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Genetic Analysis for some Quantitative Traits in some Rice Genotypes (*Oryza sativa* L.) under Normal and Water Deficit Conditions using Five Parameters Model

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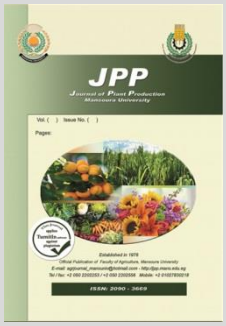

ABSTRACT

Water deficit is a significant abiotic stress that severely limits rice growth and production. Therefore, developing drought-tolerant rice genotypes is essential, especially under current water shortage conditions. In this study, eleven SSR markers revealed substantial genetic variation among parental genotypes, identifying 27 alleles with an average of 2.45 per locus and a high polymorphism information content (PIC) of 0.44. Based on this diversity, three specific crosses were generated. Five populations from each cross, including P_1, P_2, F_1, F_2, and F_3, were evaluated in two separate experiments under normal and water deficit conditions. The results showed that the overall mean values for all generations were higher under normal conditions than under water deficit conditions for most studied traits. The first cross (Sakha 107 × Nerica 7) was the best for the most studied traits under water deficit, while the third cross (Sakha Super 300 × Moroberekan) was the best under normal conditions. Scaling test results indicated that the evaluated traits did not align well with the additive-dominance model, suggesting the possibility of epistasis in trait inheritance. Dominance effects were notably high for 100-grain weight, water use efficiency, and grain yield per plant, suggesting that selection for these traits should be postponed to late generations to ensure homozygosity. The importance of additive and dominance effects varied by trait and cross under normal and water stress conditions. Among the epistatic components, the dominance effect was more significant in magnitude than the additive × additive ones in most studied traits.

Keywords: Rice, Water deficit, five populations, SSR markers, Gene action.

INTRODUCTION

Rice (*Oryza sativa* L.) is one of the most important cereal crops, serving as a staple for over one-third of the global population (Kaur *et al.* 2024). However, rice production faces substantial challenges, especially from water deficit conditions (Jarin *et al.* 2024). In addition, estimates indicated that drought impacts approximately 50% of global rice production (Chen *et al.* 2024). Moreover, water deficit significantly impairs rice growth and development by disrupting photosynthesis, metabolism, and cell enlargement (Qiao *et al.* 2024). During the vegetative stage, drought reduces leaf formation and tillering, while at the reproductive stage, it increases grain sterility and diminishes grain filling and weight, ultimately lowering yields (AbdAllah *et al.* 2013). Consequently, it affects plant growth and physiological processes, including respiration and nutrient uptake (Shao *et al.* 2008; Zampieri *et al.* 2023).

Generally, grain yield decreased by more than 50% under drought conditions, depending on the stress's timing, duration, and severity. In Egypt, 30% of paddy fields, especially in terminal areas, are affected by water shortage, thus reducing the total yield by 15%. In addition, the performance of developed rice varieties under water-limited conditions remains suboptimal (AbdAllah, 2010). Therefore, developing drought-tolerant genotypes is essential for global food security, particularly in the face of climate change.

Quantitative traits are controlled by multiple minor genes, each with a small effect, and are influenced by the environment. Methods typically focus on genotypic mean performance or variances to study the genetic parameters of these traits, helping estimate gene action for practical breeding (Hassan *et al.* 2023). Furthermore, understanding gene action for various characteristics is essential for deciding the most suitable breeding systems to enhance yield and drought tolerance under varying conditions (Abd EL-Aty *et al.* 2017).

Generation mean analysis is an effective method for estimating gene effects in polygenic traits, mainly due to its ability to evaluate epistatic gene effects such as additive × additive, dominance × dominance, and additive × dominance interactions. However, this knowledge is essential for formulating effective breeding strategies, especially in improving crop productivity and resilience under normal and stressful conditions. Moreover, it guides the selection of breeding strategies for optimal genetic improvement in varying environments.

Evaluating genetic diversity helps develop new genotypes with optimal traits and speeds up genotype identification in breeding programs (Salem *et al.* 2024). Moreover, biotechnological techniques have enhanced the ability to assess genetic variation at both phenotypic and genotypic levels. Further, DNA-based genetic diversity analyses provide valuable insights for designing effective breeding programs that expand the genetic base of commercially cultivated varieties.

Molecular marker technology is a powerful tool for assessing genetic variation in rice, offering a more reliable and efficient approach than morphological traits (Naaz *et al.* 2022). Unlike morphological markers, DNA-based markers provide greater accuracy, consistency, and repeatability. Among these, microsatellites (SSRs) are especially useful due

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to their ability to transmit co-dominantly, their multiple allele variation, high genomic representation, and minimal DNA requirements, making them highly effective for analyzing genetic differences among rice genotypes (Li *et al.* 2023 and Mukta *et al.* 2024).

Therefore, the objectives of the present study were to (1) investigate genetic diversity among local and exotic parental rice genotypes using SSR markers, (ii) determine the nature and magnitude of gene action governing the inheritance of some root, physiological, and agronomic traits in three specific rice crosses using generation means analysis under both normal and water deficit conditions.

MATERIALS AND METHODS

Plant materials

Six genetically diverse rice (*Oryza sativa* L.) genotypes, three local varieties (Sakha 107, Sakha 105, and Sakha Super 300), and three exotic genotypes, (Nerica 7, Vandana, and Moroberekan) from Africa Rice Center (WARDA), were used for this study (Table 1). These genotypes were selected based on their diversity in several agronomic and physiological characteristics and their drought tolerance to water deficit.

Table 1. Name, pedigree, origin, and type of genotypes used in this study.

Name	Pedigree	Origin	Drought tolerance reaction	type
Sakha 107	Giza 177 /BLI	Egypt	Tolerant	Japonica
Sakha 105	GZ5581-46-3/GZ4316-7-1-1	Egypt	Sensitive	Japonica
Sakha Super 300	-	Egypt	moderate	Japonica
NERICA 7	WAB 56-104/ CG14//WAB56-104	Ivory Cost	Tolerant	Indica
Vandana	C 22/Kalakeri	India	Tolerant	Indica
Moroberekan	IR 8-24-6- (M307 H5)	Guinea	Tolerant	Tropical japonica

Molecular Analysis

Genomic DNA extraction

Genetic diversity among the selected parental genotypes was analyzed using SSR markers. Genomic DNA was extracted from fresh leaves of the 14-day-old seedlings using the CTAB method (Doyle and Doyle 1990). The quality and quantity of the extracted DNA were evaluated with a NanoDrop ND-1000 UV-Vis spectrophotometer (NanoDrop Technologies, Delaware, USA) using 2 µL of each sample. The DNA samples were diluted in TE buffer (10 mM Tris-HCl, 1 mM EDTA, pH 8.0) for PCR amplification to achieve a final concentration of 30 ng/µL.

PCR Amplification and Gel Electrophoresis

Eleven SSR markers (Table 2) were utilized in this study (Chen *et al.* 1997; McCouch *et al.* 2002; Sasaki *et al.* 2005). PCR amplification reactions were prepared in 15 µL volumes, each containing 1.5 µL of template DNA, 1 µL of both forward and reverse SSR primers, 7.5 µL of PCR master mix (ROVALAB 2x Red PCR Master Mix, Kantstr., Germany), and 4.5 µL of ddH_2O.

Amplifications were performed in a PerkinElmer GeneAmp PCR System 2400 with the following cycling conditions: initial denaturation at 94°C for 5 minutes, 35 cycles of denaturation at 94°C for 1 minute, annealing at 55°C for 30 seconds, and extension at 72°C for 1 minute, followed by a final extension at 72°C for 7 minutes. The PCR products were separated on 3% agarose gels in 0.5X TAE buffer and stained with ethidium bromide (0.5 µg/mL). Gels were visualized and photographed using a Biometra Biodoc Analyze system to observe the amplified DNA fragments. The sizes of the DNA bands were estimated by comparing their migration with a 50 bp DNA ladder (MBI Fermentas) used as a molecular size reference.

SSR data analysis

The amplified bands for each SSR marker were scored as (1) for presence and (0) for absence, creating a binary data matrix. Allele diversity was assessed by calculating the number of alleles, major allele frequency, and polymorphic information content (PIC), as Botstein *et al.* (1980) described. Genetic similarity between inbred lines was calculated using Jaccard's (1908) index, and a dendrogram was constructed using UPGMA in PAST software.

Table 2. Name and sequence of the SSR primers used in this study.

