. Row spacing was set at 20 × 20 cm. Standard agricultural practices were followed for planting, fertilizing, and maintaining plots.

Two irrigation treatments were tested in 2023: the well-watered condition (normal) regime every four days (6000 m³/fed) and a water-deficit treatment (WD) regime every twelve days (3500 m³/fed). Sixty plants from each P₁, P₂, and F₁ population, 150 plants from BC₁ and BC₂, and 200 plants from F₂ were selected, harvested, and threshed individually to assess yield and yield components.

Various vegetative traits of both control and treated rice plants were measured after the water deficit condition ended. (RL) was measured using a centimeter scale, and the number of roots per plant (NRP) was recorded at the maximum tillering stage. (RV) was determined in cubic centimeters Root volume by immersing the roots in a water-filled measuring cylinder. The (RSR) was calculated at the maximum tillering stage using the formula: root/shoot ratio = Root dry weight (g)/ Shoot dry weight (g). Vegetative and yield component traits, such as NDH, Cc, PH, PL, NPP, NFP, TGW, SP, and GYP, were recorded according to the method outlined by IRRI (2002). Relative water content (RWC%) was determined using the method described by Barrs and Weatherly (1962). Flag leaf area (FLA) was measured at the flowering stage, following the manual method proposed by Yoshida *et al.*, (1962). Leaf rolling (LR), used as an indicator of drought tolerance, was assessed on a 1-9 scale based on visual estimation, following the method by De Datta *et al.*, (1988).

Heterosis was calculated according to Falconer and Mackey (1996). and appropriate LSD values were computed to test the significance of heterotic effects using the formula suggested by Wynne *et al.*, (1970). The relative potence ratio (P) was applied to assess the degree and direction of dominance, following the formula by Mather and Jinks

(1971). Scaling tests (A, B, and C) were calculated based on the formula suggested by Evans *et al.*, (2002). Gene effects were estimated according to Mather (1949) and Hayman (1958). The expected genetic variance for VBC₁, VBC₂, and VF₂, additive (1/2 D) and dominance (1/4 H) components, was derived following Mather (1949). Heritability in both broad and narrow sense was determined according to Powers *et al.*, (1950) and Warner (1952), respectively. Finally, expected and predicted values of genetic advance (GS and GS%) were calculated using the method by Johnson *et al.*, (1955).

RESULTS AND DISCUSSION

Results

Means of the parents and their generations:

As shown in Figures 1 and 2, the results indicated significant variation in trait means between the two parents across most studied traits. The F₁ mean values surpassed the higher parent values for traits such as RL, RV, NRP, RSR, Cc, PL, NPP, NFP, TGW, and GYP in all crosses. Additionally, values of F₁ were higher than the highest parent for RWC in CI, NDH and FLA in CII, and PL and SP in the first cross under well-watered conditions and the second cross under both conditions. Conversely, the means of F₁ were intermediate between the parents for NDH and FLA in CI, PH and SP in CI under WD, and RWC in the second cross under well-watered treatment. For LR under both conditions and RWC in CII under WD, F₁ values were lower than the lowest parent. F₂ values exceeded the highest parent values for traits such as RV, RSR, Cc, NDH, NPP, and GYP in all crosses. Other characters, including RL and NRP in CI, PH and FLA in CII, PL in the first cross under WD and CII under both treatments, NFP and SP in CI under well-watered and CII under both treatments, TGW in CII under well-watered and CI under both treatments, and RWC in CII under normal treatment, also showed values higher than the highest parent. In the remaining traits, values generally fell between the two parents, except LR in CI under both treatments, RL, and RWC in CII under WD, which were lower than the lowest parent.

BC₁ mean values were higher than the highest parent for RV, NRP in I, RSR, NDH, PH, PL in CII, RWC, Cc in both crosses under well-watered treatment, FLA in CII under WD, NPP and GYP in the first cross under both conditions and the second cross well-watered treatment, TGW in CI under normal conditions and CII under (WD), and SP in CI under well-watered treatment and CII under both treatments. Values of BC₁ were lower than the lowest parent for RWC in CII under both conditions, RV and NRP in CII under well-watered treatment, and LR in CI under well-watered conditions, while other traits had intermediate values between the parents. BC₂ mean values surpassed the highest parent for RV, NPP, NFP, and GYP in the second cross, RSR and PH in CII, RL and NRP in the first cross under WD, NDH and SP in the first cross under N treatment and CII under both treatments, PL in CI under WD and CII under both conditions, RWC in both crosses under N treatment, Cc in the first cross under both treatments and the second cross under WD, and FLA in CII under well watered. The other crosses for these traits were generally intermediate between the parents, except for TGW and LR in the first cross under both treatments, and RL, FLA, and RWC in the CII under WD, which were lower than the lowest parent.

