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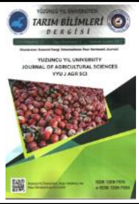

Research Article

Genetic Control and Combining Ability Effects of Certain Yield Traits in Cowpea (*Vigna unguiculata* L. (Walp)) under Conditions of Drought Stress

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Abstract: This research was undertaken to assess genetic control and combining effects of some essential traits of yield under drought stress. Forty-two hybrids under water-stressed and well-watered conditions were tested in field experiments for two years. Evaluation of the various genetic components of variation was performed. Both the additive (D) and the dominant (H1) variance components were important in most of the traits suggesting both additive and non-additive gene effects under both conditions. The study showed that the minimum number of genes under water-stressed (WS) conditions ranged from 0.02 for pod length to 16.13 for days to 50% flowering. The narrow-sense heritability ranged from 24% for the number of pods per plant and pod length to 66% for the number of days to 50% flowering under WS condition. The impacts of SCA and GCA have been determined. In both conditions IT93K-432-1 and IT97K-499-35 showed the strongest GCA results on both of the traits. Danila×IT93K-432-1, Danilla×IT97K-499-35, and TVu7778×IT99K-573-2-1 have been observed to have the best SCA effect under both conditions for most of the traits. In most traits, additive and non-additive gene effects plus additive × additive and additive × dominance gene interactions were common. In summary, additive and non-additive gene actions were detected; however, there was a preponderance of non-additive gene action in both conditions. As a result, the enhancement of these traits would involve a repetitive selection technique as a result of the prevalence of the dominant gene effect, which would allow favorable recombination of the genes in both conditions in later generations.

Kuraklık Stresi Koşullarında Börülcede (*Vigna unguiculata* L. (Walp)) Belirli Verim Özelliklerinde Genetik kontrol ve Birleşme Yeteneğinin Etkileri

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Anahtar Kelimeler
Birleşme yeteneği,
Börülce,
Kuraklık toleransı,
Epistaz,

Öz: Bu araştırma, kuraklık stresi altında verime ait bazı temel özelliklere genetik kontrol ve uygulamaların ortak etkilerini değerlendirmek için yapılmıştır. Su stresli ve iyi sulanmış koşullar altında kırk iki hibrit, arazi deneylerinde iki yıl boyunca test edildi. Varyasyonun çeşitli genetik bileşenlerinin değerlendirilmesi yapıldı. Hem eklemeli (D) hem de baskın (H1) varyans bileşenleri, her iki koşulda da hem eklemeli hem de eklemeli olmayan gen etkilerini düşündüren özelliklerin çoğunda önemliydi. Çalışma, su stresi (WS) koşulları altında minimum gen sayısının, % 50 çiçeklenme döneminde, bakla uzunluğu için 0.02 ila 16.13 arasında değiştiğini gösterdi. Dar anlamda kalıtsallık, bitki başına bakla sayısı ve bakla uzunluğu için % 24'ten gün sayısı için % 66'ya, WS koşulunda % 50 çiçeklenmeye kadar değişmektedir. SCA ve GCA'nın etkileri belirlendi. Her iki koşulda da IT93K-432-1 ve IT97K-499-35, her iki özellik üzerinde de en güçlü GCA sonuçlarını gösterdi. Danila × IT93K-432-1, Danilla × IT97K-499-35 ve TVu7778 × IT99K-573-2-1'in, özelliklerin çoğu için her iki koşulda da en iyi SCA etkisine sahip olduğu gözlemlendi. Çoğu özellikte, eklemeli ve eklemeli olmayan gen etkilerinden artı eklemeli × eklemeli ve eklemeli × baskın gen etkileşimleri yaygındı. Özetle, eklemeli ve eklemeli olmayan gen aktiviteleri tespit edildi; fakat, her iki koşulda da eklemeli olmayan gen eyleminin üstünlüğü vardı. Sonuç olarak, bu özelliklerin geliştirilmesi, baskın gen etkisinin prevalansının bir sonucu olarak her iki koşulda da genlerin sonraki nesillerde uygun şekilde yeniden birleştirilmesine izin verecek tekrarlayan bir seçim tekniğini içerecektir.

Genotipler, Katkısız.

