RESEARCH ARTICLE

Elucidation of the mechanism for drought stress through combining ability and gene action in groundnut

Ousmane Sanogo^{1,4}, Sory Sissoko², Safiatou Sangare³, Ibrahima Zan Doumbia³, Pangirayi B. Tongoona¹, Kwadwo Ofori¹, Samuel Offei¹, Haile Desmae⁴

- 1. West Africa Centre for Crop Improvement, University of Ghana, PMB 30, Accra, Ghana
- 2. Université des Sciences, des Techniques et des Technologies de Bamako, (USTTB), BP: E 423 Bamako, Mali
- 3. Institut d'Économie Rurale IER, BP: 262 Bamako, Mali
- 4. International Crop Research Institute for the Semi-Arid Tropics (ICRISAT), BP: 320 Bamako, Mali

Corresponding authors email Id: ouzbi777@gmail.com

Manuscript received: January, 7, 2020; Decision on manuscript, February 19, 2020; Manuscript accepted: April 1, 2020

Abstract

Groundnut is a major food, feed and cash crop in Mali. However, drought stress is a major constraint to this crop production. Study was carried out to estimate the combining ability effects and to assess the mode of gene action for pod yield and drought related traits in groundnut. Four females (ICGV 93305, ICGV 91317, ICGV 86024 and ICIAR 19 BT) were crossed with three drought tolerant males (ICGV 97182, ICGV 87378 and ICGS 44) using North Carolina mating design II. The 6 parents and their 90 F2s progenies were evaluated in 2 x 10 alpha lattice design with 3 replicates in dry season. Combining ability showed significant variation for most traits in both water regimes based on mean squares due to females, males and their interaction. Additive gene actions were more important than non-additive gene actions in controlling almost all the traits under both water regimes. On the basis of GCA effects, ICGV 87378 (with 2602 kg/ha) and ICIAR19BT (with 3016.7 kg/ha) were found good general combiners for drought stress and pod yield under well-watered condition for male and female parent, respectively. Likewise, under water-stressed condition, ICGV 87378 (with 1500 kg/ha) and ICGV 91317 (with 2013.9 kg/ha) were the good combiners for drought stress and pod yield as male and female parents, respectively. ICGV 86024/ ICGV 873378 (with 4041.67 Kg/ha) and ICIAR 19BT/ICGS 44 (with 2597.22 Kg/ha) were the best specific crosses for drought and pod yield in this study. The combiners could be therefore used as important parents for drought study while their combinations are recommended for pure lines selection and further seed production.

Keywords: Groundnut, drought stress, combining ability, gene action, yield

Introduction

In Mali, groundnut production is estimated at 338,458 tons cultivated on 220,000 ha of area (FAOSTAT, 2015). It is the most important food legume accounting for almost 71% of the overall legume production in the country (CPS, 2012).

Groundnut production in Mali is low and less than 1000 kg/ ha (FAOSTAT, 2015). Ntare et al., (2012) pointed out drought as the most important constraint for groundnut production in this country. Moreover, drought occurring at reproductive phase is the most damaging form to the groundnut production (Coulibaly, 2013). This form of drought occurs from pegging to maturity period i.e 52 to 90 days after sowing (DAS) and it terms as end of season or terminal drought (Jogloy et al., 1996; Upadhyaya, 2005). Several researchers (Nageswara Rao et al., 1989; Vorasoot et al., 2003; Prasad et al., 2009) observed a decrease in yield and yield components (total dry weight, pod yield, seed yield, number of seeds per plant and seed weight) for all cultivars under water-limited conditions. Haro et al. (2008) observed a decrease in pod and seed growth rates by approximately 30% followed by decrease of individual seed weight from 563 to 428 mg under drought. Ravi et al., (2011) proposed the development of varieties that are better adapted to water-limited conditions. This option can partially tackle recurrent yield loss in the harsh climate conditions of the Sahel zone in Mali where farmers mostly used landraces that are susceptible to drought. The development of drought groundnut requires tolerant identification and crossing of suitable parents. Combining ability study provides guidelines for plant breeders. It helps selecting suitable parents and their combinations in breeding programs (Jogloy et al., 2005; John and Reddy, 2015). Combining ability is the relative ability of a genotype to transmit its desirable performance to its progenies (Mothilal and Ezhil, 2010; John and Reddy, 2015). The information about the relative contribution of components of variation i.e., additive, non-additive and epistasis, is essential for effective plant improvement. General combining ability is associated with genes which are additive in effects while specific combining ability is attributed primarily

to deviations from the additive scheme caused by dominance and epistasis (Chahal and Gosal, 2006; Stoskopf et al., 2006; Hallauer et al., 2010). In self-pollinated crops like groundnut, pure line selection is needed and additive genes expressed as GCA are more important than nonadditive genes (SCA). The information on combining ability and mode of gene action responsible for drought tolerance would certainly help in improving tolerance in groundnut and enhance yield. Such knowledge of genetic information is prerequisite but is lacking in groundnut breeding in Mali. Therefore, the aims of this study were to estimate general and specific combining ability, and to assess the mode of gene action of drought related traits and yield components in groundnut.