Marker name	Chromosome number	Repeat motif	Sequence (5'-3')	Annealing temperature (º)	Expected PCR product size (bp)
RM1261	12	$(AG)_{16}$	F: GTCCATGCCCAAGACACAAC R: GTTACATCATGGGTGACCCC	50	167
RM201	9	$(CT)_{17}$	F: CTCGTTTATTACCTACAGTACC R: CTACCTCCTTTCTAGACCGATA	55	142-158
RM223	8	$(CT)_{25}$	F: GAGTGAGCTTGGGCTGAAAC R: GAAGGCAAGTCTTGGCACTG	55	148-165
RM242	9	$(CT)_{26}$	F: GGCCAACGTGTGTATGTCTC R: TATATGCCAAGACGGATGGG	55	196-225
RM246	1	$(CT)_{20}$	F: GAGCTCCATCAGCCATTCAG R: CTGAGTGCTGCTGCGACT	55	113-116
RM263	2	$(CT)_{34}$	F: CCCAGGCTAGCTCATGAACC R: GCTACGTTTGAGCTACCACG	55	157-196
RM279	2	$(GA)_{16}$	F: GCGGGAGAGGGATCTCCT R: GGCTAGGAGTTAACCTCGCG	55	164-174
RM28048	12	$(CGC)_{8}$	F: TTCAGCCGATCCATTCAATTCC R: GCTATTGGCCGGAAAGTAGTTAGC	55	93-94
RM324	2	$(CAT)_{21}$	F: CTGATTCCACACACTTGTGC R: GATTCCACGTCAGGATCTTC	55	134-175
RM3805	6	$(GA)_{19}$	F: AGAGGAAGAAGCCAAGGAGG R: CATCAACGTACCAACCATGG	55	110
RM518	4	$(TC)_{15}$	F: CTCTTCACTCACTCACCATGG R: ATCCATCTGGAGCAAGCAAC	55	171

***All data were obtained from https://archive.gramene.org/markers/**

Field experiments

During the 2021 season, three crosses were generated using the six selected genetically diverse parental genotypes to obtain F_1 seeds: Cross I (Sakha 107 × Nerica 7), Cross II

(Sakha 105 × Vandana), and Cross III (Sakha Super 300 × Moroberekan). In the second season, 2022, the hybrid seeds (F_1 seeds) of the three crosses were sown to give the F_2 seeds. Moreover, the same parents were crossed again to produce F_1 seeds. The new hybrid seeds and part of the seeds obtained from F_1 selfed plants (F_2 seeds) were kept in the refrigerator for the final experiment. In the third season (2023), the F_1 and F_2 plants were selfed to produce F_2 and F_3 seeds, respectively. In the fourth season (2024), the five population of each cross, P_1, P_2, F_1, F_2, and F_3 were evaluated under two irrigation regimes; well-watered or non-stress (NS) and water-deficit (WD) conditions in separated experiments at the experimental farm of Sakha Agricultural Research Station, Rice Research Department, Kafr El-Sheikh Governorate (31° 08'N latitude, 30° 58'E Longitude), Field Crops Research Institute, Agricultural Research Center, Egypt. The physical and chemical properties of the soil samples before the rice planting season 2024 are illustrated in Table 3, according to Black *et al. (*1965).

Table 3. Some chemical and physical properties of experimental field soils before rice planting season 2024.

Properties	Soil depth (cm)	
	0-30 cm	30-60 cm
Chemical Analysis		
EC (ds/m)	1.56	0.94
pH	7.82	7.95
Organic matter (%)	1.62	1.20
Soluble Cations, meq/L:		
Ca^{++}	5.03	1.97
Mg^{++}	5.55	1.83
Na^{+}	15.15	13.66
K^{+}	0.18	0.06
Soluble Anions, meq/L:		
$Co3^{--}$	--	--
$Hco3^{-}$	3.13	2.82
$So4^{--}$	9.93	3.66
Cl^{-}	12.50	11.04
Physical Analysis		
Sand (%)	18.07	19.41
Clay (%)	54.20	51.68
Silt (%)	27.73	28.91
$CaCo_3$ (%)	3.81	3.68
Soil texture	Clayey	Clayey

A Randomized Complete Block Design (RCBD) with three replications was used in each experiment. The non-stress (NS) or well-watered condition was performed using continuous flooding every 4 days with an adequate depth of submersion that ensured all surface areas were covered by water in each irrigation incident. The water-deficit (WD) treatment was performed using irrigation every 12 days without standing water. The stress condition was applied 15 days after the transplantation. The water applied irrigation quantities for each treatment were measured using a flow meter under well-watered and water-deficit conditions (13,200 and 8290 m^3/ha), respectively. The agricultural practices involving sowing and transplanting were a single plant on a hill, and each row consisted of 25 plants with 20 × 20 cm spaces between seedlings. It grew in three rows for P_1, P_2, and F_1; however, 30 rows were used for the F_2 population, and 15 rows were used for the F_3 generation per replicate for each cross. Nitrogen fertilizer at 160 kg N ha^{-1} rate was applied in two phases as urea (46.0% N): two-thirds was utilized as basal and blended into dry soil before flooding irrigation, and one-third was applied at the maximum tillering stage. Phosphorous was applied at 40 kg P_2O_5 ha^{-1} as super-phosphate (15% P_2O_5), and potassium at a rate of 50 kg K_2O kg/ha as potassium sulfate (48% K_2O). Zinc fertilizer was applied at a rate of 25 kg/ha $ZnSO_4$. Other standard agricultural practices, such as weed control and disease protection, were conducted according to the recommended package at the Rice Research Department.

Data Collection

Data were recorded on 10 randomly selected plants for each P_1, P_2, and F_1 generation, 150 plants from the F_2 population, and 75 plants from the F_3 generation. The evaluated traits included maximum root length (cm), number of roots per plant, root volume (cm^3), number of root xylem vessels, root xylem vessel area (mm^2), days to 50% heading, chlorophyll content (mg/ds^{-1}), leaf rolling, relative water content (%), plant height (cm), pollen fertility (%), panicle length (cm), number of panicles per plant, 100-grain weight (g), sterility percentage (%), grain yield per plant (g), and water use efficiency (g/ml). All measurements were recorded for the three crosses under normal and water-deficit conditions, following the protocols established by IRRI (2013).

Gene action determination

Scaling tests (C and D) were computed for each trait to ascertain if the additive-dominance model or non-allelic gene interaction was adequate. However, these scales were found to be significant in indicating the existence of non-allelic interactions. According to Evans *et al.* (2002), the variance means for these estimations were shown, and the significance from zero was tested using a *t*-test. A five-parameter model was used to calculate estimates of different gene effects, allelic interactions, and their significance test (Hayman 1958).

Epistasis type

When dominance (h) and dominance × dominance (l) gene effects have the same sign, the form of epistasis known as complementary epistasis (C) is identified. In contrast, duplicate epistasis (D) is identified when the sign differs.

Statistical analysis

The analysis of variance for five generations (P_1, P_2, F_1, F_2, and F_3) was statistically analyzed based on individual plant using TNAUSTAT (http://sourceforge.net/projects/dosbox/).

RESULTS AND DISCUSSION

Molecular genetic diversity among selected parents

Eleven microsatellite markers were utilized to examine the genetic diversity among the tested parental genotypes. PCR-amplified products for the eleven SSR markers are shown in Figure 1. The alleles number per locus varied from 2 to 4, with an average of 2.45 alleles per locus (Table 4). The number of effective alleles per locus varied from 1.38 to 3.6, with a mean of 1.97 alleles. The mean number of alleles per locus detected in this study was higher than those reported by Gaballah *et al.* (2021), who observed averages of 1.28. However, it was lower than those reported by Naaz *et al.* (2022), Mukta *et al.* (2024), and Salem *et al.* (2024), who observed averages of 4, 4.75, and 4.61 alleles, respectively.

The variation in allele numbers may be attributed to the genetic architecture of the genotypes and the specific SSR markers used. The major allele frequency averaged 0.65, ranging from 0.33 to 0.83. This finding indicates that 65% of the tested genotypes exhibited a shared major allele across the loci examined, consistent with results reported by Pradhan *et al.* (2023) and Guha *et al.* (2024). The polymorphic information content (PIC) measures the ability of a marker to

detect polymorphisms, reflecting its discriminating power. The PIC ranged from 0.28 to 0.80, averaging 0.44 (Table 4). This indicates that markers exhibit a high level of informativeness. The mean PIC value observed in this study was close to those reported by Nachimuthu *et al.* (2015) and Pradhan *et al.* (2023), who detected an average of 0.42 and 0.43, respectively. SSR markers with PIC values > 0.50 are considered highly informative Botstein *et al.* (1980). In this study, RM223, RM518, and RM3805, with PIC values exceeding 0.61, demonstrated high discriminatory power and are valuable for exploring genetic diversity in rice genotypes for drought tolerance Khan *et al.* (2022).