1.Introduction

Nigeria has been confirmed to be the world's highest producer of nearly 47 million metric tons of beans from an estimated 4.5 million hectares per year, making it Africa's top producer of pulses and the world's fourth-largest producer of cowpea (Daily Trust 2019, Unpublished). In Nigeria more than 60 million people consume cowpea products daily. CGIAR (Unpublished) stated that Cowpea (*Vigna unguiculata* L. (Walp)) was a protein-rich grain which supplements cereals and other tuber crops as well. It also provides livestock feed and fixes soil nitrogen to increase nutrients in the soil. It is usually grown in the African, Asian, European, United States, and Central and South American semi-arid tropics. The grains contain 25 per cent protein and other minerals and vitamins. The crop is an edible crop which has made a significant contribution to the survival of millions in both the southern and northern parts of the country (Singh et al., 1999).

The importance of Cowpea cuts across its use as the staple food and cash crop. Nearly every part of the crop is useful; grains are useful because they provide relatively poor urban communities with inexpensive and nutritious food (Singh et al., 1999). "Cowpea leaves are also found to be sold in Benin, Cameroon, Ethiopia, Ghana, Kenya, Malawi, Mali, Tanzania and Uganda" (Barret, 1987), the above-ground parts of cowpea are also harvested for fodder, except for pods, and they are also found to symbiotically fix atmospheric nitrogen by nodule bacteria (Rhizobium sp) as a vital supplement to soil fertility status (Barret, 1987).

Nevertheless, biotic and abiotic factors are the main constraints to cowpea development in Nigeria. Attaching the crop to biotic factors such as insect pests and diseases thus decreases yield (Hall and Patell, 1987; Ajeigbe HA et al., 2008). Drought is one of Nigeria's main abiotic factors affecting cowpea development (IITA, 2000; Ishiyaku and Aliyu, 2013). However, cowpea as a plant has been recorded to be highly drought-tolerant, particularly the spreading cultivars, but under extreme drought it has suffered significantly, resulting in a substantial reduction in yield. Singh et al. (1985) and Shimelis and Shiringani (2010) reported that cowpea has a higher yield than other crops under drought stress. The irregular pattern of rainfall as a result of climate change has plunged the agricultural communities into unemployment and then famine. The water stress issue can be solved by having a practical and efficient modern irrigation network, or by breeding for genotypes that are resistant to drought. Given the high cost of introducing a modern irrigation scheme, however, breeding for drought-tolerant genotypes would be more acceptable and cheaper. Three major approaches for breeding tolerant genotypes have been suggested; the first approach is to evaluate and search for drought tolerant under optimum (non-water stress) condition for high yield varieties, expecting a high correlation between results in optimum and stress conditions (Johnson and Frey, 1967) and that varieties with higher yields under normal conditions may also perform better under water stress, but this may be influenced by genotypes, which may eventually interfere with yield. The second approach involves breeding for high yield varieties under water stress, this approach is struggling as the severity of drought is highly variable from year to year and as a result environmental selection pressure shifts from generation to generation and even low heritability will exacerbate the problem (Jiban Mitra, 2001). However, the mechanism by which plants adapted under water stress – drought escape, drought avoidance and drought tolerance – do not help high yield which is the ultimate target of breeders (Jiban Mitra, 2001), the third approach which may also serve as an alternative to the two morphological incorporations described above and agronomic and physiological function of resistance to drought in high yielding genotypes; The desired goals of evolving high yielding drought tolerant genotypes (Ishiyaku and Aliyu, 2013) would thus be accomplished by simultaneous selections under water stressed and non-water stressed environments for yield under nonwater stressed and stability under water stressed. It will be useful to classify the correct hybrid combinations by evaluating the combination of parental ability to select drought-tolerant genotypes in cowpea in breeding programs (Hira Lal, 2009; Kadam, 2013).

Hence the purpose of this study was to understand genetic control by evaluating different genetic parameters and evaluating screened diverse drought tolerance cowpea genotypes for general and specific combining capacity of certain yield traits under drought-stressed condition.

