RESEARCH ARTICLE

SABRAO Journal
of Breeding and Genetics
53 (2) 139-156, 2021

GENETIC BEHAVIOR OF THE PHYSIOLOGICAL, NUTRIENT, AND YIELD TRAITS OF RICE UNDER DEFICIT IRRIGATION CONDITIONS

M.M. GABALLAH*, R.Y. EL-AGOURY, S.M. SAKR and A.A. ZIDAN

Department of Rice Research and Training Center, Field Crops Research Institute, Agricultural Research Center, Sakha, Kafr-El-Sheikh, Egypt
*Corresponding author email: mahmoudgab@yahoo.com
Email addresses of coauthors: roshdyrrtc@gmail.com, drshimaamagdy89@gmail.com, abdozidan2011@yahoo.com

SUMMARY

Given that water deficit is the main challenge to rice (*Oryza sativa* L.) production in Egypt, the development of drought-tolerant genotypes through classical breeding is the main strategy for increasing rice yield in Egypt. The present study aimed to generate new populations by crossing tolerant rice genotypes with local adapted cultivars. During 2019, seven rice genotypes were crossed in a half-diallel mating design to generate 21 F_1 hybrids. During 2020, the parental genotypes and their F_1 hybrids were grown and assessed with a randomized complete block design with three replications for chlorophyll pigments, antioxidants, nutrients, and yield components under water deficit conditions at Sakha Research Station, Kafr El-Sheikh, Egypt. General combining ability (GCA): specific combining ability (SCA) ratios were found to be less than unity for all studied traits, except for peroxidase (PA) activity. This result indicated the importance of nonadditive genetic variance in determining the performance of these half-diallel hybrids for various traits. Three rice parental genotypes, i.e., N-22, Azucena, and Giza-179, were identified as good general combiners for physiological and yield traits under water stress conditions. Under water stress conditions, the F1 hybrids Azucena × Giza-177, Sakha-104 × Giza-179, IRAT-112 × Azucena, and Azucena × Giza-179 showed desirable SCA effects for the majority of the physiological and yield traits. The F1 hybrids Azucena × Giza-179, Azucena × Giza-177, Azucena × Sakha-104, N-22 × Giza-179, and Sakha-104 × Giza-179 demonstrated promising mean performance for chlorophyll pigment (a, b) and carotenoid content, proline content, catalase and PA activities, soluble sugar content, abscisic acid, and polyphenol oxidase, as well as grain yield and its components. These promising populations could be used in future breeding programs to develop drought-tolerant and high-yielding rice genotypes.

Keywords: Half-diallel crosses, chlorophyll content, proline content, polyphenol oxidase, combining ability, heterosis, grain yield, *Oryza sativa* L.

Key findings: Breeding for drought tolerance is one of main strategies for increasing rice (*Oryza sativa* L.) production under drought conditions. The evaluation of half-diallel crosses among diverse and adapted rice genotypes under water deficit conditions revealed that F_1 hybrids showed enhanced drought tolerance and grain yield compared with their parental genotypes.

Manuscript received: December 18, 2020; Decision on manuscript: January 25, 2021; Accepted: February 8, 2021.

Communicating Editor: Dr. Naqib Ullah Khan

INTRODUCTION

Water scarcity is becoming an intensifying problem faced by crop plants worldwide. This situation is particularly true in Egypt, where water resources for irrigation are limited and dependent only on the Nile River, which contains approximately 55 billion cubic meters of water (Gaballah and Abdallah, 2015). Thus, the development of rice (*Oryza sativa* L.) genotypes tolerant to water stress is considered of vital importance in the future. Plant response to drought conditions is complex, and plants adopt several mechanisms when encountering drought; these mechanisms include a) drought escape through rapid development that allows plants to complete their life cycle before water stress, b) drought avoidance through increasing water uptake and decreasing transpiration rate by restricting stomatal conductance and leaf area, and c) tissue turgor maintenance during water stress through osmotic adjustment to allow survival under water stress (Zain *et al.,* 2014).

Grain yield is a complex trait and depends on all the biochemical and physiological processes occurring in a plant during crop development. In crop plants, water deficit conditions affect chlorophyll contents with time period and intensity. These effects have been described in different species. The ratios of chlorophyll contents vary under drought conditions. Carotenoids have vital roles and provide benefits for plants to tolerate water deficit stress conditions (Sahebi *et al.,* 2018). Drought stress inhibits the synthesis of chlorophyll a/b and decreases the content of binding proteins, leading to reductions in light-harvesting pigment proteins related to photosystem II (Fahad *et al.,* 2017). The chlorophyll and carotenoid levels in different field crops under drought stress have been studied.

Drought may cause nutrient deficits even in fertilized fields given that soil physiochemical properties can lead to the decreased mobility and absorbance of single nutrients (Faralli *et al.,* 2019). Increased abscisic acid (ABA) in plants causes rapid stomatal closure in reaction to drought stress, finally resulting in reduced transpiration rate and moisture retention in leaves (Zu *et al.,* 2017). Furthermore, water potential and proline and chlorophyll contents are significantly correlated with rice drought tolerance and consequently can be used as criteria to assess the degree of leaf injury under drought stress conditions (Zu *et al.,* 2017). Physiological traits are indirect indicators of drought tolerance, thus controlling their application. In breeding for drought tolerant upland rice, simple, rapid, and accurate methods for distinguishing between drought-tolerant and drought-susceptible rice cultivars are considered to be highly desirable. The effective assessment of drought tolerance in rice has become a key point in breeding for water deficit tolerance.

Plants tolerate different abiotic stresses, and the accumulation of polyphenols in response to these stresses aids plants to adapt to unfavorable environments (Lum *et al.,* 2014). Therefore, the concentration of phenols in plant tissue is a good indicator for predicting the degree of abiotic stress tolerance in plants and varies greatly in different plant genotypes under exposure to an array of external factors. Polyphenols influence plant growth and development processes, participate in seed germination and biomass accumulation, and improve plant metabolism (Mcclung *et al.,* 2020). The biosynthesis of metabolites, including polyphenols, increases in plants in response to abiotic stresses. Phenolics increase plant tolerance against different stress conditions, such as heavy metals, salinity, temperature, drought, pesticides and ultraviolet (UV) radiation (Kar and Mishra, 1976).

The genetic analysis of biochemical and physiological traits and grain yield and its related traits can provide interesting information about gene action types. Such an approach will be helpful for determining the appropriate selection method to improve various traits in populations. It can recognize genotypes possessing the most dominant and recessive alleles responsible for the expression of a certain trait. Such information empowers breeders to conduct the efficient selection of segregating generations, thus leading to the improvement of breeding materials for various traits under water stress conditions.

In diallel analysis, general combining ability (GCA) is related to additive gene action, whereas specific combining ability (SCA) affects dominance and epistasis variances. Many parental cultivars with great agronomic potential may perform poorly in the F_1 generation because of genetic hindrance in various cross combinations. Therefore, crossing in a diallel design is an effective procedure for the identification, measurement, and selection of superior rice genotypes (Akanksha and Jaiswal, 2019). Selection may be successful during the early generations once additive gene action is predominant and can be effective at later generations in case effects are fixed in homozygous lines.

The present investigation aimed to estimate GCA and SCA; the nature of gene action; the heterotic effects relative to the mid- and better parents for physiological traits and grain yield and its related traits; and phenotypic correlation coefficients among all the studied traits under water stress conditions.

MATERIALS AND METHODS

Plant material and experimental design

The present investigations were performed at the Rice Research and Training Center (RRTC), Sakha Research Station, Kafr El-Sheikh, Agricultural Research Center, Egypt. Seven rice genotypes were crossed in a half-diallel mating design by following Method II and Model I (Griffing, 1956). Rice parental genotypes were obtained from the genetic germplasm bank resources of RRTC (Table 1). During 2019, seven rice genotypes were planted on three successive planting dates with 10-day intervals to overcome the differences in flowering time among genotypes. Thirty-day-old seedlings of each parent were individually transplanted in the field in five rows with a length of 5 m. During the flowering period, these parental genotypes were crossed in a half-diallel mating design to produce 21 F_1 hybrid seeds (Butany, 1961).

During the 2020 cropping season, seven parental genotypes and their 21 F_1 hybrids were evaluated under water stress conditions (flush irrigation every 12 days), which were imposed after 15 days from transplanting till the harvesting date. The 30-day-old seedlings of the 28 rice genotypes were transplanted in a randomized complete block design with three replications under water stress conditions. Each replication comprised five rows of each parent and F_1 hybrid. Each row was 5 m long, and a distance of 20 cm × 20 cm was maintained between and within rows. The plot size was 6 m^2. The weather parameters during the first and second cropping seasons at Sakha Research Station, Egypt, are given in Figure 1. The soil texture was clay, and soil samples were taken before land preparation at the depth of 0–30 cm from the soil surface. The soil samples were completely mixed, dried, and ground and then physically and chemically analyzed in accordance with Black *et al*. (1965) (Table 2).

Table 1. Rice genotypes with their parentage, origin and type used in this study.

Genotypes	Parentage	Origin	Type
Giza-177	Giza171/ Yumji No.1// PiNo.4	Egypt	Temperate *japonica* type, sensitive to drought, short stature, early duration, and resistant to blast
Sakha-108	Sakha101/HR5824-B-3-2-3// Sakha101	Egypt	Temperate *japonica* type, sensitive to drought, short stature, moderate duration, and resistant to blast
Sakha-104	GZ4096-8-1/ GZ4100-9-1	Egypt	Temperate *japonica* type, sensitive to drought, moderate stature, moderate duration, and susceptible to blast
Giza-179	GZ6296/ GZ1368	Egypt	Indica/*japonica* type, moderate tolerance to drought, short stature, early duration, and resistance to blast
IRAT-112	IRAT 13/ Dourado Precoce	Côte d'Ivoire	Tropical *japonica* type, tolerant to drought (Upland) – long stature, late duration, and susceptible to blast
Nagina-22 (N-22)	Selected from Rajbhog.	India	*Indica* type, tolerant to drought, long stature, late duration, and resistance to blast
Azucena	Exotic	Philippine	Tropical *japonica*, tolerance to drought (upland), long stature, late duration, and resistance to blast

Table 2. Chemical and physical properties of the experimental field soil.