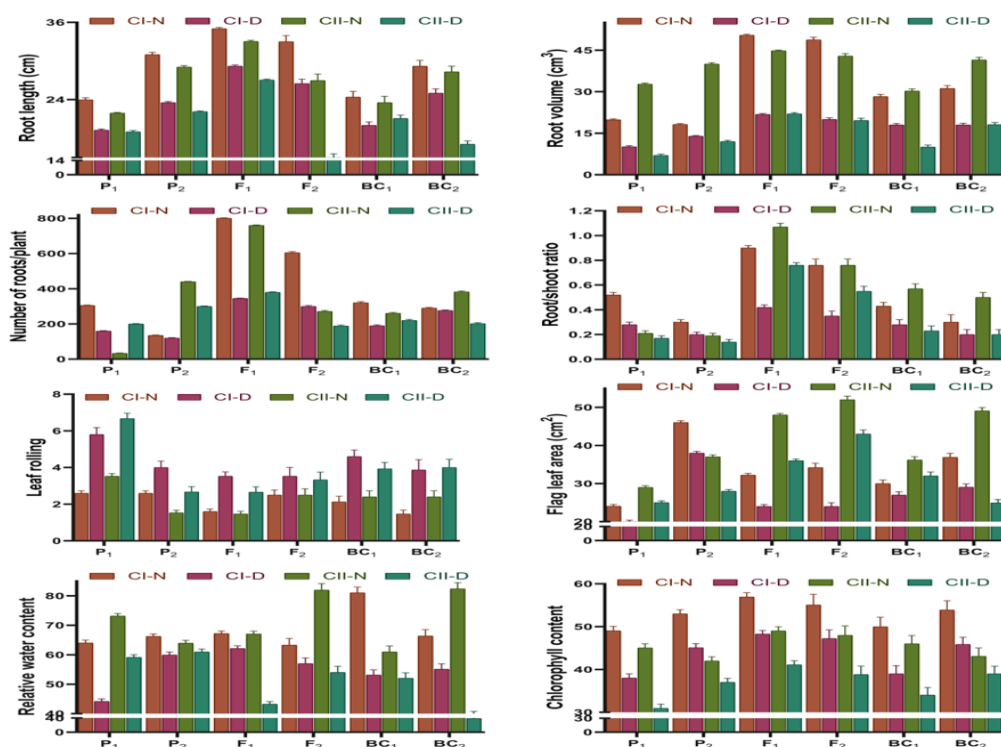


Fig. 1. Means and standard error of the six populations for root and physiological traits in both crosses (CI: Sakha106 × Nerica7, and CII: Giza177 × GZ 10848-1-2-2-1 (Giza183)) under normal condition (N) and water deficit (WD) conditions.

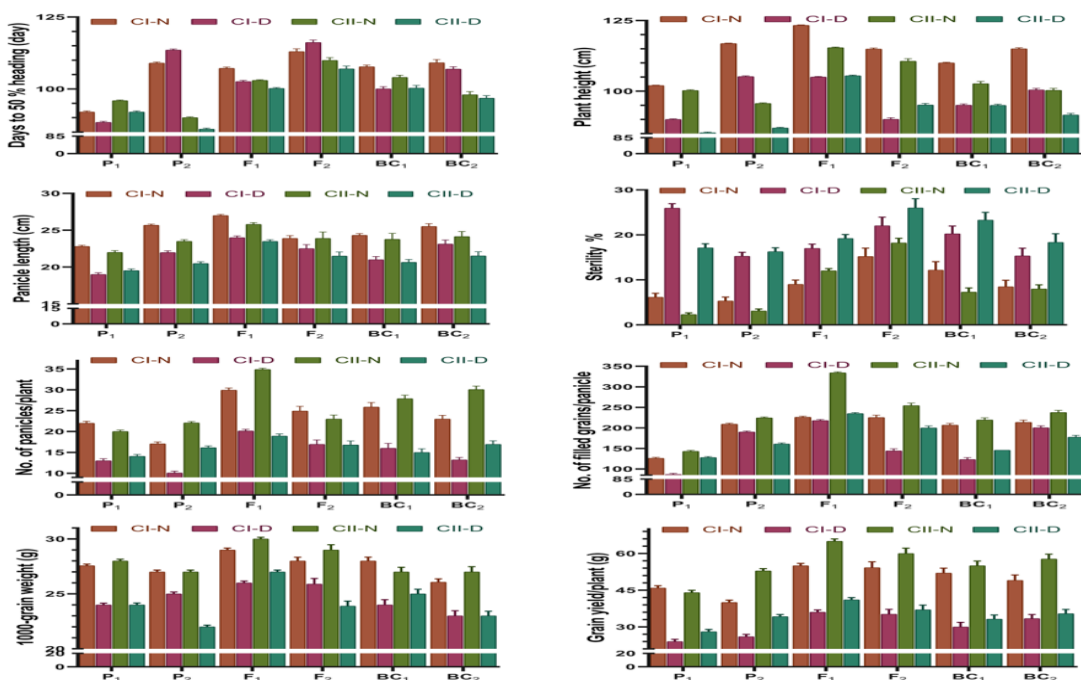


Fig. 2. Means and standard error of the six populations for agronomic and yield components traits in both crosses (CI: Sakha106 × Nerica7, and CII: Giza177 × GZ 10848-1-2-2-1 (Giza183)) under normal condition (N) and water deficit (WD) conditions.

Estimates of heterosis, degree of dominance and inbreeding depression:

As shown in Table 1, the degree of dominance exceeded unity (± 1.0) for traits such as RL, RV, NRP, RSR, RWC, Cc, PL, NPP, NFP, TGW, GYP, NDH, and FLA in

(CII) under both treatments. For PH and SP in CII under well-watered treatment and LR in CII under well-watered treatment and CI under WD, over-dominance appeared significant in influencing these traits

Table 1. Estimates of heterosis as a deviation from mid-parents (MP), better-parent (BP), degree of dominance and Inbreeding depression (%) for rice root, physiological and yield components traits for the two studied crosses under normal (N) and water stress (WD) conditions.

