



Combining ability analysis of groundnut (*Arachis hypogaea* L.) genotypes for yield and related traits under drought-stressed and non-stressed conditions

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Abstract Genetic advancement and gains in yield and related traits are dependent on the selection of best combiner parents and progenies under the prevailing growing conditions. This study was conducted to determine the combining ability effects of eight selected drought-tolerant groundnut parental lines and their F₂ progenies under drought-stressed (DS) and non-stressed (NS) conditions to determine the gene actions involved in the inheritance of the studied traits and identify the best parents and progenies for further improvement of the crop for moisture stress tolerance. Experiments were conducted at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) in India during 2020 cropping season. Data on some of the important physiological, yield and yield component traits were collected. The general combining ability (GCA) effects of parents were significant ($P < 0.05$) for all assessed traits

under all testing conditions, except for PB under DS and NS conditions in the glasshouse. The specific combining ability (SCA) effects of progenies were significant ($P < 0.05$) for all traits, except for PH across all testing environments and PB under field conditions. The genotype ICGV 10178 was the best general combiner with positive contribution and significance to SCMR, PY, SHP, KY, TBM and HI and reduced SLA. Crosses ICGV 10178 × ICGV 11369, ICGV 10373 × ICGV 15083, ICGV 98412 × ICGV 15094 and ICGV 10178 × ICGV 98412 were the best specific combiners for enhanced pod yield and drought tolerance. The GCA was found predominant over the SCA effect for the inheritance of PY, KY and TBM. Higher GCA: SCA ratios were recorded for PY and KY under both DS and NS conditions, and SCMR, SLA and TBM under DS condition suggesting the predominant role of additive genes conditioning the inheritance of these traits. Therefore, the above new progenies are useful populations for developing improved pure line groundnut varieties with high pod yield and drought tolerance.

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Introduction

Groundnut (*Arachis hypogaea* L., $2n = 4x = 40$), is a nutrient-rich food legume and oilseed crop cultivated mainly in the semi-arid tropics where recurrent drought is common. Groundnut is a predominantly self-pollinating crop with about 5% cross-pollination depending on season and genotype. For example, during the post-rainy season higher outcrossing rate was reported compared with the rainy season and the Spanish type of groundnut shows a higher outcrossing level than the Virginia type (Reddy et al. 1993). Climate change studies predicted increased rainfall variability, likely affecting crop production and productivity under water-limited environments (Watson et al. 2015).

Groundnut yield is affected by drought stress at different growth stages (Rao et al. 1985; Meisner and Karnok 1992) reported 49% and 37% unshelled yield reduction in groundnut due to drought stress during flowering and early pod-filling stages, respectively. Thus, breeding groundnut genotypes with high pod yield potential along with drought-tolerant and desirable agronomic traits is an overriding consideration to sustain groundnut production and productivity. Most groundnut breeding programs had been using yield and surrogate traits such as specific leaf area, chlorophyll content, biomass production, and harvest index for drought tolerance screening (Nigam et al. 2005). However, the inheritance of traits associated with drought adaptation are likely to be genetically complex and governed by polygenes (Ravi et al. 2011). Further, drought tolerance is subject to genotype \times environment interaction (Ravi et al. 2011; Falke et al. 2019).

Knowledge of combining ability effects and mode of gene action responsible for regulating expression of different traits is a prerequisite in planning appropriate breeding strategies for biotic and abiotic stress tolerance (Kiani et al. 2007). The diallel mating design is the most widely used method to determine the combining ability effect and the nature of gene action involved in yield and yield-influencing traits (Falconer and Mackay 1996; Sprague and Tatum 1942) introduced the concept of general combining ability (GCA) and specific combining ability (SCA) effects. GCA of parents is associated with additive gene effects, while the SCA effect of progenies is attributed to dominance and epistasis gene actions (Rojas and Sprague 1952).

Combining ability analysis enables the selection of the best parents and progenies with desirable GCA and SCA effects, in that order, in plant breeding programs. Significantly higher GCA effects is attributed to polygenes with minor gene effect; hence pure line, recurrent or single seed descent selection methods can be effective for enhanced response to selection (Singh and Narayanan 2017). Conversely, a significantly higher SCA effect reveals the predominance of non-additive gene action, and in this case, heterosis breeding is more rewarding in sexually reproducing crops if cost-effective and efficient hybridization techniques are available. If the estimated values of GCA and SCA effects for a trait becomes equal, this suggests an equal contribution of additive and non-additive genetic variance; hence population improvement can be adopted to develop superior genotypes (Singh and Narayanan 2017). In groundnut breeding for drought tolerance, Sanogo et al. (2020) reported a significant GCA effect for pod yield, harvest index, biomass production and shelling percentage, while a significant SCA effect was found for chlorophyll meter reading based on soil-plant analysis development (SPAD) under both drought-stressed and non-stressed conditions.

In Ethiopia, groundnut is one of the most important food and oil crops grown under rainfed conditions. The major groundnut producer regions in the country are Oromia (contributing to 59.2% of the total national production), Benshangul-Gumuz (24.83%), Amhara (7.43%), and Harari (3.29%) (CSA 2018). The total land coverage and national mean yield of groundnut in Ethiopia are estimated to be 80, 842 ha and 1.76 tons/ha, respectively (CSA 2018). In these agro-ecologies, water stress due to erratic rain distribution is the major impediment to crop production. In Eastern Ethiopia, where groundnut is a major crop, drought stress occurring during the flowering stage is a key abiotic constraint (Abady et al. 2019a). A limited number of introduced groundnut varieties were released for cultivation in the country (MoANRs 2016). However, these varieties are late maturing and low yielding and were not bred for drought tolerance. Therefore, there is a need to develop groundnut varieties with high yielding and drought stress tolerance that are adapted for cultivation under rainfed and drought-affected agro-ecologies. In an attempt to develop high yielding and drought-tolerant groundnut cultivars, information on combining ability and mode of gene action

responsible for drought tolerance has paramount importance. There is a dearth of information on combining ability effects and genetic analysis of groundnut to guide selection and cultivar development, especially for moisture stress tolerance, in Ethiopia. Consequently, 100 groundnut genotypes were phenotyped under field conditions and genotyped with high-density single nucleotide polymorphism (SNP) markers at ICRISAT/India to select drought-tolerant and genetically superior parents for breeding. Accordingly, some complementary lines were selected based on their yield potential, biomass production, early maturity and drought tolerance. The selected lines should be bred to develop drought-tolerant and locally adapted cultivars under Ethiopian conditions or similar agro-ecologies. Therefore, the objective of this study was to determine the combining ability effects of eight selected drought-tolerant, agronomical superior and complementary groundnut parental lines and their F₂ progenies under drought-stressed and non-stressed conditions to determine the gene actions involved in the inheritance of the studied traits and identify the best parents and progenies for further improvement of the crop for moisture stress tolerance.

Materials and methods

Study site, plant materials, crosses and mating design

The experiments were conducted at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru in India. ICRISAT is situated at a latitude of 17.51° N and a longitude of 78.27° E with an altitude 545 m above sea level. Eight parents were selected for crosses based on selected based on field phenotypic evaluations and SNP genotyping aiming at yield potential, biomass production, early maturity, drought tolerance and genetic diversity. The details of groundnut parents used for crosses are presented in Table 1. The eight parents consisted of five Spanish bunch type (such as genotypes ICGV 15083, ICGV 10178, ICGV 98412, ICGV 96174 and ICGV 11396) and three Virginia bunch type (ICGV 06175, ICGV 10373 and ICGV 15094). Parent ICGV 98412 is a high yielding genotype with a medium maturity period released for cultivation in Ghana and

Ethiopia (Abady et al. 2019b). Parent ICGV 15083 has high oleic acid content and was released in India (ICRISAT 2020). All the remaining genotypes are advanced breeding lines acquired from ICRISAT/India. The selected parents showed varied maturity duration. Genotypes ICGV 06175 and ICGV 15083 attain physiological maturity at 110 days after sowing (DAS), making them early maturing genotypes for drought tolerance breeding. Genotypes ICGV 10373, ICGV 10178, ICGV 96174, ICGV 11396 and ICGV 15094 attain maturity at 120 DAS, while ICGV 98412 mature in 130 DAS. The stress tolerance index was used to assess the drought tolerance level of the assessed genotypes.

The parents were grown in poly-house under controlled temperatures and light conditions at ICRISAT during 2019/20. Growing media was prepared with a mixture of red soil, sandy soil and farmyard manure with a ratio of 4:3:1, respectively. The media was autoclaved at 200 °C for 2 h on two occasions to ensure soil health. Crosses were performed using a half-diallel mating design without reciprocals to obtain 28 F₁ families. Each parent was grown in five plastic pots, and three seeds were sown in each pot and staggered planted. Hand emasculating and pollination were carried out according to the technique developed by Nigam et al. (1990).

Growing parents and the F₂ families

The genotypes were evaluated under drought-stressed (DS) and non-stressed (NS) conditions in a controlled environment (glasshouse condition) and under non-stressed field conditions during 2019 and 2020. The experiments involved 28 F₂ families and eight parents. The experiments were conducted using a 4 × 9 alpha lattice design with two replications. Growing media for the glasshouse experiment was prepared as described above. Under glasshouse conditions, the genotypes were grown in plastic pots, and three seeds were sown in each pot and evaluated under DS and NS conditions. The pots were maintained with regular irrigation until flowering for both treatments. Stress was imposed at the flowering stage by withholding water until wilting symptoms appeared (Vaidya et al. 2016). For the NS treatment, sufficient irrigation was supplied until physiological maturity. Under field conditions, seed of each genotype were sown in a single row of 4-meter-long with 30 cm between rows

Table 1 Description of groundnut parents used for crosses

No	Genotype	Market type	Breeding history	Seed shape	Seed size	Pod constriction	Maturity class	Drought tolerance
1	ICGV 06175	Virginia bunch	ABL	Round	Small	Moderate	Early	Tolerant
2	ICVG 10373	Virginia bunch	ABL	Round	Medium	Slight	Medium	Tolerant
3	ICGV 15083	Spanish bunch	Cultivar	Elongated	Large	Moderate	Early	Tolerant
4	ICGV 10178	Spanish bunch	ABL	Flat	Large	Slight	Medium	Tolerant
5	ICGV 98412	Spanish bunch	Cultivar	Elongated	Large	Moderate	Medium	Semi-tolerant
6	ICGV 96174	Spanish bunch	ABL	Round	Large	Slight	Medium	Semi-tolerant
7	ICGV 11396	Spanish bunch	ABL	Flat	Medium	Slight	Medium	Semi-tolerant
8	ICGV 15094	Virginia bunch	ABL	Round	Medium	Moderate	Medium	Semi-tolerant

ABL advanced breeding line

and 10 cm between plants. Weather data during field trial is presented in Table 2. The mean annual rainfall during 2020 was 43.9 mm. The field experiment was conducted with supplementary irrigation to evaluate genotypes under optimal conditions. The mean minimum and mean maximum temperatures during the experimental period were 22.70 and 30.96 °C, respectively.