Materials and methods

Experimental conditions and genetic resources

The study was conducted at ICRISAT Station Samanko (12°54'W and 8°04'N, 331 m) at 25 km South-West from Bamako, in the Sudano-Sahelian zone of Mali. The soils are poor in organic matter and light with the pH 5.0. Relative humidity, temperature readings for the period of experiments were recorded daily by an automated weather station. The average ambient temperature during this period was 26.07°C, with a standard deviation STDEV= 9.55% and the average relative humidity was 27.17% with a standard deviation STDEV of 16.56%. There was no rainfall during crop growth. The experimental material consisted of the four drought susceptible females crossed to three drought tolerant males using North Carolina mating design II according to Comstock and Robinson (1948). The female parents (ICGV 93305, ICGV 91317, ICGV 86024 and ICIAR 19 BT) were locally adapted varieties with at least one desired attribute (high yield potential, short duration. tolerance Aflatoxin

contamination and diseases) but susceptible to drought stress. On contrast, the male parents (ICGV 97182, ICGV 87378 and ICGS 44) were reported drought tolerant as they exhibited high SPAD values with low SLA values, TE, and HI (Upadhyaya, 2005; Hamidou et al., 2012). Seed of F_1 were selfed to generate more seed at F_2 . Parents and their 12 F2's were planted in 2 x 10 alpha lattice design with three replications during the 2014/2015 dry season for evaluation. Each genotype was grown in a single plot of 4 m row with 0.20 x 0.60 m spacing. The irrigation water management described by4 was partly modified and applied as followed: the waterstressed (WS) block, full irrigation was provided till 50 days after sowing (DAS). At 50 DAS, drought stress was imposed for 14 days and irrigation was resumed at the 15th day to bring the soil up to saturation. Then, drought stress was imposed for 10 days, followed by irrigation up to saturation. After that, drought stress was imposed for 7 days followed by irrigation up to harvest. This technique was supposed to mimic the end-of-season drought since water was withheld during the critical stage of the reproductive phase. The well-watered (WW) block received full irrigation throughout the life cycle of the crop (from sowing to harvesting period). Plants were irrigated one to two times per week with 20 mm of water until end-ofseason (pod filling to pod maturity) at seven day interval depending on the prevailing weather conditions. Except for the different irrigation treatments, all field management practices were uniform for both the well-watered and waterstressed experiments.

Data collection and analysis

Data were collected from an average of 10 plants /plot on the following traits: 50% Plants flowering (days), Soil Plant Analysis Development SPAD Chlorophyll Meter Reading (SCMR at 60 DAS and 80 DAS), Specific Leaf Area (SLA at 60 DAS and 80 DAS, cm2.g-1),

plant biomass at harvest, 100-sound seed weight (g), shelling percentage (%), harvest index (g) and pod yield (g). Analysis of variance for yield and drought related traits were performed with SAS 9.3 software using the model described by Comstock and Robinson (1948). Genotypes were considered as fixed effects, while replications and water regime were considered as random effects.

Results and discussion

Observed variability under well-and waterstressed environments

Analysis of variance indicated the presence of significant variation among genotypes (Table 1). Significant interaction between genotypes and environments for drought related traits and for yield and yield components were found for SCMR 60 DAS, GY, and BIO. The differences between crosses and their parents were significant for most traits. Partitioning revealed that parents x environments interactions were significant for SCMR 60 DAS. Progenies F2 crosses vs parents x environment interactions were significant for all traits except for 50% DF. Partitioning of the crosses x environment mean squares into variation due to males x environment and females x environments interactions showed significant with GCA x environment effect for HSW and BIO 80 DAS in the females x environment interaction. Combining ability of the traits revealed significant differences among parents, crosses and parents x crosses for most the measured traits under both environments (well-watered and water-stressed). This indicated the existence of adequate genetic variation among the parents used in the crosses and their response to wellwatered and water-stressed conditions. Similar results were observed by Lal and Kumar, (2012) and Avinash et al., (2017) studying genetic variability of parents and crosses under contrasting environments in maize.