Properties	2019		2020	
	0–20 cm	20–40 cm	0–20 cm	20–40 cm
Electric conductivity (ds m^{-1})	2.0	2.1	2.0	2.2
PH	8.2	8.3	8.0	8.1
Organic matter (%)	1.3	1.3	1.2	1.2
$CaCo_3$ (%)	3.7	3.1	3.8	3.2
Soluble ions (meq $^{-1}$):				
Ca^{++}	5.1	4.8	5.4	5.2
Mg^{++}	2.1	2.0	2.4	2.3
Na^{+}	12.0	13.1	11.8	12.3
K^{+}	0.4	0.5	0.6	0.5
Co_3^{--}	-	-	-	-
Hco_3^{-}	3.5	3.8	3.7	4.2
Cl^{-}	14.8	14.9	15.2	15.9
So_4^{--}	1.3	1.7	1.2	1.9
Available P (ppm)	12.6	12.0	14.2	14.3
Available Zn (ppm)	0.7	0.7	0.8	0.8
Available Fe (ppm)	5.2	5.1	6.1	6.0
Available Mn (ppm)	2.1	2.3	2.5	2.1

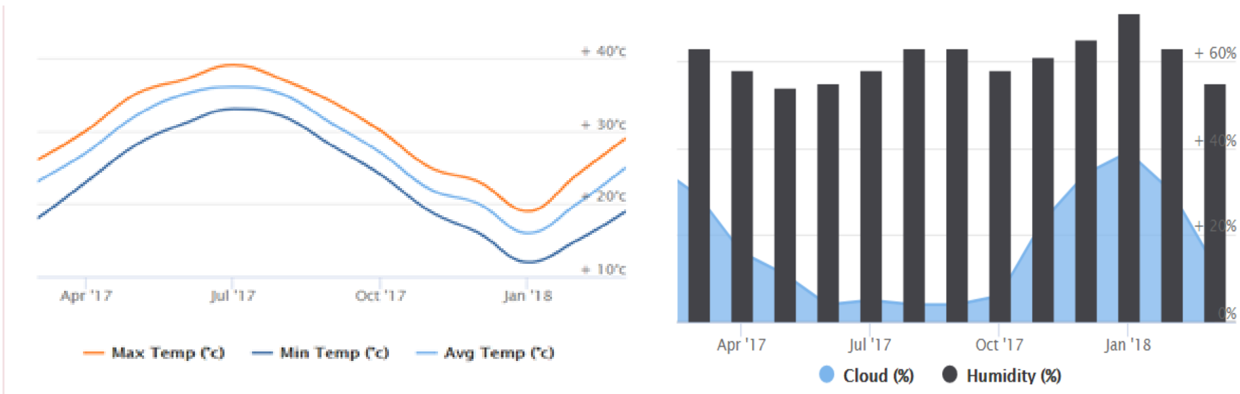

Figure 1. Weather parameters during the first and second cropping seasons in Sakha Research Station, Egypt.

Physiological traits

Photosynthetic pigments

At 30 days after transplanting, total chlorophyll content (TCH) was determined in five leaves via measurement with SPAD meter 502 (Minolta Inc; Lincoln, NE, USA). Chlorophyll a (CHA), chlorophyll b (CHB), and carotenoid contents were measured at maximum tillering stage under water shortage environment. CHA and CHB were measured in accordance with Lohithaswa *et al.* (2013) as follows:

$$CHA\ (mg\ g^{-1}) = [12.7 \times (OD_{663}) - 2.69 \times (OD_{645})] \times V/1000 \times W$$

$$CHB\ (mg\ g^{-1}) = [22.9 \times (OD_{645}) - 4.68 \times (OD_{663})] \times V/1\ 000 \times W$$

Where, V = volume of extract, W = weight of fresh leaves, OD = optimal density

Carotenoid content was calculated as follows (Robbelen *et al.*, 1957):

$$Carotenoid\ (mg\ g^{-1},\ CAR) = Acar/EM \times 100$$

Where, the unit of carotenoids is in fresh weight,

$$Acar = [(OD_{480}) + 0.114 \times (OD_{663})] - 0.638 \times (OD_{645}),\ Em = 2500.$$

Photosynthetic pigments were determined by using the spectrophotometric method in accordance with Moran (1982).

Determination of antioxidant and mineral content

Crude enzyme extracts were prepared by homogenizing 500 mg of leaf tissue in extraction buffer containing 0.5% Triton X-100 and 1% polyvinylpyrrolidone in 100 mM potassium phosphate buffer (pH 7.0) with a chilled mortar and pestle. These extracts were used to determine the enzymatic activities of the antioxidant proteins. The homogenate was centrifuged at 15 000 rpm for 20 min at 4 °C. The supernatant was used in the enzymatic assays as described below.

Proline content

Free proline was extracted from 200 mg of leaf sample in 3% (w/v) aqueous sulfosalicylic acid and estimated by using ninhydrin reagent in accordance with Bates *et al.* (1973). The organic toluene phase containing the chromophore was separated, and the absorbance of the red color that had developed was read at 520 nm. Proline content (PC) was determined by using the calibration curve and expressed as mg g^{-1} fresh weight.

Assay of catalase activity

The assay mixture had a total of 3 mL containing 0.5 mL of 0.2 M phosphate buffer (pH 7.0), 0.3 mL of (v/v) H_2O_2, and 0.1 mL of enzyme. The final volume was made up to 3 mL by adding distilled water. The change in optical density was measured at 240 nm at 0 and 3 min on a UV–Vis spectrophotometer (Chapman and Pratt, 1978). The results were expressed as μmol H_2O_2 $min^{-1}g^{-1}$ protein.

Assay of peroxidase activity

The 3 mL assay mixture contained 1.5 mL of 0.1 M phosphate buffer (pH 7.0), 1 mL freshly prepared 10 m Mguaiacol, 0.1 mL of enzyme extract and 0.1 mL of 12.3 mM H_2O_2. Absorbance was read at 436 nm and then increase in the absorbance was noted at the interval of 30s on UV-Vis spectrophotometer (Chapman and Pratt, 1978).

Soluble sugar

Sucrose was measured spectrophotometrically by using the method of Ibrahim and Jaafar (2011). The samples (0.5 g and 0.25 mm) were placed in 15 mL conical tubes then brought to the volume of 10 mL with distilled water. The mixture was vortexed and later incubated for 10 min. Anthrone reagent was prepared by dissolving anthrone (0.1 g) in 95% sulfuric acid (Fisher Scientific, Omaha, NE, USA, 50 mL). Sucrose was used as a standard stock solution to prepare a standard curve for the quantification of sucrose in the sample. Ground dry sample was centrifuged with distilled water at a speed of 3400 rpm for 10 min and then filtered to obtain the supernatant. The sample (4 mL) was mixed with anthrone reagent (8 mL) and placed in a water bath set at 100 °C for 5 min before the measurement at 620 nm by using a spectrophotometer (Model UV160U; Kyoto, Japan). Soluble sugar (SS) content was expressed as mg sucrose g^{-1} dry sample**.**

ABA concentration

A leaf sample (c. 1 g) was taken at 30 days from transplanting and ground in liquid N_2 then extracted with 10 mL of isopropanol/HCl buffer at 4 °C for 30 min. After the addition of 20 mL of dichloromethane, the mixture was shaken rigorously, kept at 4 °C for 30 min, and then centrifuged at 4 °C for 10 min at 12 000 × *g*. The lower organic phase was collected, dried with N_2 gas, dissolved in 400 mL of methanol (0.1% formic acid), and subjected to ultrahigh-performance liquid chromatography tandem mass spectrometry detection by using an Acquity UPLC Xevo TQ system (Waters) with an Acquit UPLC R BEH C18 column. The column temperature was set at 40 °C and the eluent flow was set at 0.3 mL min^{-1}. Mobile phase A (water:methanol (98:2, v/v) with 0.05% formic acid and 5 mM ammonium acetate) and mobile phase B (acetonitrile) were set in gradient mode (time [min] of solvent A [%]:solvent B [%], 0:90:10, 4:100:0, 5:90:10, 6:90:10). Mass spectrometry analysis was performed with multiple reactions monitoring under negative and positive ion switching scanning.

Polyphenol oxidase

The 5 mL assay mixture for polyphenol oxidase (PPO) activity consisted of the same assay mixture as that of peroxidase (PA) without H_2O_2. The absorbency of the formed purpurogallin was measured at 420 nm. PA and PO activities were expressed in absorbency units.

Nitrogen content

Nitrogen content (N) was determined by following the method of Barrs and Weatherly (1962) by using the micro-Kjeldahl method in accordance with Jackson (1973). The results were expressed as mg nitrogen.

Potassium and sodium

Potassium (K) and sodium (Na) were determined by using flame photometry in accordance with Chapman and Pratt (1978).

Yield and yield attributes

At harvest, 10 plants were collected randomly for the estimation of plant height, number of panicles per plant (NPP), 100-grain weight (HGW, g), and spikelet fertility percentage (FP %). A total of 25 randomly selected plants from each replication for each genotype were harvested, dried, threshed, and the grain yield per plant (GYP) was determined at the moisture content of 14%. All data were recorded in accordance with the standard evaluation system (IRRI, 2016).

Statistical analysis

All traits were subjected to analysis of variance in accordance with randomized complete block design with three replications. The genetic parameters were further estimated after obtaining the significant differences among the genotypes for various traits. SCA and GCA effects were calculated by using Method-2 and Model-1 (Griffing, 1956). Treatment means were compared and separated on the basis of least significant difference. All the analyses were performed with analysis of variance technique by means of 'Agrobase' computer software package.

RESULTS

The analysis of variance indicated highly significant differences among genotypes, crosses, parents, and parents × crosses for all studied traits under water stress conditions (Table 3). GCA and SCA variances were highly significant for all the studied characters. The GCA:SCA ratios were found to be less than unity for almost all the studied traits, except for PA, for which the ratio was more than unity.

Mean performance

The mean performance of the parental genotypes and their F_1 hybrids for the 14 studied characteristics is presented in Table 4. The mean performance of the genotypes revealed varied values for various traits. For CHA, the best genotypes were the crosses Azucena × Giza-179, Azucena × Giza-177, N-22 × Giza-179, IRAT-112 × Azucena, IRAT-112 × N-22, and N-22 × Sakha-108, which showed the highest mean values of 2.75–3.02 mg g^{-1}.

For CHB, the hybrid combinations Azucena × Giza-177, Azucena × Giza-179, N-22 × Giza-179, and Sakha-104 × Giza-179 produced superior values that varied from 2.07 mg g^{-1} to 2.13 mg g^{-1}. The genotypes N-22 × Giza-179 and N-22 × Azucena and N-22 showed increased values for CAR content. The hybrid combinations Azucena × Giza-179, N-22 × Giza-179, and Azucena × Giza-177 revealed the desirable mean values for TCH that ranged from 5.9 6 mg g^{-1} to 6 mg g^{-1}.

For PC, the maximum mean values were obtained by the crosses IRAT-112 × Giza-177, Azucena × Giza-177, and Sakha-104 × Giza-179 and ranged from 0.79 mg g^{-1} to 0.81 mg g^{-1} fresh weight. However, the best mean values for ABA were found in hybrid combinations, viz., Azucena × Sakha-104, Azucena × Giza-177, and Azucena × Giza-179 and varied between 0.29 g^{-1} to 0.32 ng ABA g^{-1} fresh weight. For SS content, the best mean performance was shown by hybrid combinations, i.e., IRAT-112 × Azucena, Azucena × Giza-177, and Sakha-104 × Giza-179 and varied from 19.67 mg sucrose g^{-1} to 19.76 mg sucrose g^{-1}. The hybrid combinations IRAT-112 × Giza-177, Azucena × Giza-177, IRAT-112 × Azucena, N-22 × Giza-179, Sakha-104 × Giza-179, and IRAT-112 × N-22 exhibited the highest mean values for catalase (CAT) content that ranged from 38.26 μmol min^{-1} g^{-1} to 39.34 μmol min^{-1} g^{-1} protein.