Data collected

DF were recorded by counting the number of days from sowing to when 50% of the total plant stand had reached flowering. Soil plant analysis development (SPAD) chlorophyll meter reading (SCMR) was recorded at 80 days after sowing from three trifoliates of each plant between 8:00 to 9:30 am. The SCMRs were recoded using Minolta SCMR-502 m (Tokyo, Japan), and the reading was taken as described by Rao et al. (2001). Leaf area was measured using a leaf area scanner, and leaves were oven-dried at 80 °C for 48 h. SLA was calculated based on the formula suggested by Rao et al. (2001) as follow:

$$SLA = \text{Leaf area (cm}^2\text{)}/\text{Leaf dry weight (g)}$$

PH (cm) was measured from ten randomly sampled plants from the soil surface to the tip of the main stem. PB was recorded as the average number of primary branches from the ten plants. PY (g plant⁻¹) was recoded as the average pod weight of ten sample plants. SHP (%) for each genotype was calculated from a random sample of pods weighing 200 g, as the proportion of shelled seed weight to the total weight of

the unshelled pods. KY (g plant⁻¹) was estimated as the product of pod yield per plant and shelling outturn and TBM (g plant⁻¹) was recorded as the mean total biomass weight of ten sample plants during physiological maturity of the crop. HI (%) was computed as a ratio of pod weight to total biomass (Mukhtar et al. 2013).

Data analysis

Analysis of variance

The data collected were subjected to analysis of variance using SAS version 9.3 Software (SAS Institute Inc., 2011). Treatment means were separated using the least significant difference (LSD) test at 5% significance level.

Combining ability analysis

Data were subjected to combining ability analysis using a half-diallel (Method II, Model I) approach of Griffing (1956) with Model I and Method II. The linear mathematical model used for the half-diallel per experiment was as follows:

$$Y_{ij} = \mu + g_i + g_j + s_{ij} + \frac{1}{bc} \sum \sum e_{ijkl}$$

where Y_{ij} = the value of a character measured on cross of i th and j th parents; μ = the population mean; g_i = the general combining ability effect of the i th parent; g_j = the general combining ability effect of the j th parent; s_{ij} = the specific combining

Table 2 Monthly weather data during the field trial at ICRISAT/India in 2020

Month	Rainfall (mm)	Tmax (°C)	Tmin (°C)	RHmax (%)	RHmin (%)
June	6.37	33.45	24.05	87.8	63.9
July	7.37	31.35	23.05	90.61	71.25
August	9.69	28.92	22.65	91.87	79.32
September	8.38	30.77	22.59	93.43	76.83
October	12.09	30.33	21.14	93.52	73.35

Tmax, average maximum temperature; Tmin, average minimum temperature; RHmax, average maximum relative humidity; RHmin, average minimum relative humidity

ability effect of the cross between *I*th and *j*th parents such that $s_{ij} = s_{ji}$ and $e_{ijk} =$ the environmental effect associated with *ijk*th observation; *b* and *c* = number of blocks and sample plants, respectively.

The GCA and SCA effects were computed using the AGD-R (Analysis of Genetic Designs in R) software version 5.0 (Francisco et al. 2015). The variance components of GCA and SCA were calculated as per the formula provided in Singh and Chaudhary (1977).

Variance due to GCA

$$\frac{1}{P-1} \sum_{gi} 2 = \frac{M_g - M'_e}{P+2}$$

Variance due to SCA

$$\frac{2}{P(P-1)} \sum_{i<j} s_{ij}^2 = M_s - M'_e$$

Narrow sense heritability was calculated according to Singh and Chaudhary (1977). The predominance of additive versus non-additive gene action was compared from the ratio of components of GCA variance to SCA variance (Baker 1978). The closer the GCA to SCA ratio to unity is, the greater would be the magnitude of additive genetic effects, while the ratio much less than unity suggests a predominant role of non-additive gene effects conditioning trait inheritance.

Results

Analysis of variance

Analysis of variance revealed significant ($p < 0.05$) difference among parents and F2 progenies for all

assessed traits, except PB under both drought-stressed (DS) and non-stressed (NS) conditions in the glasshouse and SHP under NS in the field condition (Table 3). Both GCA \times environment and SCA \times environment interactions were significant ($p < 0.05$) for DF, PB, PY, SHP and KY under NS conditions. In addition, the GCA \times environment interaction effects of these traits were higher than their respective entries \times environment interaction values. Under all testing environments, the GCA effects of the parents showed significant differences for all the traits except PB under DS condition. Furthermore, significant SCA effects were noted for DF, SCMR, PY, SHP, KY, TBM and HI under DS and NS conditions. The relative importance of GCA and SCA effects ranged from 0.01 for PB to 1 for PH under DS condition and 0.06 for DF to 0.99 for TBM. High narrow sense heritability (h^2_n) values were recorded for PY (56.38%) and KY (52.34%) under NS condition, while higher h^2_n values were recorded for SCMR, SLA, PY, KY and TBM with values of 53.56%, 61.24%, 46.64%, 53.69% and 66.46% in that order.

Mean performance

The early flowering genotypes under DS, were ICGV 15094 (29 days) and crosses ICGV 15083 \times ICGV 11396 (29 days), ICGV 06175 \times ICGV 96174 (30 days), ICGV 15083 \times ICGV 98412 (30 days) and ICGV 06175 \times ICGV 15083 (30 days) (Table 4). Under the NS glasshouse condition, the highest mean value for plant height was recorded for the parent ICGV 06175 and crosses ICGV 10178 \times ICGV 96174, ICGV 15083 \times ICGV 11396 and ICGV 15083 \times ICGV 98412 (Table 5).

Table 3 Analysis of variance showing mean square values due to environments (ENV), replications (REP), general combining ability (GCA) effects of the parents, specific combining ability (SCA) effects of crosses for the nine phenotypic traits and chlorophyll meter reading (SCMR) evaluated under non-stressed and drought-stressed conditions

Non-stressed													
Source of variation	df	PB	PH	PY	SHP	KY	SCMR	SLA	TBM	HI	Source of var.	df	
ENV	1	330.03**	215.11*	33994.14**	1263.04**	881.67**	629.25**	REP	1	2.0Ins	98.26ms	699.38**	1.38ns
REP(ENV)	2	0.68*	1.84*	50.82*	56.36*	78.08ns	28.90*	Entries	35	2.0Ins	98.26ms	699.38**	1.38ns
Entries	35	9.37*	5.62ns	61.36*	100.59**	83.58ns	43.60**	GCA	7	24.01*	2275.92*	231.37**	127.17*
GCA	7	8.49*	6.28*	153.41*	315.16**	138.98**	127.83**	SCA	28	53.23*	3664.74*	744.84**	352.66**
SCA	28	9.59*	5.46*	38.35ns	46.95**	69.56*	22.54**	Residual	29	11.351	704.73	58.06	56.84
Entries × ENV	35	0.942*	5.35*	22.91ns	27.95*	79.68*	11.48*	δ ² g		1.27	157.12	17.33	7.03
GCA × ENV	7	1.09*	5.84*	39.74ns	58.34*	153.00*	17.78*	δ ² s		41.88	2960.01	686.78	295.82
SCA × ENV	28	0.91*	5.23*	18.70ns	20.36*	61.55*	9.90*	Baker's ratio		0.03	0.05	0.03	0.02
Residual	58	0.33	2.66	30.09	11.80	29.46	4.08	h ² n		4.54	7.90	4.45	3.84
δ ² g		0.816	0.0362	12.332	30.336	10.952	12.375						
δ ² s		9.26	2.8	8.26	35.15	40.1	18.46						
Baker's ratio		0.09	0.01	1.49	0.86	0.27	0.67						
h ² n		14.54	1.31	39.14	56.38	23.95	52.34						
Drought-stressed													
Source of variation	df	DF	PB	PH	SCMR	SLA	PY	SHP	KY	TBM	HI	Source of var.	df
REP	1	0.12**	0.11ns	19.51*	37.77**	1152.60ms	15.74**	2.23**	2.00*	179.24ns	35.17*		
Entries	35	4.66**	1.68ns	28.11*	18.53**	2475.78*	70.00**	110.33**	27.80**	258.36**	332.68**		
GCA	7	3.24**	2.54ns	42.27*	50.40**	5795.99*	234.65**	187.89**	97.31**	802.65**	916.14**		
SCA	28	5.02**	1.46ns	25.98ns	10.62*	1645.73ns	33.51**	90.94**	13.05**	122.29*	217.68**		
Residual	29	0.18	1.84	14.88	4.5	1044.24	2.37	11.39	0.92	45.91	32.98		
δ ² g		0.306	0.07	2.739	4.59	475.175	20.114	17.65	9.639	75.674	88.316		
δ ² s		4.84	0.38	11.1	6.12	601.49	31.14	79.55	12.13	76.38	184.7		
Baker's ratio		0.06	0.18	0.25	0.75	0.79	0.65	0.22	0.79	0.99	0.48		
h ² n		10.87	8.75	33.04	53.56	61.24	46.64	30.74	53.69	66.46	12.57		

δ²g, variance of GCA; δ²s, variance of SCA; h²n, narrow-sense heritability; df, degrees of freedom; DF, days to 50% flowering; PB, number of primary branches per plant; PH, plant height (cm); SLA, specific leaf area (cm² g⁻¹); PY, pod yield per plant (g); SHP, shelling percentage (%); KY = kernel yield per plant (g); TBM, total biomass yield per plant (g); HI, harvest index (%); ns, non-significant

*Significant at $p \leq 0.05\%$
 **Significant at $p \leq 0.01$

Table 4 Mean values for the nine phenotypic traits and chlorophyll meter reading (SCMR) among eight groundnut parents and 28 F₂ families under drought-stressed glasshouse conditions