Characters	Cross	Heterosis %				Potence ratio (%)		Inbreeding depression (%)	
		MP		BP		N	WD	N	WD
		N	WD	N	WD				
Root length	I	27.47**	36.45**	13.01**	24.08**	2.15	3.66	5.80	9.25
	II	29.65**	28.75**	13.67**	22.26**	2.11	5.41	18.38**	44.57
Root volume	I	164.80**	81.16**	176.92**	56.46**	-37.64	5.14	3.31**	8.26
	II	23.19**	131.58**	12.00**	83.33**	2.32	5.00	4.32	10.76
Number of roots/plant	I	263.99**	146.57**	493.09**	187.67**	-6.83	-10.26	24.38**	13.09**
	II	105.40**	52.01**	72.76**	26.65**	5.58	2.60	64.34**	50.41**
Root/shoot ratio	I	119.02**	71.90**	199.33**	106.62**	-4.44	-4.28	15.40	15.87
	II	435.33**	389.66**	463.51**	459.61**	-87.07	-31.17	29.02	27.38
Days to 50% heading	I	6.67**	1.62**	-1.65**	-9.63**	0.79	0.13	-5.41**	-13.22
	II	10.75**	12.54**	14.36**	16.42**	-3.41	-3.76	-6.73	-6.79**
Plant height	I	12.70**	7.58**	5.53**	-0.19**	1.87	0.97	6.81**	14.22**
	II	17.80**	22.40**	20.63**	21.23**	-7.58	23.16	4.13**	9.80**
Leaf rolling	I	-38.46**	-27.89**	-38.46**	-11.67**	1.00	1.52	-56.25	0.00
	II	-42.11**	-42.86**	-4.35	0.00	1.07	1.00	-70.45	-25.00
Flag leaf area	I	-8.66**	-17.19**	-30.45**	-36.80**	-0.28	-0.55	-6.91**	0.05**
	II	45.40**	35.85**	29.64**	28.57**	3.73	6.33	-8.32**	-19.46**
Relative water content	I	3.20**	19.47**	1.48	3.76**	1.89	1.29	5.85**	8.28**
	II	-2.15**	-27.96**	4.89**	-29.06**	0.32	-18.13	-22.19**	-24.86**
Chlorophyll content	I	11.60**	16.12**	7.42**	7.00**	2.98	1.89	3.32**	2.16**
	II	12.66**	21.03**	16.75**	11.10**	-3.61	2.35	2.13**	5.55**
Panicle length	I	11.32**	17.17**	5.09**	9.26**	1.91	2.37	11.48	6.25
	II	13.41**	17.41**	9.79**	14.68**	4.07	7.31	7.36	8.47
No. of panicles/plant	I	53.24**	74.57**	75.39**	100.00**	-4.22	-5.86	16.70**	15.89**
	II	65.77**	25.39**	58.01**	17.36**	13.39	3.71	34.03	11.27**
No. of filled grains/panicle	I	34.90**	57.40**	8.10**	14.74**	1.41	1.54	0.22**	33.93**
	II	82.00**	62.70**	49.00**	45.96**	3.70	5.47	23.91**	14.88**
1000-grain weight	I	6.29**	6.12**	7.41**	4.00**	-6.06	3.00	3.45	0.38
	II	9.09**	17.39**	11.11**	22.73**	-5.00	-4.00	3.33	11.48
Sterility %	I	57.14**	-17.49**	69.34**	11.41*	-7.93	0.67	-68.65**	-29.51**
	II	344.90**	15.04**	288.76**	18.06**	23.88	-5.89	-51.37**	-35.33**
Grain yield/plant	I	28.11**	44.00**	37.50**	38.46**	-4.11	11.00	1.45**	2.22**
	II	34.21**	31.91**	22.95**	20.08**	3.74	3.24	7.69**	9.90**

The degree of dominance was close to unity (± 1.0) for LR in CI under normal conditions and CII under water deficit. However, it was lower than unity for NDH and FLA in CI under both conditions, and for PH and SP in CI under WD, suggesting incomplete dominance for these traits.

Table 1 also shows, highly significant positive of heterosis (as deviations from mid- and better-parent values) for traits such as RL, RV, NRP, RSR, Cc, PL, NPP, NFP, TGW, GYP, and NDH, except in CI for better-parent heterosis under both treatments. Positive heterosis (as deviations from mid- and better-parent values) was observed in FLA in CII and RWC in CI, excluding the better-parent values under normal conditions. Conversely, significant negative heterosis (as deviations from mid- and better-parent values) was noted for traits such as LR (except in CII for better-parent heterosis under both conditions), FLA in CII, RWC in CII (excluding the better-parent heterosis under normal conditions), NDH in CI for better-parent heterosis under both conditions, PH for better-parent heterosis in CI under WD, and SP for mid-parent heterosis in CI under water deficit.

High inbreeding depression was significant for traits such as NRP, PH, Cc, NFP, and GYP across both crosses and conditions. NPP, RWC in CI under both conditions, RL in CII, and RV in CI under normal conditions also showed highly significant positive inbreeding depression. In contrast, SP under both conditions, FLA under both treatments (except CI under WD), RWC in CI under both conditions, and NDH

in CI under well-watered treatment and CII under WD showed significantly negative inbreeding depression.

Estimates of genetic components of generation mean:

The data in Table 2 illustrated that the scaling test parameters (A, B and C) estimated for roots, agro-physiological and yield component traits in the two studied crosses under both conditions. All of the computed permeates of scaling test were statistically significant except LR under WD for CI, Cc and PH for CI and CII under normal and CII under WD, PL for CII under normal and CI under WD and NPP for CI under normal and CII under WD which were affected by allelic interaction.