2. Material and Methods

The experiment was performed at the Ibadan University Teaching and Research Farm. The varieties of the cowpea used are maintained by the unit of genetic resources of the International Institute for Tropical Agriculture. Genotypes are of varying resistance to drought (Table 1). In the screenhouse, ten genotypes of cowpea were evaluated using the box screening approach proposed by Singh (1991). Two seeds of each of the ten cowpea lines were planted in a pot filled with rich garden soil and then thinned two weeks after planting, to one plant per pot. The crossing block consisted of 10 mainly Latin square consisting of ten parental lines. Each column on the Latin square is a mating unit in various units with crosses between parents. Pollen from the first parent is transmitted to the second parent in each cell. The second parent's pollen is passed on to the third parent etc. From a preliminary screening experiment, crosses were selected for diallel analysis in a dialect system involving the ten parental lines, with different drought tolerances. At Teaching and Research Farm, University of Ibadan during the dry season, November to February, parental lines, 21F1, and 21RF1 hybrids were selected for evaluation in an RCBD with three replications (3 replicas for each water regime). The experiment was conducted for 2 years during the dry season from October to February of 2014/2015 and 2015/2016. Through entrance was grown 3 m long in a single row plot with a row spacing 75 cm apart and 20 cm apart within a row. Two seeds were sown per hole and subsequently thinned to one seed per hole. Upon sowing, all the plants were watered before the trifoliolate leaves appeared upon which watering on water-stressed plots was suspended. Irrigation was developed by irrigating the plots with additional water whenever necessary, while on the other plot it was kept entirely during the growing season. The soil moisture content of the parcels has also been periodically calculated. Throughout the growing season crop management has been consistent. The following agronomic characteristics were gathered at the reproductive stage, the number of days to 50 percent flowering, number of days to 50 percent ripe pod. And the following data were collected at maturity: number of pods per plant, number of seeds per pod, length of pods, 100 seed weights and total seed weight. Method 1 model II Griffing (1956), adapted for partial diallel, and was used to combine capacity analysis of the dialel crosses using F1 and RF1. Genetic variance components were measured using Hayman's formulae (1954), as shown by Askel (1963).

Descriptive statistical methods have been used to independently obtain means and variances for each system (Steel 1997). According to Griffing (1956), the genetic variation in the materials was partitioning into general combining capacity and specific combining ability.

3. Results

Table (1) showed the characteristic of cowpea parents used:

Table 1. Characteristics of the ten cowpea parents used

NO	Parent	Source	Growth Habit	Level of Drought Tolerance
1	P1	Landrace	SS	HTD
2	P2	IITA	SS	TD
3	P3	-	E	HSD
4	P4	-	E	MTD
5	P5	-	E	TD
6	P6	-	E	HTD
7	P7	-	SS	MTD
8	P8	-	E	HSD
9	P9	-	E	VMTD
10	P10	-	S	TD

P1 = Danilla, P2 = IT92KD-357-3, P3 = TVU7778, P4 = TVU12349, P5 = IT93K-432-1, P6 = IT97K-499-35, P7 = IT89KD-288, P8 = IT98K-205-8, P9 = IT98K-491-4, P10 = IT91K-513. SS = Semi Spreading, E = Erect. HTD = Highly Tolerance of Drought, TH = Tolerance of Drought, MTD = Moderately Tolerance of Drought, VMTD = Very Moderately Tolerance of Drought, HSD = Highly Susceptible of Drought.

3.1. The genetic component of variance.

Table 2 shows partial diallel mean square values for all yielding characters under water-stressed (WS) and well-watered (WW) conditions. The GCA, SCA, and RCA (General Combining Ability, Specific Combining Ability, and Reciprocal Combining Ability, respectively) were all significant for all characteristics under both conditions.

However, the values for the total seed weight property in terms of component D in Table 3 are insignificant in both conditions. In addition, the D values for the number of pods per plants (NPP) under well-watered (WW) conditions and the number of seeds per plant (NSP) under water- stress (WS) conditions are also insignificant.

The genetic components of variance (Table 3), additive (D) and dominance (H1) were very significant under both conditions, except for pod length under WS and total seed weight under WW for variance component D, but all were significant under both conditions for variance component H1. The other components of dominant variation H2 and h2 under both conditions were also important to most of the traits.