Entry	DF	PB	PH	SCMR	SLA	POD	SHP	KY	TBM	HI
<i>Parents</i>										
ICGV 06175	33	8	31.5	45.3	231.87	10.7	66.36	7.10	46.00	30.31
ICGV 10373	31	7.5	24.875	47.4	121.18	8.60	53.53	4.60	37.35	29.67
ICGV 15083	33	7.25	33	46.95	181.35	15.70	59.47	9.35	48.05	48.54
ICGV 10178	35	6.25	35.25	48.25	164.36	18.15	61.10	11.06	54.70	49.64
ICGV 98412	32	6.5	33.25	51.75	245.96	9.80	50.98	5.00	35.85	38.13
ICGV 96174	32	6.5	27	44.3	262.88	5.45	65.79	3.60	25.80	29.91
ICGV 11396	34	7.5	25.5	47.85	194.46	10.80	56.95	6.15	45.50	31.33
ICGV 15094	29	8.5	26	47.3	237.34	2.95	42.73	1.30	29.05	10.65
Mean	32.38	7.25	29.55	47.39	204.8	10.27	57.11	6.02	40.29	33.52
<i>Crosses</i>										
ICGV 06175 × ICGV 15094	33	6.75	34	43.55	251.84	12.65	46.31	5.85	46.95	36.93
ICGV 10373 × ICGV 15094	35	8.25	26.25	48.2	181.23	8.40	59.03	4.90	39.90	26.68
ICGV 15083 × ICGV 15094	33	8	32.5	49.7	188.96	6.80	60.29	4.10	57.80	13.33
ICGV 10178 × ICGV 15094	32	9.25	22.75	52.2	177.55	17.35	64.73	11.25	54.95	46.32
ICGV 98412 × ICGV 15094	34	7	28.75	50.8	169.71	13.85	53.85	7.40	41.90	49.31
ICGV 96174 × ICGV 15094	32	6.25	23.75	39.85	245.95	8.15	42.83	3.50	33.35	36.33
ICGV 11396 × ICGV 15094	32	8.25	31.25	46.85	164.68	9.60	51.94	5.10	48.00	24.85
ICGV 06175 × ICGV 11396	33	7.25	28.25	51.3	194.86	11.85	55.94	6.65	38.35	45.40
ICGV 10373 × ICGV 11396	32	8.25	25	49	196.11	8.85	59.33	5.25	37.35	31.51
ICGV 15083 × ICGV 11396	29	9.25	26.25	47.75	159.24	8.15	50.24	4.10	43.45	23.12
ICGV 10178 × ICGV 11396	31	7.25	25.75	48.45	156.86	21.35	65.81	14.05	60.75	54.19
ICGV 98412 × ICGV 11396	33	6.25	25.75	49.3	147.95	10.95	46.54	5.10	42.50	34.70
ICGV 96174 × ICGV 11396	32	6.5	24.25	46.75	215.22	3.50	51.62	1.80	32.00	11.99
ICGV 06175 × ICGV 96174	30	6.25	19.75	45.7	190.91	13.10	50.02	6.55	48.55	37.26
ICGV 10373 × ICGV 96174	32	7.25	24.75	42	166.18	12.40	62.41	7.70	40.10	44.35
ICGV 15083 × ICGV 96174	33	8.25	29.5	42.05	167.51	8.00	61.33	4.90	46.25	22.47
ICGV 10178 × ICGV 96174	34	7.5	24.5	47.65	131.96	20.90	63.99	13.4	62.30	50.91
ICGV 98412 × ICGV 96174	33	8.25	26.5	45.3	195.91	12.10	54.55	6.60	42.45	40.15
ICGV 06175 × ICGV 98412	31	6.5	26	47.2	201.56	11.30	49.19	5.60	43.90	34.17
ICGV 10373 × ICGV 98412	33	7.25	24	53.65	200.16	11.85	63.79	7.55	40.45	41.97
ICGV 15083 × ICGV 98412	30	6	22	49.9	176.9	20.70	43.35	8.95	64.55	47.36
ICGV 10178 × ICGV 98412	33	6.25	33	51.35	180.93	22.65	67.32	15.25	67.10	51.32
ICGV 06175 × ICGV 10178	32	8	29	44.55	132.96	20.20	61.72	12.45	56.90	55.06
ICGV 10373 × ICGV 10178	34	7.75	27.5	51.2	166.68	20.40	61.98	12.60	62.30	48.65
ICGV 15083 × ICGV 10178	32	7	27.25	45.8	145.43	28.65	49.34	14.15	70.05	69.84
ICGV 06175 × ICGV 15083	30	9	33.5	47.4	214.28	17.50	62.61	10.95	55.75	45.80
ICGV 10373 × ICGV 15083	34	7.5	25.5	48.45	146.26	23.40	65.99	15.45	63.45	58.42
ICGV 06175 × ICGV 10373	32	8.5	23.75	45.55	194.41	9.15	62.39	5.70	35.55	35.38
Mean	32.29	7.49	26.82	47.55	180.79	14.06	56.73	8.10	49.18	39.92
Grand mean	32.43	7.43	27	47.51	186.12	13.22	56.81	7.64	47.20	38.49
CV (%)	1.34	18.24	14.23	4.46	18.04	11.62	5.98	12.53	15.18	14.87
LSD (5%)	0.88	2.77	7.98	4.34	68.68	3.14	6.95	1.95	14.66	11.71

Table 4 continued

Entry	DF	PB	PH	SCMR	SLA	POD	SHP	KY	TBM	HI
F test	**	ns	ns	*	*	**	**	**	**	**

DF, days to 50% flowering; PB, number of primary branches per plant; PH, plant height (cm); SLA, specific leaf area ($\text{cm}^2 \text{g}^{-1}$); Pod, pod yield per plant (g); SHP, shelling percentage (%); KY = kernel yield per plant (g); TBM, total biomass yield per plant (g); HI, harvest index (%), CV (%); percentage of coefficient of variation; LSD, Least significant difference; F, Fisher's, ns, non-significant

*Significant at $p \leq 0.05\%$

**Significant at $p \leq 0.01$

The highest SCMR values were recorded for the parents ICGV 98412 and ICGV 10178 and crosses ICGV 10373 \times ICGV 98412 and ICGV 10178 \times ICGV 15094, ICGV 10178 \times ICGV 98412, ICGV 06175 \times ICGV 11396 and ICGV 10373 \times ICGV 10178 under DS condition. The lowest SLA values were recorded for the parents ICGV 10373 and ICGV 10178 and crosses ICGV 10178 \times ICGV 96174, ICGV 06175 \times ICGV 10178 (and ICGV 15083 \times ICGV 10178 under DS condition. Under NS conditions in the glasshouse, the highest SLA values were recorded for the parent ICGV 98412 and crosses ICGV 15083 \times ICGV 98412, ICGV 15083 \times ICGV 96174 and ICGV 96174 \times ICGV 15094.

The highest PY were recorded for the parents ICGV 10178 ($18.15 \text{ g plant}^{-1}$) and ICGV 15083 ($15.7 \text{ g plant}^{-1}$) and crosses ICGV 15083 \times ICGV 10178 ($28.65 \text{ g plant}^{-1}$), ICGV 10373 \times ICGV 15083 ($23.40 \text{ g plant}^{-1}$) and ICGV 10178 \times ICGV 98412 ($22.65 \text{ g plant}^{-1}$) under DS. Under NS condition in the glasshouse, the highest PY were recorded for the parents ICGV 10178 ($25.37 \text{ g plant}^{-1}$), ICGV 98412 ($23.75 \text{ g plant}^{-1}$) and ICGV 15083 ($22.9 \text{ g plant}^{-1}$) and crosses ICGV 10178 \times ICGV 98412 ($34.2 \text{ g plant}^{-1}$), ICGV 15083 \times ICGV 10178 ($31.05 \text{ g plant}^{-1}$) and ICGV 15083 \times ICGV 98412 (31.05). Under field condition, the highest PY were recorded for the parents ICGV 10178 ($15.00 \text{ g plant}^{-1}$) and ICGV 15083 ($12.80 \text{ g plant}^{-1}$) and crosses ICGV 15083 \times ICGV 98412 ($23.21 \text{ g plant}^{-1}$), ICGV 98412 \times ICGV 11396 ($23.20 \text{ g plant}^{-1}$) and ICGV 98412 \times ICGV 96174 ($23.16 \text{ g plant}^{-1}$) (Table 6).

The parents ICGV 10178 and ICGV 15083 and the crosses ICGV 10373 \times ICGV 15083, ICGV 10178 \times ICGV 98412, ICGV 15083 \times ICGV 10178 gave the highest KY values of 11.05, 9.35, 15.45, 15.25 and

$14.15 \text{ g plant}^{-1}$, respectively under DS condition in the glasshouse study. Under NS condition in the glasshouse, the highest KY were recorded for parents ICGV 98412 ($14.10 \text{ g plant}^{-1}$), ICGV 10178 ($13.70 \text{ g plant}^{-1}$) and ICGV 15083 ($12.60 \text{ g plant}^{-1}$) and crosses ICGV 10178 \times ICGV 98412 ($20.75 \text{ g plant}^{-1}$), ICGV 15083 \times ICGV 98412 ($20.00 \text{ g plant}^{-1}$) and ICGV 15083 \times ICGV 10178 ($18.10 \text{ g plant}^{-1}$). During the field study, the highest KY were recorded for the parents ICGV 10178 ($8.76 \text{ g plant}^{-1}$) and ICGV 15083 ($7.14 \text{ g plant}^{-1}$) and crosses ICGV 15083 \times ICGV 98412 ($14.32 \text{ g plant}^{-1}$), ICGV 98412 \times ICGV 11396 ($14.04 \text{ g plant}^{-1}$) and ICGV 98412 \times ICGV 96174 ($13.35 \text{ g plant}^{-1}$).

General combining ability effect of groundnut parents

The parental line ICGV 15083 exhibited a significant ($p \leq 0.05$) negative GCA effect for DF under DS condition in a desirable direction and positive GCA effects for PY, KY and TBM under both DS and NS conditions in the glasshouse (Table 7). ICGV 10178 showed significant positive GCA effects for PY and KY in all environments, positive GCA effect for SCMR and negative GCA effect for SLA under DS condition. In addition, ICGV 10178 exhibited a significant positive GCA effect for DF under DS conditions in the glasshouse and NS field conditions. ICGV 98412 exhibited significant negative GCA effect for DF and positive GCA effects for PY and KY under NS condition in the glasshouse and NS field condition. In addition, ICGV 98412 exhibited significant positive GCA effects for HI under both DS and NS conditions in the glasshouse. Due to desirable

Table 5 Mean values for the nine phenotypic traits and chlorophyll meter reading (SCMR) among eight groundnut parents and 28 F₂ families under non-stressed glasshouse conditions