Table 3. Mean squares of combining ability analysis for grain yield and its related traits under deficit irrigation conditions.

S.O.V.	df	CHA	CHB	CAR	TCH	PC	ABA	SS	CA	PA	PPO	N	P	K	NPP	HGW	FP	GYP
Reps	2	0.002	0.001	0.0003	0.01	0.0003	0.00003	0.18	0.73	10.73	2.00	0.0002	0.00002	0.0001	0.18	0.004	4.00	0.91
Genotypes	27	0.48**	0.20**	0.03**	1.30**	0.01**	0.004**	24.6**	54.1**	545.8**	100.1**	0.05**	0.002**	0.03**	42.2**	0.33**	2205**	649.9**
F_1 hybrids	20	0.56**	0.24**	0.03**	1.56**	0.01**	0.005**	29.2**	61.4**	631.5**	98.3**	0.06**	0.008**	0.04**	37.3**	0.4**	2830**	831.3**
Parents	6	0.22**	0.05**	0.02**	0.45**	0.01**	0.001**	5.9**	12.7**	319.4**	93.91**	0.01**	0.0005**	0.01**	20.6**	0.13**	456.6**	38.01**
P vs. F_1	1	0.41**	0.25**	0.001**	1.21**	0.04**	0.01	43.8**	156.1**	189.9**	171.3**	0.005**	0.0001**	0.06**	269.9**	0.16**	218.5**	692.8**
Error	54	0.002	0.001	0.0002	0.01	0.0001	0.00001	0.08	0.34	5.02	1.05	0.0001	0.00001	0.00	0.07	0.001	0.96	0.27
GCA	6	0.21**	0.03**	0.01**	0.43**	0.01**	0.005**	10.5**	15.1**	199.7**	25.3**	0.02**	0.0007**	0.01**	13.3**	0.04**	424.8**	178.1**
SCA	21	0.14**	0.07**	0.01**	0.43**	0.004**	0.001**	7.5**	18.8**	176.8**	35.6**	0.01**	0.0007**	0.01**	14.3**	0.13**	824.0**	227.6**
GCA/SCA	-	0.001	0.0003	0.001	0.002	0.0001	0.00001	0.03	0.11	1.67	0.35	0.00004	0.000001	0.00002	0.023	0.001	0.32	0.09
Error	54	0.16	0.05	0.17	0.11	0.15	0.12	0.16	0.09	0.13	0.08	0.15	0.12	0.09	0.10	0.03	0.06	0.09

**: highly significant at $P \leq 0.01$. CHA: chlorophyll a, CHB: chlorophyll b, CAR: carotenoid content, TCH: total chlorophyll content, PC: proline content, ABA: abscisic acid content, SS: soluble sugar content, CA: catalase content, PA: peroxidase content, PPO: polyphenol oxidase, N: nitrogen content, P: phosphorus content, K: potassium content, NPP: number of panicles per plant, HGW: 100-grain weight, FP: fertility percentage, GYP: grain yield per plant.

Table 4. Mean performances of the parental genotypes and F_1 hybrids for various traits under deficit irrigation conditions.

Genotypes	CHA	CHB	CAR	TCH	PC	ABA	SS	CA	PA	PPO	N	P	K	NPP	HGW	FP	GYP
IRAT-112	2.61	1.64	0.94	5.19	0.63	0.19	15.03	29.30	124.54	60.70	0.70	0.20	0.31	13.44	3.07	79.76	32.05
IRAT-112 × N-22	2.79	1.92	0.93	5.64	0.76	0.28	19.03	38.26	151.36	61.91	0.79	0.22	0.62	17.00	3.18	92.40	55.00
IRAT-112 × Azucena	2.81	1.97	0.88	5.66	0.77	0.26	19.76	38.68	148.89	65.44	0.76	0.23	0.59	20.00	2.20	94.85	54.00
IRAT-112 × Giza-177	2.53	1.72	0.83	5.08	0.81	0.23	19.15	39.34	135.68	66.09	0.69	0.21	0.49	18.01	2.67	51.57	28.61
IRAT-112 × Sakha-104	2.12	1.65	0.77	4.54	0.71	0.22	14.65	28.57	121.44	49.89	0.41	0.15	0.41	12.66	2.14	18.50	13.39
IRAT-112 × Giza-179	2.15	1.53	0.66	4.35	0.69	0.21	17.16	33.46	142.20	66.73	0.59	0.16	0.29	13.53	2.76	16.65	27.05
IRAT-112 × Sakha-108	2.36	1.39	0.71	4.46	0.65	0.23	11.00	29.05	123.46	49.00	0.43	0.15	0.30	13.63	2.17	16.55	12.66
N-22	2.50	1.64	0.95	5.10	0.70	0.25	11.71	34.86	148.16	54.31	0.63	0.20	0.43	16.43	2.68	45.79	28.75
N-22 × Azucena	2.36	1.78	0.96	5.10	0.76	0.26	18.82	36.70	155.98	59.14	0.65	0.22	0.28	21.00	2.54	85.00	46.00
N-22 × Giza-177	1.63	1.72	0.83	4.18	0.62	0.22	13.01	25.37	107.82	61.93	0.47	0.16	0.38	17.00	2.92	71.87	35.00
N-22 × Sakha-104	2.69	1.82	0.87	5.38	0.73	0.22	19.03	37.10	157.64	56.73	0.60	0.21	0.31	17.88	2.54	93.38	49.66
N-22 × Giza-179	2.84	2.07	0.99	5.90	0.75	0.27	19.22	38.63	157.18	60.28	0.73	0.22	0.56	17.00	2.53	92.12	54.00
N-22 × Sakha-108	2.75	1.70	0.78	5.24	0.62	0.25	14.08	27.45	120.42	53.15	0.63	0.19	0.44	12.74	2.38	86.27	36.28
Azucena	2.16	1.42	0.71	4.29	0.77	0.20	14.87	28.99	123.22	52.21	0.59	0.21	0.45	8.82	2.38	62.73	22.40
Azucena × Giza-177	2.85	2.13	0.92	5.90	0.79	0.29	19.72	38.70	152.36	65.13	0.79	0.23	0.62	19.00	2.25	92.13	59.00
Azucena × Sakha-104	2.03	1.42	0.64	4.09	0.65	0.32	16.19	31.57	134.17	51.03	0.54	0.19	0.46	16.00	2.44	54.00	28.00
Azucena × Giza-179	3.02	2.10	0.88	6.00	0.75	0.29	19.06	37.32	148.86	64.14	0.84	0.22	0.60	23.00	3.47	94.00	58.00
Azucena × Sakha-108	2.04	1.39	0.81	4.24	0.69	0.19	13.94	27.18	115.50	61.56	0.43	0.15	0.37	8.94	2.34	21.86	13.92
Giza-177	2.07	1.67	0.74	4.48	0.60	0.21	14.87	29.00	127.03	51.38	0.48	0.18	0.38	9.00	2.70	77.00	30.00
Giza-177 × Sakha-104	2.00	1.89	0.70	4.60	0.63	0.19	15.77	30.76	130.76	57.65	0.51	0.18	0.40	13.18	2.62	85.69	37.50
Giza-177 × Giza-179	1.69	1.18	0.89	3.76	0.73	0.17	18.13	35.35	137.91	56.15	0.45	0.20	0.44	14.50	1.89	46.25	19.34
Giza-177 × Sakha-108	2.36	1.87	0.66	4.89	0.76	0.22	10.86	32.88	139.74	63.19	0.53	0.22	0.43	14.00	2.74	87.96	40.00
Sakha-104	2.00	1.67	0.85	4.53	0.64	0.23	15.91	31.03	131.89	63.05	0.58	0.19	0.34	12.76	2.64	68.72	30.44
Sakha-104 × Giza-179	2.47	2.07	0.94	5.48	0.79	0.27	19.67	38.38	150.54	65.26	0.76	0.23	0.56	22.02	2.78	91.62	57.08
Sakha-104 × Sakha-108	2.02	1.51	0.81	4.35	0.64	0.23	16.11	31.40	133.46	63.01	0.56	0.19	0.39	13.72	2.66	78.80	31.04
Giza-179	1.94	1.41	0.81	4.16	0.62	0.23	15.43	30.09	144.88	62.08	0.55	0.18	0.43	12.00	2.57	79.00	33.20
Giza-179 × Sakha-108	1.58	1.29	0.86	3.73	0.56	0.18	10.95	31.10	132.56	51.85	0.44	0.15	0.35	15.00	2.77	20.00	9.00
Sakha-108	1.96	1.72	0.83	4.51	0.63	0.22	15.61	30.44	141.95	49.61	0.55	0.18	0.34	11.84	2.68	76.89	31.58
$LSD_{0.05}$	0.06	0.05	0.02	0.13	0.02	0.01	0.47	0.96	3.66	1.67	0.02	0.01	0.01	0.43	0.07	1.60	0.85
$LSD_{0.01}$	0.09	0.06	0.03	0.18	0.03	0.01	0.62	1.28	4.88	2.24	0.02	0.01	0.02	0.58	0.09	2.14	1.14

CHA: chlorophyll a, CHB: chlorophyll b, CAR: carotenoid content, TCH: total chlorophyll content, PC: proline content, ABA: abscisic acid content, SS: soluble sugar content, CA: catalase content, PA: peroxidase content, PPO: polyphenol oxidase, N: nitrogen content, P: phosphorus content, K: potassium content, NPP: number of panicles per plant, HGW: 100-grain weight, FP: Spikelet fertility %, GYP: grain yield per plant (g $plant^{-1}$).

The highest mean values for PA content were recorded for the crosses N-22 × Sakha-104, N-22 × Giza-179, and N-22 × Azucena and varied from 155.98 μmol $min^{-1}g^{-1}$ to 157.64 μmol $min^{-1}g^{-1}$ protein. For PPO, the cross combinations IRAT-112 × Giza-179, IRAT-112 × Giza-177, IRAT-112 × Azucena, Sakha-104 × Giza-179, and Azucena × Giza-177 provided the highest mean values, i.e., 66.73, 66.09, 65.44, 65.26, and 65.13 Ug^{-1} FW, respectively. For N content, the crosses Azucena × Giza-179, IRAT-112 × N-22, and Azucena × Giza-177 recorded high mean values that varied from 0.79 g to 0.84 g. The crosses IRAT-112 × Azucena, Azucena × Giza-177, and Sakha-104 × Giza-179 presented the maximum values for P content of 0.23 g. For K content, the genotypes IRAT-112 × N-22, Azucena × Giza-177, Azucena × Giza-179, and IRAT-112 × Azucena provided superior values that ranged from 0.59 g to 0.62 g.