Table 1: Mean squares for drought intermittent traits, yield and yield components of crosses and their parents grown across well-watered and water-stressed conditions

Sources of variation df	J p	50%DF	SCMRf	SLAf	SCMRz	SLAz	BIO	PY	HSW	H	SP
Environment (E)	1	0.35	537.1***	73027.59**	376.48***	5424.31	1.00***	235.6***	298.94** 2.51		966.39**
Rep within E	4	1.96	1.18	439.51	9857.83	450.39	24.31	38.70**	3.14	52.48**	34.82
Genotypes (G)	18	952.32***	143.6***	80080.16***	67804.73***	60841.78***	54.1***	66.1***	725.26*** 466.2***		966.06***
Parents (P)	9	43.52***	58.42**	15935.79*	55.79***	11537.56***	53.24**	23.8***	15.67	0.02***	169.79*
P vs C	1	16832.5***	2048.3***	1345826.6***	1034395.5***	1025924.5***	309.9***	814.0***	12958.9**	12958.9** 8063.7***	16368.6***
Progenies	11	4.36***	16.89***	0.13**	16886.81*	0.19*	31.38*	21.26**	0.16**	29.81**	0.16***
GCA female	3	23.94***	6.37	23491.23*	5.2	2549.5	0.23**	53.94**	68.34***	59.85**	332.51**
GCA male	2	5.06	1.91	3705.67	1.4	6963.64	0.01	14.65	1.05	33.14	55.61
SCA	9	17.31***	46.89***	17978.31	58.08***	10232.35**	0.18**	22.79	49.74**	16.56	225.26*
ExG	18	2.15	14.09**	3524.94	8141.19	517.72	39,41**	11.36	3.3	9.04	31.88
ExP	9	4.21	32.82**	7509.26	4.42	466.03	7.26	3.03	6.54	0	42.81
ExPvsC	1	13.53	49.19*	18392.82**	27829.11*	6522.40**	543.1***	130.1**	19.01*	81.5**	316.87**
ExC	11	0	89.0	0.05	10789.61	0.04	11.16	5.11	0.1	7.38	0.02
ERROR	106	4.05	10.56	2830.47	10.56 2830.47 6563.44 933.21 17.66	933.21		9.54	4.99	9.42	29.59

Where, *P<0.05, **P<0.01, ***p<0.001, respectively. PY= pod yield (kg ha⁻¹), 50%DF= Day to 50% flowering (days), SCMRf=SPAD meter reading at 60DAS, SCMRZ=SPAD meter reading at 80DAS, SLAf= Specific leaf area (cm² g¹) at 60DAS, SLAz=Specific leaf area (cm² g¹) at 80DAS, HSW=hundred seed weight (g), SP=Shelling percentage (%).

Performance of parental lines and crosses for pod yield and other traits in field under wellwatered and water-stressed conditions

Comparative studies among the parents and crosses reflect the insight of the tolerance for drought stress. In comparing the two water regimes, there was general reduction in performance of the parental lines under drought stress conditions for PY and most of the traits (Tables 2 and 3). Some genotypes showed large reduction whereas others had small reduction under drought stress. Large reduction in performance was observed for traits in some parental lines under water-stressed condition. With ICIAR 19 BT, PY was 3016.67 kg/ha under well-watered condition and 1601.85 kg/ha under water-stressed conditions (1414 kg reduction).conditions while other genotypes showed low reduction in performance under the same. Alhassan, 2013; Coulibaly, 2013, used ICIART 19 BT as parental lines showing better performance in cross combination. The genotype ICGV 87378, ICGS 44 and ICIAR 19BT might exhibit maternal or epistasis effects reported by Upadhyaya and Nigam (1998).

Similarly, PY was 2666.70 kg /ha and 1331.00 kg/ha for ICGV 86024 respectively under wellwatered condition and under water-stressed condition. The opposite was recorded with ICGV 93305 with 1609.80 kg/ha as PY under well-watered condition and 1021 kg/ha under water-stressed condition. The same genotype had the lowest pod yield among parent lines under both well-watered and water-stressed conditions DAS under water-stressed condition. Parental lines performance decreasing was observed while ICIAR 19 BT showed the highest performance in both water regimes despite having the highest reduction in PY. All the parental lines scored higher SCMR 60 DAS under water-stressed condition while only the male parents showed higher SLA 60 under