Entry	DF	PB	PH	SCMR	SLA	POD	SHF	KY	TBM	HI
<i>Parents</i>										
ICGV 06175	33.5	8	30.5	58.1	140.27	14.75	63.67	9.35	44.8	33.44
ICGV 10373	33	6.5	24	53.4	129.57	12.2	59.83	7.45	34.45	35.73
ICGV 15083	34	7.5	28.5	51.7	194	22.9	55.01	12.60	61.20	37.43
ICGV 10178	35	5.75	28	57.75	220.38	25.35	54.07	13.70	61.70	41.07
ICGV 98412	32	6.5	27.25	54.25	224.41	23.75	59.49	14.10	41.00	59.05
ICGV 96174	32	5	29.25	52.15	148.31	14.3	63.60	9.10	54.95	26.03
ICGV 11396	35	7.5	24.75	48.2	124.97	14	43.09	6.05	46.15	30.57
ICGV 15094	30	7	21	50.4	167.15	12.5	52.19	6.55	49.85	25.52
Mean	33.06	6.72	26.66	53.24	168.63	17.47	56.37	9.86	49.26	36.10
<i>Crosses</i>										
ICGV 06175 × ICGV 15094	36	7.25	27.5	53.75	138.47	17.65	59.84	10.75	55.75	31.73
ICGV 10373 × ICGV 15094	35	6.75	23	52	181.7	9.6	47.99	4.60	32.75	30.44
ICGV 15083 × ICGV 15094	33.5	8.25	27	55.2	119.32	19.1	56.81	10.85	55.10	34.68
ICGV 10178 × ICGV 15094	32	7.25	28.75	55.25	151.59	23.5	59.07	13.85	63.10	37.21
ICGV 98412 × ICGV 15094	35	6.25	27	52.4	145.1	16.6	55.93	9.30	56.65	29.52
ICGV 96174 × ICGV 15094	32	6	26.75	50.3	218.98	11.85	57.82	6.90	36.05	41.62
ICGV 11396 × ICGV 15094	33	7.75	31	46.05	128.6	16.8	44.53	7.55	53.75	31.26
ICGV 06175 × ICGV 11396	34.5	7	32	54.1	197.15	17.3	50.87	8.80	53.90	32.10
ICGV 10373 × ICGV 11396	32.5	6.25	25.75	52.25	147.68	16.45	57.37	10.00	40.30	40.31
ICGV 15083 × ICGV 11396	34	9	31.25	53.25	148.54	21.9	66.54	14.60	54.50	40.77
ICGV 10178 × ICGV 11396	32.5	6.75	30.25	54.75	154.71	21.6	58.00	12.50	63.40	34.04
ICGV 98412 × ICGV 11396	33	7	30	55.05	155.35	19.7	60.91	12.00	42.50	46.35
ICGV 96174 × ICGV 11396	33.5	6.25	31	53	168.89	16.9	52.02	8.85	53.90	31.42
ICGV 06175 × ICGV 96174	31	4.75	24.25	51.3	159.67	13.85	59.72	8.35	40.6	34.37
ICGV 10373 × ICGV 96174	34	6	27.25	53.35	189.43	13.25	64.26	8.50	34.65	38.19
ICGV 15083 × ICGV 96174	33	6.25	24.5	52.4	224.3	25.3	64.83	16.40	50.6	50.38
ICGV 10178 × ICGV 96174	35.5	8.25	34	55.8	169.96	25.6	63.88	16.35	61.85	41.39
ICGV 98412 × ICGV 96174	32	6.25	21.75	51.05	158.25	24.05	61.29	14.75	49.6	48.51
ICGV 06175 × ICGV 98412	32.5	7.75	19.5	53.8	183.2	14.6	50.95	7.50	37.15	38.23
ICGV 10373 × ICGV 98412	33	6.75	23.5	48.6	186.47	16.25	62.37	10.40	42.45	36.52
ICGV 15083 × ICGV 98412	32.5	6.75	31.25	55.05	226.28	31.05	64.30	20.00	67.75	45.84
ICGV 10178 × ICGV 98412	34	6.5	29	59.45	207.7	34.2	60.66	20.75	71.3	48.95
ICGV 06175 × ICGV 10178	32	6.5	30.5	54.85	117.56	22.75	56.62	12.85	51.15	44.44
ICGV 10373 × ICGV 10178	35	6.5	26.75	50.7	190.2	18.9	62.66	11.85	50.15	37.69
ICGV 15083 × ICGV 10178	34	6.25	25.75	65.05	163.05	31.05	58.41	18.10	71.15	43.57
ICGV 06175 × ICGV 15083	32.5	6.25	26.75	54.25	91.02	12.1	52.33	6.35	47.35	25.35
ICGV 10373 × ICGV 15083	35	7	24.25	55.8	177.23	9.35	49.14	4.60	33.65	26.42
ICGV 06175 × ICGV 10373	32.5	5.25	27.25	52.75	166.49	9.25	54.84	5.15	42.35	21.84
Mean	33.39	6.74	27.41	53.63	166.67	18.95	57.64	11.16	50.48	37.26
Grand mean	33.31	6.73	27.24	53.54	167.1	18.61	57.35	10.87	50.2	36.99
CV (%)	1.64	18.49	12.16	6.33	16.52	16.87	8.18	20.55	15.72	20.69
LSD (5%)	1.12	2.54	6.77	6.94	56.47	6.42	9.59	4.56	16.15	15.66

Table 5 continued

Entry	DF	PB	PH	SCMR	SLA	POD	SHP	KY	TBM	HI
F test	**	ns	*	*	*	**	*	**	*	*

DF, days to 50% flowering; PB, number of primary branches per plant; PH, plant height (cm); SLA, specific leaf area ($\text{cm}^2 \text{g}^{-1}$); Pod, pod yield per plant (g); SHP, shelling percentage (%); KY = kernel yield per plant (g); TBM, total biomass yield (g); HI, harvest index (%); CV (%); percentage of coefficient of variation; LSD, Least significant difference; F, Fisher's, ns, non-significant; * significant at $p \leq 0.05\%$ and ** significant at $p \leq 0.01$

Table 6 Mean values for the six phenotypic traits among eight groundnut parents and 28 F_2 families under non-stressed field conditions

Entry	DF	PH	PB	PY	SHP	KY
<i>Parents</i>						
ICGV 06175	35.5	59	7	11.62	46.32	5.288
ICGV 10373	37	54.5	7	8.10	69.18	5.278
ICGV 15083	36	57	9	12.80	55.85	7.14
ICGV 10178	39	67	9	15.00	58.35	8.757
ICGV 98412	34	48.5	6	9.76	49.06	4.802
ICGV 96174	35	57	8	11.00	57.49	6.345
ICGV 11396	39	59	12	4.74	60.37	2.794
ICGV 15094	33	55.5	9.5	9.29	57.00	5.291
Mean	36.06	57.19	8.44	10.29	56.70	5.712
<i>Crosses</i>						
ICGV 06175 × ICGV 15094	40	59	8.5	14.4	44.36	6.39
ICGV 10373 × ICGV 15094	39	55	16.5	10.02	48.66	4.88
ICGV 15083 × ICGV 15094	36	51	11.5	8.78	56.19	4.96
ICGV 10178 × ICGV 15094	36.5	65	9	16.25	57.75	9.39
ICGV 98412 × ICGV 15094	39	59	8	14.68	57.62	8.47
ICGV 96174 × ICGV 15094	34	58.5	12	9.77	46.91	4.52
ICGV 11396 × ICGV 15094	35.5	56.5	10.5	8.27	47.67	3.93
ICGV 06175 × ICGV 11396	36.5	65.5	9.5	11.66	49.51	5.61
ICGV 10373 × ICGV 11396	37	50.5	11.5	5.21	50.80	2.63
ICGV 15083 × ICGV 11396	36	60	7	9.08	46.79	4.28
ICGV 10178 × ICGV 11396	35.5	75	8.5	16.40	52.28	8.58
ICGV 98412 × ICGV 11396	35.5	58	6.5	23.20	60.50	14.04
ICGV 96174 × ICGV 11396	35.5	55.5	8	8.32	54.22	4.58
ICGV 06175 × ICGV 96174	33	60	9.5	10.73	32.15	2.73
ICGV 10373 × ICGV 96174	35.5	58	7.5	15.79	53.05	8.39
ICGV 15083 × ICGV 96174	35.5	58	11.5	20.82	53.81	11.21
ICGV 10178 × ICGV 96174	39.5	65	10.5	10.48	47.13	4.98
ICGV 98412 × ICGV 96174	37	53	11	23.16	57.85	13.35
ICGV 06175 × ICGV 98412	36	55.5	11.5	13.48	45.44	6.06
ICGV 10373 × ICGV 98412	36	53	9.5	17.98	52.20	9.38
ICGV 15083 × ICGV 98412	35	61.5	5.5	23.21	61.70	14.32
ICGV 10178 × ICGV 98412	37	64	9	14.16	44.77	6.27
ICGV 06175 × ICGV 10178	34	65	8.5	14.47	50.01	7.22

Table 6 continued

Entry	DF	PH	PB	PY	SHP	KY
ICGV 10373 × ICGV 10178	39	60	7	12.96	55.06	7.11
ICGV 15083 × ICGV 10178	35.5	51	7	18.80	60.30	11.35
ICGV 06175 × ICGV 15083	36	51	9	7.54	41.50	3.17
ICGV 10373 × ICGV 15083	39	50.5	8.5	6.48	53.93	3.38
ICGV 06175 × ICGV 10373	36	55.5	10.5	8.66	48.90	3.96
Means	36.42	58.20	9.39	13.38	51.11	6.97
Mean	36.34	57.97	9.18	12.69	52.39	6.69
CV (%)	1.69	11.49	21.03	30.35	12.39	27.74
LSD (5%)	1.25	13.62	3.95	7.88	2.04	3.79
F test	**	ns	*	*	*	**

DF, days to 50% flowering; PB, number of primary branches per plant; PH, plant height (cm); PY, pod yield per plant (g); SHP, shelling percentage (%); KY = kernel yield per plant (g); CV (%); percentage of coefficient of variation; LSD, Least significant difference; F, Fisher's, ns, non-significant; *Significant at $p \leq 0.05\%$ and **Significant at $p \leq 0.01$

Table 7 General combining ability effects for the nine phenotypic traits and chlorophyll meter reading (SCMR) of eight parental genotypes of groundnut evaluated in the glasshouse (drought-stressed and non-stressed conditions) and non-stressed field conditions

Traits	Env.	Parents							
		ICGV 06175	ICGV 10373	ICGV 15083	ICGV 10178	ICGV 98412	ICGV 96174	ICGV 11396	ICGV 15094
DF	DS	- 0.39*	0.41*	- 0.44*	0.71ns	0.11ns	- 0.14ns	0.01ns	- 0.29*
DF	NS	- 0.19ns	0.31*	0.26ns	0.51*	- 0.39*	- 0.49*	0.31*	- 0.34*
DF	NSF	- 0.46*	0.84**	- 0.21ns	0.79**	- 0.36*	- 0.71*	0.24ns	- 0.11ns
PB	DS	0.13ns	0.28ns	0.26ns	- 0.14ns	- 0.64ns	- 0.37ns	0.10ns	0.38ns
PB	NS	0.01ns	- 0.31ns	0.41ns	- 0.11ns	- 0.04ns	- 0.69ns	0.44ns	0.29ns
PB	NSF	- 0.16ns	0.24ns	- 0.46ns	- 0.51ns	- 0.96*	0.34ns	0.29ns	1.24*
PH	DS	1.04ns	- 2.03**	1.57ns	1.34ns	0.57ns	- 1.98*	- 0.93ns	0.44ns
PH	NS	0.36ns	- 1.94*	0.26ns	1.58ns	- 0.87ns	0.28ns	1.56ns	- 1.22ns
PH	NSF	0.78ns	- 3.03ns	- 2.48ns	5.73*	- 2.08ns	0.03ns	1.73ns	- 0.65ns
SCMR	DS	0.91ns	- 0.96ns	1.25ns	2.95*	0.20ns	- 1.04ns	- 1.70*	- 1.61ns
SCMR	NS	- 1.18*	0.52ns	- 0.27ns	1.01ns	2.34*	- 2.97**	0.75ns	- 0.19ns
SLA	DS	11.21ns	- 34.04*	- 7.20ns	- 4.01ns	3.46ns	17.77*	- 5.13ns	17.95*
SLA	NS	- 17.0*	- 19.3	12.3ns	13.5*	11.0ns	8.2ns	- 9.9ns	1.2ns
POD	DS	- 0.18ns	- 0.73ns	2.56**	6.88**	0.4ns	- 2.99**	- 2.31**	- 3.63**
POD	NS	- 3.06*	- 5.01**	2.81*	6.07**	3.64*	- 0.82ns	- 0.89ns	- 2.75*
POD	NSF	- 1.01ns	- 2.10*	0.60ns	1.92*	3.51*	0.68ns	- 2.26*	- 1.35ns
SHP	DS	0.96ns	3.06*	0.08ns	4.58**	- 3.08*	0.7ns	- 1.6ns	- 37.52
SHP	NS	- 0.37ns	0.21ns	0.61ns	1.12ns	1.92ns	3.48*	- 3.98*	- 2.99*
SHP	NSF	- 6.67*	2.98ns	1.47ns	1.28ns	0.70ns	- 1.11ns	1.14ns	0.2ns
KY	DS	- 0.08ns	- 0.04ns	1.25**	4.65**	- 0.23ns	- 1.71**	- 1.44**	- 2.41**
KY	NS	- 1.94*	- 2.78*	1.83*	3.58**	2.51*	0.05ns	- 1.14*	- 2.09*
KY	NSF	- 1.45*	- 0.99*	0.67ns	1.22*	2.13*	0.22ns	- 1.10*	- 0.71ns
TBM	DS	- 0.69ns	- 3.1ns	7.26*	11.90**	- 1.03ns	- 6.82*	- 3.14ns	- 4.39*