As shown in Table 3, mean effect parameters (*m*) were highly significant for all traits. Additive gene action (*d*) was critical in the inheritance of most traits, except NRP, PH and GYP, RL in the CII under WD treatment, RSR in the CI under WD condition and the CII under both conditions, RV, LR, FLA and RWC in the CI under WD, Cc in the CI and CII under normal condition, NDH and NFP in the CI under well-watered treatment, PL and NPP in the CII under both treatments, TGW in the CI under WD and the CII under well-watered treatment, SP in the CI under well-watered treatment and the CII under both conditions. Dominance gene action (*h*) was influential in most traits across the studied crosses, except for GYP, PH in the CI under well-watered treatment and the CII under both conditions, RL in the CII under both treatments, RV and RWC in the CI under WD, RSR in the CI under WD and the CII under well-watered treatment, LR and PL in the CI

under WD and the CII under both treatments, FLA and TGW in the CI under normal condition, Cc and NPP in the CI under both treatments and CII under WD, NFP in the CI and CII under normal treatment and SP in the CI under normal

condition and the CII under WD condition. Additive x additive type of gene interaction (*i*) played an effective role in all the crosses, except RL, LR and GYP in the CII under both treatments, PL in the CII under

Table 2. Scaling test for adequacy of additive and dominance model of rice root, physiological and yield components characters for the two studied crosses under normal (N) and water deficit (WD) conditions.

Character	cross		A	B	C
Root length	I	N	-10.20±1.80**	-7.63±1.87**	6.97±3.87
		WD	-8.47±1.10**	-2.73±1.37*	4.80±2.76
	II	N	-7.87±2.00**	-5.44±1.77**	-9.18±4.07*
		WD	-4.83±1.07**	-15.06±1.03**	-36.15±2.29**
Root volume	I	N	-13.73±1.62**	-6.20±2.08**	56.07±3.97**
		WD	4.07±1.16**	0.27±1.30	12.33±2.55**
	II	N	-17.00±1.57**	-1.87±1.95	9.13±3.68*
		WD	-9.00±1.65**	2.27±1.61	15.53±3.43**
Number of roots/plant	I	N	-464.13±11.82**	-355.53±9.13**	380.73±23.68**
		WD	-125.20±10.38**	87.47±7.63**	229.60±20.31**
	II	N	-538.93±10.22**	-435.07±9.61**	-1176.13±22.07**
		WD	-139.47±11.68**	-275.60±10.09**	-506.40±24.84**
Root/shoot ratio	I	N	-0.55±0.07**	-0.59±0.11**	0.42±0.21*
		WD	-0.14±0.08	-0.22±0.08**	0.08±0.16
	II	N	-0.14±0.09	-0.26±0.09**	0.50±0.20*
		WD	-0.47±0.08**	-0.49±0.08**	0.38±0.17*
Leaf rolling	I	N	0.07±0.65	-1.27±0.45**	1.60±1.13
		WD	-0.13±0.84	0.20±1.17	-2.73±2.02
	II	N	-0.20±0.68	1.80±0.68**	2.00±1.40
		WD	-1.47±0.81	2.67±0.99**	-1.33±1.81
Flag leaf area	I	N	3.93±1.96*	-4.23±2.20	2.78±4.62
		WD	9.98±1.79**	-3.96±1.82*	-10.02±3.97*
	II	N	-4.60±1.78**	13.16±1.80**	45.97±3.95**
		WD	3.05±2.15**	-14.14±1.87*	47.04±4.47*
Relative water content	I	N	30.85±4.06**	-0.68±4.45	-11.55±9.17
		WD	0.00±3.65	-11.85±3.85**	-0.32±7.95**
	II	N	-18.25±4.25**	33.81±4.38**	56.60±9.17**
		WD	1.74±3.81	-26.72±4.27**	9.44±8.54
Chlorophyll content	I	N	-5.98±4.64	-2.15±4.51	4.27±10.21
		WD	-8.27±4.00*	-1.62±3.55	9.22±8.43
	II	N	-2.07±4.04	-4.89±4.15	6.85±8.99
		WD	-3.97±3.77	-0.09±3.74	5.15±8.21

Table 2.cont.

Character	cross		A	B	C
Days to 50% heading	I	N	16.27±1.29**	2.07±2.27	36.60±3.94**
		WD	9.13±1.57**	-2.27±1.69	57.53±3.52**
	II	N	9.20±1.49**	2.93±2.15	47.73±3.87**
		WD	8.47±1.89**	7.33±1.79**	49.53±3.89**
Plant height	I	N	-5.33±10.06	-10.20±10.24	-5.80±22.42
		WD	-4.87±8.93	-9.27±10.34	-44.93±21.17*
	II	N	-10.33±9.95	-10.40±9.32	15.80±21.40
		WD	-0.80±9.67	-9.27±9.22	-2.73±20.90
Panicle length	I	N	-1.19±0.52*	-1.68±0.79*	-6.91±1.52**
		WD	-1.00±0.93	0.30±1.13	1.03±2.27
	II	N	-0.27±1.66	-1.01±1.41	-1.50±3.51
		WD	-1.73±0.85*	-0.94±1.17	-0.99±2.27
No. of Panicles /plant	I	N	-0.20±2.26	-1.00±1.88	0.80±4.60
		WD	-1.13±2.41	-3.80±1.33**	4.40±4.33
	II	N	0.87±1.75	3.20±1.70	-19.80±3.89**
		WD	-3.00±1.84	-1.20±1.81	-0.87±4.02
No. of filled grains/ panicle	I	N	61.47±9.25**	-7.73±11.04	114.93±22.88**
		WD	-58.73±9.58**	-7.33±9.77	-136.87±21.19**
	II	N	-38.60±11.15**	-83.53±10.97**	-18.53±24.58
		WD	-71.40±8.81**	-41.20±9.58**	41.27±19.94*
1000-grain weight	I	N	-0.57±0.74	-3.87±0.65**	-0.57±1.43
		WD	-2.00±0.99**	-5.00±0.97**	2.60±2.08
	II	N	-4.00±0.87**	-3.00±0.99**	1.00±1.95
		WD	-1.00±0.87	-3.00±0.88**	-4.40±1.84*
Sterility %	I	N	9.19±3.92*	2.64±3.11	31.31±7.73**
		WD	-2.46±3.68	-1.61±3.62	12.86±7.98*
	II	N	0.25±1.91	1.06±1.92	43.39±4.23**
		WD	10.21±3.66**	1.19±4.03	32.18±8.42**
Grain yield/ plant	I	N	3.13±4.20	3.00±4.64	20.93±9.80*
		WD	0.00±3.96	4.80±3.55	18.80±8.22*
	II	N	1.00±3.99	-2.40±4.19	13.13±8.99*
		WD	-2.73±3.57	-4.47±3.72*	3.60±7.95

