

GENETIC ANALYSIS OF RICE GENOTYPES WITH CONTRASTING RESPONSE TO AEROBIC CONDITIONS

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Abstract

Climate change and emerging water scarcity have seriously threatened the rice production systems which necessitate developing drought tolerant genotypes for ensuring food security. A trial was conducted to explore the genetic divergence among rice genotypes with an ultimate aim to sort out drought tolerant genotypes with high grain yield potential. The trial was comprised of seven rice genotypes along with their twenty one hybrids grown under aerobic conditions. The results revealed that hybrids of Azucena × Giza177 and Azucena × Giza179 remained superior by recording the maximum leaf diffusive resistance, leaf transpiration rate, and grain yield. In contrast, IRAT112 × N22 and IRAT112 × Azucena hybrids exhibited the lowest stomatal conductance. Besides rice hybrids, three parents N22, Azucena and Giza179 were identified as promising general combiners in terms of drought tolerance, physiological robustness and better grain yield components and thus these might be recommended as potent candidates for future breeding programs to increase drought tolerance. Additionally, grain yield per plant was positively correlated with leaf diffusive resistance, net photosynthesis rate, CO₂ concentration, photosynthetic active radiation, panicles numbers, 100-grain weight, and fertility percentage, while it had negative association with stomatal conductance, leaf transpiration rate, leaf temperature, and leaf rolling. Moreover, the crosses of Azucena × Giza177, IRAT 112 × Azucena, IRAT 112 × N22, and Azucena × Giza179 showed good SCA effects and significant heterosis indicating that the hybrid combinations could be an introgression to drought.

Key words: Drought, Physiological, Grain yield components, Correlation coefficient.

Introduction

Globally, climate change and frequently occurring drought spells are causing serious decline in crops yield which may compromise food security and zero hunger sustainable development goal (Luo *et al.*, 2022, Zhang *et al.*, 2022, Zhang *et al.*, 2022b). The productivity and nutritional quality of water intensive crops like rice have been reduced drastically under drought (Xu *et al.*, 2022, Zaghum *et al.*, 2022). The water intensive crops such as rice is one of the most strategic crops for ensuing the food and nutritional security of rapidly increasing population worldwide (Abbas *et al.*, 2021, Haque *et al.*, 2021, Hakim *et al.*, 2021). In Egypt, irrigation resources are rapidly squeezing for rice that requires 1,400 liters of water to produce 1 kg paddy (Abdallah, 2015). Resultantly, rice exports has sharply reduced leading to sharp decline in grower's income and foreign exchange earnings (Frege *et al.*, 2022, Fonta *et al.*, 2022). Therefore, developing drought tolerant genotypes of rice are the need of time in order to cope with water deficiency under changing climate scenario (Furqan *et al.*, 2022, Gaballah *et al.*, 2022, Wang *et al.*, 2022).

Drought stress (DS) imparts numerous deleterious effects on rice plants growth and development which leads to significant decline in paddy yield (Abdelrahman *et al.*, 2022). One of the pronounced DS effects include reduced radiation absorption by canopy causing decline

in radiation use efficiency and decreased harvest index (Chukwu *et al.*, 2022). Likewise, DS impaired rice growth and reduced seedling biomass, stomatal conductance, photosynthesis, plant water relations, and starch metabolism (Ndikuryayo *et al.*, 2022). It was revealed that drought sensitive rice cultivars showed numerous morphological and physiological interruptions in response to drought which ultimately reduced paddy yield (Minh *et al.*, 2022). Rice plants responses to DS are complex such as drought escape by fast development that allows plants to complete their cycle much earlier than optimal condition. Additionally, another plant response to DS is called drought avoidance which takes place via increasing water uptake and reducing transpiration rate by the decrease stomatal conductance and leaf area (El-Mouhamady *et al.*, 2022). Moreover under DS, rice plants might exhibit drought tolerance by maintaining tissue turgor through osmotic adjustment that allows plants to conserve limited water in plant tissues (Zain *et al.*, 2014). To mitigate the deleterious effects of drought on rice plants, targeted crop breeding efforts for enabling rice plants to biosynthesize metabolites for boosting protein outputs are direly needed (Krishnan *et al.*, 2022). Likewise, Kumar *et al.*, (2022) opined that yield traits of rice such as days to maturity, spikelets fertility percentage, relative water content and stomatal conductance might be manipulated through effective breeding efforts to ameliorate DS induced morpho-physiological alterations.

Table 1. Details of seven rice genotypes used in the present study.

Name	Parentage	Origin	Type
Giza177	Giza171/ Yumji No.1// PiNo.4	Egypt	Japonica type, sensitive to drought, short stature, early duration and resistance to blast
Sakha108	Sakha101/ HR5824-B-3-2-3 // Sakha101	Egypt	Japonica type, sensitive to drought, short stature, early duration and resistance to blast
Sakha104	GZ4096-8-1/ GZ4100-9-1	Egypt	Japonica type, sensitive to drought, short stature, early duration and sensitive to blast
Giza179	GZ6296/ GZ1368	Egypt	Indica/Japonica type – moderate tolerance to drought, short stature, early duration and resistance to blast
IRAT112	IRAT 13/ Dourado Precoce	Côte d'Ivoire	Japonica type , tolerant to drought (Upland) – long stature, late duration and sensitive to blast
Nagina-22 (N22)	Selected from Rajbhog.	India	Indica type, tolerant to drought, long stature, late duration and resistance to blast
Azucena	-	Philippine	japonica, tolerance to drought (upland), long stature , late duration and resistance to blast

Besides, stomatal regulation in rice plants exposed to drought must be studied because it plays critical role in the regulating water transpiration and CO₂ uptake (Pan *et al.*, 2022). The stomatal aperture is governed by the turgor pressure difference among the guard cells adjacent the pore and the bulk leaf epidermis. With the aim of optimize CO₂ uptake and water losses DS, rice plants tend to control stomatal aperture (Ghaley *et al.*, 2012). The existing genetic pool of rice is quite diverse and integrated research efforts might explore the superior genotypes for boosting paddy yield (Lou *et al.*, 2022, Tao *et al.*, 2022). Different rice cultivars respond differently to DS owing to their genotypic variation in terms of morphological traits and physiological adjustments (Bhat *et al.*, 2022, Crofts *et al.*, 2022, Faysal *et al.*, 2022). Genetic analysis for physiological traits and grain yield of rice genotypes may determine the gene action for the expression of a particular trait. Moreover, assessing the nature and role of alleles (dominant or recessive) in controlling trait of interest might also assist to develop drought tolerant rice genotypes. In diallel analysis, general combining ability is related to additive gene action and specific combining ability is concern as dominance and epistasis variances (Li *et al.*, 2022, Rahman *et al.*, 2022). Several cultivars, besides their good agronomic performances, it performs poorly in the F₁ generation caused by genetic hindrance in varied cross combinations (Salem *et al.*, 2022). Therefore, crossing in a diallel design is the effective and specific technique for the identification, measurement and selection of superior genotypes (Hussain *et al.*, 2022, Sreewongchai *et al.*, 2021). Selection could be successful in the early generations since the additive gene action is predominant and later on selection can be done once the acquired effects get fixed in the homozygous lines. Thus, it was hypothesized that genetic variance exist among rice genotypes and their crossing might produce rice hybrids having greater yield potential under DS. The present study aimed to estimate the general and specific combining ability effects, nature of gene action, heterotic effects in F₁ hybrids. Moreover, phenotypic correlation among physiological, and yield related traits was objectively performed in order to sort out the nature of relationship among these traits under water stress conditions.