drought stress condition for SLA at 80 DAS and SCMR at 80 DAS. General reduction in performance of the crosses was noticed under drought stress condition for most of the traits comparing the two water regimes (Tables 4 and 5). The performance of PY decreased from 2521.32 kg/ha under well-watered condition to 1492.01 kg/ha under water-stressed condition (1029.31 kg/ha reduction) for all crosses. Some crosses showed large reduction for PY while low reduction was observed for other. In ICGV 86024/ICGV 87378, PY was 4041.67 kg/ha under well-watered condition and 1805.56 kg/ha under water-stressed condition (2236.11kg/ha reduction). This was followed by ICIAR 19 BT/ICGV 97182 which had 2041.66 kg/ha reduction of PY (2944.44 kg/ha under wellwatered condition and 902.78 kg/ha under water-stressed condition). These two crosses had the largest difference in pod yield under waterstressed condition. In ICGV 93305/ICGV 97182, the reduction of PY was small (491.67 kg/ha with 1902.78 kg/ha under well-watered condition and 1411.11 kg/ha under waterstressed condition). Decreasing of crosses performance under drought stress for yield components (BIO, HI, SP and HSW) were observed but trend in 50%DF was similar for all crosses under both water regimes. Similar results in yield and yield attributes were reported by Songsri et al., (2008) and Wunna et al., (2009) in groundnut

The crosses ICGV 93305/IGCS 44 and ICIAR 19BT/ICGS 44 had the highest SCMR 60 DAS under water-stressed conditions while ICGV 91317/ICGV 97182 and ICIAR 19 BT showed the highest SCMR 60 DAS and 80 DAS under water-stressed condition. The lowest SLA 60 DAS and 80 DAS under water-stressed conditions were found with ICGV 93005/IGCS 44 and ICGV 86024/ICGV 87378, respectively. Similar reduction in SLA and increase of SCMR in groundnut were reported by Coulibaly (2013).

Journal of Genetics, Genomics & Plant Breeding 4(2) 54-67 (April, 2020) ISSN (Online): 2581-3293

Table 2: Performance of parental lines evaluated under well-watered (WW) condition

Genotypes	50%DF	SCMRf	SLAf	SCMRz	SLAz	HSW	HI	BIO	SP	PY
			<u> </u>	Female	<u> </u>	l		I		l
ICGV 93305	32	39.0	195.7	43.0	176.1	22.3	0.3	18.1	29.8	1609.8
ICGV 91317	30	37.4	292.6	40.9	209.8	22.3	0.6	18.6	17.6	2792.1
ICGV 86024	32	37.5	347.1	40.6	195.4	22.5	0.5	19.3	21.8	2666.7
ICIAR 19BT	33	38.7	256.3	41.4	206.2	25.7	0.5	22.4	21.1	3016.7
SE±	2	3.4	96.4	2.8	73.8	3.5	0.2	3.2	6.9	706.4
Male										
ICGV 97182	32	37.6	287.1	40.7	208.8	23.5	0.5	19.2	20.8	2559.4
ICGV 87378	31	38.4	259.3	41.7	176.3	21.3	0.5	20.5	22.0	2602.8
ICGS 44	32	38.4	272.4	41.9	205.4	24.8	0.5	19.1	24.9	2401.8
SE±	2	3.4	121.0	3.1	70.9	3.4	0.2	3.6	8.2	916.3

Where, PY= pod yield (kg ha⁻¹), 50% DF= Day to 50% flowering (days), SCMRf=SPAD meter reading at 60DAS, SCMRz=SPAD meter reading at 80DAS, SLAf= Specific leaf area (cm² g⁻¹) at 60DAS, SLAz=Specific leaf area (cm² g⁻¹) at 80DAS, HSW=hundred seed weight (g), SP=Shelling percentage (%),HSW=hundred seed weight (g), HI= Harvest index, BIO= Biomass (Kg), SP=Shelling percentage (%).

Table 3: Performance of parental lines evaluated under water-stressed condition

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Genotypes	50%DF	SCMRf	SLAf	SCMRz	SLAz	HSW	HI	BIO	SP	PY	
				Fen	nale						
ICGV 93305	32	41.9	186.0	45.5	172.7	20.5	0.2	14.4	32.3	1021.3	
ICGV 91317	30	43.4	246.6	45.6	182.5	23.6	0.5	15.8	24.3	2013.9	
ICGV 86024	32	44.3	183.1	46.1	169.2	21.7	0.3	15.7	34.0	1331.0	
ICIAR 19BT	33	44.7	221.1	47.0	193.6	25.5	0.3	18.1	29.0	1601.9	
SE±	2	3.0	62.7	3.4	52.6	4.0	0.2	4.4	10.8	644.3	
Male											
ICGV 97182	32	43.5	223.8	46.2	205.7	22.5	0.3	15.6	30.6	1481.3	
ICGV 87378	31	43.3	208.1	45.9	172.7	22.4	0.3	16.9	28.1	1500.0	
ICGS 44	32	43.9	195.8	46.0	160.0	23.6	0.3	15.5	31.0	1494.8	
SE±	2	3.2	67.7	3.4	49.7	4.5	0.2	4.7	11.5	759.3	