Table 3. Genetic components of generation means for root, physiological and yield components traits for the two studied crosses under normal (N) and water stress (WD) conditions.

Character	Cross	Mean F ₂ generation	<i>d</i>	<i>h</i>	<i>i</i>	<i>j</i>	<i>l</i>	
Root length	I	N	33.00**	-4.80**	-17.25**	-24.80**	-1.28	42.63**
		WD	26.50**	-5.00**	-8.20**	-16.00**	-2.87**	27.20
	II	N	26.97**	-4.80**	3.42	-4.13	-1.22**	17.45**
		WD	15.00**	4.00	22.31	16.27	5.12	3.62
Root volume	I	N	48.73**	-2.93*	-44.63**	-76.00**	-3.77**	95.93**
		WD	20.00**	0.00	1.77	-8.00**	1.90*	3.67
	II	N	42.87**	-11.20**	-19.57**	-28.00**	-7.57**	46.87**
		WD	19.63**	-8.13**	-9.77*	-22.27**	-5.63**	29.00**
Number of roots/plant	I	N	605.50**	30.67**	-619.70**	-1200.40**	-54.30**	2020.07**
		WD	300.00**	-86.33**	-62.13**	-267.33**	-106.33**	305.07**
	II	N	271.07**	-121.87**	592.20**	202.13**	-51.93*	771.87**
		WD	188.50**	18.00*	221.40**	91.33**	68.07**	323.73**
Root /shoot ratio	I	N	0.76**	0.13*	-1.08**	-1.57**	0.02	2.71**
		WD	0.35**	0.08	-0.26	-0.44*	0.04	0.79**
	II	N	0.76**	0.07	-0.03	-0.90**	0.06	1.30**
		WD	0.55**	0.03	-0.74**	-1.34**	0.01	2.30**
Leaf rolling	I	N	2.50**	0.67	-3.80**	-2.80*	0.67	4.00*
		WD	3.53**	0.73	1.43	--	--	--
	II	N	2.50**	0.00	-1.47	-0.40	-1.00*	-1.20
		WD	3.33**	-0.07	0.53	2.53	-2.07**	-3.73
Flag leaf area	I	N	34.22**	-6.90**	-6.12	-3.08	4.08**	3.38
		WD	24.01**	-2.03	11.06*	16.05**	6.97**	-22.08**
	II	N	52.01**	-12.90**	-22.41**	-37.41**	-8.88**	28.84**
		WD	43.02**	7.10**	-48.62**	-58.12**	8.60**	69.21**
Relative water content	I	N	63.29**	14.66**	43.80**	41.72**	15.77**	-71.88**
		WD	57.03**	-1.96	-1.40	-11.53	5.92*	23.39
	II	N	81.96**	-21.43**	-42.51**	-41.04**	-26.0**	25.48
		WD	54.02**	13.30**	-51.22**	-34.42**	14.23**	59.41**
Chlorophyll content	I	N	55.06**	-3.90	-6.48	--	--	--
		WD	47.22**	-6.86**	-12.42	-19.12*	-3.32	29.02*
	II	N	48.00**	2.94	-8.30**	--	--	--
		WD	38.83**	-4.98*	-2.07	--	--	--

Table 3. cont.

Character	Cross	Mean F ₂ generation	<i>d</i>	<i>h</i>	<i>i</i>	<i>j</i>	<i>l</i>	
Days to 50% heading	I	N	113.00**	-1.40	-11.57*	-18.27**	7.10**	-0.07
		WD	116.17**	-6.87**	-49.03**	-50.67**	5.70**	43.80**
	II	N	109.93**	6.07**	-25.60**	-35.60**	3.13*	23.47**
		WD	107.00**	3.53**	-22.57**	-33.73**	0.57	17.93**
Plant height	I	N	114.93**	-5.00	4.17	--	--	--
		WD	90.07**	-5.40	38.20**	30.80**	2.20	-16.67*
	II	N	110.63**	2.33	-19.10	--	--	--
		WD	95.13**	3.40	11.97	--	--	--
Panicle length	I	N	23.90**	-1.19**	6.79**	4.04*	0.25	-1.17
		WD	22.50**	-2.13**	1.78	--	--	--
	II	N	23.90**	-0.38	3.28	--	--	--
		WD	21.50**	-0.87	1.80	-1.68	-0.40	4.35*
No. of panicles/plant	I	N	24.93**	2.87**	8.40	--	--	--
		WD	16.93**	2.80**	-0.73	-9.33	1.33	14.27*
	II	N	23.00**	-2.20	37.70**	23.87**	-1.17	-27.93**
		WD	16.80**	-1.93	0.50	--	--	--
No. of filled grains/panicle	I	N	225.50**	-6.93	-2.73	-61.20*	34.60**	7.47
		WD	144.03**	-77.20**	150.30**	70.80**	-25.70**	-4.73
	II	N	254.33**	-18.20*	47.00	-103.60**	22.47**	225.73**
		WD	200.03**	-31.67**	-63.30**	-153.87**	-15.10*	266.47**
1000-grain weight	I	N	28.00**	1.93**	-2.15	-3.87*	1.65**	8.30**
		WD	25.90**	1.00	-8.10**	-9.60**	1.50*	16.60**
	II	N	29.00**	0.00	-5.50*	-8.00**	-0.50	15.00**
		WD	23.90**	2.00**	4.40*	0.40	1.00	3.60*
Sterility %	I	N	15.20**	3.69	-16.20	-19.48*	3.27	7.65
		WD	22.03**	4.92*	-20.54*	-16.94	-0.43	21.02**
	II	N	18.22**	-0.80	-32.76**	-42.09**	-0.41	40.79**
		WD	26.00**	4.94	-18.26	-20.78*	4.51	9.37
Grain yield/plant	I	N	54.20**	3.00	-2.73	-14.80*	0.07	8.67*
		WD	35.20**	-3.40	-3.00	-14.00*	-2.40	9.20*
	II	N	60.00**	-2.73	2.03	-14.53*	1.70	15.93*
		WD	37.00**	-2.20	-0.87	-10.80	0.87	18.00*