The F_1 hybrids Azucena × Giza-179, Sakha-104 × Giza-179, N-22 × Azucena, and IRAT-112 × Azucena presented the highest values for NPP. These values varied from 20 to 23. For HGW, the heaviest grains with maximum mean values were found in the F_1 hybrids Azucena × Giza-179 and IRAT-112 × N-22 and the parental genotype IRAT-112. The hybrid combinations IRAT-112 × Azucena, Azucena × Giza-179, and N-22 × Sakha-104 presented the highest mean values for FP. These values varied from 93.38% to 94.85%. The highest mean values for GYP were found for the cross combinations of Azucena × Giza-177, Azucena × Giza-179, Sakha-104 × Giza-179, and IRAT-112 × N-22 and ranged from 45.00 g $plant^{-1}$ to 49.00 g $plant^{-1}$.

Combining ability analysis

GCA

GCA effects were found to differ significantly from zero in most cases (Table 5). The parental genotypes N-22, IRAT-112, and Azucena showed highly significant and positive GCA effects for CHA and might be good general combiners for the trait. By contrast, the genotypes N-22, Giza-177, Sakha-104, and Azucena exhibited highly significant and positive GCA effects for CHB and could be good general combiners for this trait. For CAR, the parental genotypes N-22 and Giza-179 showed highly significant and positive GCA effects. Therefore, the parents N-22, IRAT-112, and Azucena exhibited highly significant and positive GCA effects for TCH and could be considered as good general combiners for the trait. The parental genotypes Azucena, IRAT-112, and N-22 had highly significant and positive GCA effects for PC. The genotypes N-22, Azucena, and Sakha-104 had highly significant and positive GCA effects for ABA.

The parental genotypes Azucena, Giza-179, Sakha-104, and IRAT-112 were identified as good general combiners for SS given their highly significant and positive GCA effects for the trait. Highly significant and positive GCA effects were found for the parents Giza-179, N-22, Azucena, and IRAT-112 for the trait CA, and the parents Giza-179, N-22, and Azucena performed better and revealed the highest GCA effects for PA. The parental genotypes Giza-179, IRAT-112, and Giza-177 showed the highest GCA effects for PPO. The genotypes Azucena, N-22, IRAT-112, and Giza-179 exhibited highly significant and positive GCA effects for N. The parents N-22, Azucena, and Giza-177 were found as good general combiners for P. The parents Azucena, Giza-179, and Giza-177 were confirmed as good general combiners for K. For NPP, the parental genotypes N-22, Giza-179, and Azucena demonstrated highly significant and positive GCA effects and were considered as good general combiners. The parents N-22, Giza-179, and IRAT-112 showed highly significant and positive GCA effects for HGW. The parental genotypes N-22, Giza-177, Azucena, and Sakha-104 were identified as good general combiners for FP. The parents N-22, Azucena, and Giza-179

Table 5. General combining ability effects of the parental genotypes for various traits under deficit irrigation conditions.

Genotypes	CHA	CHB	CAR	TCH	PC	ABA	SS	CA	PA	PPO	N	P	K	NPP	HGW	FP	GYP
IRAT-112	0.18^{**}	-0.01^{**}	0.01^{**}	0.18^{**}	0.01^{**}	-0.01^{**}	0.29^{**}	0.31^{**}	-2.77^{**}	1.24^{**}	0.03^{**}	-0.003^{**}	-0.01^{**}	0.06	0.05^{**}	-9.72^{**}	-2.58^{**}
N-22	0.19^{**}	0.09^{**}	0.07^{**}	0.35^{**}	0.01^{**}	0.02^{**}	-0.18^{**}	1.12^{**}	5.52^{**}	-0.84^{**}	0.04^{**}	0.01^{**}	0.002^{**}	1.59^{**}	0.07^{**}	8.34^{**}	6.16^{**}
Azucena	0.12^{**}	0.01^{**}	-0.01^{**}	0.12^{**}	0.04^{**}	0.02^{**}	1.00^{**}	0.55^{**}	0.57	0.17	0.05^{**}	0.01^{**}	0.044^{**}	0.49^{**}	-0.09^{**}	3.31^{**}	2.86^{**}
Giza-177	-0.13^{**}	0.04^{**}	-0.03^{**}	-0.13^{**}	−0.002	-0.01^{**}	-0.20^{**}	-0.30^{**}	-4.30^{**}	0.40^{*}	-0.04^{**}	0.001^{**}	0.012^{**}	-0.83^{**}	-0.03^{**}	5.77^{**}	0.16
Sakha-104	-0.12^{**}	0.02^{**}	-0.02^{**}	-0.11^{**}	-0.01^{**}	0.004^{**}	0.56^{**}	-0.36^{**}	−0.58	0.04	-0.02^{**}	-0.002^{**}	-0.023^{**}	−0.02	-0.04^{**}	2.43^{**}	−0.05
Giza-179	-0.08^{**}	-0.05^{**}	0.02^{**}	-0.11^{**}	-0.01^{**}	-0.001^{*}	0.76^{**}	1.25^{**}	6.89^{**}	2.14^{**}	0.02^{**}	-0.001^{**}	0.027^{**}	0.88^{**}	0.06^{**}	-2.10^{**}	1.43^{**}
Sakha-108	-0.15^{**}	-0.10^{**}	-0.04^{**}	-0.29^{**}	-0.04^{*}	-0.01^{**}	-2.23^{**}	-2.58^{**}	-5.33^{**}	-3.15^{**}	-0.07^{**}	-0.02^{**}	-0.05^{**}	-2.16^{**}	-0.04^{**}	-8.03^{**}	-7.99^{**}
S.E. (gi)	0.01	0.00	0.002	0.01	0.002	0.001	0.05	0.10	0.40	0.18	0.002	0.001	0.001	0.047	0.01	0.17	0.09
S.E. (gi-gj)	0.01	0.01	0.004	0.02	0.003	0.001	0.08	0.16	0.61	0.28	0.003	0.001	0.002	0.072	0.01	0.27	0.14
$LSD_{0.05}$	0.01	0.01	0.005	0.03	0.004	0.001	0.10	0.21	0.80	0.37	0.004	0.001	0.003	0.09	0.02	0.35	0.19
$LSD_{0.01}$	0.02	0.01	0.01	0.04	0.01	0.002	0.14	0.28	1.07	0.49	0.005	0.002	0.003	0.13	0.02	0.47	0.25

*,**: significant and highly significant at $P \leq 0.05$ and $P \leq 0.01$, respectively. CHA: chlorophyll a, CHB: chlorophyll b, CAR: carotenoid content, TCH: total chlorophyll content, PC: proline content, ABA: abscisic acid content, SS: soluble sugar content, CA: catalase content, PA: peroxidase content, PPO: polyphenol oxidase, N: nitrogen content, P: phosphorus content, K: potassium content, NPP: number of panicles per plant, HGW: 100-grain weight, FP: fertility percentage, GYP: grain yield per plant.

Table 6. Specific combining ability effects of the F_1 hybrids for various traits under deficit irrigation conditions.