Where, PY= pod yield (kg ha⁻¹), 50% DF= Day to 50% flowering (days), SCMRf=SPAD meter reading at 60DAS, SCMRz=SPAD meter reading at 80DAS, SLAf= Specific leaf area (cm² g⁻¹) at 60DAS, SLAz=Specific leaf area (cm² g⁻¹) at 80DAS, HSW=hundred seed weight (g), SP=Shelling percentage (%), HSW=hundred seed weight (g), HI= Harvest index, BIO= Biomass (Kg), SP=Shelling percentage (%).

Table 5: Performance of parental lines evaluated under water-stressed (WS) condition

Crosses	50%DF	SCMRf	SLAf	SCMRz	SLAz	HSW	н	BIO	SP	PY
ICGV 93305 /										
ICGV 97182	32	41.42	196.46	44.73	194.89	19.75	0.31	14.35	26.85	1411.11
ICGV 93305 /										
ICGV 87378	31	39.85	190.35	44.84	175.48	20.03	0.16	14.87	31.34	819.44
ICGV 93305 /										
ICGS 44	33	44.56	171.28	46.78	147.75	21.76	0.17	13.90	38.70	833.33
ICGV 91317 /										
ICGV 97182	31	47.04	211.38	50.85	166.40	26.67	0.62	15.27	23.37	2416.67
ICGV 91317 /										
ICGV 87378	30	41.80	292.47	43.74	211.22	19.33	0.48	16.23	20.06	2069.44
ICGV 91317 /										
ICGS 44	29	41.37	236.00	42.12	169.85	24.86	0.30	15.83	29.41	1555.56
ICGV 86024 /										
ICGV 97182	31	43.29	191.00	45.35	192.64	20.00	0.20	17.57	39.37	1194.44
ICGV 86024 /										
ICGV 87378	30	46.15	175.45	48.40	144.13	24.67	0.39	16.57	29.31	1805.56
ICGV 86024 /										
ICGS 44	34	43.33	182.89	44.50	170.68	20.33	0.23	12.85	33.43	993.05
ICIAR 19BT /	o =	42.40	20121	42.00	2 50 04	22.40	0.45	4 7 00	22.07	000 50
ICGV 97182	35	42.40	296.26	43.89	268.81	23.49	0.17	15.03	32.95	902.78
ICIAR 19BT /	22	15.16	174 10	16.60	160.10	25.60	0.21	20.10	21.56	1205.56
ICGV 87378	33	45.46	174.10	46.62	160.13	25.60	0.21	20.10	31.56	1305.56
ICIAR 19BT /	21	46.21	102.01	50.47	151.01	27.22	0.52	10.20	22.54	2507.22
ICGS 44	31	46.31	193.01	50.47	151.81	27.33	0.53	19.30	22.54	2597.22
Mean	32	43.58	209.22	46.02	179.48	22.82	0.31	15.99	29.91	1492.01
SE ±	1.5	2.39	58.94	2.20	43.48	3.59	0.09	4.29	9.70	497.00
LSD _{0.05}	2.3	3.66	95.53	4.05	84.79	6.61	0.17	6.2	19.85	814.28

PY= pod yield (kg ha⁻¹), 50%DF= Day to 50% flowering (days), SCMRf=SPAD meter reading at 60DAS, SCMRz=SPAD meter reading at 80DAS, SLAf= Specific leaf area (cm² g⁻¹) at 60DAS, SLAz=Specific leaf area (cm² g⁻¹) at 80DAS, HSW=hundred seed weight (g), SP=Shelling percentage (%), HSW=hundred seed weight (g), HI= Harvest index, BIO= Biomass (Kg), SP=Shelling percentage (%)

Relative contributions of combining ability effects

Specific combining ability is regarded as an indication of loci with dominance variance (non-additive effects) and all the three types of epistatic interaction components if epistasis were present. They include additive \times dominance and dominance \times dominance interactions. GCA contributions to genotypic sum of squares varied from 24% for SCMR 60 DAS to 92% for HSW under well-watered environments while SCA varied from 8% for HSW to 76% for SCMR 60 DAS (Fig. 1). The contribution of GCA_m (2%) and GCA_f (57%) to genotypic sum of squares for pod yield was highly significant under well-

watered environments while SCA was 41% under well-watered environment. SCA accounted for 76%, 61 % and 58% of the variation respectively for SCMR 60 DAS, SCMR 80 DAS and SLA 80 DAS. GCA accounted for most of the variation observed in pod yield, SP, BIO, HI, HSW, SLA 60 DAS and 50 % DF.