Materials and Methods

Experiment details: The investigations were carried out during 2019 and 2020 rice growing seasons at the Rice Research and Training Center Farm, Sakha Research Station, Kafr El-Sheikh, Agricultural Research Center, Egypt. The station coordinates are 31° 05 N latitude and 30° 57 E longitude. For this tria, seven rice genotypes were selected and crossed in a half-diallel mating design (Method II, Model I excluded reciprocal (Table 1). A total of 21 hybrids along with parental genotypes were evaluated under DS (flush irrigation every twelve days) was imposed after 15 days from transplanting till harvesting date. In 2019 season, the rice genotypes were planted in three successive dates of planting at ten-day intervals in order to overcome the differences in flowering time among these parental genotypes. Thirty days old seedlings of every parent were individually transplanted

in five rows in the field. Every row was five meter long and contained twenty five hills. During flowering time, the crossing program with all possible combinations among the seven parental genotypes excluding reciprocals were carried out following the method suggested by Butany 1961. In 2020 season, 30 days old seedlings of 28 rice genotypes (7 parents plus 21 F₁'s) were transplanted in a randomized complete block design (RCBD) with three replications under DS conditions. Each replicate comprised 5 rows of each parent and F₁ hybrids. The rows were 5 m long and 20 x 20 cm apart were maintained between and within rows, and the plot size was 6 m². The meteorological features during the both crop seasons at Sakha research stations are given in Fig. 1.

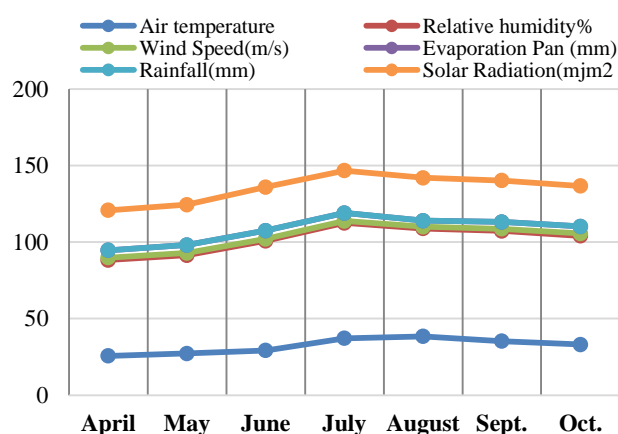


Fig. 1. Meteorological records of the studied area during growing seasons.

Physiological traits: The evaluation of stomata, diffusive conductance and the CO₂ rates and water vapor exchange are important parameters for estimating carbon (C) and water content of plants. A portable porometer “steady-state porometer, LICOR, LI-1600, Lincoln, NE, USA” is designated for assessing the steady-state CO₂ and H₂O exchange degrees of leaves. The entire porometer comprises an open gas exchange in its system that displays the variations in concentrations levels of CO₂ and H₂O incoming and exit a cuvette that is fixed on or around leaves. Data of leaf diffusive resistance (LDR) was determined through the equation: $LDR (s\ cm^{-1}) = (DR_{ad} \times DR_{ab}) / (DR_{ad} + DR_{ab})$. Here, DR_{ad} and DR_{ab} exemplify the diffusive resistance of the adaxial and abaxial surfaces, correspondingly (Schulze *et al.*, 1982). Stomatal conductance (SC) was measured in the fully expanded flag leaf. Net photosynthetic rate (NPR, A) used for the g_s models was estimated as follows: $A = A_{max} \times f(PAR)$, PAR in this equation was obtained from the on-site PAR measurements at which the measurements took location) in the morning, round noon and afternoon). Where, PAR is the photo-synthetically active radiation ($\mu mol\ m^{-2}\ s^{-1}$). CO₂ concentration (CO₂) was calculated. Leaf transpiration rate (LTR) was dignified directly on the same leaf. It signifies the sum of the rates for the adaxial and abaxial surfaces. Leaf temperature (LT) was determined by the thermocouple of the steady-state porometer pressed against the adaxial and abaxial surfaces of the leaf, and the leaf-to-air temperature gradient ($T_L - T_A$) was measured by using the atmospheric temperature. The cuvette temperature was

measured using Linearized thermistor at the ambient air temperature and the humidity around the leaf. This device might also be utilized to calculate the response of CO₂ curves in the field. Adaxial and abaxial diffusive resistances were determined on the upper fully expanded leaf with a steady-state porometer was collected during the measurement.

Morphological traits: The morphological traits were estimated using ten randomly selected plants from each replication for determination of leaf rolling (LR), days to heading (DTH), the number of panicles/plant (NPP), 100-grain weight (TGW), fertility percentage (FP) and grain yield/plant (GYP) were recorded at the time of harvest. Moreover, water use efficiency (WUE) was measured from the grain yield divided by the quantity of irrigation water applied in treatments.

Statistical analysis: The analysis of variance (ANOVA) was conducted for recorded data according to randomized complete block design (RCBD) with three replications (Steel *et al.*, 1997). The general combining ability and specific combining ability were calculated using model I and method II, where block and variety effects are fixed assumed and one set of the hybrids were used with the parents. All statistical analysis was performed using analysis of variance method by means of "Agrobase" computer software package. The means of treatment were compared by least significant differences at 5 percent probability level.

Results

The ANOVA indicated significant ($p \leq 0.01$) differences among genotypes, crosses, parents and parents \times crosses for all studied traits under DS conditions (Table 2). Both general (GCA) and specific (SCA) combining ability variances were found to be significant ($p \leq 0.01$) for all the studied characters. The GCA/SCA ratios were found to be less than unity for all studied traits, except CO₂ concentration and PAR which recorded higher ratios than unity values.

Mean performance: Mean values of the parental genotypes and the F₁ hybrids for the fourteen studied characters have been presented in Table 3. The mean performance of the studied traits varied from combination to other. The earliness was found with crosses Sakha104 \times Sakha108, IRAT112 \times Giza179 and IRAT112 \times Sakha108 as well as parent Sakha108 under water shortage conditions. For leaf diffusive resistance, the hybrids Azucena \times Giza177, Azucena \times Giza179, Sakha104 \times Giza179 and IRAT112 \times N22 remained superior under DS conditions. However, the genotypes IRAT112 \times N22, IRAT112 \times Azucena, N22 \times Azucena and N22 \times Sakha104 confirmed the decreased values for stomatal conductance. The crosses Azucena \times Giza177, Azucena \times Giza179, Sakha104 \times Giza179, and IRAT112 \times N22 reported improved leaf transpiration rates. Therefore, the lowest value for leaf temperature was found for Azucena \times Giza177, Azucena \times Giza179, Sakha104 \times Giza179, and IRAT112 \times N22. With respect to leaf rolling, the lowest rolling scores were recorded by

genotypes Azucena, IRAT112 × Azucena, IRAT112 × N22 and N22 × Azucena. Concerning the net photosynthetic rate, the genotypes Azucena × Giza177, Azucena × Giza179, Sakha104 × Giza179 and IRAT112 × N22 exhibited the maximum values. The genotypes Azucena × Giza177, Azucena × Giza179, Sakha104 × Giza179 and IRAT112 × N22 produced the superior value for CO₂ concentration. Regarding PAR, the highest value was obtained for the crosses Azucena × Giza177, Azucena × Giza179, Sakha104 × Giza179 and IRAT112 × N22. The hybrids Azucena × Giza179, Sakha104 × Giza179, N22 × Azucena and IRAT112 × Azucena recorded the maximum number of panicles per plant otherwise, the genotypes Azucena × Giza179, IRAT112 × N22, IRAT112, and N22 × Giza177 gave the heaviest mean values for 100-Grain weight. The best genotypes for fertility percentage were recorded by IRAT112 × Giza177, IRAT112 × Azucena, Giza177 × Sakha104 and Azucena × Giza179 whereas the crosses Azucena × Giza177, Azucena × Giza179, Sakha104 × Giza179, and IRAT112 × N22 exhibited the highest values for grain yield per plant. The highest mean values for WUE was recorded for genotypes Azucena × Giza177, Azucena × Sakha108, N22 × Sakha104, and Azucena × Giza179.