WD treatment, FLA in the CI under well-watered treatment, RWC in the CI under WD condition, NPP in the CI under WD, TGW in the CII under WD. Additive x dominance (*j*) interaction was essential for most traits except for RSR, LR, Cc, PH, PL, NPP, SP and GYP, RL in the CI under normal treatment and the CII under WD treatment, NDH in the CII under WD and TGW in the CII under both treatments.

Dominance x dominance type of gene interaction (*l*) played an important role in the inheritance of all the studied characters, except FLA, NDH and PL in the CI under well-watered treatment, RWC in the CI under WD condition and the CII under normal condition, SP in the CI under normal treatment and the CII under WD, LR in the CII under both conditions, NPP in the CI under both conditions, RL in the CI and CII

under WD, RV in the CI under WD condition and TGW in the CII under WD treatment.

Estimates of genetic variance, heritability and genetic advance:

Data summarized in Table 4 revealed that additive genetic variance ($\frac{1}{2} D$) was higher than dominance genetic variance ($\frac{1}{4} H$) for FLA, Cc, PH, PL, NPP, NFP, SP and GYP for CI and CII, indicating that ($\frac{1}{2} D$) played a major role than

that of the additive variance in the inheritance of these traits. While ($\frac{1}{4} H$) was higher than ($\frac{1}{2} D$) for RL, RV, NRP, RSR, LR, RWC, NDH and TGW, these findings indicated that the dominance variance played an important role in the inheritance of these traits for CI and CII.

Table 4. Estimates of additive ($\frac{1}{2} D$) and, dominance genetic variance ($\frac{1}{4} H$), broad and narrow-sense heritabilities and genetic advance (G.S %) for rice root, physiological and yield components traits for the two studied crosses under normal (N) and water stress (WD) conditions.

Character	Cross	Genetic variance		Heritability		G.s	G.s %
		1/2 D	1/4 H	Broad- sense	Narrow- sense		
Root length	I	N	0.22	0.61	90.69	23.94	142.79
		WD	0.19	0.25	93.11	40.03	211.65
	II	N	0.30	0.69	97.10	29.26	226.25
		WD	0.11	0.18	92.39	35.42	275.14
Root volume	I	N	0.25	0.60	89.97	26.53	109.06
		WD	0.09	0.17	70.18	23.51	146.80
	II	N	0.17	0.49	81.20	20.55	88.55
		WD	0.19	0.26	67.97	28.86	244.99
Number of roots/plant	I	N	15.69	11.60	82.94	47.68	93.05
		WD	11.19	9.68	84.85	45.48	154.88
	II	N	13.07	9.68	80.28	46.13	186.61
		WD	18.89	12.26	85.28	51.71	341.55
Root/shoot ratio	I	N	0.001	0.002	81.07	47.32	664.10
		WD	0.001	0.002	70.49	10.56	235.78
	II	N	0.001	0.002	75.25	37.33	484.76
		WD	0.001	0.002	67.66	9.62	141.36
Leaf rolling	I	N	0.01	0.05	74.70	8.77	195.51
		WD	0.02	0.10	52.70	9.48	261.61
	II	N	0.02	0.08	82.64	14.79	413.64
		WD	0.02	0.07	51.35	13.09	336.95
Flag leaf area	I	N	0.54	0.48	82.26	43.50	292.63
		WD	0.39	0.32	78.27	42.63	347.87
	II	N	0.40	0.33	79.66	43.46	164.17
		WD	0.51	0.46	83.24	43.79	227.01
Relative water content	I	N	1.63	2.57	84.43	32.72	237.56
		WD	1.07	1.72	76.42	29.28	201.77
	II	N	1.42	2.68	83.05	28.80	161.02
		WD	1.15	2.29	80.61	26.91	212.17
Chlorophyll content	I	N	2.81	2.40	84.55	45.64	423.69
		WD	1.95	1.38	80.38	47.00	417.61
	II	N	1.94	1.89	81.30	41.14	383.42
		WD	1.61	1.40	77.28	41.33	432.45

Table 4. cont.