Under drought environment, the overall contributions of GCA (GCA $_m$ plus GCA $_f$) sum of squares to the total variation among genotypes varied from 11% for SCMR at 80 DAS to 73% for BIO while SCA varied from 41% for HSW to 91% for SCMR 80 DAS (Figure 2). GCA contributed up to 60% of the

sum of squares for pod yield, 67% for SLA 80 DAS, 66% for SLA 60 DAS, 65% for 50%DF, 52% for HI and 39% for SCMR 60 DAS. The percentage of GCA $_{\rm f}$ (55%) was higher than GCA $_{\rm m}$ (5%) and SCA (40%) for pod yield. The GCA $_{\rm f}$ was larger than GCA $_{\rm m}$ for all traits except for SLA 80 DAS. Similarly, GCA $_{\rm f}$ was larger for all traits than SCA except for SCMR 80 DAS (89%) and SCMR 60 DAS (61%) sum of squares.

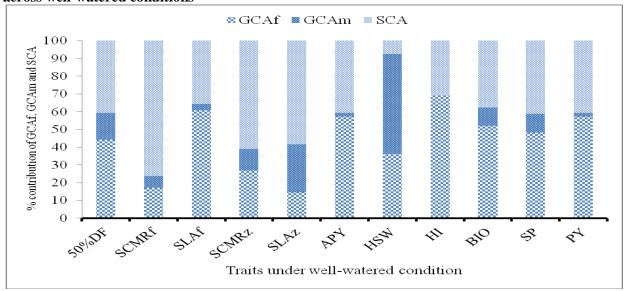
Among females, ICIAR 19BT and ICGV 91317 had consistently greater values for GCA_f and significant GCA_f effects in most of the traits. Correspondingly, ICGS 44, and ICGV 87378 consistently showed greater GCA_m effects. These four parental lines (ICIAR 19BT, ICGV 91317, ICGV 87378 and ICGS 44) were likely to contribute favourable alleles in a pure line selection programme for drought tolerance improvement. Such lines could be used as parents to form a pool population that could be improved for tolerance to drought. This also suggests that these inbreds are tolerant to drought as confirmed by high pod yield performance of inbreds ICGV 87378 and ICGS 44 under drought. The female parental lines ICIAR 19BT, ICGV 91317 that were earlier identified as susceptible to drought (Hamidou et al., 2012; Alhassan, 2013) showed tolerant level to drought in current study. This situation might be due to the procedure of imposing the drought stress based on intensity of drought, the stress length and interval between two subsequent irrigations.

In addition to its early maturity that contributes to escaping drought, ICIAR 19BT could therefore be considered as a potential parent under drought conditions. Similarly, the high yielding and aflatoxin tolerant variety ICGV 91317 was identified by (Nigam *et al.*, 2009) as one of the best parental lines in this study. Further studies could be done to confirm the actual findings on the tolerance level of ICIAR

19BT and ICGV 97317. Yield performance of ICIAR 19BT with 3016.67 kg/ha and 1606.85 kg/ha respectively under well-watered and water-stresses conditions was the most attractive general combiner. This was followed by ICGV 91317 with high GCA_f effects. The male parental line ICGV 87378 with 2602.78 kg/ha under well-watered condition and 1500 Kg/ha under drought stress conditions was the best combiner with high GCA_m effects followed by ICGS 44. In actual study, high SCMR and low SLA which are desirable for identifying drought tolerance genotype, did not always lead to higher pod yield. Krishnamurthy et al. (2007) also reported poor relationship between pod yield and these traits. Although SCA values were presented here, their importance is minimal in groundnut breeding because selections are based on pure lines rather on hybrids development. SCA effects cannot be fixed in inbred groundnut genotypes (Tongoona, Pers. comm). Important parameters were the effects of GCA_m and that of GCA_f. These estimates provided additive genes that can be exploited in pure line selection of the highly self-pollinated groundnut crop.