Table 7 continued

Traits	Env.	Parents							
		ICGV 06175	ICGV 10373	ICGV 15083	ICGV 10178	ICGV 98412	ICGV 96174	ICGV 11396	ICGV 15094
TBM	NS	- 3.40ns	- 10.67*	5.06*	10.36**	- 0.25ns	- 1.47ns	0.27ns	0.10ns
HI	DS	0.41ns	- 0.02ns	3.09*	12.91**	2.88*	- 4.32*	- 5.81*	- 9.14**
HI	NS	- 3.81*	- 3.01ns	0.89ns	3.64ns	7.90*	0.49ns	- 1.56ns	- 4.55*

Env., environments; DS, drought-stressed; NS, non-stressed; NSF = non-stressed at field condition; DF, days to 50% flowering; PB, number of primary branches per plant; PH, plant height (cm); SLA, specific leaf area ($\text{cm}^2 \text{g}^{-1}$); PY, pod yield per plant (g); SHP, shelling percentage (%); KY = kernel yield per plant (g); TBM, total biomass yield per plant(g); HI, harvest index (%); GCA values of parents in a row followed by ns are non-significant

*Significant at $p \leq 0.05\%$

**Significant at $p \leq 0.01$

GCA effects for PY, KY and HI the parental lines ICGV 10178, ICGV 15083 and ICGV 98412 These lines could be recommended to breed drought stress tolerance.

Specific combining ability effect of crosses

During the glasshouse study under DS conditions, higher and significantly negative SCA effects in a desirable direction were detected for DF by the families ICGV 15083 \times ICGV 11396, ICGV 10178 \times ICGV 11396 and ICGV 06175 \times ICGV 15083 (Table 8). Under NS conditions in the glasshouse, ICGV 10178 \times ICGV 96174 and ICGV 15083 \times ICGV 98412 exhibited significant positive SCA effects for PH, which is desirable for breeding groundnut genotypes for increased plant height (Table 9). Crosses ICGV 10373 \times ICGV 15094 and ICGV 06175 \times ICGV 98412 showed significantly positive SCA effects for PB under field conditions (Table 10). These are desirable families for enhanced biomass yield in groundnut.

Families ICGV 06175 \times ICGV 11396, ICGV 10178 \times ICGV 15094 and ICGV 10373 \times ICGV 98412 displayed significant positive SCA effect for SCMR under DS condition. Under DS condition, significant negative SCA effect for SLA was recorded for ICGV 06175 \times ICGV 96174, whereas significant positive SCA for SLA were recorded for ICGV 15083 \times ICGV 96174, ICGV 15083 \times ICGV 98412, ICGV 96174 \times ICGV 15094 and ICGV 10178 \times ICGV 98412 under NS condition in the glasshouse.

Under DS condition, significant positive SCA effects for PY were recorded for ICGV 10373 \times ICGV 15083, ICGV 15083 \times ICGV 10178, ICGV 15083 \times ICGV 98412, ICGV 98412 \times ICGV 15094 and CGV 10178 \times ICGV 96174. Under NS condition in glasshouse, significant positive SCA effects for PY were noted for ICGV 15083 \times ICGV 98412, ICGV 10178 \times 98412, ICGV 06175 \times ICGV 15094 and ICGV 15083 \times ICGV 96174. Under field condition, ICGV 98412 \times ICGV 11396, ICGV 15083 \times ICGV 96174, ICGV 98412 \times ICGV 96174 and ICGV 15083 \times ICGV 98412 displayed significant positive SCA effects for PY.

Under DS condition, crosses such as ICGV 10373 \times ICGV 10178, ICGV 10178 \times ICGV 15094, ICGV 10178 \times ICGV 96174, ICGV 10178 \times ICGV 11396 and ICGV 06175 \times ICGV 10178 exhibited significant positive SCA effects for KY. Under NS condition in the glasshouse, ICGV 15083 \times ICGV 98412, ICGV 06175 \times ICGV 15094, ICGV 10178 \times ICGV 98412, ICGV 15083 \times ICGV 96174 and ICGV 10373 \times ICGV 11396 exhibited significant positive SCA effects for KY. Under field condition families ICGV 98412 \times ICGV 11396, ICGV 15083 \times ICGV 98412, ICGV 98412 \times ICGV 96174, ICGV 15083 \times ICGV 96174 and ICGV 15083 \times ICGV 10178 expressed significant positive SCA effects for KY.

Discussion

The development of promising groundnut genotypes with high yield potential and drought tolerance would

Table 8 Specific combining ability effects for the nine phenotypic traits and chlorophyll meter reading (SCMR) of 28F₂ groundnut families under drought-stressed condition in the glasshouse

Crosses	Traits									
	DF	PB	PH	SCMR	SLA	PY	SHP	KY	TBM	HI
ICGV 06175 × ICGV 15094	1.24**	- 1.20ns	5.09ns	- 2.60ns	2.65ns	3.24*	- 6.77*	0.53ns	- 5.03ns	7.16ns
ICGV 10373 × ICGV 15094	2.44**	0.15ns	0.42ns	0.35ns	19.12ns	- 0.46ns	3.84ns	- 0.91ns	- 3.61ns	- 2.66ns
ICGV 15083 × ICGV 15094	1.29**	- 0.08ns	3.07ns	2.64ns	- 14.55ns	- 5.35**	8.09*	- 3.35**	- 7.87ns	- 152.96
ICGV 10178 × ICGV 15094	- 0.86*	1.58ns	- 6.46*	3.87*	9.91ns	0.88ns	8.03*	3.20**	4.79ns	4.06ns
ICGV 98412 × ICGV 15094	1.74**	- 0.18ns	0.32ns	1.14ns	- 36.51ns	3.86*	4.80*	- 0.87ns	- 0.54ns	17.08**
ICGV 96174 × ICGV 15094	- 0.01ns	- 1.2	- 2.13ns	- 4.50*	16.45ns	1.55ns	- 10.00**	- 2.69**	- 5.24ns	11.29*
ICGV 11396 × ICGV 15094	- 0.16ns	0.33	4.32ns	- 1.22ns	18.60ns	2.32*	1.42ns	1.39*	4.58ns	1.30ns
ICGV 06175 × ICGV 11396	1.44**	- 0.43ns	0.72ns	4.22*	- 24.20ns	1.13ns	- 0.23ns	0.70ns	8.86ns	12.29*
ICGV 10373 × ICGV 11396	- 0.86*	0.43ns	0.54ns	0.22ns	- 33.71ns	- 1.32ns	1.05ns	1.81*	2.82ns	- 1.16ns
ICGV 15083 × ICGV 11396	- 3.01**	1.45ns	- 1.81ns	- 0.24ns	- 29.19ns	- 5.32**	- 5.05*	- 2.28*	- 1.39ns	- 12.66*
ICGV 10178 × ICGV 11396	- 1.66**	- 0.15ns	- 2.08ns	- 0.82ns	- 24.43ns	3.56*	6.02*	2.82**	10.03*	8.59*
ICGV 98412 × ICGV 11396	0.44ns	- 0.65ns	- 1.31ns	- 1.30ns	- 11.44ns	- 0.36ns	- 5.60*	0.90ns	3.09ns	- 0.86ns
ICGV 96174 × ICGV 11396	- 0.31ns	- 0.68ns	- 0.26ns	1.46ns	41.21*	- 35.28	- 4.29ns	- 0.62ns	- 7.76*	- 16.38**
ICGV 06175 × ICGV 96174	- 1.91ns	- 0.95ns	- 6.73*	2.34ns	- 54.54*	3.06*	- 8.45*	- 1.73*	- 1.59ns	2.67ns
ICGV 10373 × ICGV 96174	- 0.71*	- 0.10ns	1.34ns	- 3.06*	14.58ns	2.91*	1.83ns	0.18ns	- 2.62ns	10.19*
ICGV 15083 × ICGV 96174	1.14**	0.93ns	2.49ns	- 2.22ns	- 5.48ns	- 4.79**	3.74ns	0.29ns	11.12*	- 14.80**
ICGV 10178 × ICGV 96174	0.99*	0.58ns	- 2.28ns	2.10ns	9.63ns	3.79*	1.91ns	3.19**	9.03*	3.82ns
ICGV 98412 × ICGV 96174	1.09**	1.83*	0.49ns	- 1.58ns	52.91*	1.47ns	0.11ns	- 2.18**	- 9.30*	3.10ns
ICGV 06175 × ICGV 98412	- 0.66*	- 0.43ns	- 3.03ns	- 1.47ns	- 13.75ns	- 2.14*	- 5.50*	0.24ns	- 1.51ns	- 7.61*
ICGV 10373 × ICGV 98412	0.04ns	0.18ns	- 1.96ns	3.28*	18.61ns	- 1.04ns	6.99*	0.35ns	6.31ns	0.61ns
ICGV 15083 × ICGV 98412	- 2.11**	- 1.05ns	- 7.56*	0.32ns	- 12.92ns	4.52**	- 10.46**	0.60ns	3.69ns	2.89ns
ICGV 10178 × ICGV 98412	- 0.26ns	- 0.40ns	3.67ns	0.49ns	3.14ns	2.15*	9.01**	- 5.88**	- 16.29**	- 2.96ns
ICGV 06175 × ICGV 10178	- 0.76*	0.58ns	- 0.81ns	- 2.79*	24.15ns	0.28ns	- 0.62ns	2.14*	1.98ns	3.24ns
ICGV 10373 × ICGV 10178	0.94*	0.18ns	0.77ns	2.16ns	26.65ns	1.03ns	- 2.47ns	6.60**	12.09*	- 2.73ns
ICGV 15083 × ICGV 10178	- 0.71*	- 0.55ns	- 3.08ns	- 2.45ns	25.39ns	5.99**	- 12.13**	- 0.80ns	- 13.67*	15.33**
ICGV 06175 × ICGV 15083	- 1.61**	1.18ns	3.47ns	1.33ns	1.08ns	1.90ns	4.77*	- 1.82*	- 7.87ns	3.79ns
ICGV 10373 × ICGV 15083	2.09**	- 0.48ns	- 1.46ns	0.68ns	- 30.34ns	8.35**	6.04*	- 2.96**	- 3.65ns	16.85*
ICGV 06175 × ICGV 10373	- 0.46ns	0.65ns	- 2.68ns	- 1.31ns	22.32ns	- 3.15*	1.55ns	- 0.38ns	0.17ns	- 3.51ns