SCA Effects	CHA	CHB	CAR	TCH	PC	ABA	SS	CA	PA	PPO	N	P	K	NPP	HGW	FP	GYP
IRAT-112 × N-22	0.13^{**}	0.15^{**}	0.03^{**}	0.30^{**}	0.05^{**}	0.04^{**}	2.89^{**}	3.93^{**}	11.48^{**}	2.85^{**}	0.12^{**}	0.02^{**}	0.20^{**}	0.21^{**}	0.45^{**}	26.59^{**}	16.67^{**}
IRAT-112 × Azucena	0.22^{**}	0.28^{**}	0.06^{**}	0.55^{**}	0.02^{**}	0.02^{**}	2.44^{**}	4.92^{**}	13.96^{**}	5.37^{**}	0.08^{**}	0.03^{**}	0.13^{**}	4.30^{**}	-0.36^{**}	34.07^{**}	18.97^{**}
IRAT-112 × Giza-177	0.19^{**}	0.00	0.04^{**}	0.22^{**}	0.11^{**}	0.01^{**}	3.03^{**}	6.44^{**}	5.62^{**}	5.79^{**}	0.10^{**}	0.01^{**}	0.07^{**}	3.64^{**}	0.05^{**}	-11.67^{**}	-3.73^{**}
IRAT-112 × Sakha-104	-0.24^{**}	-0.06^{**}	-0.04^{**}	-0.34^{**}	0.02^{**}	-0.01^{**}	-2.22^{**}	-4.27^{**}	-12.34^{**}	-10.05^{**}	-0.19^{**}	-0.04^{**}	0.02^{**}	-2.53^{**}	-0.47^{**}	-41.40^{**}	-18.73^{**}
IRAT-112 × Giza-179	-0.24^{**}	-0.10^{**}	-0.19^{**}	-0.54^{**}	-0.01^{*}	-0.01^{**}	0.08	-1.00^{**}	0.95	4.69^{**}	-0.06^{**}	-0.03^{**}	-0.16^{**}	-2.56^{**}	0.05^{**}	-38.72^{**}	-6.55^{**}
IRAT-112 × Sakha-108	0.03^{**}	-0.19^{**}	-0.09^{**}	-0.24^{**}	-0.01^{*}	0.01^{**}	-3.08^{**}	-1.58^{**}	-5.57^{**}	-7.75^{**}	-0.12^{**}	-0.03^{**}	-0.06^{**}	0.58^{**}	-0.44^{**}	-32.89^{**}	-11.52^{**}
N-22 × Azucena	-0.24^{**}	-0.01^{**}	0.07^{**}	-0.18^{**}	0.01^{*}	0.00	1.97^{**}	2.13^{**}	12.76^{**}	1.14^{**}	-0.03^{**}	0.01^{**}	-0.20^{**}	3.77^{**}	-0.04^{**}	6.16^{**}	2.23^{**}
N-22 × Giza-177	-0.72^{**}	-0.09^{**}	-0.04^{**}	-0.85^{**}	-0.08^{**}	-0.01^{**}	-2.64^{**}	-8.34^{**}	-30.53^{**}	3.71^{**}	-0.13^{**}	-0.04^{**}	-0.06^{**}	1.10^{**}	0.28^{**}	-9.44^{**}	-6.07^{**}
N-22 × Sakha-104	0.32^{**}	0.02^{**}	-0.01^{**}	0.33^{**}	0.04^{**}	-0.03^{**}	2.62^{**}	3.45^{**}	15.57^{**}	-1.14^{**}	-0.01^{**}	0.01^{**}	-0.10^{**}	1.17^{**}	-0.09^{**}	15.41^{**}	8.80^{**}
N-22 × Giza-179	0.44^{**}	0.34^{**}	0.07^{**}	0.85^{**}	0.05^{**}	0.02^{**}	2.61^{**}	3.36^{**}	7.64^{**}	0.31	0.08^{**}	0.02^{**}	0.11^{**}	-0.61^{**}	-0.20^{**}	18.68^{**}	11.66^{**}
N-22 × Sakha-108	0.42^{**}	0.03^{**}	-0.08^{**}	0.37^{**}	-0.04^{**}	0.01^{**}	0.46^{**}	-3.99^{**}	-16.90^{**}	-1.53^{**}	0.07^{**}	0.00	0.06^{**}	-1.83^{**}	-0.26^{**}	18.77^{**}	3.36^{**}
Azucena × Giza-177	0.57^{**}	0.39^{**}	0.14^{**}	1.10^{**}	0.05^{**}	0.06^{**}	2.89^{**}	5.56^{**}	18.96^{**}	5.89^{**}	0.19^{**}	0.02^{**}	0.14^{**}	4.19^{**}	-0.23^{**}	15.86^{**}	21.23^{**}
Azucena × Sakha-104	-0.27^{**}	-0.30^{**}	-0.16^{**}	-0.73^{**}	-0.08^{**}	0.07^{**}	-1.40^{**}	-1.51^{**}	-2.95^{**}	-7.85^{**}	-0.08^{**}	-0.01^{**}	0.01^{**}	0.38^{**}	-0.04^{**}	-18.93^{**}	-9.56^{**}
Azucena × Giza-179	0.69^{**}	0.45^{**}	0.04^{**}	1.18^{**}	0.02^{**}	0.04^{**}	1.27^{**}	2.62^{**}	4.27^{**}	3.16^{**}	0.18^{**}	0.02^{**}	0.10^{**}	6.49^{**}	0.90^{**}	25.60^{**}	18.96^{**}
Azucena × Sakha-108	-0.22^{**}	-0.21^{**}	0.03^{**}	-0.40^{*}	-0.01^{*}	-0.04^{**}	-0.86^{**}	-3.69^{**}	-16.87^{*}	5.88^{**}	-0.14^{**}	-0.04^{**}	-0.05^{**}	-4.53^{**}	-0.13^{**}	-40.60^{**}	-15.70^{**}
Giza-177 × Sakha-104	-0.05^{**}	0.14^{**}	-0.07^{**}	0.03	-0.05^{**}	-0.03^{**}	-0.61^{**}	-1.46^{**}	-1.49^{**}	-1.45^{**}	-0.02^{**}	-0.01^{**}	-0.02^{**}	-1.12^{**}	0.09^{**}	10.29^{**}	2.64^{**}
Giza-177 × Giza-179	-0.39^{**}	-0.50^{**}	0.07^{**}	-0.82^{**}	0.04^{**}	-0.05^{**}	1.55^{**}	1.51^{**}	-1.80^{**}	-5.05^{**}	-0.12^{**}	0.003^{**}	-0.02^{**}	-0.69^{**}	-0.74^{**}	-24.62^{**}	-17.00^{**}
Giza-177 × Sakha-108	0.34^{**}	0.25^{**}	-0.10^{**}	0.49^{**}	0.11^{**}	0.02^{**}	-2.73^{**}	2.87^{**}	12.24^{**}	7.28^{**}	0.05^{**}	0.04^{**}	0.04^{**}	1.85^{**}	0.21^{**}	23.03^{**}	13.08^{**}
Sakha-104 × Giza-179	0.37^{**}	0.41^{**}	0.11^{**}	0.89^{**}	0.11^{**}	0.03^{**}	2.33^{**}	4.60^{**}	7.11^{**}	4.42^{**}	0.17^{**}	0.04^{**}	0.13^{**}	6.02^{**}	0.16^{**}	24.10^{**}	20.95^{**}
Sakha-104 × Sakha-108	−0.01	-0.09^{**}	0.04^{**}	-0.07^{**}	0.00	0.01^{**}	1.75^{**}	1.45^{**}	2.25^{**}	7.46^{**}	0.06^{**}	0.01^{**}	0.04^{**}	0.76^{**}	0.14^{**}	17.21^{**}	4.33^{**}
Giza-179 × Sakha-108	-0.48^{**}	-0.25^{**}	0.04^{**}	-0.69^{**}	-0.09^{**}	-0.04^{**}	-3.61^{**}	-0.47^{**}	-6.12^{**}	-5.81^{**}	-0.10^{**}	-0.03^{**}	-0.05^{**}	1.14^{**}	0.15^{**}	-37.06^{**}	-19.19^{**}
$LSD_{0.05}$ (Sii)	0.02	0.01	0.01	0.04	0.01	0.002	0.15	0.26	0.99	0.45	0.005	0.001	0.003	0.12	0.02	0.43	0.23
$LSD_{0.01}$ (Sii)	0.022	0.012	0.012	0.043	0.013	0.0021	0.16	0.30	1.16	0.53	0.01	0.005	0.004	0.14	0.022	0.51	0.27
$LSD_{0.05}$ (Sij)	0.02	0.02	0.01	0.05	0.01	0.002	0.17	0.36	1.36	0.62	0.01	0.002	0.004	0.16	0.03	0.60	0.32
$LSD_{0.01}$ (Sij)	0.03	0.02	0.01	0.06	0.01	0.003	0.22	0.45	1.72	0.79	0.01	0.002	0.006	0.20	0.03	0.75	0.40

*, **: significant and highly significant at $P \leq 0.05$ and $P \leq 0.01$, respectively. CHA: chlorophyll a, CHB: chlorophyll b, CAR: carotenoid content, TCH: total chlorophyll content, PC: proline content, ABA: abscisic acid content, SS: soluble sugar content, CA: catalase content, PA: peroxidase content, PPO: polyphenol oxidase, N: nitrogen content, P: phosphorus content, K: potassium content, NPP: number of panicles per plant, HGW: 100-grain weight, FP: fertility percentage, GYP: grain yield per plant.

exhibited highly significant and positive GCA effects for GYP and were considered as good general combiners for grain yield.

SCA

The estimation of SCA effects for various F_1 hybrids is provided in Table 6. Eleven out of 21 crosses showed highly significant and positive SCA effects for CHA. Ten F_1 hybrids demonstrated highly significant and positive SCA effects for CHB. For CAR, 12 crosses out of 21 showed highly significant and positive SCA effects. Ten cross combinations were confirmed to exhibit highly significant and positive SCA for TCH. Highly significant and positive SCA were found in 11 crosses for PC, in eight crosses for ABA, and in 12 crosses for SS and CA.

Eleven crosses out of 21 presented highly significant and positive SCA effects for PA, whereas 12 out of 21 F_1 hybrids were found to be promising for PPO. Ten crosses showed highly significant and positive SCA effects for N content. On the other hand, 11 crosses out of 21 recorded highly significant and positive SCA effects for P. However, 12 crosses showed highly significant and positive SCA effects for K content. Highly significant and positive SCA effects were confirmed in 14, 10, 12, and 12 F_1 hybrids for NPP, HGW, FP and GYP, respectively.

Heterosis

The estimates of heterosis relative to the mid- and the better parents for all the studied traits under drought conditions are presented in Tables 7 and 8. Favorable heterosis and heterobeltiosis in the studied crosses were considered to be positive directions for the studied traits. For CHA, highly significant and positive heterosis over the mid- and better parent were found in 13 and 17 F_1 hybrids, respectively. For CHB, 14 and 16 F_1 crosses demonstrated highly significant and positive heterosis over the mid- and better parents, respectively. Nine and 12 F_1 hybrid combinations were found to show highly significant and positive heterosis and heterobeltiosis for CAR, respectively. With respect to TCH, 12 and 14 F_1 hybrid combinations showed highly significant and positive heterosis and heterobeltiosis, respectively. Sixteen and 19 F_1 hybrids out of 21 demonstrated highly significant and positive heterosis over the mid- and better parents for PC.

Fifteen and 16 hybrid combinations demonstrated highly significant and positive heterosis related to the mid- and better parents for ABA (Tables 7 and 8). For SS, 15 and 16 hybrid combinations were found to be highly significant with positive heterosis over the mid- and better parents. Sixteen out of 21 F_1 hybrids illustrated positive and highly significant heterosis over the mid- and better parents for CA. Twelve and thirteen crosses were found to be highly significant with positive heterosis and heterobeltiosis, respectively, for PA. Highly significant and positive heterosis and heterobeltiosis were recorded in 14 and 18 crosses for PPO. Highly significant and positive heterosis over the mid- and better parents were presented by 10 and 14 crosses for N content and 12 and 15 crosses for P content. Fourteen and 16 crosses were found to be highly significant with positive heterosis over the mid- and better parents for K content. With respect to NPP, 18 and 20 crosses showed highly significant and positive heterosis and heterobeltiosis, respectively.

For HGW, eight and 10 F_1 hybrid combinations were confirmed to show highly significant and positive heterosis over the mid- and better parents, respectively. For FP, 13 out of 21 F_1 hybrids exhibited highly significant and positive heterosis over the mid- and better parents. Fourteen crosses showed highly significant and positive heterosis over the mid- and better parents for GYP.

Correlation coefficient

Correlation coefficient analysis revealed that CHA had highly significant and positive correlations with CHB, TCH, PC, ABA, SS, CA, PA, N, P, K, NPP, FP, and GYP and significant positive correlations

Table 7. Heterotic effects (over the mid-parent) in F_1 hybrids for various traits under deficit irrigation conditions.