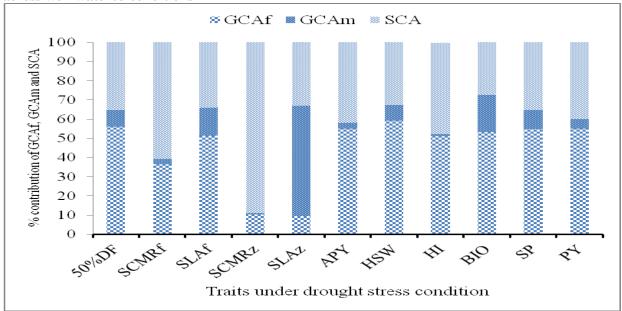
To select the two best progenies, Arunga et al., (2010) suggested that SCA effects should be used in combination with progeny means of the GCA effects of the respective parents. These authors believed that for self-pollinated crops, a combination of SCA value of the progeny and its mean performance would tend to increase the concentration of favourable alleles. Most of the studies also rely on GCA, SCA along with mean performance to choose best performing line. Based on these considerations, the following two combinations (progenies), ICIAR 19BT/ ICGS 44 and ICGV 91317/ ICGV 87378 out of the twelve were selected. These progenies, derived from the four good combiners showed high yield under both well-watered and water-stressed environments.

Figure 1: Percentage contributions of GCA and SCA effects to total variance for selected traits across well-watered conditions



PY= pod yield (kg ha⁻¹), 50%DF= Day to 50% flowering (days), SCMRf=SPAD meter reading at 60DAS, SCMRz=SPAD meter reading at 80DAS, SLAf= Specific leaf area (cm² g⁻¹) at 60DAS, SLAz=Specific leaf area (cm² g⁻¹) at 80DAS, HSW=hundred seed weight (g), SP=Shelling percentage (%). GCAm=General Combining ability for male, GCAf = General Combining ability for female, GCAm + GCAf=GCA. SCA= Combining ability of crosses

Figure 2: Percentage contributions of GCA and SCA effects to total variance for selected traits across well-watered conditions



PY= pod yield (kg ha⁻¹), 50%DF= Day to 50% flowering (days), SCMRf=SPAD meter reading at 60DAS, SCMRz=SPAD meter reading at 80DAS, SLAf= Specific leaf area (cm² g⁻¹) at 60DAS, SLAz=Specific leaf area (cm² g⁻¹) at 80DAS, HSW=hundred seed weight (g), SP=Shelling percentage (%). GCAm=General Combining ability for male, GCAf = General Combining ability for female, GCAm + GCAf=GCA. SCA= Combining ability of crosses.

GCA effects of female and male parents for various traits under drought stress and wellwatered conditions in field

Limited studies have been reported in groundnut reporting combining ability study under drought stress. In the present study three genotypes ICGV 91317, ICGV 86024 and ICIAR 19 BT had significantly positive GCAf effects for pod yield while ICGV 93305 showed significantly negative GCAf effect for pod vield under wellwatered-condition. **ICGV** 91317 showed significantly GCAf effect for days to 50% flowering and shelling percentage while ICGV 93305 had significantly positive GCAf for shelling percentage. ICIAR 19 BT had significantly positive GCAf effect for hundred seed weight and biomass under well-watered conditions. The genotypes ICGV 97182 and ICGV 87378 showed significantly positive GCAm effects for pod yield under well-watered conditions (Table 6).

Under water-stressed condition, ICGV 91317 and ICIAR 19 BT had significant and positive GCAf effects while ICGV 93305 and ICGV 86024 showed significantly negative GCAf effects. ICGV 93305 showed significantly negative GCAf effect for chlorophyll content at 60 DAS. ICIAR 19 BT had significantly positive GCAf effects for days to 50% flowering and hundred seed weight under drought stress condition. Under well-watered conditions, all genotypes had significantly positive GCAm effects except for ICGV 97182 which showed significantly negative GCAm effects.

Furthermore, significant GCA and SCA for traits is an indication of more involvement of additive and non-additive gene actions. The greater importance of GCA effects than SCA effects for most measured traits under both moisture regimes and environments (pots and field) indicating the preponderance of additive effects. Progress in selection could be made at late stage