DF, days to 50% flowering; PB, number of primary branches per plant; PH, plant height (cm); SCMR, chlorophyll meter reading; SLA, specific leaf area (cm² g⁻¹); PY, pod yield per plant (g); SHP, shelling percentage (%); KY = kernel yield per plant (g); TBM, total biomass yield per plant (g); HI, harvest index (%); SCA values of traits in a column followed by ns are ns, non-significant

*Significant at $p \leq 0.05\%$

**Significant at $p \leq 0.01$ among crosses

Table 9 Specific combining ability effects for the nine phenotypic traits and chlorophyll meter reading (SCMR) of 28F₂ groundnut families under non-stressed glasshouse condition

Traits		DF	PB	PH	SCMR	SLA	POD	SHP	KY	TBM	HI
Crosses											
ICGV 06175 × ICGV 15094	3.21**	0.21ns	1.12ns	1.35ns	-12.83ns	4.83*	5.84*	3.91*	8.85ns	3.09ns	
ICGV 10373 × ICGV 15094	1.71**	0.04ns	-1.08ns	1.37ns	1.09ns	-1.26ns	-6.59*	-1.39ns	-6.89ns	1.00ns	
ICGV 15083 × ICGV 15094	0.26ns	0.81ns	0.72ns	0.16ns	-29.69ns	0.42ns	1.82ns	0.25ns	-0.27ns	1.34ns	
ICGV 10178 × ICGV 15094	-1.49**	0.34ns	1.14ns	-0.04ns	-6.77ns	1.55ns	3.58ns	1.49ns	2.43ns	1.11ns	
ICGV 98412 × ICGV 15094	2.41**	-0.74ns	1.84ns	3.01ns	-34.13ns	-2.91ns	-0.36ns	-1.98ns	6.59ns	-10.83*	
ICGV 96174 × ICGV 15094	-0.49ns	-0.34ns	0.44ns	2.20ns	42.48*	-3.21ns	-0.03ns	-1.92ns	-12.78*	8.68ns	
ICGV 11396 × ICGV 15094	-0.29ns	0.29ns	3.42ns	-1.94ns	-30.18ns	1.82ns	-5.86*	-0.08ns	3.18ns	0.36ns	
ICGV 06175 × ICGV 11396	1.06*	-0.19ns	2.84ns	-2.12ns	33.49ns	2.63ns	-2.14ns	1.01ns	6.83ns	0.46ns	
ICGV 10373 × ICGV 11396	-1.44**	-0.61ns	-1.11ns	1.81ns	-45.28*	3.73ns	3.79ns	3.06*	0.49ns	7.89ns	
ICGV 15083 × ICGV 11396	0.11ns	1.41ns	2.19ns	-1.36ns	-12.83ns	1.36ns	12.54**	3.05*	-1.04ns	4.44ns	
ICGV 10178 × ICGV 11396	-1.64**	-0.31ns	-0.13ns	0.35ns	-16.01ns	-2.20ns	3.50ns	-0.81ns	2.56ns	-5.04ns	
ICGV 98412 × ICGV 11396	-0.24ns	-0.14ns	2.07ns	-1.66ns	-36.25*	-1.67ns	5.62ns	-0.23ns	-7.73ns	3.01ns	
ICGV 96174 × ICGV 11396	0.36ns	-0.24ns	1.92ns	0.68ns	-19.97ns	-0.01ns	-4.84ns	-0.92ns	4.90ns	-4.51ns	
ICGV 06175 × ICGV 96174	-1.64**	-1.31ns	-3.63ns	-0.86ns	1.33ns	-0.90ns	-0.75ns	-0.63ns	-4.73ns	0.68ns	
ICGV 10373 × ICGV 96174	0.86*	0.26ns	1.67ns	-4.18ns	1.78ns	0.46ns	3.21ns	0.37ns	-3.42ns	3.71ns	
ICGV 15083 × ICGV 96174	-0.09ns	-0.21ns	-3.28ns	0.05ns	68.26*	4.69*	3.37ns	3.66*	-3.20ns	12.00*	
ICGV 10178 × ICGV 96174	2.16**	2.31*	4.89*	2.76ns	4.57ns	1.72ns	1.93ns	1.85ns	2.75ns	0.25ns	
ICGV 98412 × ICGV 96174	-0.44ns	0.24ns	-4.91*	0.30ns	-28.02ns	2.61ns	-1.46ns	1.33ns	1.11ns	3.12ns	
ICGV 06175 × ICGV 98412	-0.24ns	1.04ns	-7.23*	-2.55ns	22.13ns	-4.60*	-7.95*	-3.94*	-9.41ns	-2.86ns	
ICGV 10373 × ICGV 98412	-0.24ns	0.36ns	-0.93ns	-4.83*	-3.91ns	-1.00ns	2.89ns	-0.19ns	3.16ns	-5.37ns	
ICGV 15083 × ICGV 98412	-0.69ns	-0.36ns	4.62*	7.31*	44.45*	5.98*	4.41ns	4.80*	12.73*	0.05ns	
ICGV 10178 × ICGV 98412	0.56ns	-0.09ns	1.04ns	-1.69ns	39.57*	5.87*	0.27ns	3.79*	10.98*	0.40ns	
ICGV 06175 × ICGV 10178	-1.64**	-0.14ns	1.32ns	-1.46ns	-22.63ns	1.11ns	-1.49ns	0.34ns	-6.02ns	7.60ns	
ICGV 10373 × ICGV 10178	0.86*	0.19ns	-0.13ns	1.97ns	20.70ns	-0.78ns	3.97ns	0.18ns	0.25ns	0.06ns	
ICGV 15083 × ICGV 10178	-0.09ns	-0.79ns	-3.33ns	-4.35*	25.15ns	3.55ns	-0.69ns	1.82ns	5.52ns	2.04ns	
ICGV 06175 × ICGV 15083	-0.89*	-0.91ns	-1.11ns	-0.74ns	-39.82*	-6.27*	-5.27ns	-4.41*	-4.52ns	-8.73ns	
ICGV 10373 × ICGV 15083	1.11*	0.16ns	-1.31ns	1.78ns	17.08ns	-7.07*	-9.04*	-5.31*	-10.95*	-8.45ns	
ICGV 06175 × ICGV 10373	-0.94*	-1.19ns	1.59ns	2.73ns	4.05ns	-1.30ns	-2.35ns	-1.00ns	6.21ns	-8.34ns	

DF, days to 50% flowering; PB, number of primary branches per plant; PH, plant height (cm); SCMR, chlorophyll meter reading; SLA, specific leaf area (cm² g⁻¹); PY, pod yield per plant (g); SHP, shelling percentage (%); KY = kernel yield per plant (g); TBM, total biomass yield per plant (g); HI, harvest index (%); SCA values of traits in a column followed by ns are ns, non-significant

*Significant at $p \leq 0.05\%$ and **Significant at $p \leq 0.01$ among crosses

Table 10 Specific combining ability effects for the six phenotypic traits of 28F₂ groundnut families under non-stressed field conditions

Traits						
Crosses	DF	PB	PH	POD	SHP	KY
ICGV 06175 × ICGV 15094	4.23**	− 1.76ns	0.93ns	4.07ns	− 1.53ns	1.86ns
ICGV 10373 × ICGV 15094	1.93**	5.84**	0.73ns	0.77ns	− 6.87ns	− 0.11ns
ICGV 15083 × ICGV 15094	− 0.02ns	1.54ns	− 3.82ns	− 3.17ns	2.16ns	− 1.70ns
ICGV 10178 × ICGV 15094	− 0.52ns	− 0.91ns	1.98ns	2.98ns	3.92ns	2.19ns
ICGV 98412 × ICGV 15094	3.13**	− 1.46ns	3.78ns	− 0.17ns	4.37ns	0.36ns
ICGV 96174 × ICGV 15094	− 1.52*	1.24ns	1.18ns	− 2.25ns	− 4.54ns	− 1.68ns
ICGV 11396 × ICGV 15094	− 0.97*	− 0.21ns	− 2.52ns	− 0.81ns	− 6.01ns	− 0.96ns
ICGV 06175 × ICGV 11396	0.38ns	0.19ns	5.03ns	2.24ns	2.69ns	1.47ns
ICGV 10373 × ICGV 11396	− 0.42ns	1.79ns	− 6.17ns	− 3.12ns	− 5.66ns	− 1.97ns
ICGV 15083 × ICGV 11396	− 0.37ns	− 2.01ns	2.78ns	− 1.96ns	− 8.17ns	− 1.98ns
ICGV 10178 × ICGV 11396	− 1.87**	− 0.46ns	9.58ns	4.04ns	− 2.49ns	1.76ns
ICGV 98412 × ICGV 11396	− 0.72ns	− 2.01ns	0.38ns	9.26*	6.31ns	6.32**
ICGV 96174 × ICGV 11396	− 0.37ns	− 1.81ns	− 4.22ns	− 2.79ns	1.84ns	− 1.24ns
ICGV 06175 × ICGV 96174	− 2.17**	0.14ns	1.23ns	− 1.64ns	− 12.43*	− 2.73*
ICGV 10373 × ICGV 96174	− 0.97*	− 2.26ns	3.03ns	4.51ns	− 1.17ns	2.46*
ICGV 15083 × ICGV 96174	0.08ns	2.44ns	2.48ns	6.84*	1.09ns	3.63*
ICGV 10178 × ICGV 96174	3.08**	1.49ns	1.28ns	− 4.82ns	− 5.40ns	− 3.15*
ICGV 98412 × ICGV 96174	1.73**	2.44ns	− 2.92ns	6.27*	5.90ns	4.31*
ICGV 06175 × ICGV 98412	0.48ns	3.44*	− 1.17ns	− 1.72ns	− 0.95ns	− 1.31ns
ICGV 10373 × ICGV 98412	− 0.82*	1.04ns	0.13ns	3.87ns	− 3.84ns	1.56ns
ICGV 15083 × ICGV 98412	− 0.77ns	− 2.26ns	8.08ns	6.40*	7.17ns	4.82**
ICGV 10178 × ICGV 98412	0.23ns	1.29ns	2.38ns	− 3.98ns	− 9.57*	− 3.77*
ICGV 06175 × ICGV 10178	− 2.67**	− 0.01ns	0.53ns	0.86ns	3.04ns	0.75ns
ICGV 10373 × ICGV 10178	1.03*	− 1.91ns	− 0.67ns	0.43ns	− 1.55ns	0.19ns
ICGV 15083 × ICGV 10178	− 1.42*	− 1.21ns	− 10.22*	3.57ns	5.19ns	2.76*
ICGV 06175 × ICGV 15083	0.33ns	0.44ns	− 5.27ns	− 4.75ns	− 5.66ns	− 2.74*
ICGV 10373 × ICGV 15083	2.03**	− 0.46ns	− 1.97ns	− 4.73ns	− 2.88ns	− 2.99*
ICGV 06175 × ICGV 10373	− 0.72ns	1.24ns	− 0.22ns	− 0.93ns	0.23ns	− 0.29ns