General combining ability effects (GCA): General combining ability effects were found significantly different for several traits under investigation (Table 4). The parents Sakha108, Giza177, Giza179 and Sakha104 showed significant ($p \leq 0.01$) and negative GCA effects for DTH and it is could be good general combiner for the said trait. While the parents N22, Azucena, Giza177 and Giza179 gave significant ($p \leq 0.01$) and positive GCA for LDR. The parents that exhibited significant ($p \leq 0.01$) and negative GCA effects was desirable and could be good general combiner for these traits so, the genotypes N22, Azucena and Giza179 were found as good general combiners for SC, Azucena, Giza177 and N22 for LTR, Azucena, Sakha104 and Giza179 for LT and Azucena, N22, IRAT 112 and Sakha104 for LR. Otherwise, the highly significant and positive values of GCA effects were desirable for the traits that have high contribution to yield. However, the genotype Azucena, Giza177 and N22 for NPR. Concerning the CO₂ concentration the genotypes N22, Azucena, Giza179, Giza177 and Sakha104 obtained high significant and positive GCA effects. Regarding PAR the three parents Azucena, N22 and Giza179 illustrated good combiners. The desired parent's performance for NPP, N22, Giza179, Azucena and IRAT 112 were observed highly significant and positive GCA effects. Regardless the HGW the parents N22, Giza179 and IRAT 112 showed highly significant and positive GCA effects The two parents N22 and Giza177 gave the GCA effects positive and highly significant for FP. Concerning the GYP the parents, N22 Azucena, Giza179 and Giza177 illustrated good combiner where the GCA had highly significant and positive effects. The parents N22, Azucena and Sakha108 exhibited highly significant and positive GCA effects for WUE.

Specific combining ability (SCA): Evaluations of SCA for the crosses are given in Table 4. For DTH, ten out of 21 hybrids showed negative and significant ($p \leq 0.01$) SCA

effects. Concerning LDR, ten crosses were found to be significant ($p \leq 0.01$) and positive SCA effects. Eleven out of 21 hybrids illustrated negative SCA effects and significant ($p \leq 0.01$) for SC and TR. For LT, the eight crosses i.e., Azucena × Giza177, Sakha104 × Giza179, Azucena × Giza179, IRAT 112 × N22, IRAT 112 × Azucena, N22 × Sakha108, Giza177 × Sakha108, and N22 × Giza179 revealed significant ($p \leq 0.01$, $p \leq 0.05$) and negative SCA effects. Fourteen out of 21 F1 hybrids were found to be significant ($p \leq 0.01$, $p \leq 0.05$) with negative SCA effects for LR. On the other hand, the positive and significant ($p \leq 0.01$) SCA effects were found with ten crosses for NPR. Eleven crosses out of 21 were recorded with significant ($p \leq 0.01$) and positive SCA effects for CO₂ concentration. Twelve out of 21 crosses showed highly significant and positive SCA for PAR. Concerning to NPP, fourteen crosses reported highly significant and positive SCA effects, otherwise the ten crosses were highly significant and positive SCA for HGW. With respect to fertility percentage, 12 crosses exhibited highly specific combing ability effects. Regardless, the grain yield /plant twelve crosses out twenty one had confirmed highly significant and positive SCA effects. Eleven crosses were observed highly significant and positive SCA effects for WUE.

Heterosis: Estimates of heterosis relative to mid and the better parent for all the studied traits under drought conditions are presented in Table 5. Favorable heterosis and heterobeltiosis in the studied crosses was considered negative and positive direction for studied traits. Fore days to heading the negative and significant heterosis over mid and better parent were found in nine and thirteen crosses, respectively. For diffusive resistance, 13 and 14 crosses out of 21 hybrids showed significant ($p \leq 0.01$) and positive heterosis over mid parent and better parents, respectively. Consequently, the 12 hybrid combinations were found to be significant ($p \leq 0.01$) and negative heterosis and heterobeltiosis for stomatal conductance, respectively. With respect to LTR, twelve and thirteen hybrids had shown significant ($p \leq 0.01$) and negative heterosis and heterobeltiosis, respectively. Eleven crosses demonstrated significant ($p \leq 0.01$) and negative heterosis over mid and better parents for LT. Sixteen and seventeen cross combinations were found with significant ($p \leq 0.01$) and negative heterosis related to mid and better parents for LR. Regardless, net photosynthetic rate thirteen and fourteen hybrid combinations found to be highly significant and positive heterosis over mid-parent and better parent thus, the twelve crosses out from twenty one illustrated positive and highly significant heterosis over mid-parent and better parent heterosis for CO₂ concentration. Therefore, there are non-crosses found for PAR significant over mid and better parent. Highly significant and positive heterosis were found with eighteen and twenty crosses for number of panicles/plant, eight and ten crosses for 100-grain weight, twelve crosses for fertility percentage, thirteen and fourteen crosses for grain yield per plant for over mid-parent and better parent heterosis, respectively. With respect to WUE, fifteen and sixteen crosses had shown highly significant and positive heterosis over mid and better parent.

Table 2. Mean squares analysis of variances and combining ability analysis for yield attributes and grain yield of rice genotypes.

S.O.V.	d.f.	Days to heading	Leaf diffusive resistance (s cm-1)	SC (cm s-1)	Leaf transpiration rate (µg cm-2 s-1)	Leaf temperature (°C)	Leaf rolling	Net photosynthetic rate
Replications	2	4.92	0.15	0.000002	0.88	0.47	0.01	0.07
Genotypes	27	769.04**	14.00**	0.0002**	75.10**	2.10**	8.84**	86.2**
F1	20	785.83**	17.69**	0.0003**	93.71**	2.64**	9.75**	112.4**
Parents	6	816.26**	0.35**	0.0001**	6.36**	0.32**	6.96**	1.33**
P vs F1	1	149.89**	21.96**	0.0004**	115.3**	2.11**	1.81**	72.2**
Error	54	2.46	0.07	0.000001	0.49	0.25	0.01	0.04
G.C.A	6	807.74**	4.47**	0.00005**	14.4**	0.61**	6.27**	20.64
S.C.A	21	98.81**	4.72**	0.00009**	28.06**	0.73**	2.00**	31.08**
GCA/SCA		0.82	0.02	0.0000001	0.16	0.08	0.003	0.01
Error	54	0.92	0.11	0.064583	0.06	0.09	0.35	0.07
Total	83							

Table 2. (Cont'd.).

S.O.V.	d.f.	CO2	Photosynthetically active radiation (µmol s-1 m-2)	Number of panicles per plant	1000 grains weight (g)	Fertility percentage (%)	Grain yield per plant (g)	Water use efficiency UE
Replications	2	38.68	9881.06	0.18	0.00	6.57	0.91	0.0004
Genotypes	27	10292.47**	1404046.3**	42.2**	0.33**	2359.9**	649.9**	0.34**
F1	20	13035.4**	1764248.1**	37.34**	0.40**	3009.1**	831.3**	0.42**
Parents	6	986.5**	96133.1**	20.68	0.13**	372.9**	38.01**	0.04**
P vs F1	1	11268.0**	2047489.7**	269.9**	0.16**	1298.1**	692.7**	0.67**
Error	54	15.66	4080.55	0.07	0.002	1.94	0.27	0.0003
G.C.A	6	1983.4**	355262.2**	13.3**	0.04**	921.9**	178.1**	0.05**
S.C.A	21	3844.3**	500230.6**	14.2**	0.13**	747.9**	227.6**	0.13**
GCA/SCA		5.22	1360.18	0.02	0.001	0.65	0.09	0.0001
Error	54	0.06	0.08	0.10	0.03	0.14	0.09	0.04
Total	83							

** is high significant at probability 0.01

Table 3. The genotypes mean performances under water deficit for studied characters.