with traits having additive gene effects. These results agree with the findings of Ali et al., (1995) who reported that GCA estimates were greater than SCA effects for shelling percentage, pod yield in F_1 and F_2 generations. In a 6 x 6 full diallel mating design, Lal et al., (2006) reported both additive and non-additive effects governing SCMR with preponderance of the former while SLA and HI were mainly additive genes in nature. Similar results were obtained by Nava and Larysse (1997) who reported predominance of additive gene action for pod yield, kernel yield, and shelling percentage. Other researchers reported presence of both additive and non-additive gene effects in controlling pod yield, and shelling percentage in groundnut (Upadhyaya and Nigam, 1998). Dwivedi et al. (1998) found significant GCA effects for harvest index when studying 6 parent diallel cross in groundnut while Parmar et al., (2000) reported significance GCA and SCA effects for pod yield, shelling percentage and hundred seed weight. However, the present results are not in line with the findings of Upadhyaya et al., (1998) who reported that nonadditive gene effects predominantly for pod yield and kernel yield and shelling outturn when using a line x tester analysis. Current findings are in the agreement of the earlier researchers of John et al., (2011) and Coulibaly (2013) who indicated non-additive genes controlling pod yield, biomass, 50% date to flowering and shelling percentage. Differences may arise due to the differences in the set of germplasm, and the specific environment of the study as well their interaction.

In the present findings, high x high general combiners for drought and yield traits did not always lead to better performing combinations. This result was in line with the findings of Ahmhad *et al.*, (2017) when studying wheat seed quality traits.

Table 6: Estimates of GCA effects and standard errors of parental lines evaluated under well-watered conditions

watered to		50%								
994	DX7		COLUDA	OT A 6	COMP	CT. A	TTOTAL	DIO	CIP.	***
GCA	PY	DF	SCMRf	SLAf	SCMRz	SLAz	HSW	BIO	SP	HI
				GCA	\f					
ICGV										
93305	-470.71**	0.25	-1.64*	-23.2	-0.57	-11.25	-2.31	-1.62	2.38	-0.1
ICGV										
91317	521.88**	-1.64*	-0.18	37.40	-0.45	0.16	0.80	-0.21	-5.63	0.16
ICGV										
86024	-160.99**	0.03	0.67	-26.11	0.06	-20.78	-1.15	-0.33	4.13	-0.04
ICIAR										
19BT	109.84**	1.36*	1.14	11.9	0.97	11.25	2.66*	2.15	-0.89	-0.01
SE ±	706.4	0.47	0.73	35.97	0.87	16.81	1.30	1.14	3.90	1.30
GCAm										
ICGV										
97182	-10.76**	0.36	-0.04	14.56	0.19	22.22	-0.34	-0.43	0.72	0.01
ICGV										
87378	7.99**	-0.47	-0.27	-1.13	-0.12	-15.21	-0.41	0.95	-1.84	0.00
ICGS 44	2.78**	0.11	0.31	-13.42	-0.05	-22.22	0.75	-0.52	1.11	0.00
SE ±	916.3	0.40	0.63	31.15	0.75	14.56	1.13	0.99	3.38	1.13

*, ***, ****, indicates significance at P<0.05, P<0.01 and P<0.001, respectively. PY= pod yield (kg ha⁻¹), 50%DF= Day to 50% flowering (days), SCMRf=SPAD meter reading at 60DAS, SCMRz=SPAD meter reading at 80DAS, SLAf= Specific leaf area (cm² g⁻¹) at 60DAS, SLAz=Specific leaf area (cm² g⁻¹) at 80DAS, HSW=hundred seed weight (g), SP=Shelling percentage (%)HSW=hundred seed weight (g), HI= Harvest index, BIO= Biomass (Kg), SP=Shelling percentage (%)

Conclusion

In conclusion efforts were made to study the performance of the parents and their crosses in order to estimate the mode of gene action of drought related traits and yield components in groundnut. This study revealed that additive gene effects were more important than nonadditive gene effects in controlling most of the traits under both water regimes. Good combiners and combinations showed low SLA with high SCMR and high pod yield under drought stress conditions. The best four good combiners identified were ICIAR 19BT and ICGV 91317 for the female and ICGS 44 and ICGV 87378 for the male parents. The good combiners were useful to identify two crosses: ICGX-IS 13005 (ICGV 91317/ICGV 87378) and ICGX-IS 13012 (ICIAR 19BT/ICGS 44), which were high yielding under both water regimes resulting from cross combinations of these lines. The combiners could be therefore used as important parents for drought study while their combinations are recommended for pure lines selection and further seed production.

Acknowledgements

The authors are very thankful to Alliance for Green Revolution in Africa (AGRA) for funding this research work. Authors also would like to acknowledge the help and the technical support received from the International Crop Research Institute for the Semi-Arid Tropics (ICRISAT), Hyderabad, India and West Africa Centre for Crop Improvement (WACCI) Noguchie Link, Accra, Ghana.

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Journal of Genetics, Genomics & Plant Breeding 4(2) 54-67 (April, 2020) ISSN (Online): 2581-3293

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