DF, days to 50% flowering; PB, number of primary branches per plant; PH, plant height (cm); SCMR, chlorophyll meter reading; SLA, specific leaf area ($\text{cm}^2 \text{g}^{-1}$); PY, pod yield per plant (g); SHP, shelling percentage (%); KY = kernel yield per plant (g); TBM, total biomass yield per plant (g); HI, harvest index (%); SCA values of traits in a column followed by ns are ns, non-significant; *Significant at $p \leq 0.05\%$ and **Significant at $p \leq 0.01$ among crosses

enhance the production and productivity of the crop under dry-land conditions. The analysis of variance (Table 3) revealed significant differences among test parents and crosses for most of the assessed traits across all testing environments. This finding indicates that parents and the new crosses exhibited considerable variability for most of the studied traits. Similar trends were reported in previous findings (Zongo et al. 2017; Chavadhari et al. 2017). The present study

showed that the mean PH for the test genotypes under DS was shorter than under NS conditions in glass-house and field conditions (Tables 4 and 5). These results agreed with the findings of Arruda et al. (2015), who pinpointed 34% plant height reduction in groundnut due to mid-season moisture stress. In groundnut, strong positive associations between plant height and pod yield under optimum environments were reported by Zongo et al. (2017) and Kamdar et al. (2020). Taller

plants have better radiation interception and total biomass productivity than shorter plants (Mathew et al. 2019). Drought stress affects plant growth rates primarily through reductions in radiation use efficiency of the plant (Jamieson et al. 1995). This implies that selection of taller plants under drought-prone areas could also be associated with enhanced biomass production.

Groundnut genotypes with the capability to maintain high chlorophyll content and biomass yield under drought-stressed conditions could show better tolerance to drought (Oppong-Sekyere et al. 2019; Songsri et al. 2008). The mean values of total biomass for crosses were higher than their parents under both DS and NS conditions in the glasshouse (Tables 4 and 5). Under DS condition, the highest TBM was recorded for the parents ICGV 10178 and ICGV 15083 and crosses ICGV 15083 \times ICGV 10178, ICGV 10178 \times ICGV 98412 and ICGV 15083 \times ICGV 98412. These genotypes can be used in groundnut breeding programs to enhance biomass production under stress environments in Ethiopia. Genotypes with higher TBM were recommended for production under intermittent drought in groundnut (Ratnakumar et al. 2009). Higher TBM production under drought-stressed conditions is associated with the genotypes' root system to mobilize water from the soil for stem elongation and biomass accumulation. This refers to the transpiration efficiency of the genotypes (Vadez et al. 2014).

In the present study, the highest pod yield was recorded for ICGV 10178 under both moisture conditions. Identifying genotypes with high and stable yield performance under drought-stressed and non-stressed environments is pertinent to ensure production and productivity of groundnut (Shrief et al. 2020). Drought stress during the flowering and grain filling stage can drastically cause pod yield reduction in groundnut. This is associated with a reduction in shelling percentage, as expressed by the decrease in the weight ratio of the seeds and the pods (Ratnakumar and Vadez 2011). This suggests that the selection of genotypes with high shelling percentage and/or seed yield could help to sustain groundnut production in drought stress and non-stressed environments. The following crosses with high SHP: ICGV 10178 \times ICGV 98412, ICGV 10373 \times 15083 and ICGV 178 \times ICGV 11396 under DS condition in the glasshouse and, ICGV 15083 \times ICGV 96174,

ICGV 10373 \times ICGV 96174 and ICGV 15083 \times ICGV 98412 under NS condition in the glasshouse and, ICGV 15083 \times ICGV 98412, ICGV 98412 \times ICGV 11396 and ICGV 15083 \times ICGV 10178 under field conditions are useful groundnut populations for enhanced shelling outturn in drought-prone areas.

Strong and positive associations between harvest index and pod yield in groundnut have been reported in previous findings (Sanogo et al. 2019; Oppong-Sekyere et al. 2019). HI is a useful trait to improve pod yield in groundnut. The present study identified the following crosses with high HI values: ICGV 15083 \times ICGV 10178, ICGV 10373 \times ICGV 15083 and ICGV 10178 \times ICGV 11396 under DS condition in the glasshouse and, ICGV 15083 \times ICGV 96174, ICGV 10178 \times ICGV 98412, ICGV 98412 \times ICGV 96174 and ICGV 98412 \times ICGV 96174 under NS condition in the glasshouse. The above selected crosses with enhanced harvest indices under drought-stressed and non-stressed environments are suitable candidates for future variety development and release.

SCMR is used to measure leaf chlorophyll concentration. It is a useful trait to identify drought-tolerant genotypes in groundnut (Sheshshayee et al. 2006). In this study, a wider SCMR range was recorded for crosses than their parents under DS and NS conditions in the glasshouse (Tables 4 and 5). This result presents an opportunity to select genotypes with higher chlorophyll content which would enable to maintain high photosynthetic capacity and productivity under drought stress environments. Groundnut genotypes that maintain higher SCMR and lower SLA values under drought stress should be more tolerant to drought and hence maintain higher WUE under severe drought conditions (Songsri et al. 2009). Reduced SLA is facilitated by increasing leaf thickness, which results in thicker cell wall to prevent water loss by evaporation and to achieving the aim of higher water use efficiency (Zhou et al. 2020). Under DS conditions, low SLA was recorded for the parents ICGV 10373 and ICGV 10178, and crosses ICGV 10178 \times ICGV 96174 and ICGV 06175 \times ICGV 10178. Under NS glasshouse conditions, the highest SLA values were recorded for the parent ICGV 98412 and crosses ICGV 15083 \times ICGV 98412 and ICGV 15083 \times ICGV 96174. Genotypes with higher SLA values were recommended for areas where sufficient moisture is available. Zhou et al. (2020) reported that selection of plants with high SLA helps to enhance photosynthetic

capacity and productivity in maize crop. Sheshshayee et al. (2006) reported strong relation between SLA and SCMR under well-watered conditions in groundnut. This suggests that the selection of genotypes with higher SLA under optimum conditions could help enhance the photosynthetic capacity and productivity in groundnut.

The GCA \times environment interaction effects for DF, PB, PY, SHP and KY under NS conditions were higher than entries \times environment interaction values. This suggests a higher contribution of GCA than the environment for the expression of these traits. Information on GCA effects of parents helps to estimate the genetic potential of a breeding material for traits of interest (Amelework et al. 2015). ICGV 15083, ICGV 06175 and ICGV 15094 were the best combiner genotypes for breeding early flowering genotypes. Early maturity is a novel drought escape mechanism that would otherwise occur during flowering and pod filling stages. Parental line ICGV 10178 exhibited significant positive GCA effects for SCMR, PY, SHP, KY, TBM and HI under DS condition and significant positive GCA effect for SLA under NS glasshouse condition (Table 7). This suggests the predominant role of additive gene effect in controlling the inheritance of these traits. Rantakumar and Vader (2011) reported that water stress during flowering and pod filling stages reduced pod initiation and thereby reduced harvest index in groundnut. ICGV 98412 exhibited a significant positive GCA effect for HI under both DS and NS conditions in the glasshouse (Table 7). Under DS condition, a significant negative GCA effect for SLA was recorded for ICGV 10373, whereas a significant positive GCA effect for SLA was recorded for ICGV 10178 under NS condition. This result suggests that the two genotypes can enhance water use efficiency in groundnut under the drought-stressed environments with an effective photosynthetic capacity of the crop under optimum conditions (Upadhyaya et al. 2011).

Information on SCA effects of crosses is useful to identify best specific combiners for economic traits. Crosses ICGV 06175 \times ICGV 11396, ICGV 10178 \times ICGV 15094 and ICGV 10373 \times ICGV 98412 showed significant positive SCA effects for SCMR under DS and CGV 15083 \times ICGV 98412 under NS condition in the glasshouse. A strong and positive association between SCMR and water use efficiency was reported by Sheshshayee et al. (2006) and Janila et al. (2015).

Arunyanark et al. (2008) suggested SCMR as a surrogate trait for breeding drought tolerance in groundnut. The selection of genotypes with high SCMR and best combiners enable to enhance drought tolerance in groundnut breeding.

Under DS, ICGV 10373 \times ICGV 15083 and ICGV 98412 \times ICGV 15094 exhibited significant positive SCA effects for pod yield, shelling percentage and harvest index. Passiour et al. (1986) reported that HI is directly related to water use efficiency under stress conditions. Thus, these crosses could be selected for high pod yield and HI under drought stress environments. The present study identified ICGV 10178 \times ICGV 98412 with significant SCA effects for SLA, PY, KY and TBM and, ICGV 15083 \times ICGV 96174 with significant positive SCA effects for SLA, PY, KY and HI and, ICGV 15083 \times ICGV 98412 with significant positive SCA effects for PH, SCMR, SLA, PY, KY and TBM. These crosses are selected for further genetic advancement and to breed promising groundnut genotypes with improved yield and yield components under drought stress environments.

Conclusions

The present study determined the combining ability effects of eight selected drought-tolerant groundnut parental lines and 28 F₂ families under drought-stressed (DS) and non-stressed (NS) conditions. ICGV 10178 was the best general combiner with a positive contribution to SCMR, PY, SHP, KY, TBM and HI. Crosses ICGV 10178 \times ICGV 11369, ICGV 10373 \times ICGV 15083, ICGV 98412 \times ICGV 15094 and ICGV 10178 \times ICGV 98412 were the best specific combiners for enhanced pod yield and drought tolerance. Higher GCA: SCA ratios were recorded for PY and, KY under NS conditions and SCMR, SLA and TBM under DS conditions suggesting the predominant role of additive genes conditioning the inheritance of these traits. Therefore, the selected families are useful populations for developing improved pure line groundnut varieties with high pod yield and drought tolerance.

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Declarations

Conflict of interest The authors declared no conflict of interest.