Genotypes	Days to heading	Leaf diffusive resistance (s cm-1)	SC (cm s-1)	Leaf transpiration rate ($\mu\text{g cm}^{-2} \text{s}^{-1}$)	Leaf temperature ($^{\circ}\text{C}$)	Leaf rolling	Net photosynthetic rate
IRAT112	119.82	15.71	0.06	41.89	30.29	2.04	11.72
IRAT112×N22	103.07	19.15	0.05	35.42	28.90	1.00	15.51
IRAT112×Azucena	128.70	18.36	0.05	37.50	29.10	0.99	14.04
IRAT112×Giza177	89.90	15.63	0.07	44.47	30.79	7.32	10.78
IRAT 112×Sakha104	86.64	13.84	0.07	43.61	29.90	2.92	8.99
IRAT112×Giza179	81.69	15.15	0.07	44.14	30.60	5.23	10.51
IRAT112×Sakha108	86.35	13.04	0.07	43.88	30.49	2.91	8.94
N22	117.06	15.39	0.07	43.74	30.30	4.10	11.32
N22 × Azucena	133.00	18.20	0.05	38.20	29.38	1.00	13.48
N22 × Giza177	95.88	15.81	0.06	38.94	29.68	4.08	12.36
N22 × Sakha104	95.36	18.16	0.05	37.67	29.21	1.00	13.77
N22 × Giza179	102.27	18.30	0.05	37.65	29.11	3.93	13.94
N22 × Sakha108	103.91	15.69	0.06	38.22	29.31	2.94	12.69
Azucena	122.67	14.65	0.07	42.94	29.80	0.98	10.03
Azucena × Giza177	108.53	22.10	0.05	20.33	27.60	2.96	37.80
Azucena × Sakha104	125.62	14.89	0.07	43.17	29.90	3.99	11.14
Azucena × Giza179	105.00	19.42	0.05	34.07	27.80	1.00	17.68
Azucena × Sakha108	118.46	14.15	0.07	44.07	30.21	2.95	9.19
Giza177	91.50	15.21	0.07	42.77	29.82	5.08	11.29
Giza177 × Sakha104	90.60	16.02	0.06	38.51	29.60	4.06	13.30
Giza177 × Giza179	90.57	14.27	0.07	42.87	29.60	5.97	9.82
Giza177 × Sakha108	92.00	16.18	0.06	38.20	29.40	4.00	13.27
Sakha104	98.29	15.20	0.07	42.21	29.53	3.88	11.29
Sakha104 × Giza179	105.07	19.41	0.05	35.29	27.86	1.00	16.34
Sakha104 × Sakha108	69.59	15.19	0.07	41.21	29.50	4.90	11.35
Giza179	90.00	15.60	0.06	39.67	29.70	4.00	12.20
Giza179 × Sakha108	87.00	12.99	0.08	46.36	31.19	4.00	8.27
Sakha108	81.99	15.29	0.06	40.33	29.50	5.00	11.55
LSD 0.05	2.56	0.42	0.0018	1.15	0.81	0.15	0.33
LSD 0.01	3.42	0.56	0.0025	1.53	1.09	0.20	0.44

Table 3. (Cont'd.).

Genotypes	CO ₂	Photosynthetically active radiation ($\mu\text{mol s}^{-1} \text{m}^{-2}$)	Number of panicles per plant	1000 grains weight (g)	Fertility percentage (%)	Grain yield per plant (g)	Water use efficiency
IRAT112	254.17	3965.00	13.44	3.07	89.92	32.05	0.87
IRAT112×N22	346.67	4981.67	17.00	3.18	92.40	55.00	1.30
IRAT112×Azucena	304.62	4900.00	20.00	2.20	94.85	54.00	1.12
IRAT112×Giza177	227.05	3730.30	18.01	2.67	99.95	28.61	0.84
IRAT 112×Sakha104	198.62	3354.67	12.66	2.14	18.50	13.39	0.40
IRAT112×Giza179	214.74	3672.00	13.53	2.76	16.65	27.05	1.34
IRAT112×Sakha108	171.16	3157.33	13.63	2.17	16.55	12.66	1.40
N22	228.05	3749.33	16.43	2.68	91.39	28.75	0.86
N22 × Azucena	283.58	4692.00	21.00	2.54	85.00	46.00	1.09
N22 × Giza177	266.54	4037.85	17.00	2.92	91.87	35.00	1.07
N22 × Sakha104	287.82	4720.21	17.88	2.54	93.38	49.66	1.50
N22 × Giza179	300.77	4752.00	17.00	2.53	92.12	54.00	1.35
N22 × Sakha108	266.13	4062.27	12.74	2.38	86.27	36.28	1.09
Azucena	207.77	3511.20	8.82	2.38	62.73	22.40	0.66
Azucena × Giza177	397.16	5600.00	19.00	2.25	80.13	59.00	1.62
Azucena × Sakha104	224.36	3666.12	16.00	2.44	54.00	28.00	0.84
Azucena × Giza179	365.92	5525.33	23.00	3.47	94.00	58.00	1.44
Azucena × Sakha108	202.69	3389.80	8.94	2.34	21.86	13.92	1.62
Giza177	227.35	3800.00	9.00	2.70	87.00	30.00	0.92
Giza177 × Sakha104	271.22	4185.72	13.18	2.62	94.75	37.50	1.13
Giza177 × Giza179	202.91	3441.67	14.50	1.89	85.58	19.34	0.60
Giza177 × Sakha108	280.93	4186.00	14.00	2.74	87.96	40.00	1.20
Sakha104	244.32	3826.18	12.76	2.64	68.72	30.44	0.90
Sakha104 × Giza179	361.23	5168.77	22.02	2.78	91.62	57.08	0.74
Sakha104 × Sakha108	245.23	3861.00	13.72	2.66	88.70	31.04	0.93
Giza179	256.58	4031.67	12.00	2.57	79.00	33.20	1.00
Giza179 × Sakha108	153.85	3100.00	15.00	2.77	20.00	9.00	0.27
Sakha108	252.26	3987.64	11.84	2.68	86.83	31.58	0.96
LSD 0.05	6.46	104.31	0.43	0.07	2.27	0.85	0.03
LSD 0.01	8.63	139.26	0.58	0.09	3.03	1.14	0.04

Table 4. General combining ability for traits studied under water deficit conditions.

GCA effects	Days to heading	Leaf diffusive resistance (s cm-1)	SC (cm s-1)	Leaf transpiration rate (µg cm-2 s-1)	Leaf temperature (°C)	Leaf rolling	Net photosynthetic rate
IRAT 112	1.13**	-0.32**	0.001**	1.51**	0.42**	-0.24**	-1.27**
N22	6.86**	0.74**	-0.004**	-0.63**	-0.04	-0.50**	0.09**
Azucena	17.64**	0.78**	-0.002**	-1.78**	-0.33**	-1.31**	2.20**
Gizal77	-6.15**	0.11**	0.002**	-1.15**	-0.03	1.32**	1.81**
Sakha104	-4.05**	-0.17**	0.001**	0.52**	-0.17**	-0.11**	-0.68**
Gizal79	-6.03**	0.15**	-0.001**	0.05	-0.11*	0.28**	-0.29**
Sakha108	-9.40**	-1.29**	0.003**	1.48**	0.28**	0.56**	-1.86**
LSD 0.05 (gi)	0.28	0.05	0.0002	0.13	0.09	0.02	0.04
LSD 0.01 (gi)	0.43	0.07	0.0003	0.19	0.14	0.03	0.05
LSD 0.05 (gi - gj)	0.56	0.09	0.0004	0.25	0.18	0.03	0.07
LSD 0.01 (gi - gj)	0.75	0.12	0.001	0.33	0.24	0.04	0.10

(Table 4. Cont'd.).

GCA effects	CO2	Photosynthetically active radiation (µmol s-1 m-2)	Number of panicles per plant	1000 grains weight (g)	Fertility percentage (%)	Grain yield per plant (g)	Water use efficiency
IRAT 112	-10.94**	-127.45**	0.06*	0.05**	-8.13**	-2.58**	-0.02**
N22	15.33**	207.96**	1.59**	0.07**	14.66**	6.16**	0.09**
Azucena	13.81**	213.62**	0.49**	-0.09**	-4.07**	2.86**	0.08**
Gizal77	3.43**	-10.17	-0.83**	-0.03**	13.59**	0.16**	-0.0004
Sakha104	0.83*	-29.36**	-0.02	-0.04**	-1.50**	-0.05	-0.11**
Gizal79	4.77**	94.45**	0.88**	0.06**	-3.77**	1.43**	-0.06**
Sakha108	-27.24**	-349.04**	-2.16**	-0.04**	-10.77**	-7.99**	0.01**
LSD 0.05 (gi)	0.71	11.38	0.05	0.01	0.25	0.09	0.003
LSD 0.01 (gi)	1.08	17.39	0.07	0.012	0.38	0.14	0.005
LSD 0.05 (gi - gj)	1.41	22.82	0.09	0.02	0.50	0.19	0.01
LSD 0.01 (gi - gj)	1.88	30.39	0.13	0.02	0.66	0.25	0.01

*, ** is significant and high significant at probability 0.05 and 0.01, respectively

Table 4. Specific combining ability estimated for studied traits under drought conditions.