F_1 Hybrids	CHA	CHB	CAR	TCH	PC	ABA	SS	CA	PA	PPO	N	P	K	NPP	HGW	FP	GYP
IRAT-112 × N-22	9.07**	17.13**	−1.48**	9.71**	14.33**	25.42**	42.33**	19.27**	11.01**	7.66**	18.82**	8.37**	69.02**	13.84**	10.69**	47.19**	80.94**
IRAT-112 × Azucena	17.79**	29.07**	6.79**	19.51**	9.80**	32.94**	32.19**	32.72**	20.19**	15.92**	17.33**	11.86**	56.31**	79.68**	−19.21**	33.14**	98.35**
IRAT-112 × Giza-177	8.15**	3.97**	−0.47**	5.22**	32.19**	12.34**	28.08**	34.96**	7.86**	17.95**	16.74**	7.41**	43.62**	60.54**	−7.60**	−34.20**	−7.79**
IRAT-112 × Sakha-104	−8.05**	−0.48**	−13.89**	−6.55**	11.49**	3.10**	−5.29**	−5.28**	−5.29*	−19.37**	−35.56**	−24.41**	26.32**	−3.38**	−24.95**	−75.08**	−57.14**
IRAT-112 × Giza-179	−5.46**	0.43**	−24.03**	−7.00**	10.95**	1.24**	12.66**	12.66**	5.56*	8.70**	−5.46**	−14.85**	−21.67**	6.33**	−1.98**	−79.03**	−17.08**
IRAT-112 × Sakha-108	3.21**	−17.07**	−19.72**	−8.00**	3.68**	10.24**	−28.17**	−2.75**	−7.34**	−11.16**	−30.42**	−22.54**	−6.46**	7.80**	−24.53**	−78.87**	−60.21**
N-22 × Azucena	1.26**	16.44**	15.29**	8.70**	3.30**	15.21**	41.59**	14.96**	14.96**	11.03**	6.36**	7.17**	−37.06**	66.36**	0.57**	56.65**	79.86**
N-22 × Giza-177	−28.71**	3.88**	−1.92**	−12.71**	−4.56**	−5.04**	−2.12**	−20.54**	−21.64**	17.19**	−15.18**	−16.38**	−5.65**	33.72**	8.65**	17.06**	19.15**
N-22 × Sakha-104	19.48**	10.00**	−3.90**	11.83**	8.33**	−8.87**	37.74**	12.60**	12.58**	−3.32**	−1.39**	7.08**	−20.21**	22.52**	−4.29**	63.08**	67.82**
N-22 × Giza-179	27.84**	35.67**	12.34**	27.47**	13.71**	11.72**	41.61**	18.96**	7.28**	3.58**	23.91**	14.98**	31.21**	19.61**	−3.53**	47.64**	74.34**
N-22 × Sakha-108	23.44**	1.37**	−12.45**	9.04**	−5.84**	4.92**	3.08**	−15.93**	−16.98**	2.29*	7.90**	−1.37**	14.29**	−9.84**	−11.28**	40.64**	20.27**
Azucena × Giza-177	34.81**	38.06**	26.65**	34.60**	15.14**	42.16**	32.62**	33.48**	21.77**	25.74**	47.11**	18.59**	49.14**	113.2**	−11.35**	31.87**	125.1**
Azucena × Sakha-104	−2.40**	−8.10**	−18.21**	−7.20**	−8.21**	50.27**	5.19**	5.20**	5.19**	−11.45**	−8.37**	−4.08**	15.22**	48.27**	−2.63**	−17.84**	5.98**
Azucena × Giza-179	47.38**	48.64**	15.58**	42.07**	7.74**	35.51**	25.81**	26.34**	11.05**	12.24**	46.85**	13.43**	36.29**	120.9**	40.32**	32.65**	108.6**
Azucena × Sakha-108	−0.67**	−11.57**	4.39**	−3.66**	−1.58**	−9.04**	−8.53**	−8.53**	−12.88**	20.93**	−24.81**	−22.65**	−6.98**	−13.4**	−7.36**	−68.68**	−48.43**
Giza-177 × Sakha-104	−1.60**	13.17**	−11.48**	2.14**	1.96**	−12.64**	2.49**	2.49**	1.00	0.77	−3.55**	−1.59**	10.98**	21.10**	−1.89**	17.60**	24.09**
Giza-177 × Giza-179	−15.64**	−23.38**	14.19**	−13.05**	19.29**	−24.02**	19.69**	19.65**	1.44	−1.03	−12.17**	9.26**	9.12**	38.13**	−28.35**	−40.71**	−38.79**
Giza-177 × Sakha-108	17.21**	10.37**	−16.16**	8.79**	24.00**	2.68**	−28.73**	10.64**	3.90*	25.14**	3.28**	22.63**	18.83**	34.35**	1.82**	14.31**	29.92**
Sakha-104 × Giza-179	25.42**	34.31**	13.18**	26.23**	25.08**	18.01**	25.53**	25.57**	8.78**	4.32**	34.06**	24.99**	45.54**	77.89**	6.88**	24.04**	79.38**
Sakha-104 × Sakha-108	2.04**	−10.72**	−3.73**	−3.82**	1.35**	2.01**	2.21**	2.17**	−2.53	11.87**	−0.21**	2.49**	14.66**	11.54**	0.16**	8.23**	0.09
Giza-179 × Sakha-108	−18.91**	−17.53**	4.60**	−13.95**	−10.10**	−19.74**	−29.44**	2.77**	−7.57**	−7.15**	−19.73	−16.39**	−9.41**	25.84**	5.48**	−74.34**	−72.21**
$LSD_{0.05}$	0.07	0.05	0.02	0.14	0.02	0.01	0.49	1.01	3.88	1.77	0.02	0.01	0.01	0.46	0.07	1.70	0.90
$LSD_{0.01}$	0.10	0.07	0.04	0.21	0.03	0.01	0.75	1.53	5.87	2.69	0.03	0.01	0.02	0.69	0.11	2.57	1.37

*, **: significant and highly significant at $P \leq 0.05$ and $P \leq 0.01$, respectively. CHA: chlorophyll a, CHB: chlorophyll b, CAR: carotenoid content, TCH: total chlorophyll content, PC: proline content, ABA: abscisic acid content, SS: soluble sugar content, CA: catalase content, PA: peroxidase content, PPO: polyphenol oxidase, N: nitrogen content, P: phosphorus content, K: potassium content, NPP: number of panicles per plant, HGW: 100-grain weight, FP: fertility percentage, GYP: grain yield per plant.

Table 8. Heterotic effects (over better-parent) in F_1 hybrids for various traits under deficit irrigation conditions.

F1 hybrids	CHA	CHB	CAR	TCH	PC	ABA	SS	CA	PA	PPO	N	P	K	NPP	HGW	FP	GYP
IRAT-112 × N-22	11.47**	17.30**	−0.57**	10.65**	20.57**	44.95**	62.45**	30.58**	21.53**	13.98**	25.74**	8.55**	101.93**	26.48**	18.87**	101.78**	91.32**
IRAT-112 × Azucena	30.20**	39.15**	23.46**	32.04**	22.16**	34.60**	32.89**	33.44**	20.84**	25.33**	27.95**	13.11**	92.81**	126.73**	−7.41**	51.21**	141.0**
IRAT-112 × Giza-177	22.33**	5.02**	12.67**	13.50**	35.53**	17.23**	28.75**	35.66**	8.94**	28.64**	43.68**	14.37**	60.92**	100.15**	−1.26**	−33.03**	−4.65**
IRAT-112 × Sakha-104	5.99**	0.67**	−9.68**	0.23*	12.70**	12.37**	−2.49**	−2.48*	−2.49	−17.81**	−29.11**	−21.39**	33.68**	−0.81*	−18.76**	−73.08**	−56.01**
IRAT-112 × Giza-179	10.94**	8.51**	−18.15**	4.45**	11.87**	10.89**	14.18**	14.18**	14.18**	9.94**	7.56**	−9.33**	−5.98**	12.71**	7.56**	−78.93**	−15.59**
IRAT-112 × Sakha-108	20.51**	−15.01**	−14.86**	−1.11**	4.06**	17.48**	−26.79**	−0.86	−0.87	−1.23	−20.54**	−17.23**	−1.02**	15.08**	−19.0**	−78.48**	−59.91**
N-22 × Azucena	9.35**	25.73**	34.68**	18.97**	8.70**	31.31**	60.66**	26.61**	26.59**	13.27**	9.43**	8.55**	−35.30**	138.07**	6.90**	85.62**	105.3**
N-22 × Giza-177	−21.26**	4.78**	12.16**	−6.70**	3.33**	4.76**	11.06**	−12.52**	−15.12**	20.53**	−2.08**	−11.11**	0.00	88.89**	9.15**	56.95**	21.7**
N-22 × Sakha-104	34.45**	11.11**	1.76**	18.86**	12.97**	−3.79**	62.42**	19.54**	19.52**	4.45*	2.29**	11.18**	−10.46**	40.10**	−3.57**	103.91**	72.75**
N-22 × Giza-179	46.39**	46.81**	22.22**	41.83**	20.97**	17.39**	64.08**	28.38**	8.49*	10.98**	32.73**	22.22**	31.74**	41.67**	−1.56**	101.17**	87.84**
N-22 × Sakha-108	40.66**	3.74**	−6.25**	16.14**	−0.32**	13.27**	20.19**	−9.82**	−15.17**	7.14**	15.99**	5.22**	28.28**	7.62**	−11.17**	88.39**	26.19**
Azucena × Giza-177	37.68**	50.46**	29.07**	37.64**	31.67**	46.46**	32.62**	33.51**	23.65**	26.76**	64.58**	27.78**	62.73**	115.40**	−5.30**	46.88**	163.3**
Azucena × Sakha-104	1.42**	0.30**	−10.21**	−4.59**	0.92**	61.62**	8.88**	8.91**	8.89*	−2.26	−7.63**	0.92**	33.30**	81.39**	2.69**	−13.91**	24.98**
Azucena × Giza-179	55.67**	48.94**	23.46**	44.23**	20.97**	46.46**	28.18**	28.75**	20.81**	22.84**	52.73**	22.22**	39.53**	160.74**	46.04**	49.86**	158.8**
Azucena × Sakha-108	4.45**	−2.11**	13.30**	−1.15**	9.93**	−4.33**	−6.27**	−6.24**	−6.26*	24.10**	−21.53**	−16.36**	7.64**	1.39**	−1.39**	−65.14**	−37.88**
Giza-177 × Sakha-104	0.09	13.33**	−4.77**	2.69**	5.70**	−8.92**	6.08**	6.08**	2.93	12.21**	6.96**	0.67**	17.16**	46.41**	−0.69**	24.68**	24.99**
Giza-177 × Giza-179	−12.82**	−16.31**	19.59**	−9.70**	21.28**	−20.40**	21.94**	21.90**	8.57*	9.28**	−5.76**	9.26**	16.14**	61.16**	−26.54**	−39.94**	−35.53**
Giza-177 × Sakha-108	20.60**	11.98**	−10.81**	9.15**	26.67**	4.76**	−26.97**	13.38**	10.01*	27.38**	10.42**	23.04**	25.47**	55.56**	2.16**	14.39**	33.33**
Sakha-104 × Giza-179	27.40**	46.91**	16.13**	31.82**	27.50**	18.56**	27.50**	27.54**	14.14**	5.13**	38.27**	27.86**	64.04**	83.54**	8.24**	33.32**	87.52**
Sakha-104 × Sakha-108	3.21**	−9.54**	−2.71**	−3.63**	2.83**	4.19**	3.22**	3.18**	1.19	27.03**	3.29**	5.20**	14.69**	15.88**	1.04**	14.67**	1.96*
Giza-179 × Sakha-108	−18.56**	−8.51**	6.17**	−10.34**	−9.68**	−17.63**	−29.03**	3.36**	−6.61	4.52**	−19.46**	−16.11**	2.13**	26.68**	7.78**	−73.99**	−71.50**
$LSD_{0.05}$	0.10	0.07	0.03	0.21	0.03	0.01	0.74	1.52	5.82	2.66	0.03	0.01	0.02	0.69	0.11	2.55	1.36
$LSD_{0.01}$	0.19	0.13	0.06	0.39	0.06	0.02	1.36	2.79	10.69	4.89	0.05	0.02	0.03	1.26	0.21	4.67	2.49

*,**: significant and highly significant at $P \leq 0.05$ and $P \leq 0.01$, respectively. CHA: chlorophyll a, CHB: chlorophyll b, CAR: carotenoid content, TCH: total chlorophyll content, PC: proline content, ABA: abscisic acid content, SS: soluble sugar content, CA: catalase content, PA: peroxidase content, PPO: polyphenol oxidase, N: nitrogen content, P: phosphorus content, K: potassium content, NPP: number of panicles per plant, HGW: 100-grain weight, FP: fertility percentage, GYP: grain yield per plant.