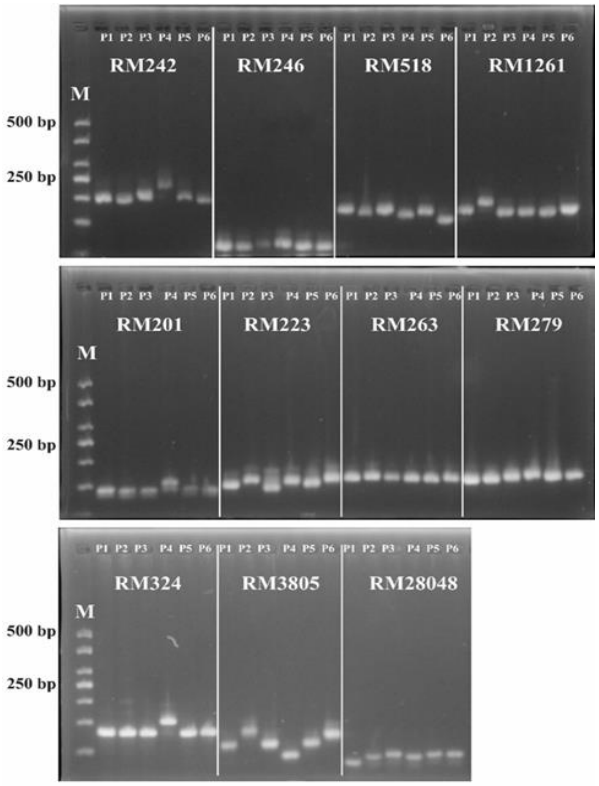

Figure 1. PCR-amplified products for the eleven SSR markers with the six parental rice genotypes. P1: Sakha 107, P2: Nerica7, P3: Sakha 105, P4: Vandana, P5: Sakha Super 300, P6: Moroberekan, and M: 50 bp DNA ladde.

Table 4. Genetic features of the eleven SSR markers utilized in this study.

Marker Name	Chromosome number	Number of Alleles	Effective number of alleles	Major Allele Frequency	PIC
RM246	1	2	1.80	0.67	0.44
RM201	9	2	1.38	0.83	0.28
RM263	2	2	1.80	0.67	0.44
RM242	9	2	1.38	0.83	0.28
RM3805	6	3	2.57	0.50	0.61
RM223	8	4	3.60	0.33	0.72
RM279	2	2	1.80	0.50	0.44
RM28048	12	2	1.38	0.83	0.28
RM518	4	3	2.57	0.50	0.61
RM1261	12	3	2.00	0.67	0.50
RM324	2	2	1.38	0.83	0.28
Mean	-	2.45	1.97	0.65	0.44

The genetic similarity, as determined by SSR markers, ranged from 0.1 to 0.83, with an average of 0.42 (Table 5). This indicates relatively high genetic diversity among the selected parental genotypes, reflecting a wide array of diverse genes. These results align with the findings of Gaballah *et al.* (2021), Li *et al.* (2023), and Hemasai *et al.* (2024).

Table 5. Genetic similarity matrix among the tested genotypes based on SSR analysis.

Genotypes	Sakha 107	Nerica 7	Sakha 105	Vandana	Sakha Super 300
Sakha 107	1				
Nerica 7	0.30	1			
Sakha 105	0.70	0.37	1		
Vandana	0.10	0.37	0.22	1	
Sakha Super 300	0.57	0.37	0.83	0.22	1
Moroberekan	0.40	0.40	0.61	0.23	0.61

The highest similarity was detected between Sakha 105 and Sakha Super 300. However, the lowest genetic similarity was between Vandana and Sakha 105. The dendrogram, generated from the genetic distance matrix, classified the genotypes into two main clusters, with internal sub-clusters displaying varying levels of diversity (Figure 2). Group I consisted of Nerica 7 and Vandana, both indica types and drought-tolerant genotypes. Group II included four genotypes, further divided into two sub-groups: the first sub-group contained Sakha 107, Sakha 105, and Sakha Super 300, all japonica types, while the second sub-group included the tropical japonica Moroberekan. This result agrees with that obtained by Khan *et al.* (2022), who found that SSR markers separate indica and japonica varieties into distinct groups. Similarly, Gaballah *et al.* (2021) observed that genotypes clustered into two groups representing japonica and indica genotypes.

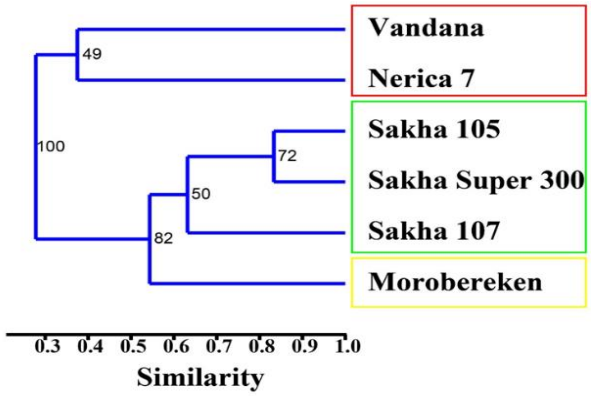

Figure 2. Dendrogram for the six rice genotypes constructed from SSR data using UPGMA and similarity matrix computed according to the Jaccard coefficient.

Generations mean

Data in Table 6 showed the mean performance of the five populations, P_1, P_2, F_1, F_2, and F_3, for studied traits of three crosses under normal and water deficit conditions. The validity of parental differences and genetic variance within F_2 and F_3 populations in normal and water deficit stress conditions were examined. Generally, the differences between each of the two parents were found to be highly significant.

Regarding maximum root length (Table 6), the mean values of P_2 and F_1 were slightly higher than P_1, F_2, and F_3 in the three crosses under normal and water deficit conditions. While root length in the third cross (Sakha Super 300 × Moroberekan) was superior compared to other crosses for

five populations P_1 (32.82 and 26.54 cm), P_2 (34.78 and 30.76 cm), F_1 (34.21 and 29.98 cm), F_2 (27.84 and 20.70 cm) and F_3 (26.19 and 20.77 cm) under normal and water deficit conditions, respectively.

For the number of roots/plant, the mean value of F_1 followed by P_1 was higher than that of P_2, F_2, and P_3 under normal and water stress conditions in the three crosses, while the first cross (Sakha 107 × Nerica 7) was the superior one and higher for the number of roots per plant compared to other crosses for five populations P_1 (266.01) and P_2 (219.20); and populations F_1 (288.36), F_2 (218.11) and F_3 (225.50) under water deficit conditions (Table 6).

Concerning root volume, the mean value of F_1 was slightly higher than P_1, P_2, F_2, and F_3 under normal and water deficit conditions in the three crosses.

Table 6. Mean performance and standard error of five-parameters for studied traits in the three crosses under non-stress and water deficit conditions.