SCA effects	Days to heading	Leaf diffusive resistance (s cm-1)	SC (cm s-1)	Leaf transpiration rate (µg cm-2 s-1)	Leaf temperature (°C)	Leaf rolling	Net photosynthetic rate
IRAT 112 × N22	-5.65**	2.55**	-0.009**	-5.36**	-1.05**	-1.59**	3.74**
IRAT 112 × Azucena	9.20**	1.72**	-0.011**	-2.13**	-0.56**	-0.79**	0.16**
IRAT 112 × Giza177	-5.80**	-0.35**	0.008**	4.21**	0.83**	2.91**	-2.72**
IRAT 112 × Sakha104	-11.1**	-1.85**	0.005**	1.68**	0.08	-0.06**	-2.01**
IRAT 112 × Giza179	-14.1**	-0.86**	0.009**	2.67**	0.72**	1.87**	-0.89**
IRAT 112 × Sakha108	-6.11**	-1.53**	0.003**	0.98**	0.22*	-0.74**	-0.88**
N22 × Azucena	7.76**	0.50**	-0.006**	0.70**	0.18	-0.52**	-1.76**
N22 × Giza177	-5.56**	-1.22**	0.0001	0.82**	0.18	-0.07**	-2.49**
N22 × Sakha104	-8.19**	1.41**	-0.009**	-2.12**	-0.14	-1.72**	1.42**
N22 × Giza179	0.71*	1.23**	-0.007**	-1.68**	-0.30**	0.82**	1.19**
N22 × Sakha108	5.72**	0.06	-0.002**	-2.54**	-0.50**	-0.45**	1.52**
Azucena × Giza177	-3.69**	5.03**	-0.012**	-16.6**	-1.61**	-0.38**	20.84**
Azucena × Sakha104	11.29**	-1.90**	0.009**	4.53**	0.83**	2.08**	-3.33**
Azucena × Giza179	-7.35**	2.32**	-0.009**	-4.11**	-1.33**	-1.30**	2.82**
Azucena × Sakha108	9.48**	-1.52**	0.006**	4.46**	0.69**	0.37**	-4.09**
Giza177 × Sakha104	0.07	-0.10	-0.004**	-0.76**	0.23*	-0.48**	-0.78**
Giza177 × Giza179	2.02**	-2.17**	0.006**	4.07**	0.17	1.04**	-4.65**
Giza177 × Sakha108	6.82**	1.18**	-0.007**	-2.04**	-0.42**	-1.21**	0.37**
Sakha104 × Giza179	14.41**	3.26**	-0.012**	-5.18**	-1.43**	-2.49**	4.37**
Sakha104 × Sakha108	-17.7**	0.47**	0.003**	-0.69**	-0.18	1.12**	0.94**
Giza179 × Sakha108	1.69**	-2.04**	0.015**	4.92**	1.45**	-0.17**	-2.52**
LSD 0.05 (Sii)	0.69	0.11	0.0005	0.31	0.22	0.04	0.09
LSD 0.01 (Sii)	0.81	0.13	0.001	0.36	0.26	0.05	0.10
LSD 0.05 (Sij)	0.95	0.16	0.001	0.43	0.30	0.06	0.12
LSD 0.01 (Sij)	1.21	0.20	0.0009	0.54	0.38	0.07	0.15

Table 4. (Cont'd.).

SCA Effects	CO ₂	Photosynthetically active radiation ($\mu\text{mol s}^{-1} \text{m}^{-2}$)	Number of panicles per plant	1000 grains weight (g)	Fertility percentage (%)	Grain yield per plant (g)	Water use efficiency
IRAT 112 × N22	83.57**	792.0**	0.21**	0.45**	11.89**	16.67**	0.19**
IRAT 112 × Azucena	43.05**	704.7**	4.30**	-0.36**	33.06**	18.97	0.02
IRAT 112 × Giza177	-24.1**	-241.2**	3.64**	0.05**	20.50	-3.73**	-0.18**
IRAT 112 × Sakha104	-49.9**	-597.6**	-2.53**	-0.47**	-45.86**	-18.73**	-0.51**
IRAT 112 × Giza179	-37.8**	-404.1**	-2.56**	0.05**	-45.44**	-6.55**	0.38**
IRAT 112 × Sakha108	-49.3**	-475.3**	0.58**	-0.44**	-38.54**	-11.52**	0.37**
N22 × Azucena	-4.26**	161.2**	3.77**	-0.04**	0.42	2.23**	-0.12**
N22 × Giza177	-10.9**	-269.0**	1.10**	0.28**	-10.37**	-6.07**	-0.06**
N22 × Sakha104	12.9**	432.4**	1.17**	-0.09**	6.23**	8.80**	0.47**
N22 × Giza179	21.9**	340.4**	-0.61**	-0.20**	7.25**	11.66**	0.28**
N22 × Sakha108	19.3**	94.2**	-1.83**	-0.26**	8.39**	3.36**	-0.05**
Azucena × Giza177	121.2**	1287**	4.19**	-0.23**	-3.38**	21.23**	0.50**
Azucena × Sakha104	-48.9**	-627.2**	0.38**	-0.04**	-14.42**	-9.56**	-0.17**
Azucena × Giza179	88.6**	1108**	6.49**	0.90	27.85**	18.96**	0.38**
Azucena × Sakha108	-42.5**	-583.9**	-4.53**	-0.13**	-37.29**	-15.70**	0.48**
Giza177 × Sakha104	8.2**	116.1**	-1.12**	0.09**	8.67**	2.64**	0.20**
Giza177 × Giza179	-64.0**	-751.7**	-0.69**	-0.74**	1.77**	-17.00**	-0.37**
Giza177 × Sakha108	46.0**	436.1**	1.85**	0.21**	11.15**	13.08**	0.15**
Sakha104 × Giza179	96.9**	994.5**	6.02**	0.16**	22.91**	20.95**	-0.13**
Sakha104 × Sakha108	12.9**	130.2**	0.76**	0.14**	26.99**	4.33**	-0.01*
Giza179 × Sakha108	-82.3**	-754.5**	1.14**	0.15**	-39.45**	-19.19**	-0.72**
LSD 0.05 (Sii)	1.75	28.17	0.12	0.02	0.61	0.23	0.01
LSD 0.01 (Sii)	2.05	33.10	0.14	0.02	0.72	0.27	0.01
LSD 0.05 (Sij)	2.41	38.88	0.16	0.03	0.85	0.32	0.01
LSD 0.01 (Sij)	3.05	49.17	0.20	0.03	1.07	0.40	0.01

*, ** is significant and high significant at probability 0.05 and 0.01, respectively

Table 5. Estimates of heterosis relative to mid-parent and better parent for all the studied traits under stress conditions.