The variance variable D ranged from 72.2±16.8 for the number of pods per plant to 3.2±2.3 for the length of the pods both under WS. The H1 variance variable ranged from 914.7±120.8 for total seed weight to 14.1±1.2 for the number of seeds per pod both under the WW conditions. The Fr-component whose value indicates the proportion of dominant (+ sign) or recessive (-sign) alleles showed significant values ranging from 603.3±130.0 for total seed weight in WW condition to 4.6±5.3 for the pod length in WS condition. The calculated ratio (H1/D) 1/2 of genetic components that provide valuable information about the degree**,** order, and course of dominance ranged from 4.36 for total seed weight to 1.51 for the number of days to the first day that both flowered under WW. The ratio h2/H2 estimates the number of gene groups showing a certain dominance ranged from 6.13 for the number of days to first flowering to 0.03 for 100SW both under WS. The ratio H2/4H1 estimates the relative mean allelic frequencies for parents ranging from 1.18 for total seed weight under WS to 0.07 for 100SW under WW and the number of days for the first flowering under WS. The heritability of the narrow sense (Hns) ranged from 0.66 for the number of days to the first flowering to 0.24 for the number of pods per plant and the length of the pods under WS.

3.2. General combining ability effects

Combining ability Effects (Table 4) estimates the parents' comparative effect (GCA) and cross-combination (Table 5) (SCA) in relation to each other.

Danilla, IT92KD-357-3, TVU7778, TVU12349, IT97K-499-35, and IT89KD-288 had a relatively high GCA effect on the number of days to flower, thus appearing to possess unfavorable alleles under both conditions. IT93K-432-1, IT89KD-288, IT98K-205-8, IT98K-491-4, and IT99K-513-21 had low to negative GCA effects. The same trend has been observed for the number of days to the first ripe pod under both conditions. As for the number of pods per plant, under well-watered conditions, TVU7778, IT93K-432-1, and IT97K-499-35, had relatively high positive, meaningful GCA effects, while TVU12349 and IT89KD-288 had relatively high negative GCA effect. TVU12349, and IT89KD-288 had a high negative GCA value under water-stressed conditions, while Danilla, TVU7778, IT93K-432-1, and IT98K-205-8 were intermediates. The number of seeds per pod had a strongly positive, major GCA effect under well-watered conditions for IT92KD-357-3, TVU7778, and IT97K-499-35, while TVU7778, and IT97K-499-35 were relatively good water-stressed combiners due to their high positive GCA effect. Danilla, IT92KD-357-3, TVU7778, IT93K-432-1, had a fairly strong positive GCA effect for 100-seed weight and have therefore good combination capability under both conditions. As for total seed weight, TVU7778, IT93K-432-1, and IT97K-499-35 had strong positive GCA effects and thus good seed weight combiners under well-watered environment. However, under water-stressed circumstances, Danilla, TVU7778, and IT97K-499-35 had major positive GCA impacts, and thus were strong combiners. With respect to the pod length, Danilla, IT92KD-357-3 and IT97K-499-35, had a fairly high positive GCA effect and therefore good combiners capability under both conditions.

Table 2. Mean square values of partial diallel for yield characteristics of cowpea crosses under water-stress (WS) and well-watered (WW) conditions