Character	Cross	Genetic variance		Heritability		G.s	G.s %
		1/2 D	1/4 H	Broad- sense	Narrow- sense		
Days to 50 % heading	I	N	0.27	0.51	85.15	29.55	51.45
		WD	0.25	0.34	81.50	34.40	51.79
	II	N	0.17	0.69	94.43	18.98	34.06
		WD	0.23	0.58	88.80	24.92	45.83
Plant height	I	N	12.69	11.40	81.73	43.05	419.00
		WD	10.67	10.03	79.66	41.07	478.82
	II	N	11.94	10.33	82.82	44.40	428.73
		WD	11.15	9.83	81.98	43.56	477.27
Panicle length	I	N	0.07	0.05	84.97	51.41	164.16
		WD	0.13	0.12	81.31	42.10	211.88
	II	N	0.37	0.32	92.65	49.68	370.37
		WD	0.13	0.11	82.31	44.29	232.95
No. of panicles /plant	I	N	0.53	0.48	81.93	42.98	394.45
		WD	0.50	0.41	82.35	45.37	579.84
	II	N	0.44	0.37	88.52	48.05	410.42
		WD	0.40	0.32	77.93	43.26	509.59
No. of filled grains/panicle	I	N	14.93	10.31	82.26	48.65	246.17
		WD	10.66	10.03	79.45	40.95	298.87
	II	N	15.67	15.08	85.61	43.63	211.81
		WD	8.79	8.49	75.75	38.52	189.50
1000-grain weight	I	N	0.02	0.07	77.37	17.25	43.41
		WD	0.07	0.16	89.05	27.60	112.00
	II	N	0.05	0.15	88.11	21.66	73.38
		WD	0.05	0.13	85.92	22.82	88.23
Sterility %	I	N	1.38	1.26	77.18	40.33	1010.65
		WD	1.50	1.30	76.58	40.96	731.96
	II	N	0.45	0.41	82.32	43.04	497.31
		WD	1.65	1.75	81.85	39.83	643.12
Grain yield/plant	I	N	2.45	2.32	84.16	43.25	391.35
		WD	1.59	1.45	77.90	40.71	470.59
	II	N	1.93	1.91	81.44	40.95	305.39
		WD	1.45	1.41	78.37	39.71	422.43

Broad sense heritability (BSH) estimates were larger than their corresponding ones of narrow sense heritability (NSH) for all the studied crosses for CI and CII. High (BSH) was estimated for all traits under both treatments for CI and CII, except LR under WD treatment was moderate. (NSH) ranged from low to moderate in the two crosses.

High estimates of expected genetic advance were recorded in all the crosses under both conditions for CI and CII, except NDH under both treatments and TGW in the CI under normal treatment were moderate.

Discussion:

Drought stress poses a significant challenge to rice production, leading to substantial economic losses, particularly exacerbated by ongoing global climate change. Given the projected rise in global food demand, there is a pressing need to bolster crop productivity on rainfed lands susceptible to drought. To meet production targets in these areas, the development of drought-tolerant rice varieties is imperative, making genetic enhancement for drought tolerance a paramount focus of future research endeavors. However, breeding for such varieties presents a complex and challenging task due to the intricate nature and multigenic control of drought-tolerant traits, posing a major bottleneck for current research efforts Hassan (2013). Nonetheless, significant strides have been made over the past two decades in understanding the mechanisms underlying adaptation and tolerance to drought stress in rice. This study aims to elucidate recent advancements in the adaptation of rice to drought tolerance, particularly focusing on root systems, agro-physiological traits, and yield components.

Backcross breeding, indeed, facilitates the transfer of desired traits from one variety (the donor parent) to another (the recurrent parent) by repeated backcrossing with the recurrent parent. This method allows breeders to retain the genetic background of the recurrent parent while introducing the desired trait from the donor parent. If the trait of interest is produced by a dominant gene like tolerant to water deficit, the process is relatively straightforward. In each backcross generation, the breeder selects individuals from the progeny that exhibits the desired trait and backcrosses them with the recurrent parent. The breeder can then select individuals from these progenies with the highest level of similarity to the recurrent parent for further breeding or for release as a new variety. This approach has been quite successful for transferring root, physiological and yield parameters especially under water deficit conditions. One of the most successful examples in rice is the transfer of submergence tolerance Satya and Sarkar (2018). Overall, backcross breeding is a powerful tool for introducing specific traits into elite genetic backgrounds, enabling breeders to develop improved varieties with desired characteristics.

The F_1 , F_2 , BC_1 and BC_2 means were higher than the highest parent or lower than the lowest parent for among studied traits for Sakha106 x Nerica7 (CI) and Giza177 x GZ 10848-1-2-2-1 (Giza183) (CII) under both treatments; these findings suggested that over dominance played a major role in the inheritance of these traits. On the contrary, values of F_1 , F_2 , BC_1 and BC_2 were intermediated between the two parents suggesting the presence of partial dominance in the inheritance in the other remaining traits under both treatments Guilengue et al., 2020 and Hassan et al., (2023). In addition, The ratio of degree of dominance which was between zero

and unity, suggesting partial or incomplete dominance might be played a remarkable role in the inheritance of a few studied traits, while it was greater than unity for among traits under normal and water deficit condition, suggesting that a complete dominance played an important role in the inheritance of this trait Gaballah et al., (2021) and Sakran et al., (2022).

The estimates of heterosis were significant and positive for all root traits, chlorophyll content and yield components traits under both treatments for Sakha106 x Nerica7 and Giza177 x Giza183 suggested that heterosis played an important role in the inheritance of these traits under both conditions. Similar results were reported by Hassan (2013), Hassan (2017b), Ouyang et al., (2022) and Daher et al., (2023). Highly significant positive inbreeding depression, were obtained for some of studied traits for CI and CII and it was high significant negative for some other traits under WD condition El-Gamal (2013), Gao and Gao (2016) and El-Malky and Al-Daej (2023). These results are logic and expected since the expression of heterosis in F_1 will be followed by a considerable reduction in F_2 due to homozygosity due to segregation. The results are in accordance with those reported by Rahman et al., (2022) and Hassan et al., (2023).