Characteristics	Cross	P_1		P_2		F_1		F_2		F_3	
		NS	WD	NS	WD	NS	WD	NS	WD	NS	WD
Maximum root length (cm)	I	26.52±0.31	22.85±0.38	31.18±0.27	27.35±0.26	30.45±0.52	26.83±0.56	24.46±0.84	21.51±0.81	25.31±0.86	21.55±0.74
	II	25.32±0.22	18.28±0.18	27.23±0.23	23.63±0.19	27.93±0.32	21.19±0.33	23.29±0.39	18.54±0.37	25.09±0.39	18.81±0.37
	III	32.82±0.15	26.54±0.16	34.78±0.11	30.76±0.20	34.21±0.17	29.98±0.15	27.84±0.47	20.70±0.40	26.19±0.36	20.77±0.34
Number of roots per plant	I	331.00±0.60	266.01±0.34	244.51±0.51	219.20±0.38	348.85±0.92	288.36±0.96	280.39±1.85	218.11±1.31	280.84±1.75	225.50±1.28
	II	342.47±0.74	249.62±0.52	239.88±0.58	222.6±0.37	335.5±1.04	235.96±1.58	158.30±2.43	210.03±2.58	175.58±2.06	212.59±1.96
	III	350.18±0.34	267.76±1.29	218.53±1.15	184.46±1.40	350.08±1.45	256.92±1.82	277.47±3.04	198.3±2.43	287.97±2.74	220.58±2.06
Root volume (cm^3)	I	68.94±0.32	42.13±0.23	55.05±0.31	37.46±0.33	75.15±0.46	45.61±0.48	68.98±0.77	34.35±0.73	70.01±0.70	41.22±0.68
	II	66.29±0.20	31.21±0.20	56.49±0.13	35.72±0.18	75.94±0.37	45.26±0.33	65.56±0.62	30.53±0.61	60.08±0.45	32.32±0.42
	III	84.68±0.22	49.40±2.16	55.82±0.15	37.53±0.13	83.91±0.32	49.25±0.38	68.15±0.72	38.07±0.67	62.83±0.44	39.72±0.37
Root xylem vessels number	I	4.16±0.14	4.00±0.16	5.00±0.16	4.90±0.19	4.40±0.16	4.18±0.08	4.76±0.22	4.72±0.21	3.97±0.23	3.65±0.23
	II	4.10±0.12	4.10±0.11	4.70±0.12	4.70±0.12	4.70±0.12	4.60±0.19	4.38±0.21	4.73±0.22	3.81±0.31	3.49±0.27
	III	5.00±0.12	4.20±0.13	8.90±0.14	8.30±0.12	7.06±0.20	6.80±0.19	7.14±0.30	6.05±0.31	5.71±0.19	5.08±0.17
Root xylem vessels area (mm^2)	I	0.33±0.0049	0.29±0.0024	0.57±0.0058	0.47±0.0025	0.52±0.0066	0.46±0.0058	0.51±0.0194	0.46±0.0194	0.55±0.0278	0.40±0.0279
	II	0.32±0.0037	0.28±0.0037	0.55±0.0049	0.50±0.0024	0.50±0.0051	0.45±0.0058	0.48±0.0141	0.41±0.0136	0.45±0.0138	0.38±0.0137
	III	0.48±0.0032	0.39±0.0024	0.62±0.0032	0.56±0.0040	0.55±0.0049	0.48±0.0058	0.45±0.0200	0.41±0.0185	0.46±0.0134	0.31±0.0130
No. of days to 50% heading(day)	I	96.96±0.19	87.67±0.23	101.30±0.26	95.36±0.27	95.55±0.49	89.82±0.40	93.82±0.90	88.82±0.89	86.15±0.77	83.95±0.76
	II	97.23±0.20	88.32±0.25	109.11±0.19	100.66±0.20	97.22±0.18	91.11±0.30	100.29±1.34	95.29±1.34	90.35±0.84	88.15±0.84
	III	125.65±0.32	117.05±0.25	122.02±0.33	113.56±0.38	118.42±0.45	105.27±0.57	112.27±0.97	102.77±0.90	98.02±0.91	90.54±0.85
Chlorophyll content (mg/ds^{-1})	I	44.95±0.19	38.41±0.15	39.78±0.14	37.07±0.18	46.11±0.24	42.01±0.23	38.30±0.37	34.05±0.42	43.20±0.60	39.96±0.48
	II	46.29±0.13	38.44±0.23	42.80±0.16	40.05±0.18	45.42±0.29	39.79±0.22	41.92±0.88	39.58±0.86	38.72±0.48	35.61±0.54
	III	41.37±0.24	38.46±0.25	35.31±0.28	31.39±0.18	44.41±0.34	38.57±0.41	37.51±0.50	34.33±0.57	39.37±0.46	36.17±0.68
Leaf rolling	I	2.10±0.13	3.40±0.16	1.70±0.19	2.50±0.18	2.12±0.24	3.44±0.26	2.89±0.44	3.82±0.32	2.54±0.43	3.18±0.42
	II	2.78±0.16	5.70±0.14	2.16±0.10	2.48±0.12	1.86±0.28	4.38±0.17	3.38±0.34	3.93±0.37	2.86±0.33	4.45±0.38
	III	2.42±0.19	5.30±0.24	1.70±0.20	2.30±0.20	2.30±0.30	3.10±0.29	3.48±0.40	4.93±0.42	1.27±0.47	3.18±0.44
Relative water content (%)	I	93.68±0.22	88.96±0.22	90.21±0.23	87.62±0.21	96.22±0.30	88.65±0.24	84.16±0.56	77.74±0.46	77.13±0.33	71.48±0.31
	II	88.97±0.20	85.76±0.26	91.09±0.14	87.11±0.21	86.05±0.44	82.91±0.30	80.54±0.71	76.77±0.68	79.06±0.69	70.46±0.63
	III	94.96±0.18	86.35±0.25	91.91±0.18	88.02±0.25	93.86±0.42	88.97±0.42	87.26±0.73	81.77±0.67	81.07±0.65	76.48±0.62
Plant height (cm)	I	96.40±0.22	83.88±0.28	128.88±0.22	116.25±0.24	120.04±0.27	114.30±0.31	127.43±0.90	119.11±1.00	115.70±1.15	108.39±1.12
	II	101.83±0.25	87.99±0.42	167.98±0.35	132.16±0.32	131.82±0.60	123.09±0.64	159.11±1.41	126.94±1.26	156.62±1.39	132.66±1.06
	III	116.00±0.17	106.30±0.38	160.89±0.31	128.60±0.19	134.23±0.76	126.09±0.70	169.18±1.38	127.95±1.17	149.68±1.13	125.31±1.05
Pollen fertility (%)	I	96.50±0.17	89.20±0.22	96.72±0.23	91.31±0.11	96.56±0.24	83.38±0.23	93.68±0.35	83.03±0.52	90.57±0.56	78.63±0.50
	II	95.52±0.19	80.21±0.14	95.82±0.22	87.46±0.17	93.68±0.24	71.59±0.30	91.65±0.90	66.04±0.83	87.26±1.01	65.3±0.85
	III	96.76±0.12	91.34±0.24	97.06±0.23	92.23±0.27	96.52±0.56	88.94±0.35	94.32±0.31	86.00±0.72	90.44±0.68	80.33±0.68
Panicle length (cm)	I	24.77±0.09	20.30±0.17	26.42±0.22	22.61±0.16	25.49±0.24	19.26±0.14	24.31±0.46	17.51±0.43	22.09±0.42	17.92±0.33
	II	25.01±0.22	16.40±0.26	26.66±0.13	21.45±0.27	23.43±0.29	17.34±0.38	21.49±0.93	16.86±0.53	20.34±1.10	16.34±1.14
	III	25.08±0.24	17.03±0.26	27.40±0.28	23.32±0.18	25.31±0.31	19.45±0.40	22.12±0.46	17.20±0.44	21.91±0.59	17.09±0.45
Number of panicles per plant	I	24.43±0.17	20.05±0.21	19.67±0.20	16.83±0.19	25.31±0.24	21.03±0.15	20.42±0.54	15.80±0.45	20.03±0.64	12.11±0.62
	II	24.44±0.19	16.35±0.13	18.21±0.17	16.24±0.21	23.64±0.22	15.80±0.17	18.79±0.50	13.54±0.46	16.54±0.56	9.93±0.52
	III	26.41±0.14	21.47±0.29	19.77±0.24	16.86±0.13	25.38±0.37	19.15±0.36	21.10±0.54	15.72±0.50	21.13±0.54	12.70±0.53
100-grain weight(g)	I	2.63±0.011	2.38±0.018	2.77±0.015	2.52±0.019	2.77±0.016	2.44±0.017	2.46±0.060	2.35±0.055	2.47±0.049	2.26±0.054
	II	2.78±0.024	2.34±0.018	2.61±0.019	2.41±0.013	2.76±0.038	2.31±0.100	2.42±0.077	2.28±0.077	2.23±0.095	1.8±0.090
	III	2.91±0.034	2.44±0.016	3.25±0.028	2.93±0.022	3.09±0.026	2.68±0.055	2.57±0.051	2.44±0.074	2.52±0.06	2.19±0.087
Sterility percentage (%)	I	7.19±0.12	16.52±0.23	7.29±0.19	15.35±0.13	11.00±0.25	21.00±0.29	11.00±0.35	22.58±0.50	10.71±0.33	20.44±0.48
	II	8.61±0.15	35.49±0.18	8.48±0.16	19.28±0.12	12.04±0.32	42.87±0.26	15.10±0.41	38.26±0.47	13.68±0.34	35.81±0.34
	III	6.90±0.15	24.14±0.26	7.64±0.19	14.51±0.23	10.72±0.28	22.60±0.30	12.08±0.35	23.04±0.40	10.51±0.37	20.97±0.34
Grain yield per plant (g)	I	41.20±0.25	32.64±0.35	36.39±0.21	30.95±0.28	46.16±0.29	35.35±0.37	42.58±0.47	30.78±0.61	41.98±0.38	30.96±0.69
	II	43.26±0.29	25.69±0.18	34.27±0.19	29.92±0.13	44.85±0.31	29.59±0.21	40.23±0.44	23.42±0.35	39.82±0.43	23.98±0.34
	III	46.36±0.22	29.61±0.25	35.97±0.18	30.22±0.28	48.08±0.33	34.32±0.32	43.26±0.49	29.43±0.41	43.32±0.40	27.33±0.33
Water use efficiency (g/ml)	I	0.84±0.0032	0.90±0.0025	0.84±0.0025	0.91±0.0032	0.85±0.0037	0.98±0.0037	0.83±0.0171	0.93±0.0174	0.77±0.0168	0.88±0.0181
	II	0.82±0.0093	0.79±0.0025	0.80±0.0037	0.92±0.0051	0.82±0.0112	0.92±0.0130	0.75±0.0174	0.79±0.0171	0.74±0.0232	0.81±0.0238
	III	0.84±0.0103	0.90±0.0097	0.87±0.0144	0.97±0.0073	0.84±0.0121	0.95±0.0116	0.79±0.0210	0.86±0.0193	0.69±0.0223	0.81±0.0228

***Cross I: Sakha 107 × Nerica 7, Cross II; Sakha 105 × Vandana, Cross III: Sakha Super 300 × Moroberekan, NS: non-stress, and WD: water-deficit.**

Concerning root xylem vessels' number (Table 6), the mean values of P_2 were higher than that of the other parent P_1 and F_1 and the segregating populations F_2 and F_3 for the three crosses under normal and water deficit conditions. The third cross, Sakha Super 300 × Moroberekan, was the superior one and higher for root xylem vessels number compared to other crosses for five populations P_1 (5.00 and 4.20) and P_2 (8.90 and 8.30) and populations F_1 (7.06 and 6.80), F_2 (7.14 and 6.05) and F_3 (5.71 and 5.08) under normal and water deficit conditions, respectively.