Table 9. Correlation coefficient determined among various traits under deficit irrigation conditions.

Traits	CHA	CHB	CAR	TCH	PC	ABA	SS	CA	PA	PPO	N	P	K	NPP	HGW	FP
CHB	0.71**															
CAR	0.38*	0.39*														
TCH	0.94**	0.88**	0.53**													
PC	0.58**	0.49**	0.30	0.59**												
ABA	0.60**	0.57**	0.22	0.62**	0.38*											
SS	0.48**	0.52**	0.45**	0.56*	0.61**	0.44**										
CA	0.60**	0.56**	0.53**	0.66**	0.74**	0.49**	0.75**									
PA	0.51**	0.51**	0.50**	0.59**	0.52**	0.50**	0.63**	0.87**								
PPO	0.30	0.45**	0.28	0.40*	0.44**	0.20	0.50**	0.46**	0.31*							
N	0.82**	0.73**	0.54**	0.87**	0.58**	0.65**	0.68**	0.72**	0.62**	0.55**						
P	0.68**	0.66**	0.48**	0.74**	0.70**	0.53**	0.64**	0.77**	0.70**	0.45**	0.83**					
K	0.54**	0.57**	0.32*	0.60**	0.58**	0.60**	0.51**	0.58**	0.39*	0.38*	0.66**	0.62**				
NPP	0.52**	0.62**	0.54**	0.64**	0.52**	0.62**	0.57**	0.76**	0.62**	0.45**	0.67**	0.60**	0.47**			
HGY	0.18	0.35*	0.15	0.27	-0.14	0.19	0.01	0.05	0.10	0.29	0.40*	0.16	0.09	0.26		
FP	0.51**	0.72**	0.37*	0.65**	0.27	0.43**	0.51**	0.40*	0.48**	0.38*	0.66**	0.78**	0.45**	0.41**	0.35*	
GYP	0.71**	0.89**	0.47**	0.85**	0.52**	0.65**	0.69**	0.68**	0.69**	0.56**	0.84**	0.82**	0.61**	0.70**	0.36*	0.86**

*, **: Significant and highly significant at 0.05 and 0.01 probability, respectively. CHA: chlorophyll a, CHB: chlorophyll b, CAR: carotenoid content, TCH: total chlorophyll content, PC: proline content, ABA: abscisic acid content, SS: soluble sugar content, CA: catalase content, PA: peroxidase content, PPO: polyphenol oxidase, N: nitrogen content, P: phosphorus content, K: potassium content, NPP: number of panicles per plant, HGW: 100-grain weight, FP: fertility percentage, GYP: grain yield per plant.

with CAR (Table 9). CHB had highly significant and positive correlations with TCH, PC, ABA, SS, CA, PA, PPO, N, P, K, NPP, FP, and GYP and significant positive correlations with CAR and HGW. CAR revealed highly significant and positive correlations with TCH, SS, CA, PA, N, P, NPP, and GYP and significant positive correlations with K and FP. TCH presented highly significant and positive correlations with PC, ABA, CA, PA, N, P, K, NPP, FP, and GYP and significant positive correlations with SS and PPO. PC had highly significant and positive correlations with SS, CA, PA, PPO, N, P, K, NPP, and GYP and significant positive correlations with ABA. ABA revealed highly significant and positive correlations with SS, CA, PA, N, P, K, NPP, FP, and GYP.

The trait SS had highly significant and positive correlations with CA, PA, PPO, N, P, K, NPP, FP, and GYP (Table 9). CA recorded highly significant and positive correlations with PA, PPO, N, P, K, NPP, and GYP and significant positive correlations with FP. PA had highly significant and positive correlations with N, P, NPP, FP, and GYP and significant positive correlations with PPO and K. PPO showed highly significant and positive correlations with N, P, NPP, and GYP and significant positive correlations with K and FP. N content had highly significant and positive correlations with P, K, NPP, FP, and GYP and a significant positive correlation with HGW. P content had highly significant and positive correlations with K, NPP, FP, and GYP. K revealed highly significant and positive correlations with NPP, FP, and GYP. NPP showed highly significant and positive correlations with FP and GYP. HGW had significant and positive correlations with FP and GYP. FP had a highly significant and positive correlation with GYP. GYP had highly significant and positive correlations with CHA, CHB, CAR, TCH, PC, ABA, SS, CA, PA, PPO, N, P, K, NPP, FP, and GYP and a significant positive correlation with HGW.

DISCUSSION

Significant differences were observed among genotypes (parents, crosses, and parents vs. crosses) under drought conditions for all the studied traits, implying the appreciable amount of genetic variability of the parents, crosses, and parents vs. crosses used. Thus, the evaluated genotypes could be selected for further genetic improvement on the basis of grain yield and other physiological traits under drought conditions. Highly significant genetic variability is present among lines, testers, and line × tester interactions for flag leaf area, panicle density, harvest index, biological yield per plant, and yield per plant (Saleem *et al*., 2010). Tiwari *et al*. (2011) found that parents, crosses, and parents vs. crosses are highly significant for various traits, i.e., days to 50% flowering, effective tillers per plant, panicle length, number of spikelets per panicle, number of fertile spikelets, spikelet fertility percent, GYP, HGW, biological yield, and harvest index. Significant parents vs. crosses populations were studied for useful heterosis, which can be used to identify improved genotypes for all the traits under water stress conditions. Previous researchers have emphasized the importance of genetic variation in the breeding of new improved rice varieties (Wang *et al.,* 2018). Combining ability analysis revealed significant GCA and SCA variances for all of the traits under drought conditions, suggesting the importance of additive and nonadditive gene actions in the expression of these traits. GCA can be applied to identify superior parental genotypes, whereas SCA helps in the identification of promising hybrids that may ultimately lead to the development of hybrid populations (Saleem *et al*., 2010). The GCA:SCA ratio is used to identify the nature of existing gene action. The GCA:SCA ratio was less than unity for all studied traits, except for PA activity indicating that the nonadditive type of gene action was of greater importance in the inheritance of all studied characters than other types of gene action. Therefore, selection based on the accumulation of nonadditive effects would be more effective and successful in improving these traits in later generations. Through combining ability analysis, Malemba *et al.* (2017) revealed that in rice, the GCA:SCA for spikelet fertility, grain yield, thousand-grain weight, and panicles/plant are controlled by nonadditive genes under drought conditions. Hybridization and then intensive selection in later generations are recommended for the improvement of traits that are governed by nonadditive gene actions. The relatively high level of GCA variances indicated the main role of additive gene action for traits, such as stomatal conductance, net photosynthetic rate, CO_2 concentration, leaf temperature, and fertility percentage, under drought conditions. Selection and pedigree breeding methods are feasible for the improvement of rice traits governed by additive gene action (Malemba *et al.,* 2017). The inheritance of amylose content and gel consistency in rice has been revealed to be predominantly governed by additive gene action. The genetic diversity existing in Rwandan rice cultivars offers opportunities to develop quality characteristics in rice (Mukamuhirwa *et al*., 2019).

The F_1 hybrids exhibited higher mean values for the majority of the physiological traits associated with drought tolerance. The results further showed that the F_1 hybrid Azucena × Giza-177 had superior values for all traits, except for HGW, under drought stress conditions. The hybrid combination Azucena × Giza-179 provided desirable mean values for most studied traits, except for CAR and PC, for which moderate values were obtained. Desirable mean values for most of the variables were shown by the F_1 cross Sakha-104 × Giza-179. The superior mean values for physiological and morphological traits were obtained in the cross combinations IRAT-112 × N-22, IRAT-112 × Azucena, and N-22 × Giza-179. Drought damages photosynthetic pigments and thylakoid membranes (Fahad *et al.,* 2017). Al-Ashkar *et al.* (2016) reported that Line-8 has the highest amount of proline under water shortage conditions and thus demonstrates the highest tolerance to water stress conditions. Five genotypes, viz., Norungan, CT-9993, Moroberekan, Nootripathu, and MDU-5, provided significantly superior mean values than the grand mean for most of the traits, and these genotypes can be used as donors in drought resistance breeding programs (Ganapathy *et al*., 2010).

Antioxidant enzymes, such as PA, CAT, and PPO, are induced by the drought stress. The enhanced expression of antioxidant enzymes assists the crop plants in adaptation under adverse environmental conditions. The cultivar IRAT-259 showed an increased percentage of antioxidant enzymes under drought stress. ABA has vital roles in modulating stomatal density and movement in response to environmental conditions. Under water shortage, ABA accumulates in roots and leaves but tends to accumulate more in roots than in foliage (Wang *et al.,* 2007). Compared with other genotypes, Azucena × Giza-177 and Azucena × Giza-179 recorded higher values of photosynthetic pigments and thylakoid membranes (CHA, CHB, and CAR) and were thus considered as drought stress tolerant. Subsequently, the F_1 hybrids Azucena × Giza-177, Azucena × Giza-179, Sakha-104 × Giza-179, IRAT-112 × N-22, IRAT-112 × Azucena, and N-22 × Giza-179 had higher mean values for antioxidants (PC, CA, PA, and PPO), nutrient content (N, P, and K), and SS and high ABA concentrations and thus exhibited high tolerance for drought stress conditions. The above crosses also revealed the best values for grain yield and its components under drought stress conditions.

The significant and positive GCA effects of the parental genotypes for the studied traits are a good indication of enhancement in tolerance to drought stress conditions. GCA effects can be applied to identify the promising parental genotypes for the further improvement of various traits of rice. They can define the average performance of each parental genotype with that of other parents and restrict the selection of parents for the further improvement of tolerance to water stress. Gramaje *et al*. (2020) reported that the estimated GCA effects help in identifying the parental genotypes with the best genetic potential to produce individuals with desirable traits after consequent selections. The genotypes N-22, Azucena, and Giza-179 were good general combiners for improving most of the traits studied under water deficit conditions. Thus, selection to enhance such traits would be practiced on the basis of mean performance and GCA effects. SCA effects can be utilized to identify particular cross combinations for various physiological and yield traits. High-yielding genotypes with higher values of chlorophyll pigments, antioxidant defense, nutrient content, and grain yield and its component under stress environments can be selected. The F1 hybrids Azucena × Giza-177, Sakha-104 × Giza-179, IRAT-112 × Azucena, Azucena × Giza-179, IRAT-112 × N-22, Giza-177 × Sakha-108, and N-22 × Giza-179 were the top-ranking populations for drought tolerance and physiological and yield components. A good combination of crosses with high SCA values are ideal for heterosis breeding, although the selection of crosses with high SCA effects do not generally lead to the direct improvement of self-pollinated crops, such as rice. Transgressive segregants can be potentially identified from the best-performing hybrids and then fixed in subsequent generations (Gramaje *et al*., 2020). All these promising crosses shared one of the good general combiner with drought tolerance, signifying that these crosses will eventually yield desirable transgressive segregants (Malemba *et al.,* 2017). The parental genotypes used in this study were genetically varied and could be selected for different traits for further improvement. Previous research has also reported similar findings in different rice populations studied under water stress conditions (Kang and Futakuchi, 2019). Desirable parental rice genotypes could be selected through different breeding methods on the basis of mean performance, combining ability, and nature of gene action (Utharasu and Anandakumar, 2013).