SV	ENV	GE	REP	P	F1	RF1	PvF1	PvRF1	E	GCA	SCA	RCA
	DF	51	2	9	20	20	1	1	102	9	20	20
NDF	WW	30.39*	2.39	58.65*	29.92*	19.91*	4.67*	22.99*	0.64	1451.39*	195916.50*	6.96*
	WS	42.12*	5.55	100.98*	23.50*	25.82*	172.60*	290.04*	0.92	1668.78*	266832.68*	3.16*
NRP	WW	57.95*	1.74	107.34*	71.76*	26.59*	18.62*	2.11*	1.95	2779.11*	547198.13*	10.69*
	WS	55.74*	18.84	134.85*	32.70*	33.94*	303.85*	285.42*	1.01	3067.54*	655787.38*	9.90*
NPP	WW	222.14*	8.42	344.63*	311.78*	70.56*	0.02^{ns}	310.79*	9.69	325.64*	18814.91*	62.43*
	WS	69.98*	18.06	221.10*	27.32*	52.08*	52.08*	35.60*	5.49	82.99*	5939.63*	3.17*
NSP	WW	10.26*	18.19	10.17*	8.62*	9.82*	8.86*	4.45*	1.00	148.18*	12262.10*	3.01*
	WS	17.97*	0.30	16.40*	16.02*	19.35*	14.11*	78.86*	1.44	136.32*	3066.48*	3.37*
POL	WW	13.11*	3.73	11.48*	15.40*	12.80*	1.37*	0.37*	0.47	221.38*	5473.84*	1.58*
	WS	12.64*	3.24	10.72*	12.65*	12.36*	11.32*	54.23*	1.46	208.78*	7843.27*	4.28*
100SW	WW	27.26*	10.95	14.80*	38.23*	21.61*	16.83*	4.32*	0.93	346.50*	18888.11*	5.03*
	WS	41.03*	0.73	36.01*	46.14*	38.79*	9.62*	90.23*	1.78	268.07*	12015.32*	11.14*
TSW	WW	300.10*	86.71	308.43*	396.84*	165.89*	0.76^{ns}	658.63*	16.45	389.89*	35835.92*	74.71*
	WS	141.66*	13.94	74.78*	139.56*	145.08*	941.21*	698.85*	4.92	293.62*	9922.88*	38.75*

per Plant (NSP), Pod Length (POL), 100 Seed weight (100SW) and Total Seed Weight (TSW)Number of Days to 50% flowering (NDF), Number of Days to 50% ripe pods (NRP), Number of Pods per Plant (NPP) and Number of Seeds. Environment (ENV), Genotypes (GE), Parent (P), First filial generation (F1), Reciprocal first filial generation (RF1), Environmental Error (E), General Combining Ability (GCA), Specific Combining Ability (SCA) and Reciprocal Combining Ability (RCA).

Table 3. Estimates of genetic parameters for different yield characteristics under well-watered (WW) and water-stress (WS) conditions in cowpea

	GP	D	Fr	H1	H2	h^2	E	H1/D	H2/4H1	h^2/H2	Hns
NDF	WW	19.4±4.1*	30.2±9.6*	44.0±8.9*	23.3±7.5*	523.5±5.1*	0.2±1.3^{ns}	1.51	0.13	8.43	0.45
	WS	31.4±6.2*	63.3±14.4*	76.6±13.3*	22.3±11.3^{ns}	1249.9±7.0*	0.3±1.9^{ns}	1.56	0.07	16.13	0.66
NRP	WW	39.1±5.5*	74.9±35.8*	109.7±33.0*	50.9±28.1^{ns}	1579.8±1.0*	0.65±4.7^{ns}	1.67	0.12	9.07	0.46
	WS	41.9±10.6*	91.1±24.4*	120.6±22.0*	55.3±19.0*	1941.1±9.0*	0.5±3.2^{ns}	1.69	0.11	10.12	0.36
NPP	WW	26.8±40.0^{ns}	48.6±92.4^{ns}	288.9±85.2*	198.9±72.4*	96.8±48.5*	3.2±12.1^{ns}	3.29	0.17	0.49	0.39
	WS	72.2±16.8*	142.7±38.8*	174.6±35.8*	89.1±30.4*	141.8±20.4*	1.91±5.1^{ns}	1.55	0.13	1.59	0.24
NSP	WW	3.8±0.5*	5.2±1.3*	14.1±1.2*	8.0±0.9*	17.3±0.7*	0.4±0.2*	1.92	0.14	2.16	0.49
	WS	5.1±3.3^{ns}	11.8±7.6^{ns}	30.9±6.9*	18.1±5.9*	8.7±4.0*	0.5±0.9^{ns}	2.47	0.15	0.48	0.38
POL	WW	6.3±2.1*	9.2±4.8^{ns}	17.1±4.4*	8.7±3.7*	21.9±2.5*	0.2±0.0*	1.65	0.13	2.5	0.54
	WS	3.2±2.3^{ns}	4.6±5.3^{ns}	20.7±4.9*	16.4±4.2*	0.3±0.0*	0.5±0.7^{ns}	2.54	0.2	0.02	0.24
100SW	WW	12.3±3.4*	41.3±9.2*	56.1±8.5*	15.5±7.2*	4.7±4.8^{ns}	0.4±1.2^{ns}	2.14	0.07	0.3	0.57
	WS	11.5±5.0*	17.4±13.8^{ns}	50.6±12.8*	30.2±10.8	1.0±7.3*	0.6±1.8^{ns}	2.1	0.15	0.03	0.47
TSW	WW	48.1±56.8^{ns}	603.3±130.0*	914.7±120.8*	289.3±102.7*	22.7±68.4^{ns}	5.9±17.1^{ns}	4.36	0.08	0.08	0.31
	WS	23.4±15.5^{ns}	47.1±35.8^{ns}	192.5±33.0*	139.0±28.1*	777.1±18.8*	1.7±4.7^{ns}	2.87	1.18	5.59	0.29