Concerning root xylem vessels area (Table 6), the mean values of P_2 were higher than that of the other parent P_1 and F_1 and the segregating populations F_2 and F_3 for the three crosses under normal and water deficit conditions. The parent P_2 gave the higher mean values of root xylem vessel area compared with the other parent P_1 and F_1 and the segregating populations F_2 and F_3 under the two stress conditions in the three crosses. While, the third cross (Sakha Super 300 × Moroberekan) (Fig. 3) gave the superior one and higher for root xylem vessels area compared to other crosses in parents P_1 (0.48 and 0.39 mm^2), P_2 (0.62 and 0.56 mm^2) and populations F_1 (0.55 and 0.48 mm^2); on the contrary, the first cross (Sakha 107 × Nerica 7) showed the higher values compared to other crosses in segregating populations F_2 (0.51 and 0.46 mm^2) and F_3 (0.55 and 0.40 mm^2) under normal and water deficit conditions, respectively.

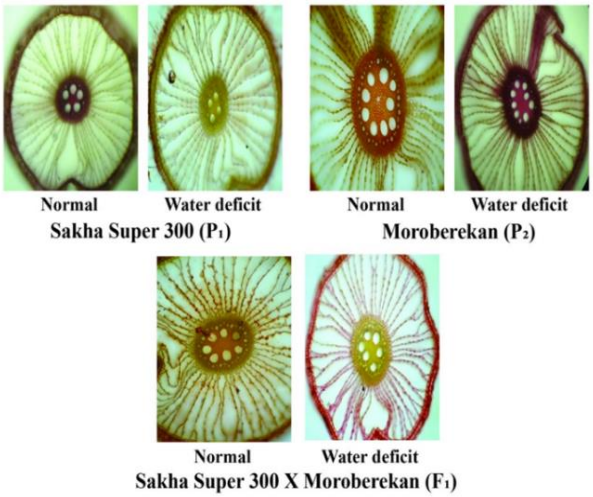

Figure 3. The pictorial illustration section of root xylem vessels in Sakha Super 300 (P_1), Moroberekan (P_2), and Sakha Super 300 × Moroberekan (F_1) under normal and water deficit conditions.

According to the days to 50% heading, the data obtained from the three crosses under normal and water deficit stress conditions (Table 6) showed that the water deficit conditions led to early maturity of about 10 days compared to other non-stress in the three crosses. In the first crosses, the segregating populations F_3 (86.15 and 83.95 days) and F_2 headed after (93.82 and 88.82 days) and matured earlier than parents P_1 (96.96 and 87.67 days) and P_2 (101.30 and 95.36 days) as well as populations F_1 (95.55 and 89.82 days) under both normal and water deficit conditions, respectively. The segregating population F_3 headed and matured earlier than the parents P_1 and P_2 and populations F_1 and F_2 in the three crosses under normal and water deficit stress conditions. This result is desirable for selecting early maturing plants in the future.

Concerning chlorophyll content (mg/ds^{-1}), the water deficit in the three crosses significantly affected chlorophyll content under water stress conditions. For chlorophyll content, the mean values in populations F_1 (46.11 and 42.01) were slightly higher than that of P_1 (44.95 and 38.41), P_2 (39.78 and 37.07), and segregating populations F_2 (38.30 and 34.05) and F_3 (43.20 and 39.96) under normal and drought stress conditions in the first cross (Table 6), respectively. In contrast, the parents Sakha 105 and Vandana in the second cross scored the highest estimates for chlorophyll content under normal and water deficit conditions.

Leaf rolling is considered the first symptom of the stress conditions reaction. For the three crosses under water deficit stress, the parent P_1 leaf rolling values were higher than the other parent P_2 and the populations F_1, F_2, and F_3 under normal and water deficit conditions. The first cross (Sakha 107 × Nerica 7) was the superior one and least for leaf rolling compared to other crosses for five populations P_1 (2.10 and 3.40) and P_2 (1.70 and 2.50); and populations F_1 (2.12 and 3.44), F_2 (2.89 and 3.82) and F_3 (2.54 and 3.18) under normal and water deficit conditions (Table 6), respectively.

Regarding relative water content (Table 6), the mean values in generation F_1 (96.22 and 88.65 %) were slightly higher than that of P_1 (93.68 and 88.96 %), P_2 (90.21 and 87.62 %), F_2 (84.16 and 77.74 %) and F_3 (77.13 and 71.48 %) under normal and water deficit conditions in the first cross, respectively. For the second cross, parent P_2 relative water content values were higher than the other parent P_1 and generation F_1 as well as the segregating populations F_2 and F_3 under two stress conditions. The third cross in parent P_1 (94.96 and 86.35 %) was higher than P_2 (91.91 and 88.02 %), F_1 (93.86 and 88.97 %), F_2 (87.26 and 81.77 %), and F_3 (81.07 and 76.48 %) under normal and water deficit conditions, respectively.

Concerning plant height under water stress conditions (Table 6), plant height was significantly affected by the water deficit. The most desirable mean values towards dwarfing were obtained with the first cross (Sakha 107 × Nerica 7) however, the shorter mean values were found for P_1 (96.40 and 83.88 cm), followed by segregating generation F_3 (115.70 and 108.39 cm), F_1 (120.04 and 114.30 cm), segregating generation F_2 (127.43 and 119.11 cm) and P_2 (128.88 and 116.25 cm) under normal and water deficit conditions, respectively. The same trend was observed in the second and the third crosses.

For pollen fertility (%) (Table 6), the mean values of P_2 were slightly higher than P_1, F_1, F_2, and F_3 under normal and water deficit conditions in the three crosses. Meanwhile, the third cross recorded the highest mean values pollen fertility compared with the other crosses, and the highest values recorded for P_2 (97.06 and 92.23 %), followed by P_1 (96.76 and 91.34 %), generation F_1 (96.52 and 88.94 %), segregating generation F_2 (94.32 and 86.00 %) and F_3 (90.44 and 80.33 %) and under normal and water deficit conditions, respectively. The same trend was observed in the first and second crosses.

For panicle length (Table 6), The mean values of P_2 followed by F_1 were slightly higher than P_1, F_2, and F_3 under normal and water deficit conditions in the three crosses. Moreover, the first cross gave the highest values of panicle length under water deficit conditions compared with the other crosses. On the other hand, the third cross gave the maximum value of panicle length under non-stress plants compared with the other crosses.

Concerning the number of panicles per plant (Table 6), the first cross data revealed that the F_1 (25.31 and 21.03) values were higher than that of the parents P_1 (24.43 and 20.05) and P_2 (19.67 and 16.83) as well as the segregating populations F_2 (20.42 and 15.80) and F_3 (20.03 and 12.11) under both normal and water deficit conditions, respectively. For the second and third crosses, data revealed that the P_1 values were higher than that of the other parent P_2 and the

segregating populations F_1, F_2, and F_3 under normal and water deficit conditions.

In the first cross the mean 100-grain weight value of P_2 (2.77 and 2.52 g) and F_1 (2.77 and 2.44 g) were higher than those of P_1 (2.63 and 2.38 g), F_2 (2.46 and 2.35 g) and F_3 (2.47 and 2.26 g) under normal and water deficit conditions, respectively. The P_2 values in the second and third crosses were higher than those of the other parent P_1 as well as the populations F_1, F_2, and F_3 under both normal and water deficit conditions.

The results in (Table 6), showed that the sterility percentage on the first cross in F_1 (11.00 and 21.00 %) and F_2 (11.00 and 22.58 %) were slightly higher than that in P_1 (7.19 and 16.52 %), P_2 (7.29 and 15.35 %) and F_3 (10.71 and 20.44 %) under normal and water deficit conditions, respectively. The same trend was observed in the second and third crosses under normal and water deficit conditions.

Concerning grain yield per plant in grams (Table 6), the mean yield of F_1 (46.16 and 35.35 g) was slightly higher than that of P_1 (41.20 and 32.64 g) and higher than P_2 (36.39 and 30.95 g), F_2 (42.58 and 30.78 g) and F_3 (41.98 and 30.96 g) under normal and water deficit conditions, respectively in the first cross. The same trend was observed in the second and third crosses under normal and water deficit stress conditions. Moreover, the first cross (Sakha 107 × Nerica 7) gave the highest mean values of grain yield per plant under water deficit conditions compared with the other crosses. On the other hand, the third cross (Sakha Super 300 × Moroberekan) gave the highest value of grain yield per plant under non-stress compared with the other crosses.

Concerning water use efficiency (Table 6), the mean values of P_2 and F_1 were higher than P_1, F_2, and F_3 under normal and water deficit conditions in the three crosses. The first cross (Sakha 107 × Nerica 7) gave the highest mean values of water use efficiency compared with the other crosses in the parents P_1 (0.84 and 0.90 g/ml) and P_2 (0.84 and 0.91 g/ml) as well as the populations F_1 (0.85 and 0.98 g/ml), F_2 (0.83 and 0.93 g/ml) and F_3 (0.77 and 0.88 g/ml) under non-stress and water shortage conditions, respectively.