Heterosis MP	Days to heading	Leaf diffusive resistance (s cm ⁻¹)	SC (cm s ⁻¹)	Leaf transpiration rate (µg cm ⁻² s ⁻¹)	Leaf temperature (°C)	Leaf rolling	Net photosynthetic rate
IRAT 112 × N22	-12.98**	23.15**	-24.20**	-17.26**	-4.60**	-67.47**	34.63**
IRAT 112 × Azucena	6.15**	20.95**	-23.25**	-11.58**	-3.14**	-34.52**	29.10**
IRAT 112 × Giza177	-14.92**	1.08**	10.01**	5.05**	2.44**	105.48**	-6.34**
IRAT 112 × Sakha104	-20.56**	-10.42**	5.96**	3.72**	-0.04	-1.46**	-21.87**
IRAT 112 × Giza179	-22.13**	-3.24**	18.02**	8.23**	2.02**	73.16**	-12.17**
IRAT 112 × Sakha108	-14.42**	-15.83**	14.54**	6.74**	1.99**	-17.31**	-23.19**
N22 × Azucena	10.96**	21.15**	-28.69**	-11.85**	-2.23**	-60.66**	26.29**
N22 × Giza177	-8.06**	3.32**	-14.85**	-9.97**	-1.26**	-11.15**	9.34**
N22 × Sakha104	-11.44**	18.72**	-28.96**	-12.33**	-2.34**	-75.05**	21.87**
N22 × Giza179	-1.22	18.09**	-23.63**	-9.72**	-2.96**	-3.01**	18.54**
N22 × Sakha108	4.41**	2.31**	-8.98**	-9.07**	-1.98**	-35.37**	11.00**
Azucena × Giza177	1.35	48.01**	-28.21**	-52.56**	-7.41**	-2.31**	254.62**
Azucena × Sakha104	13.70**	-0.24	0.97**	1.40*	0.80	64.06**	4.53**
Azucena × Giza179	-1.26	28.39**	-22.66**	-17.51**	-6.55**	-59.84**	59.07**
Azucena × Sakha108	15.77**	-5.49**	8.29**	5.85**	1.88**	-1.24**	-14.81**
Giza177 × Sakha104	-4.53**	5.34**	-13.32**	-9.38**	-0.26	-9.49**	17.81**
Giza177 × Giza179	-0.19	-7.38**	5.90**	4.01**	-0.54	31.47**	-16.36**
Giza177 × Sakha108	6.06**	6.11**	-7.41**	-8.06**	-0.88*	-20.61**	16.19**
Sakha104 × Giza179	11.60**	26.06**	-22.64**	-13.79**	-5.93**	-74.62**	39.16**
Sakha104 × Sakha108	-22.80**	-0.37	7.48**	-0.14	-0.04	10.36**	-0.65**
Giza179 × Sakha108	1.17	-15.89	33.78**	15.90**	5.37**	-11.08**	-30.37**
LSD 0.05	2.71	0.45	0.002	1.21	0.86	0.16	0.35
LSD 0.01	4.11	0.68	0.003	1.84	1.31	0.25	0.53
Heterosis BP	DITH	LDR (s cm ⁻¹)	SC (cm s ⁻¹)	LTR (µg cm ⁻² s ⁻¹)	LT (°C)	LR	NPR
IRAT 112 × N22	-13.98**	24.41**	-29.51**	-19.01**	-4.62*	-75.63**	37.03**
IRAT 112 × Azucena	4.91*	25.31**	-27.85**	-12.66**	-3.92**	-51.55**	40.00**
IRAT 112 × Giza177	-24.97**	2.73**	2.93**	3.97**	1.65	44.07**	-4.54**
IRAT 112 × Sakha104	-27.69**	-8.93**	-0.42**	3.32*	-1.29	-24.81**	-20.35**
IRAT 112 × Giza179	-31.82**	-2.90**	17.05**	5.37**	1.04	30.82**	-10.37**
IRAT 112 × Sakha108	-27.93**	-14.68**	13.22**	4.75**	0.67	-41.75**	-22.62**
N22 × Azucena	8.42**	24.22**	-29.51**	-12.66**	-3.03**	-75.63**	34.41**
N22 × Giza177	-18.09**	3.94**	-15.41**	-10.96**	-2.04	-19.69**	9.48**
N22 × Sakha104	-18.54**	19.47**	-29.75**	-13.86**	-3.59**	-75.71**	22.05**
N22 × Giza179	-12.63**	18.89**	-29.51**	-13.91**	-3.92**	-4.24**	23.16**
N22 × Sakha108	-11.23**	2.66**	-16.23**	-12.61**	-3.27**	-41.14**	12.14**
Azucena × Giza177	-11.53**	50.83**	-28.57**	-52.65**	-7.44**	-41.73**	276.92**
Azucena × Sakha104	2.40	1.62**	0.92**	0.54	0.34	2.73**	11.08**
Azucena × Giza179	-14.41**	32.54**	-27.85**	-20.65**	-6.71**	-75.00**	76.29**
Azucena × Sakha108	-3.43	-3.44**	0.71**	2.63	1.38*	-40.94**	-8.34**
Giza177 × Sakha104	-7.83**	5.37**	-13.71**	-9.97**	-0.75	-20.14**	17.83**
Giza177 × Giza179	-1.01	-6.19**	-1.67**	0.24	-0.74	17.50**	-12.99**
Giza177 × Sakha108	0.55	6.38**	-14.29**	-10.69**	-1.41*	-21.26**	17.54**
Sakha104 × Giza179	6.90*	27.72**	-27.86**	-16.39**	-6.20**	-74.98**	44.79**
Sakha104 × Sakha108	-29.20**	-0.09	-0.09**	-2.36	-0.09	-1.92**	0.53*
Giza179 × Sakha108	-3.33	-15.03**	33.33**	14.95**	5.02**	-19.94**	-28.41**
LSD 0.05	4.07	0.67	0.003	1.82	1.30	0.24	0.52
LSD 0.01	7.48	1.24	0.005	3.35	2.38	0.45	0.96

Table 5. (Cont'd.).

Heterosis MP	CO ₂	Photosynthetically active radiation ($\mu\text{mol s}^{-1} \text{m}^{-2}$)	Number of panicles per plant	1000 grains weight (g)	Fertility percentage (%)	Grain yield per plant (g)	Water use efficiency
IRAT 112 × N22	43.78**	29.15	13.84**	10.69**	1.92	80.94**	49.80**
IRAT 112 × Azucena	31.89**	31.08	79.68**	-19.21**	24.27**	98.35**	45.68**
IRAT 112 × Giza177	-5.69**	-3.92	60.54**	-7.60**	12.98**	-7.79**	-5.92**
IRAT 112 × Sakhal04	-20.31**	-13.89	-3.38**	-24.95**	-76.68**	-57.14**	-54.44**
IRAT 112 × Giza179	-15.91**	-8.16	6.33**	-1.98**	-80.29**	-17.08**	42.58**
IRAT 112 × Sakhal08	-32.41**	-20.60	7.80**	-24.53**	-81.28**	-60.21**	52.47**
N22 × Azucena	30.14**	29.25	66.36**	0.57**	10.30**	79.86**	42.99**
N22 × Giza177	17.06**	6.97	33.72**	8.65**	3.00**	19.15**	20.13**
N22 × Sakha104	21.86**	24.62	22.52**	-4.29**	16.64**	67.82**	69.60**
N22 × Giza179	24.12**	22.14	19.61**	-3.53**	8.13**	74.34**	45.06**
N22 × Sakha108	10.82**	5.01	-9.84**	-11.28**	-3.19*	20.27**	19.37**
Azucena × Giza177	82.55**	53.19	113.23**	-11.35**	7.04**	125.17**	104.64**
Azucena × Sakha104	-0.75	-0.07	48.27**	-2.63**	-17.84**	5.98**	7.35**
Azucena × Giza179	57.60**	46.50	120.93**	40.32**	32.65**	108.62**	73.15**
Azucena × Sakha108	-11.88**	-9.59	-13.43**	-7.36**	-70.76**	-48.43**	98.56**
Giza177 × Sakha104	15.00**	9.77	21.10**	-1.89**	21.69**	24.09**	23.78**
Giza177 × Giza179	-16.14**	-12.11	38.13**	-28.35**	3.11*	-38.79**	-37.52**
Giza177 × Sakha108	17.15**	7.50	34.35**	1.82**	1.20	29.92**	27.42**
Sakha104 × Giza179	44.23**	31.56	77.89**	6.88**	24.04**	79.38**	-22.12**
Sakha104 × Sakha108	-1.23	-1.18	11.54**	0.16**	14.05**	0.09	-0.21**
Giza179 × Sakha108	-39.53**	-22.69	25.84**	5.48**	-75.88**	-72.21**	-72.50**
LSD 0.05	6.85	110.53	0.46	0.07	2.41	0.90	0.03
LSD 0.01	10.37	167.44	0.69	0.11	3.65	1.37	0.04
Heterosis BP	CO ₂	PAR ($\mu\text{mol s}^{-1} \text{m}^{-2}$)	NPP	HGW (g)	FP (%)	GYP (g)	WUE
IRAT 112 × N22	52.01**	32.87	26.48**	18.87**	2.75	91.32**	50.93**
IRAT 112 × Azucena	46.61**	39.55	126.73**	-7.41**	51.2**	141.03**	68.85**
IRAT 112 × Giza177	-0.13	-1.83	100.15**	-1.26**	14.88**	-4.65**	-3.46**
IRAT 112 × Sakha104	-18.71*	-12.32	-0.81*	-18.76**	-73.08**	-56.01**	-53.73**
IRAT 112 × Giza179	-15.51*	-7.39	12.71**	7.56**	-78.93**	-15.59**	52.83**
IRAT 112 × Sakha108	-32.15**	-20.37	15.08**	-19.07**	-80.94**	-59.91**	60.24**
N22 × Azucena	36.49**	33.63	138.07**	6.90**	35.51**	105.32**	64.33**
N22 × Giza177	17.24*	7.70	88.89**	9.15**	5.60*	21.75**	24.23**
N22 × Sakha104	26.21**	25.89	40.10**	-3.57**	35.87**	72.75**	73.57**
N22 × Giza179	31.89**	26.74	41.67**	-1.56**	16.61**	87.84**	56.73**
N22 × Sakha108	16.70*	8.35	7.62**	-11.17**	-0.64	26.19**	26.45**
Azucena × Giza177	9.15**	59.49	115.40**	-5.30**	27.75**	163.35**	144.23**
Azucena × Sakha104	7.98	4.41	81.39**	2.69**	-13.91**	24.98**	26.64**
Azucena × Giza179	76.12**	57.36	160.74**	46.04**	49.86**	158.89**	117.10**
Azucena × Sakha108	-2.45	-3.46	1.39**	-1.39**	-65.14**	-37.88**	143.50**
Giza177 × Sakha104	19.29**	10.15	46.41**	-0.69**	37.86**	24.99**	25.04**
Giza177 × Giza179	-10.75*	-9.43	61.16**	-26.54**	8.33**	-35.53**	-34.80**
Giza177 × Sakha108	23.57**	10.16	55.56**	2.16**	1.30	33.33**	30.43**
Sakha104 × Giza179	47.85**	35.09	83.54**	8.24**	33.32**	87.52**	-17.88**
Sakha104 × Sakha108	0.37	0.91	15.88**	1.04**	29.07**	1.96	3.21**
Giza179 × Sakha108	-39.01**	-22.26	26.68**	7.78**	-74.68**	-71.50**	-71.98**
LSD 0.05	10.28	165.96	0.69	0.11	3.61	1.36	0.04
LSD 0.01	18.87	304.65	1.26	0.21	6.64	2.49	0.08