Significant positive heterosis over the mid- and better parents was expressed by F_1 hybrids viz., Azucena × Giza-177, Azucena × Giza-179, IRAT-112 × Azucena, N-22 × Azucena, and IRAT-112 × N-22 for the majority of the traits, indicating that these hybrids were found to be best suited to aerobic conditions and provide desirable direction for the further improvement of tolerance to drought stress conditions. Traits that are independently or in combination related to drought, such as chlorophyll pigments, antioxidants, nutrients content and yield components, may be the basis of selection in rice genotypes under moisture stress conditions (Ram *et al.,* 2019).

The correlation among various traits, particularly economic and complex characteristics, such as yield, is an important factor. Steel and Torrie (1996) mentioned that correlations are the magnitude of the level of association between traits. In this study, grain yield showed highly significant and positive correlations with the majority of the traits. The selection for one trait resulted in progress for all other traits that are positively correlated. These results are in conformity with past findings on heterosis, combining ability, and phenotypic correlation in economic traits of rice (Zaazaa and Anis, 2014).

CONCLUSIONS

The governance of physiological traits, including chlorophyll pigment, antioxidant, and nutrient contents, and yield components, including grain yield, fertility percentage, HGW, and productive tillers per plant, by nonadditive genes suggested that hybridization followed by intensive selection in later generations might be effective for the further improvement of these traits under drought conditions. Three parents, i.e., N-22, Azucena, and Giza-179, were found to be good general combiners for physiological traits and yield components under water stress conditions and hence could be utilized in future hybridization programs for the introgression of drought tolerance into elite rice lines. The F1 hybrids, viz., Azucena × Giza-179, Azucena × Giza-177, Azucena × Sakha-104, N-22 × Giza-179, and Sakha-104 × Giza-179, showed the best performance for the studied traits with desirable heterosis over the better parent. These promising populations could be used in future breeding program to develop drought-tolerant and high-yielding rice genotypes.

ACKNOWLEDGEMENTS

This publication was made possible through the support provided by Rice Research and Training Center, Egypt. The authors also express the sincere appreciation to Field Crops Research institute, Agricultural Research Center, Egypt for conducting this study.

REFERENCES

Akanksha, Jaiswal HK (2019). Combining ability studies for yield and quality parameters in basmati rice (*O. sativa* L.) genotypes using diallel approach combining ability studies for yield and quality parameters in basmati rice. *Electr. J. Plant Breed.* 10(1): 9–17.

Al-Ashkar IM, Zaazaa EI, EL-Sabagh A, Barutçular C (2016). Physio-biochemical and molecular characterization for drought tolerance in rice genotypes at early seedling stage. *J. Exp. Biol. Agric. Sci.* 4(6): 675–687.

Barrs HD, Weatherly PE (1962). Genetic studies of some physiological and shoot characters in relation to drought tolerance in rice. *Aust. J. Biol. Sci.* 15: 413–428.

Bates LS, Waklren RP, Teare ID (1973). Rapid determination of free proline water stress studies. *Plant Soil* 39: 205–207.

Black CA, Evan's DO, Ensmunger LE, White JL, Clark RC (1965). Methods of soil analysis. II. chemical and microbiological properties, American Soc. Argon Inc., Madison, Wisconsin, USA. 32–122.

Butany WT (1961). Mass emasculation in rice. *Int. Rice Com. Newsletter*. 9: 9–13.

Chapman HD, Pratt PE (1978). Methods of analysis for soils, plants and waters. Univ. of Calif., Div. *Agric. Sci. Priced Pub.* 4034: 50–169.

Din J, Khan SU, Ali I, Gurmani AR (2011). Physiological and agronomic response of canola varieties to drought stress. *J. Anim. Plant Sci.* 21(1): 78–82.

Fahad S, Bajwa AA, Nazir U, Anjum SA, Farooq A, Zohaib A, Sadia S, Nasim W, Adkins S, Saud S, Ihsan MZ, Alharby H, Wu C, Wang D, Huang J (2017). Crop production under drought and heat stress: plant responses and management options. *Front. Plant Sci.* 8(1147): 1–16.

Faralli M, Matthews J, Lawson T (2019). Exploiting natural variation and genetic manipulation of stomatal conductance for crop improvement. *Curr. Opinion in Plant Biol.* 49: 1–7.

Gaballah MM, Abdallah AA (2015). Effect of water irrigation shortage on some quantitative characters at different rice development growth stages. *World Rural Observ.* 16(2): 39–55.

Ganapathy, S., Ganesh SK, Shanmugasundaram P, Babu RC (2010). Studies on root traits for drought tolerance in rice (*O. sativa* L.) under controlled (PVC pipes) condition. *Electr. J. Plant Breed.* 1(4): 1016–1020.

Gramaje, LV, Caguiat JD, Enriquez JOS, Cruz QDD, Millas RA, Carampatana JE, Tabanao DAA (2020). Heterosis and combining ability analysis in CMS hybrid rice. *Euphytica* 216(1): 1–22.

Griffing B (1956). Concept of general and specific combining ability in relation to diallel crossing system. *Aust. J. Biol. Sci.* 9: 463–493.

Ibrahim MH, Jaafar HZE (2011). Enhancement of leaf gas exchange and primary metabolites under carbon dioxide enrichment up-regulates the production of secondary metabolites in *Labisia pumila* seedlings. *Molecules* 16: 3761–3777.

IRRI (2016). Standard Evaluation System (SES) for Rice (IRRI), Los Banios, Manila Philippines.

Jackson ML (1973). Soil chemical analysis, constable and Co$_2$. *Agric. Exp. Mad. Wisconsin.* 183–187.

Jain M, Tiwary S, Gadre R (2010). Sorbitol-induced changes in various growth and biochemical parameters in maize. *Plant, Soil and Environ.* 56(6): 263–267.

Kang D, Futakuchi K (2019). Effect of moderate drought-stress on flowering time of interspecific hybrid progenies (*O. sativa* L. × *O. glaberrima* Steud.). *J. Crop Sci. Biotechnol*. 22(1): 75–81.

Kar M, Mishra D (1976). Catalase, PA, and polyphenoloxidase activities during rice leaf senescence. *Plant Physiol*. 57(2): 315–319.

Lohithaswa ADS, Kalappanavar IK, Bandivadder TT (2013). Combining ability in tetraploid wheat for yield, yield attributing traits, quality and rust resistance over environments. *J. Agric. Sci.* 26: 190–193.

Lum MS, Hanafi MM, Akmar ASN (2014). Effect of drought stress on growth, proline and antioxidant enzyme activities of upland rice. *J. Anim. Plant Sci.* 24(5): 1487–1493.

Malemba, GM, Nzuve FM, Kimani JM, Olubayo MF, Muthomi JW (2017). Combining ability for drought tolerance in upland rice varieties at reproductive stage. *J. Agric. Sci.* 9(3): 138–150.

Mcclung AM, Rohila JS, Henry CG, Lorence A (2020). Response of US rice cultivars grown under non-flooded irrigation management. *Agron*. 10(55): 1–19.

Moran R (1982). Formulae for determination of chlorophyllous pigments extracted with n,n -dimethylformamide. *Plant Physiol*. 69(6): 1376–1381.

Mukamuhirwa A, Hovmalm HP, Bolinsson H, Ortiz R, Nyamangyoku O, Johansson E (2019). Concurrent drought and temperature stress in rice - a possible result of the predicted climate change: Effects on yield attributes, eating characteristics, and health promoting compounds. *Int. J. Environ. Res. Public Health* 16(6): 2-17.

Ram M, Kumar N, Singh S, Singh P, Bhattacharyya PK (2019). Estimation of heterosis and inbreeding depression for yield and yield components in rice (*O. sativa* L.) under drought stress conditions. *J. Pharm. Phytochem.* 8(6): 1497–1507.

Sahebi M, Hanafi MM, Rafii MY, Mahmud TMM, Azizi P, Osman M, Abiri R., Taheri S, Kalhori N, Shabanimofrad M, Miah G, Atabaki N (2018). Improvement of drought tolerance in rice (*O. sativa* L.): genetics, genomic tools, and the wrky gene family. *BioMed Res. Inter.* 1–20.

Saleem, MY, Mirza JI, Haq MA (2010). Combining ability analysis of some morphophysiological traits in basmati rice. *Pak. J. Bot*. 42(5): 3113–3123.

Steel RGD, Torrie JH (1996). Principles and procedures of statistics a biometrical approach 3rd ed McGraw Hill Book Company Inc. New York, USA. 334–381.

Tiwari, DK, Pandey P, Tripathi S, Giri SP, Dwivedi JL (2011). Studies on genetic variability for yield components. *Adv. in Agric. Bot.*. 3(1): 76–81.

Utharasu S, Anandakumar CR (2013). Heterosis and combining ability analysis for grain yield and its component traits in aerobic rice (*O. sativa* L.) cultivars. *Electr. J. Plant Breed.* 4(4): 1271–1279.

Wang S, Xia S, Peng K, Kuang F, Cao Y, Xiao L (2007). Effects of formulated fertilizer synergist on ABA accumulation, proline content and photosynthetic characteristics of rice under drought. *Rice Sci.* 14(1): 42–48.

Wang Y, Cai Q, Xie H, Wu F, Lian L, He W, Chen L, Xie H, Zhang J (2018). Determination of heterotic groups and heterosis analysis of yield performance in *indica* rice. *Rice Sci.* 25(5): 261–269.

Zaazaa EI, Anis GB (2014). Heterosis, combining ability and phenotypic correlation for some economic traits in rice (*O. sativa* L.). the mid*dle East J. Agric. Res.* 3(4): 1155–1162.

Zain NAM, Ismail MR, Mahmood M, Puteh A, Ibrahim MH (2014). Alleviation of water stress effects on MR220 rice by application of periodical water stress and potassium fertilization. *Molecules* 19: 1795–1819.

Zu X, Lu Y, Wang Q, Chu P, Miao W, Wang H, La H (2017). A new method for evaluating the drought tolerance of upland rice cultivars. *The Crop J.* 5(6): 488–498.