Generally, it could be concluded that the first cross (Sakha 107 × Nerica 7) was the best cross for most studied traits, namely maximum root length, number of roots/plants, earliness, chlorophyll content, leaf rolling, dwarfism, panicle length, number of panicles/plant, sterility percentage, grain yield per plant and water use efficiency under water deficit conditions. So, rice breeders could expect elite, promising lines for drought tolerance and use them in their breeding program mainly for drought tolerance.

In addition, the third cross (Sakha Super 300 × Moroberekan) was the best cross for most studied traits, namely maximum root length, root volume, root xylem vessels number, root xylem vessels area, leaf rolling, relative water content, pollen fertility, panicle length, number of panicles per plant, 100-grain weight, sterility percentage, grain yield per plant and water use efficiency under normal conditions. These results are in agreement with results obtained by Sultan *et al.* (2014), Ghazy (2017), and Ganapati *et al.* (2020), who found that some crosses mean performed better than others under stressed conditions.

Scaling test

Table 7 displays the estimated scaling test parameters (C and D) for the studied characteristics in the three crosses under normal and water deficit conditions. Scaling tests C and D aimed to determine how the additive-dominance model is adequate for exploring types of gene action in the inheritance of different traits. When the scale test is sufficient, the values of C and D should be zero and within the limits of their respective standard errors. The significance of any one of these scales indicates the presence of non-allelic interaction.

The mean performance and variance of the five-population mean (P_1, P_2, F_1, F_2, and F_3) were used to calculate the two scaling tests. The parameters C and D values showed significant or highly significant for most studied characteristics in the three crosses under normal and water deficit conditions, suggesting that the additive-dominance model is inadequate for these traits and indicating the role of non-allelic interaction in governing these traits more particularly dominance × dominance type of non-allelic interaction (epistasis). These results indicate that the five-parameter model adequately illustrates the type of gene action for these significant characteristics. El-Gamal (2013), Sultan *et al.* (2014), Ghazy (2017), and Hassan *et al.* (2023) found comparable outcomes. They displayed one as a minimum of calculated parameters (C and D) that were significant for the studied traits. This finding suggests that allelic interaction is necessary for the genetic regulation of these traits.

In contrast, the parameters C and D values in Table 7 were non-significant for root xylem vessels area in the second cross (cross II) under non-stress and water deficit conditions, suggesting that the interaction model failed to explain the type of gene action.

Nature of gene action and types of epistasis

Types of gene effects for the studied characteristics in the three crosses at normal and water deficit conditions are shown in (Table 8). The mean effect of a parameter (m) that reflects the contribution due to the overall mean plays the locus effect and interactions of the fixed loci was highly significant for all studied characteristics in three crosses under normal and water deficit conditions. The various genetic effects used means of the different generations Kour *et al.* (2019).

The additive gene effects (d) were positively significant for the number of roots per plant, root volume, chlorophyll content, leaf rolling, number of panicles per plant, and grain yield per plant in three crosses under normal and water deficit conditions. The results indicate that selection could be effective for these characters in early generations. The additive gene effects (d) were negatively significant for root length, root xylem vessels number, root xylem vessel area, days to heading, plant height, pollen fertility, panicle length, and 100-grain weight in the three crosses under normal and water deficit conditions except days to heading in the cross III. These results indicated that the materials in the three crosses have decreasing alleles for these characters, and selection to improve it could be adequate except for days to heading and plant height if earlier and shorter plants are desired. The results agree with those reported by AbdAllah (2010), Abdel-Hafez *et al.* (2017), and Ghazy (2017).

Concerning dominance gene effects (h) (Table 8), positive and highly significant ones were attained for most studied characteristics in three crosses under normal and water deficit conditions, revealing the importance of dominance gene effects in the inheritance of these traits. Significant dominance gene effects for root traits and grain and its components in rice have been reported by El-Gamal (2013), Sultan *et al.* (2014), Hassan *et al.* (2016), and Ghazy (2017).

Table 7. Scaling test estimate for growth traits in the three crosses under non-stress and water deficit stress conditions.

Characteristics	Cross	I		II		III	
		NS	WD	NS	WD	NS	WD
Maximum root length (cm)	C	-20.75±3.55**	-17.82±3.46**	-15.24±1.71**	-10.13±1.64**	-24.65±1.92**	-34.44±1.64**
	D	-5.40±3.84	-7.02±3.40*	1.21±1.75	-3.73±1.68*	-18.51±1.74**	-15.61±1.58**
Number of roots per plant	C	151.63±7.68**	189.48±5.60**	620.17±9.98**	104.04±10.82**	158.96±12.55**	172.87±10.55**
	D	-12.94±7.97	-19.44±5.76**	196.63±9.62**	-41.93±9.42**	28.24±12.60*	33.51±9.76**
Root volume (cm^3)	C	1.64±3.24	-33.42±3.09**	-12.44±2.58**	-35.33±2.53**	-35.71±2.96**	-33.17±3.52**
	D	18.07±3.22**	16.58±3.12**	-13.58±2.19**	1.28±2.08	-25.49±2.29**	-4.18±2.94
Root xylem vessels number	C	1.09±0.98	1.63±0.89*	-0.67±0.91	0.92±0.96	0.54±1.28	-1.89±1.29
	D	-2.82±1.05**	-3.73±1.04**	-2.33±1.31*	-4.28±1.16**	-5.32±0.99**	-4.28±0.95**
Root xylem vessels area (mm^2)	C	0.09±0.079	0.17±0.079*	0.04±0.058	-0.05±0.056	-0.38±0.081**	-0.26±0.075**
	D	0.28±0.118**	-0.10±0.118	-0.01±0.062	-0.07±0.061	-0.17±0.067**	-0.53±0.064**
No. of days to 50% heading (day)	C	-14.08±3.73**	-7.40±3.69*	0.39±5.38	9.98±5.40*	-35.43±4.03**	-30.06±3.82**
	D	-41.31±3.57**	-24.89±3.58**	-45.51±4.31**	-26.94±4.31**	-80.15±4.16**	-74.02±3.89**
Chlorophyll content (mg/ds^{-1})	C	-23.73±1.57**	-23.31±1.74**	-12.26±3.58**	0.25±3.48	-15.45±2.17**	-9.69±2.43**
	D	11.46±2.53**	16.26±2.10**	-18.03±2.62**	-15.22±2.76**	5.79±2.14**	6.18±2.98*
Leaf rolling	C	3.51±0.55**	2.48±0.51**	4.86±0.61**	-1.22±0.77	5.20±0.77**	5.93±1.10**
	D	0.58±0.60	-0.82±0.54	-0.27±0.64	1.75±0.80*	-6.00±0.45**	-4.76±0.78**
Relative water content (%)	C	-39.70±2.35**	-42.9±1.94**	-30.01±2.99**	-31.60±2.79**	-25.57±3.04**	-25.22±2.85**
	D	-43.69±1.77**	-46.15±1.58**	-24.91±3.12**	-44.56±2.89**	-37.12±2.98**	-32±2.86**
Plant height (cm)	C	44.38±3.66**	47.72±4.08**	102.99±5.78**	41.42±5.23**	131.35±5.74**	24.73±4.90**
	D	-17.36±4.94**	-4.80±4.92	38.44±6.24**	56.61±4.96**	-16.52±5.32**	10.44±4.83*
Pollen fertility (%)	C	-11.61±1.52**	-15.18±2.14**	-12.11±3.63**	-46.67±3.39**	-9.59±1.68**	-17.45±2.99**
	D	-18.31±2.37**	-32.05±2.25**	-25.58±4.42**	-38.55±3.79**	-20.68±2.79**	-34.24±3.09**
Panicle length (cm)	C	-4.92±1.91**	-11.37±1.74**	-12.58±3.76**	-5.10±2.30*	-14.62±1.98**	-10.46±1.95**
	D	-11.47±1.94**	-6.24±1.58**	-13.29±4.78**	-6.22±4.71	-9.08±2.57**	-6.37±2.01**
Number of panicles per plant	C	-13.03±2.22**	-15.74±1.86**	-14.78±2.07**	-10.03±1.9**	-12.54±2.29**	-13.73±2.16**
	D	-4.80±2.80*	-20.06±2.65**	-14.07±2.45**	-19.95±2.30**	-3.87±2.43	-18.98±2.36**
100-grain weight (g)	C	-1.10±0.24**	-0.38±0.22*	-1.24±0.32**	-0.28±0.37	-2.05±0.22**	-0.95±0.32**
	D	-0.43±0.23*	-0.54±0.24*	-1.31±0.41**	-2.11±0.41**	-1.21±0.27**	-1.48±0.38**
Sterility percentage (%)	C	7.53±1.51**	16.45±2.10**	19.23±1.84**	12.55±1.96**	12.34±1.52**	8.28±1.73**
	D	6.34±1.50**	4.76±2.18*	7.44±1.62**	11.96±1.66**	3.35±1.22**	-0.83±1.60
Grain yield per plant (g)	C	0.43±1.99	-11.19±2.60**	-6.33±1.91**	-21.12±1.48**	-5.46±2.10**	-10.77±1.80**
	D	5.18±1.83**	-1.30±3.06	1.31±1.97	-6.54±1.56**	4.43±1.91*	-9.37±1.59**
Water use efficiency (g/ml)	C	-0.07±0.030*	-0.05±0.031	-0.25±0.074**	-0.41±0.074**	-0.24±0.089**	-0.31±0.082**
	D	-0.25±0.031**	-0.16±0.036**	-0.16±0.100*	-0.06±0.101	-0.53±0.100**	-0.37±0.100**

Cross I: Sakha 107 × Nerica 7, Cross II; Sakha 105 × Vandana, Cross III: Sakha Super 300 × Moroberekan, C: complementary epistasis, D: duplicate epistasis, NS: non-stress, and WD: water-deficit. * and ** Significant at 0.05 and 0.01 probability levels, respectively.