*, ** is significant and high significant at probability 0.05 and 0.01, respectively

Table 6. Correlation coefficient determined between studied traits under water stress.

	DTH	LDR	SC	LTR	LT	LR	NPR	CO ₂	PAR	NPP	HGW	FP	GYP
LDR	0.33*												
SC	-0.33*	-0.88**											
LTR	-0.19	-0.90**	0.78**										
LT	-0.20	-0.85**	0.81**	0.87**									
LR	-0.59**	-0.49**	0.62**	0.39*	0.50**								
NPR	0.19	0.82**	-0.59**	-0.95**	-0.74**	-0.25							
CO ₂	0.26	0.96**	-0.89**	-0.90**	-0.91**	-0.47**	0.79**						
PAR	0.30	0.98**	-0.91**	-0.87**	-0.89**	-0.53**	0.76**	0.98**					
NPP	0.28	0.71**	-0.62**	-0.52**	-0.55**	-0.36*	0.46**	0.66**	0.73**				
HGW	-0.05	0.28	-0.22	-0.10	-0.15	-0.16	0.04	0.37*	0.36*	0.28			
FP	0.15	0.57**	-0.58**	-0.45**	-0.51**	-0.06	0.33*	0.63**	0.61**	0.41*	0.32		
GYP	0.29	0.95**	-0.91**	-0.81**	-0.83**	-0.47**	0.68**	0.96**	0.98**	0.70**	0.37*	0.69**	
WUE	0.12	0.51**	-0.53**	-0.53**	-0.40*	-0.25	0.47**	0.50**	0.51**	0.19	0.13	0.12	0.50**

*and ** is significant and high significant at 0.05 and 0.01 probability, respectively

Correlation: The correlation coefficient analysis exhibited that DTH had positive and significant ($p \leq 0.05$) correlation with LDR, while negative correlation with SC and LR (Table 6). In addition, negative correlation was also found between LDR and SC, LTR, LT and LR, while linear association was found with NPR, CO₂, PAR, NPP, FP, GYP and WUE. Likewise, SC had significantly positive correlation with LTR, LT and LR, while in contradiction, negative correlation was found with NPR, CO₂, PAR, NPP, FP, GYP and WUE. Moreover, LTR had significantly direct correlation with LT and LR, however it was negatively associated with NPR, CO₂, PAR, NPP, FP, GYP and WUE. Furthermore, LT remained positively correlated with LR along with having indirect association with NPR, CO₂, PAR, NPP, FP, GYP and WUE. Similarly, LR recorded positive association with CO₂, PAR, NPP and GYP. The highly significant and positive correlation was found among NPR and CO₂, PAR, NPP, FP, GYP and WUE. The CO₂ had highly significant and positive correlation with PAR, NPP, HGW, FP, GYP and WUE. Therefore the PAR had positive and highly significant correlation with NPP, HGW, FP, GYP and WUE. For NPP had significant and positive correlation was found with FP and significant ($p \leq 0.01$) correlation with GYP. The significant correlation and positive association was found among HGW and GYP. The FP had highly significant and positive correlation with GYP. For grain yield per plant, significant ($p \leq 0.01$) and positive correlation were found with LDR, NPR, CO₂, PAR, NPP, HGW and FP, however, negative correlation of FP was shown with SC, LTR, LT, and LR.

Discussion

The recorded findings proved in line with the postulated hypothesis as significant variation was recorded among rice parents and their hybrids in terms of all response variables under investigation. The existence of variability has been previously attributed to difference in genetic architecture of parents and crosses (Faysal *et al.*, 2022, Kandel *et al.*, 2022, Cheng *et al.*, 2009). Thus, selected genotypes might be evaluated further for genetic improvement to boost grain yield and other physiological traits under DS. The significant P vs. C for all traits might be attributed to heterosis that might be exploited for improving the desired traits under water shortage. These findings are in concurrence with those of previous investigations which have emphasized the need of exploiting genetic variation for breeding drought tolerant varieties of rice (Hussain *et al.*, 2022, Li *et al.*, 2022, Islam *et al.*, 2021, Wang *et al.*, 2018). In this study, parents NERICA2 and NERICA15 remained superior in terms of drought tolerance and paddy yield under DS conditions. The GCA estimates in both parents remained positive for spikelet fertility and grain yields while it was negative for leaf drying and rolling. This response might be attributed to the involvement of both additive and non-additive gene action for the expression of traits under investigation. The ratio of GCA to SCA ratio was used to explain the nature of gene action which exhibited less than unity in all studied traits, except CO₂ and PAR characteristics indicating non-additive types of gene actions played vital role in the inheritance of all studied characters, so, the selection based on the accumulation of non-additive effect might be used for

improving desired traits in the late generation. In addition to the additive gene action playing important role in inheritance, these two traits and selection could be effective in early generations. Similar to our results, Malemba *et al.*, (2017) revealed that drought tolerance traits such as spikelets fertility, grain yield, thousand grain weight and number of panicles/plant were governed by non-additive genes. Hybridization then selection in later generations would be recommended for improvement of traits governed by non-additive gene actions. The higher contribution of GCA variance (fixable genetic components) displayed the significant influence of non-additive gene action for traits like stomatal conductance, net photosynthetic rate, CO₂ concentration, leaf temperature and fertility percentage in drought conditions respectively. The pedigree breeding with simple selection are sufficient to develop traits governed by additive gene actions (Malemba *et al.*, 2017, Baldoni, 2022).