References

- Abady S, Shimelis H, Janila P (2019) Farmers' perceived constraints to groundnut production, their variety choice and preferred traits in eastern Ethiopia: implications for drought-tolerance breeding. *J Crop Improv.* 33(4):505–521. <https://doi.org/10.1080/15427528.2019.1625836>
- Abady S, Shimelis H, Janila P, Mashilo J (2019) Groundnut (*Arachis hypogaea* L.) improvement in sub-Saharan Africa: a review. *Acta Agric Scand Sect B Soil Plant Sci.* <https://doi.org/10.1080/09064710.2019.1601252>
- Amelework B, Shimelis H, Laing M (2015) Genetic variation in sorghum as revealed by phenotypic and SSR markers: implications for combining ability and heterosis for grain yield. *Plant Genet Resour.* 15:1–13. <https://doi.org/10.1017/S1479262115000696>
- Arruda IM, Moda-Cirino V, Buratto JS, Ferreira JM (2015) Growth and yield of peanut cultivars and breeding lines under water deficit. *Pesquisa Agropecuária Trop Goiânia* 45:146–154. <https://doi.org/10.1590/1983-40632015v4529652>
- Baker RJ (1978) Issues in diallel analysis. *Crop Sci* 18:533–536
- Chavadhari RM, Kachhadia VH, Vachhani JH, Virani MB (2017) Genetic variability studies in groundnut (*Arachis hypogaea* L.). *Electron J Plant Breed* 8:1288–1292. <https://doi.org/10.5958/0975-928X.2017.00184.3>
- Central Statistical Agency (CSA) (2018) Agricultural sample survey 2017/18: Report on area and production of major crops (private peasant holdings, main season), vol 1. CSA, Addis Ababa
- Falconer D, Mackay T (1996) Introduction to quantitative genetics. Longman Group Ltd., London
- Falke AB, Hamidou F, Halilou O, Harou A (2019) Assessment of groundnut elite lines under drought conditions and selection of tolerance associated traits. *Adv Agric* 2019:1–10. <https://doi.org/10.1155/2019/3034278>
- Francisco R, Gregorio A, Ángela P, José C, Juan B (2015) “AGD-R (Analysis of Genetic Designs with R for Windows) Version 5.0”. CIMMYT Research Data & Software Repository Network, V14
- Griffing B (1956) Concept of general and specific combining ability in relation to diallel crossing systems. *Aust J Biol Sci* 9:463–493
- ICRISAT (International Crops Research Institute for the Semi-Arid Tropics) (2020) New ICRISAT groundnut varieties to be available from next season. Accessed 14 December 2020. www.cgiar.org
- Jamieson PD, Martin RJ, Francis GS, Wilson DR (1995) Drought effects on biomass production and radiation-use efficiency in barley. *Field Crops Res* 43:77–86
- Janila P, Manohar S, Rathore A, Nigam SN (2015) Inheritance of SPAD chlorophyll meter reading and specific leaf area in four crosses of groundnut (*Arachis hypogaea* L.). *Indian J Genet* 75:408–412. <https://doi.org/10.5958/0975-6906.2015.00067.X>
- Kakeeto R, Melis R, Biruma M, Sibiyi J (2020) Gene action governing the inheritance of drought tolerance and selected agronomic traits in Ugandan groundnut (*Arachis hypogaea* L.) lines under drought environment. *Euphytica* 216:1–21. doi:<https://doi.org/10.1007/s10681-019-2539-6>
- Kamdar JM, Jasani MD, Ajay BC, Kumar S, Bera SK, George JJ, J.J (2020) Effect of selection response for yield related traits in early and later generations of groundnut (*Arachis hypogaea* L.). *Crop Breeding Applied Biotechnology* 20(2):e317320215. Brazilian Society of Plant Breeding. Printed in <https://doi.org/10.1590/1984-70332020v20n2a3>
- Kiani G, Nematzadeh GA, Kazemitabar SK, Alishah O (2007) Combining ability in cotton cultivars for agronomic traits. *Int J Agric Biol* 9:521–522
- Mathew I, Shimelis H, Mutema M, Clulow A, Zengeni R, Mbava N, Chaplot V (2019) Selection of wheat genotypes for biomass allocation to improve drought tolerance and carbon sequestration into soils. *J Agron Crop Sci* 2019:1–16. <https://doi.org/10.1111/jac.12332>
- Meisner CA, Karnok KJ (1992) Peanut root response to drought stress. *Agron J* 84:159–165. <https://doi.org/10.2134/agronj1992.00021962008400020007x>
- Ministry of Agriculture and Natural Resources (MoANRs) (2016) “Crop Variety Register Issue No. 19. Plant Variety Release.” Protection and Seed Quality Control Directorate. MoANRs, Addis Ababa
- Mukhtar AA, Babaji BA, Ibrahim S, Mani H, Mohammad AA, Ibrahim A (2013) Dry matter production and harvest index of groundnut (*Arachis hypogaea* L.) varieties under irrigation. *J Agric Sci* 5:153–162
- Nigam SN, Vasudeva Rao MJ, Gibbons RW (1990) Artificial hybridization in groundnut. Information Bulletin no. 29. Patancheru, A.P. 502 324, India. International Crops Research Institute for the Semi-Arid Tropics
- Nigam SN, Giri DY, Reddy AGS (2004) Groundnut seed production manual. International Crops Research Institute for the Semi-Arid Tropics, Andhra Pradesh, In: Patancheru. p 32
- Nigam SN, Chandra S, Sridevi KR, Bhukta AM, Reddy GS, Nageswara Rao RC, Wright GC, Reddy PV, Deshmukh MP, Mathur RK, Basu MS, Vasundhara S, Varman PV, Nagda AK (2005) Efficiency of physiological trait-based

- and empirical selection approaches for drought tolerance in groundnut. *Ann Appl Biol* 146:433–439
- Oppong-Sekyere D, Akromah R, Ozias-Akins P, Laary JK, Gimode D (2019) Heritability studies of drought tolerance in groundnuts using the North Carolina design II fashion and variance component method. *J Plant Breed Crop Sci* 11:234–253. <https://doi.org/10.5897/JPBCS2018.0781>
- Pereira JW, Albuquerque MB, Filho PAM, Nogueira RJMC, Lima LM, Santos RC (2016) Assessment of drought tolerance of peanut cultivars based on physiological and yield traits in a semiarid environment. *Agric Water Manag* 166:70–76
- Rao RCN, Singh S, Sivakumar MVK, Srivastava KL, Williams JH (1985) Effect of water deficit at different growth phase of peanut. I yield response. *Agron J* 77:782–786
- Rao RCN, Talwar HS, Wright GC (2001) Rapid assessment of specific leaf area and leaf chlorophyll meter. *J Agron Crop Sci* 189:175–182
- Ratnakumar P, Vadez V (2011) Groundnut (*Arachis hypogaea*) genotypes tolerant to intermittent drought maintain a high harvest index and have small leaf canopy under stress. *Funct Plant Biol* 38:1016–1023
- Ratnakumar P, Vadez V, Nigam SN, Krishnamurthy L (2009) Assessment of transpiration efficiency in peanut (*Arachis hypogaea* L.) under drought using a lysimetric system. *Plant Biol* 11:124–130. <https://doi.org/10.1111/j.1438-8677.2009.00260.x>
- Ravi K, Vadez V, Isobe S, Mir RR, Guo Y, Nigam SN, Gowda MVC, Radhakrishnan T, Bertoli DJ, Knapp SJ, Varshney RK (2011) Identification of several small main-effect QTLs and a large number of epistatic QTLs for drought tolerance related traits in groundnut (*Arachis hypogaea* L.). *Theor Appl Genet* 122:1119–1132
- Reddy LJ, Nigam SN, Reddy AGS (1993) Natural outcrossing in groundnut and its implications in groundnut breeding. *J Oilseeds Res* 10:99–104
- Rojas BA, Sprague GF (1952) A comparison of variance components in corn yield trials: III. General and specific combining ability and their interaction with locations and years. *Agron J* 44:462–466
- Sanogo O, Tongoona PB, Ofori K, Offei SK, Desmae H (2019) Evaluation of yield and yield components of some groundnut genotypes under rainfed condition in Mali using biplot analysis. *Afr J Agric Res* 14:1904–1912. <https://doi.org/10.5897/AJAR2018.13776>
- Sanogo O, Sissoko S, Sangare S, Zan ID, Tongoona PB, Ofori K, Offei SK, Desmae H (2020) Elucidation of the mechanism for drought stress through combining ability and gene action in groundnut. *J Genet Genom Plant Breed* 4:54–67
- Sheshshayee MS, Bindumadhava H, Rachaputi NR, Prasad TG, Udayakumar M, Wright GC, Nigam SN (2006) Leaf chlorophyll concentration relates to transpiration efficiency in peanut. *Ann Appl Biol* 148:7–15
- Shrief SA, El-Mohsen AA, Abdel-Lattif HM, El Soda M, Zein HS, Mabrouk MM (2020) Groundnut improvement: drought stress and water use efficiency of some groundnut genotypes grown under newly reclaimed soil. *Plant Archives* 20:1527–1536
- Singh RK, Chaudhary BD (1977) Biometrical methods in quantitative genetic analysis. Kalyani Publishers, New Delhi
- Singh P, Narayanan SS (2017) Biometrical techniques in plant breeding. Kalyani Publishers, New Delhi
- Songsri P, Jogloy S, Vorasoot N, Akkasaeng C, Patanothai A, Holbrook CC (2008) Root distribution of drought-resistant peanut genotypes in response to drought. *J Agron Crop Sci* 94:92–103
- Sprague GF, Tatum LA (1942) General versus specific combining ability in single crosses of corn. *J Am Soc Agron* 34:923–932
- Upadhyaya HD, Sharma S, Singh S, Singh M (2011) Inheritance of drought resistance related traits in two crosses of groundnut (*Arachis hypogaea* L.). *Euphytica* 177:55–66. <https://doi.org/10.1007/s10681-010-0256-2>
- Vadez V, Kholová J, Medina S, Kakkera A, Anderberg H (2014) Transpiration efficiency: new insights into an old story. *J Exp Bot* 65:6141–6153. <https://doi.org/10.1093/jxb/eru040>
- Vadez V, Kholová J, Hummel G, Zhokhavets U, Gupta SK, Hash CT (2015) LeasyScan: a novel concept combining 3D imaging and lysimetry for high-throughput phenotyping of traits controlling plant water budget. *J Exp Bot* 66:5581–5593
- Vaidya S, Vanaja M, Lakshmi NJ, Sowmya P, Anitha Y (2016) Variability in drought stress induced responses of groundnut (*Arachis hypogaea* L.) genotypes. *J Biochem Physiol* 4:149. <https://doi.org/10.4172/2168-9652.1000149>
- Watson J, Zheng B, Chapman SC, Chenu K (2015) Projected impact of future climate on drought patterns in complex rainfed environments. *Proc Environ Sci* 29:190–191
- Zhou H, Zhou G, He Q, Zhou L, Ji Y, Zhou M (2020) Environmental explanation of maize specific leaf area under varying water stress regimes. *Environ Exp Bot* 171:103932. <https://doi.org/10.1016/j.envexpbot.2019.103932>
- Zongo A, Nana AT, Sawadogo M, Abdourasmane KK, Sankara P, Ntare BR, Desmae H (2017) Variability and correlations among groundnut populations for early leaf spot, pod yield, and agronomic traits. *Agronomy* 7:52. <https://doi.org/10.3390/agronomy7030052>

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