On the contrary, dominance gene effects were negative and significant for the following number of roots per plant in the third cross (Sakha Super 300 × Moroberekan) and for chlorophyll content in the first cross (Sakha 107 × Nerica 7) and for plant height in the second crosses (Sakha 105 × Vandana) under normal and water deficit conditions. The results indicate that the alleles responsible for less value of the traits mentioned were dominant over the alleles governing the high value. It is noted that there are no significant dominance gene action effects in the chlorophyll content trait of cross III. Sultana *et al.* (2016), Patel *et al.* (2020), and Nofal and Gaballah (2024) found the same trend for 100 seeds weight and plant height.

Regarding the additive x additive type of gene action (i), positively significant effects were observed for the number of roots per plant, days to 50% heading, leaf rolling, relative water content, pollen fertility, number of panicles per plant, and water use efficiency in three crosses under normal and water deficit conditions. This indicates that early generation selection for these characters could be effective in breeding programs.

On the other hand, negatively significant effects were found for root length and root volume in the first and second crosses and for root xylem vessel area and plant height in the three crosses under normal and water deficit conditions. This indicates that effective selection for these characters could be done in the late generations. Indicated to the additive × additive gene action, it had an essential role in the inheritance of these traits. However, the duplicate type of epistasis for pollen fertility, number of panicles per plant, 100-grain weight, and grain yield per plant for three crosses could impede the improvement of this characteristic caused by early generations' selection.

These crosses could be improved by using a cyclic breeding strategy, which selects and crosses desirable recombinants to combine the advantageous genes to create an elite population. Chamundeswari *et al.* (2013), Rani *et al.* (2015), and Solanke *et al.* (2019) reported similar results; therefore, Ghazy (2017) confirmed the existence of non-additive gene action for grain yield/plant the majority of the yield components in the hybrids led to a high level of vigor in the F_1, suggesting the potential for using heterosis to increase yield. Tan *et al.* (2022) also noted a less-than-additive or negative effect on the epistasis of additive-by-additive interaction between lines.

Concerning dominance x dominance type of gene effects (l), positively significant and highly significant effects were obtained for root length, number of roots per plant, root volume, and grain yield per plant in the three crosses and for chlorophyll content in the first and third crosses under normal and water deficit conditions. These results indicated that the role of dominance x dominance gene interaction is important in the inheritance of these characters. The dominance × dominance sign component has a positive in one or both crosses, indicative of an improved effect in the character expression.

Table 8. Estimates of gene effects of the three crosses for the studied characteristics under normal and water deficit stress conditions.

Characteristics	Cross	Mean F_2 generation		d		h		i		l		Type of epistasis	
		NS	WD	NS	WD	NS	WD	NS	WD	NS	WD	NS	WD
Maximum root length (cm)	I	24.46**	21.51**	-2.33**	-2.25**	1.74	3.45	-4.53*	-2.79	20.48**	14.40*	C	C
	II	23.29**	18.54**	-0.95**	-2.67**	-1.69	1.04	-5.25**	-4.55**	21.93**	8.54**	D	C
	III	27.84**	20.70**	-0.98**	-2.11**	8.65**	6.00**	6.27**	0.44	8.18*	25.1**	C	C
Number of roots per plant	I	280.39**	218.11**	43.25**	23.40**	44.45**	27.13**	69.85**	28.18**	184.92**	226.72**	C	C
	II	158.3**	210.03**	51.30**	13.51**	72.05**	10.46	130.32**	37.63**	564.72**	82.81**	C	C
	III	277.47**	198.30**	65.83**	41.65**	20.40*	-20.34**	86.33**	32.16**	249.60**	275.17**	C	D
Root volume (cm^3)	I	68.98**	34.35**	6.94**	2.33**	1.38	-10.81**	2.11	-11.95**	21.90*	66.66**	C	D
	II	65.56**	30.53**	4.90**	2.25**	21.54**	5.05**	16.78**	-11.25**	-1.52	48.82**	D	C
	III	68.15**	38.07**	14.43**	5.93**	24.70**	3.04*	39.90**	9.13**	13.62*	38.65**	C	C
Root xylem vessels number	I	4.76**	4.72**	-0.42**	-0.45**	1.88**	2.49**	1.22*	1.86**	-5.22**	-7.16**	D	D
	II	4.38**	4.73**	-0.30**	-0.30**	1.74*	3.21**	0.84	2.41**	-2.22	-6.94**	D	D
	III	7.14**	6.05**	-1.95**	-2.05**	3.75**	3.09**	-0.26	-1.56*	-7.82**	-3.20	D	D
Root xylem vessels area (mm^2)	I	0.51**	0.46**	-0.12**	-0.09**	-0.10	0.17*	-0.41**	-0.08	0.25	-0.37*	D	D
	II	0.48**	0.41**	-0.12**	-0.11**	0.07	0.10*	-0.22**	-0.18**	-0.06	-0.03	D	D
	III	0.45**	0.41**	-0.07**	-0.08**	0.04	0.31**	-0.09*	0.15**	0.29*	-0.35*	C	D
No. of days to 50% heading (day)	I	93.82**	88.82**	-2.17**	-3.85**	21.62**	13.67**	20.85**	7.67**	-36.31**	-23.32**	D	D
	II	100.29**	95.29**	-5.94**	-6.17**	24.45**	16.24**	18.51**	7.28*	-61.19**	-49.22**	D	D
	III	112.27**	102.77**	1.81**	1.74**	42.11**	34.3**	51.15**	47.83**	-59.63**	-58.61**	D	D
Chlorophyll content (mg/ds^{-1})	I	38.30**	34.05**	2.58**	0.67**	-7.85**	-10.45**	-6.43**	-13.38**	46.92**	52.75**	D	D
	II	41.92**	39.58**	1.75**	-0.80**	10.85**	10.73**	13.47**	8.58**	-7.70	-20.63**	D	D
	III	37.51**	34.33**	3.03**	3.53**	-0.37	-2.09	-0.38	1.33	28.33**	21.16**	D	D
Leaf rolling	I	2.89**	3.82**	0.20**	0.45**	0.42	1.45**	0.60	1.86**	-3.9**	-4.41**	D	D
	II	3.38**	3.93**	0.31**	1.61**	0.38	-1.08*	1.61**	1.85**	-6.85**	3.95*	D	D
	III	3.48**	4.93**	0.36**	1.5**	5.11**	3.46**	5.59**	7.16**	-14.93**	-14.26**	D	D
Relative water content (%)	I	84.16**	77.74**	1.73**	0.67**	26.78**	23.98**	25.98**	24.95**	-5.33	-4.34	D	D
	II	80.54**	76.77**	-1.06**	-0.68**	7.63**	20.92**	9.48**	23.09**	6.80	-17.29**	C	D
	III	87.26**	81.77**	1.52**	-0.84**	20.91**	18.91**	23.53**	15.46**	-15.39*	-9.04	D	D
Plant height (cm)	I	127.43**	119.11**	-16.24**	-16.19**	26.37**	25.38**	-13.51**	-21.22**	-82.32**	-70.03**	D	D
	II	159.11**	126.94**	-33.08**	-22.09**	-11.56**	-17.82**	-74.61**	-75.01**	-86.07**	20.25*	C	D
	III	169.18**	127.95**	-22.45**	-11.15**	28.69**	5.80	-11.99**	-25.13**	-197.16**	-19.05*	D	D
Pollen fertility (%)	I	93.68**	83.03**	-0.11	-1.06**	10.22**	11.96**	10.05**	16.73**	-8.93*	-22.5**	D	D
	II	91.65**	66.04**	-0.15	-3.62**	13.05**	5.67*	14.75**	10.68**	-17.97*	10.82	D	C
	III	94.32**	86.00**	-0.15	-0.45**	11.80**	17.07**	11.89**	19.03**	-14.78**	-22.39**	D	D
Panicle length (cm)	I	24.31**	17.51**	-0.83**	-1.16**	6.72**	0.08	5.17**	-0.04	-8.73*	6.84*	D	C
	II	21.49**	16.86**	-0.82**	-2.53**	4.36	1.71	5.12*	-1.76	-0.95	-1.49	D	D
	III	22.12**	17.20**	-1.16**	-3.14**	2.69	1.78	1.30	-3.79**	7.38	5.46	C	C
Number of panicles per plant	I	20.42**	15.80**	2.38**	1.61**	4.29*	13.34**	5.79**	13.97**	10.97*	-5.77	C	D
	II	18.79**	13.54**	3.12**	0.06	9.23**	11.13**	13.15**	11.74**	0.95	-13.23**	C	D
	III	21.10**	15.72**	3.32**	2.30**	2.78	10.34**	7.13**	14.97**	11.57*	-6.99	C	D
100-grain weight (g)	I	2.46**	2.35**	-0.07**	-0.07**	0.17	0.29	-0.03	0.16	0.88	-0.22	C	D
	II	2.42**	2.28**	0.09**	-0.03**	0.73**	1.30**	0.84**	1.30**	-0.09	-2.45**	D	D
	III	2.57**	2.44**	-0.17**	-0.25**	0.47**	0.82**	0.12	0.33	1.13*	-0.71	C	D
Sterility percentage (%)	I	11.00**	22.58**	-0.05	0.59**	0.80	4.63**	-3.07**	0.74	-1.59	-15.58**	D	D
	II	15.10**	38.26**	0.06	8.11**	1.74	9.60**	-1.63	10.34**	-15.72**	-0.79	D	D
	III	12.08**	23.04**	-0.37**	4.82**	3.27**	5.21**	-0.91	11.56**	-11.99**	-12.14**	D	D
Grain yield per plant (g)	I	42.58**	30.78**	2.40**	0.84**	3.98**	2.56	1.43	0.69	6.33	13.18*	C	C
	II	40.23**	23.42**	4.50**	2.12**	4.16**	2.63*	7.06**	-3.40**	10.18**	19.45**	C	C
	III	43.26**	29.43**	5.20**	-0.31**	3.05*	8.86**	6.53**	3.84**	13.18**	1.86	C	C
Water use efficiency (g/ml)	I	0.83**	0.93**	0.002	0.003	0.17**	0.17**	0.15**	0.09**	-0.25**	-0.15*	D	D
	II	0.75**	0.79**	0.009*	-0.07**	0.08	0.03	0.09	-0.16**	0.12	0.46**	C	C
	III	0.79**	0.86**	-0.02*	-0.03**	0.30**	0.21**	0.29**	0.13*	-0.39*	-0.08	D	D