Most of the computed permeates of scaling test were statistically significant for Sakha106 x Nerica7 and Giza177 x Giza183 under both treatments, thus in turn the presence of non- allelic interaction, indicating that the additive and dominance model alone was insufficient. Besides additive and dominance effects, other factors such as non-allelic interaction, linkage, genotype \times environment (G \times E) interaction, either individually or in combination, play a role in the inheritance for roots, agro-physiological and yield component traits Hassan et al., (2016), Hassan (2017a), Hastini et al., (2021) and Rahman et al., (2022). The three types of gene interaction were important in the inheritance of among studied traits under WD condition for Sakha106 x Nerica7 and Giza177 x GZ 10848-1-2-2-1 (Giza183) Abebe et al., (2019), Ganapati et al., (2020), Rahman et al., (2022) and Hassan et al., (2023).

The ($\frac{1}{4}$ H) was higher than ($\frac{1}{2}$ D) for all root, LR, RWC, NDH and TGW for Sakha106 x Nerica7 (CI) and Giza177 x GZ 10848-1-2-2-1 (Giza183) (CII) under both treatments, these findings indicated that the dominance variance played an important role in the inheritance of these traits. In both crosses and under both treatments, all examined traits showed high values of GS %, as indicated by mean percentages, consistent with findings from a previous study Hassan et al., (2023). Furthermore, a majority of the traits exhibited elevated estimates for narrow- sense heritability, suggesting a high degree of genetic stability. This indicates that these traits may be governed by a simple inheritance pattern with a few major genes or that additive gene effects are significant contributors to their inheritance Ouyang et al., (2022). Conversely, low heritability was noted for rice plant height and yield in previous studies Tiwari et al., (2019) and Karavolias et al., (2020). However, contrasting results were reported for certain traits, such as PL, HGW Farooq et al., (2019), and NPP, where high broad-sense heritability was observed Hastini et al., (2021) and Hassan et al., (2023).

CONCLUSION

The significant result of scaling test of among studied traits for Sakha106 x Nerica7 and Giza177 x GZ 10848-1-2-

2-1 (Giza183) indicated the simple additive-dominance models not adequate to getting the relationship and the studied traits are largely influenced by additive \times additive, additive \times dominance and dominance \times dominance (non-allelic interaction component). Non-allelic interactions played a key role in the inheritance of root traits, FLA, RWC, and yield components under both treatments. In contrast, allelic interactions were notably important for traits such as LR, Cc, PH, PL, and NPP, suggesting that the additive-dominance model alone cannot fully explain the relationships among these traits. Thus, in addition to additive, dominance, and non-allelic gene effects, these traits are also affected by genotype \times environment (G \times E) interactions or genetic linkage. Therefore, it is essential to consider G \times E interactions and linkage effects to accurately assess the relationships among these traits.

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تفاعل الجينات الأليلية والغير أليلية لبعض الصفات الكمية في الأرز تحت ظروف نقص المياه

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الملخص

أجريت هذه التجارب بالمزرعة البحثية لقسم بحوث الأرز - سخا - كفر الشيخ - مصر وذلك خلال مواسم زراعة الأرز 2021، 2022 و 2023 وذلك بهدف دراسة قوة الهجين، التدهور الناتج عن التربية الداخلية والتفاعل بين الجينات الأليلية والغير أليلية والتحسين الوراثي المتوقع من الانتخاب لصفات الجذور والصفات الفسيولوجية وصفات المحصول ومكوناته في الأرز تحت ظروف نقص المياه وذلك باستخدام العشائر الستة (الأب الأول، الأب الثاني، الجيل الأول، الجيل الثاني، الهجين الرجعي الأول والهجين الرجعي الثاني) لهجينين من الأرز هما سخا 106 × نير كا 7 (الهجين الأول) و جيزه 177 × جى زد 1-2-2-1-10848 (جيزه 183) (الهجين الثاني) وتم تنفيذ التجارب في تصميم قطاعات كاملة العشوائية في ثلاثة مكررات. أوضحت النتائج أن النسبة المنوية لقيم قوة الهجين عند قياسها كإحراف عن قيم متوسط وأفضل الأبوبين كانت عالية المعنوية وموجبة في معظم الهجن لكل الصفات المدروسة تحت كلا الظروف، وكذلك وجد تأثير كل من السيادة الجزئية والسيادة الفاتقة لمعظم هذه الصفات. أظهرت النتائج أن كلاً من التأثير المضيف والسيادى للجين لعب دوراً هاماً في وراثه معظم الصفات المدروسة في كل الهجن. كذلك لعب كل من الفعل الجيني المضيف × المضيف، المضيف × السيادى والسيادى × السيادى دوراً هاماً في وراثه هذه الصفات عدا بعض الاستثناءات. أوضحت النتائج أن درجة التوريث بالمعنى الواسع كانت عالية بينما كانت درجة التوريث بالمعنى الضيق متوسطه إلى منخفضه في معظم الهجن المدروسة. كذلك أظهرت النتائج قيماً عالية للتحسين المتوقع بالانتخاب لمعظم الصفات المدروسة. توصى الدراسة بأن الهجين الثاني جيزه 177 × جى زد 1-2-2-1-10848 (جيزه 183) هو أفضل الهجن التي تستطيع أن توصى به للنمو تحت ظروف ندرة المياه وذلك لحصوله على أعلى القيم لمعظم الصفات المدروسة.