This study also entailed studying the physiological traits association with drought tolerance for parents and their offspring half-diallel crosses, whereby genotypes recorded higher leaf diffusive resistance, net photosynthetic rate, CO₂ concentration and PAR along with minimum values for days to heading, stomatal conductance, leaf transpiration rate, leaf temperature and leaf rolling. The results of this trial exhibited that genotypes, Azucena × Giza177 had desirable values for LDR, LTR, LT, NPR, CO₂, PAR, NPP, GY and WUE under DS, thus the hybrid combination Azucena × Giza179 gave better values for LTR, LT, NPR, CO₂, NPP, HGW, GY and WUE. Likewise, significantly better LTR, LT, NPR, CO₂, NPP, HGW and GY were found with crosses Sakha104 × Giza179. These findings are in agreement with previously reported results of Crofts *et al.*, (2022) and Gaballah *et al.*, (2022) whereby significant variation among rice genotypes was attributed to genetic differences which manifested in the form of varying morphological and physiological traits of rice (Salem & El-Zanaty, 2015). Additionally, physiological character diffusive resistance of stomata was reported to be associated with drought tolerance (Shrestha, 2020). Similar to our findings, Chauhan *et al.*, (1996) revealed that the cultivar Vandana transpired significantly lesser water and exhibited higher stomatal diffusive resistance than the conventional cultivar Brown Gora under moisture stressed conditions. It was also inferred that physiological traits such as stomatal conductance determined using non-destructive approaches might be relied for efficient screening of drought tolerant genotypes (Rukundo *et al.*, 2017). Similarly, it was reported that stomatal conductance was decreased with declining water potential along with significant reduction in leaf conductance and CO₂ as absorption by over 69% (Rukundo *et al.*, 2017). Moreover, Minh *et al.*, (2017) reported the rice growth duration was longest under dry cultivation (by 13.5 days compared to continuous flooding) and intermittent irrigation delayed number of tillering by five to seven days, decline the leaf transpiration rate and highest the leaf photosynthetic rate. Low transpiration rate is a desirable trait is associated with the better preservation of leaf moisture under DS (Amudha *et al.*, 2010). Leaf temperature is one of the most important factors determining energy exchange between the leaf and its environment and is strongly correlated with the physiological reactions of the plant (Khan *et al.*, 2017). Zhao *et al.*, (2015) observed that net photosynthetic rate diminished dramatically, especially under severe DS coupled with higher incidence of photosynthetic active radiation in rice. It was also inferred

that net photosynthesis rate, stomatal conductance, transpiration rate, and photosynthetic active radiation declined in plants under alternative wet and dry treatment than control treatment. The photosynthetic rate reduced with decreasing soil moisture content at the tillering stage was severe in terms of drastic effects. The key reasons for the reduction in yield was the significant reduction in the number of effective panicles, the seed setting rate and the 1000-grains weight (Lian *et al.*, 2020). Caine *et al.*, (2020) reported that the low stomatal density in rice lines assisted crop plants to conserve water. When grown at elevated atmospheric CO₂, rice plants with low stomatal density were able to preserve their stomatal conductance and tolerant drought and high temperature (40°C) for longer than control plants. Moreover, low stomatal density rice improved paddy yield, although a reduced rate of photosynthesis was also recorded by Bhat *et al.*, (2022). Furthermore, rice plants with low stomata are drought tolerant and further conservative in their water use and perform better in the future even climate change is anticipated to threaten food security.

However in this investigation, negative values of GCA were found for days to heading, stomatal conductance, transpiration rate, leaf temperature and leaf rolling while positive effects were recorded for leaf diffusive resistance, net photosynthetic rate, CO₂ concentration, PAR, HGW, FP, GYP and WUE. All these traits might be exploited to enhance drought tolerance in rice cultivars. The general combining ability effects of each parent was useful for DS tolerance. Such effects were being used to compare the average performance of every parent with other parents and enable selection of parents for more improvement to water stress tolerance. Additionally, it could be included that N22, Azucena and Giza179 considered as good combiner for improving the most traits studied under DS condition. Therefore, to improve such traits could be selection practiced based on mean performance or GCA effect (Malemba *et al.*, 2017). SCA effects provide valuable information for particular cross combination. To choose high yielding cultivars under water limited condition with a few stomatal conductance, transpiration rate, leaf temperature and leaf rolling as well as high diffusive resistance, net photosynthetic rate, intercellular CO₂ concentration, photosynthetic active radiation, high percentages of spikelet fertility and more productive tillers number / plant can be selected. Crosses Azucena × Giza177, Sakha104 × Giza179, Azucena × Giza179 and IRAT 112 × Azucena outperformed in terms of physiological and yield related traits. The outcome of all these crosses studied displayed the contribution of significant parent influencing the genetic architecture of drought tolerance attributes resulting useful lines in subsequent populations (Malemba *et al.*, 2017). This study also exhibited that parents or crosses had the best general combiners for DS related traits. The outcome displayed the importance of genetically diverse parents could be selected for improvement of different traits. Moderate DS at the early vegetative stage negatively affects many traits such as panicle number per plant, number of spikelet per plant, spikelet fertility, grain yield and harvest index probably and its relationship with flowering delay (Kang & Futakuchi 2020). Yield enhancement in rice under DS condition via suitable selection of parents considering their combining ability and mean performance followed by appropriate breeding programs depending on the nature of gene action involved (Utharasu & Anandakumar, 2013).

Significant negative heterosis over mid-parent and better parent for days to heading, stomatal conductance, transpiration rate, leaf temperature and leaf rolling was expressed in hybrids viz., Giza177 × Sakha104, N22 × Giza177, Azucena × Sakha104, Azucena × Giza179, IRAT 112 × Sakha104, and N22 × Giza179 indicating that these hybrids are best suited for aerobic conditions. In addition to the positive heterosis over mid parent and better parent for the traits such as LDR, NPR, CO₂, PAR, NPP, HGW, FP, GYP and WUE were in desirable direction to improve the rice plants to tolerance drought condition and it confirm in our study in the hybrid combinations IRAT 112 × N22, IRAT 112 × Azucena, Azucena × Giza179, N22 × Azucena and Azucena × Giza177. Drought related traits like leaf diffusive resistance, CO₂ concentration, PAR, NPP, spikelet's fertility percentage, GYP and WUE independently or in combination, might be the basis of selection under moisture stress condition (Ram *et al.*, 2020). Low stomatal conductance helps to maintain higher leaf water potential in the genotypes under stress (Amudha *et al.*, 2010).

The correlation analysis indicates vital information of association among yield attributes with paddy yield as reported by Chukwu *et al.*, (2022). Pushpam *et al.*, (2018) inferred that correlation implies a cause and effect relationship between variables. It is index of degree of relationship between two continuous variables. Correlating genetic information with physio-morphological traits regarded to drought tolerance provide information regarding traits that need to be exploited for development of drought tolerance rice cultivars through indirect selection. The study has shown grain yield had highly significantly positive correlation with LDR, NPR, CO₂, PAR, NPP, HGW and FP, while negative association was shown with SC, LTR, LT and LR. The selection for one trait gave improvement for all characteristics that had positively correlated and reduction in traits that are negatively correlated.

Conclusions

The research findings remained in line with the postulated hypothesis as significant variation existed among genotypes of rice in terms of morphological and physiological traits under water scant conditions. Drought tolerance related physiological traits including days to heading, leaf diffusive resistance, stomatal conductance, transpiration rate, leaf temperature, leaf rolling, net photosynthetic rate, CO₂ concentration and photosynthetically active radiation and grain yield components (fertility percentage, hundred grain weight and number of productive tillers / plant) were governed by non-additive genes suggesting that hybridization then selection in later generations might be recommended for development of these traits. Three parents N22, Azucena and Giza179 were superior combiners for drought physiological traits and grain yield components and thus these could be utilized in hybridization breeding program to enhancement drought tolerance to elite lines. The crosses Azucena × Giza177, IRAT 112 × Azucena, IRAT 112 × N22, and Azucena × Giza179 showed significant SCA effects for drought tolerant physiological traits and yield components. However as per combining ability, no parents or specific crosses obtained combination of all drought traits, but a combination of desirable traits might be introgression to rice genotypes to develop drought tolerant genotypes.

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