Cross I: Sakha 107 × Nerica 7, Cross II; Sakha 105 × Vandana, Cross III: Sakha Super 300 × Moroberekan, d: additive gene effects, h: dominance gene effects, i: additive x additive type of gene action, I: dominance x dominance type of gene effects, C: complementary epistasis, D: duplicate epistasis, NS: non-stress, and WD: water-deficit. * and ** Significant at 0.05 and 0.01 probability levels, respectively.

Negatively significant gene effects values were detected for root xylem vessels number, days to 50% heading, leaf rolling, plant height, pollen fertility, sterility percentage, and water use efficiency in the three crosses under normal and water deficit stress. These results indicated the scope of heterosis breeding for developing superior populations. The expression of these traits in these crosses was significantly influenced by the non-fixable gene effect, which may be taken advantage of through bi-parental mating under recurrent selection or using the population improvement concept instead of traditional methods. The dominance × dominance effect sign was negative, suggesting that these characters' expressions were being reduced.

On the other hand, the dominance × dominance component was positive for the other characters, suggesting that they enhanced the expression of those characters. You *et al.* (2006) and Ghazy (2017) observed the interaction of additive × additive had a superior effect than dominance × dominance in most crosses.

The duplicate epistasis was achieved for all studied traits in three crosses except maximum root length, number of roots per plant, and grain yield per plant in three crosses and for root volume and panicle length in the third cross (Sakha Super 300 ×

Moroberekan) and for water use efficiency in the second cross (Sakha 105 × Vandana) were complementary under normal and water deficit conditions. In traits under study, both complimentary and duplicate epistasis were found. This makes it challenging to fix genotypes with higher levels of character manifestation in duplication epistasis, as the negative influence of one parameter would cancel out the opposite effect of another. On the other hand, epistasis of complementary refers to suggestions for selection in the early generation that might be effective. Ganapati *et al.* (2020) indicate the epistasis effect; the epistasis of duplicate was mainly for entirely the traits excluding panicle length; therefore, the epistasis of duplicates, as demonstrated by Solanke *et al.* (2019), may delay the selection of a single plant. Instead, biparental mating or diallel selective mating, in which a few cycles of crossing of promising segregates in F_2 and subsequent generations are followed, may aid in integrating desired genes into a single genetic background.

CONCLUSION

In conclusion, the results indicated that some crosses performed better under stress conditions. All studied traits most desirable mean values were recorded from the first cross (Sakha 107 × Nerica 7) under water deficit stress conditions. In contrast, under normal conditions, the most desirable mean values for all studied traits were recorded from the third cross (Sakha Super 300 × Moroberekan). Generally, the characters controlled by additive gene effect can be improved by the most appropriate breeding method (the pedigree selection method). In contrast, other characters were controlled by additive and non-additive or non-additive gene effects in different crosses. Hence, those could be successfully improved by heterosis breeding or hybridization followed by the cyclic method of breeding; keeping an adequate population size would be more desirable for improving these traits.

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التحليل الوراثي لبعض الصفات الكمية لبعض التراكيب الوراثية في الأرز تحت ظروف الري العادي ونقص المياه بإستخدام نموذج العشائر الخمس

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الملخص

يعتبر نقص المياه من الإجهادات البيئية الرئيسية التي تؤثر بشكل كبير على نمو وإنتاج محصول الأرز. لذلك فإن إستنباط تراكيب وراثية جديدة من الأرز تتحمل نقص المياه وذات إنتاجية عالية أمر هام جدا، خاصةً في ظل ظروف نقص المياه الحالية. تهدف هذه الدراسة إلى تقدير التباعد الوراثي بين ست تراكيب وراثية مختلفة من الأرز (مستوردة ومحلية) بإستخدام الدلائل الجزيئية (SSR) وكذلك تقدير مكونات التباين الوراثي وطبيعة الفعل الجيني المتحكم في وراثة بعض صفات الجذور وبعض الصفات الفسيولوجية وكذلك صفات المحصول بإستخدام تحليل متوسط الأجيال تحت ظروف الري العادي ونقص المياه. أظهرت نتائج تحليل SSR وجود قدر كبير من الإختلافات الوراثية بين التراكيب الوراثية المستخدمة في هذه الدراسة ، حيث تم تحديد 27 أليلً بمتوسط 2.45 أليلً لكل موقع وأظهر محتوى تعدد الأشكال المظهرية (PIC) قيمة مرتفعة قدرها 0.44. بناءاً على هذا التنوع تم استخدام هذه التراكيب الوراثية لتكوين ثلاثة هجن مختلفة وهى (سخا 107 × نيركا 7)، (سخا 105 × فندانا) و (سخا سوبر 300 × موروبيريكان). تم تقييم الأجيال الخمسة لكل هجين وهي: الأب الأول، الأب الثاني، الجيل الأول، الجيل الثاني والجيل الثالث في تجربتين منفصلتين تحت ظروف الري العادي وظروف نقص المياه. أظهرت النتائج أن قيم المتوسطات للعشائر الخمسة في الثلاثة هجن كانت أعلى بشكل عام تحت ظروف الري العادي مقارنة بظروف نقص المياه لمعظم الصفات المدروسة. أوضحت النتائج أن الهجين الأول (سخا 107 × نيريكا 7) هو الأفضل في معظم الصفات تحت ظروف نقص المياه، بينما كان الهجين الثالث (سخا سوبر 300 × موروبيريكان) الأفضل تحت ظروف الري العادي. أظهرت الإختبارات أن فعل السيادة والإضافة للفعل الجيني الوراثي غير كافي لجميع الصفات التي تم تقييمها في الثلاثة هجن تحت ظروف الري الطبيعية ونقص المياه، مما يشير إلي وجود التفوق للفعل الجيني الوراثي في وراثة هذه الصفات. أوضحت النتائج تأثير معنوي للفعل الجيني السيادي موضحاً أن الإنتخاب لمثل هذه الصفات يجب أن يؤجل للأجيال الانعزالية المتأخرة حتي يزداد التباين الوراثي المضيف. أوضحت النتائج أيضا أهمية تأثير الفعل الجيني المضيف والسيادي في وراثة بعض صفات الجذور والمحصول في الثلاثة هجن المستخدمة في الدراسة تحت ظروف الري العادي ونقص المياه. ومن بين مكونات التفوق أوضحت النتائج أن الفعل الوراثي السيادي × السيادي ذو تأثير أكبر من الفعل الوراثي المضيف × المضيف لمعظم الصفات تحت الدراسة.