Number of Days to 50% flowering (NDF), Number of Days to 50% ripe pods (NRP), Number of Pods per Plant (NPP) and Number of Seeds per Plant (NSP), Pod Length (POL), 100 Seed weight (100SW) and Total Seed Weight (TSW).
Additive Variance (D), Proportion of dominant (+ sign) or recessive (-sign) alleles (Fr), Components of Dominance Variance (H1, H2, and h2), Environmental Variance (E), Order and Degree of Dominance ((H1 / D) ½), Mean Allelic Frequencies for parent (H2/4H1).
Number of gene group (h2 / H2), and Narrow Sense Heritability (Hns).

Table 4. General combining ability effect yield characteristics of ten cowpea parents' genotypes under water stressed (WS) and non-water stressed environments

Parents	NDF		NRP		NPP		NSP		100SW		TSW		POL	
	WW	WS	WW	WS	WW	WS	WW	WS	WW	WS	WW	WS	WW	WS
P1	6.69	6.77	9.29	9.77	1.89	1.71	0.79	1.14	3.59	3.78	0.79	2.35	2.00	1.78
P2	6.63	6.75	9.58	9.61	-1.17	0.26	2.29	1.86	4.13	2.43	1.05	0.82	3.20	2.66
P3	8.36	9.08	10.50	11.60	4.48	1.43	2.76	3.17	0.98	0.96	7.82	3.49	1.94	1.97
P4	-12.33	-13.36	-16.78	-18.18	-4.89	-3.37	-4.12	-3.36	-6.59	-5.80	-5.99	-5.41	-5.19	-4.72
P5	3.59	3.45	5.23	4.49	3.07	1.30	1.26	1.27	2.07	2.88	2.37	2.10	1.03	1.24
P6	10.73	12.05	15.35	16.05	5.28	3.35	3.35	3.39	5.57	4.86	3.97	6.70	4.23	4.83
P7	-11.86	-12.49	-16.45	-17.58	-6.61	-2.33	-3.94	-3.63	-5.82	-4.85	-5.12	-4.81	-4.91	-4.69
P8	-1.84	-1.24	-2.38	-1.73	-1.32	-1.25	-0.13	-0.81	-0.46	-1.01	-2.77	-2.00	0.27	-0.17
P9	-8.22	-8.94	-11.55	-12.60	-3.07	-0.10	-2.77	-2.89	-3.49	-3.07	-4.16	-2.82	-3.31	-3.26
P10	-1.75	-2.07	-2.80	-1.83	2.34	-1.00	0.51	-0.13	0.02	-0.19	2.04	-0.43	0.75	0.36
S.E	**0.17**	**0.20**	**0.30**	**0.21**	**0.66**	**0.50**	**0.21**	**0.25**	**0.20**	**0.28**	**0.86**	**0.47**	**0.15**	**0.26**

Number of Days to 50% flowering (NDF), Number of Days to 50% ripe pods (NRP), Number of Pods, per Plant (NPP) and Number of Seeds per Plant (NSP), Pod Length (POL), 100 Seed weight (100SW) and Total Seed Weight.

3.3. Specific combining ability

With respect to the number of days to 50 per cent flowering (Table 5), all crosses except IT92KD-357-3×IT97K-499-35, Danilla×IT92KD-357-35, Danilla×IT97K-499-35 and TVU7778×IT97K-499-35 expressed positive SCA effects for this trait under well-watered conditions, the same was observed under water-stressed conditions except TVU7778×IT97K-499-35 and Danilla×IT98K-205-8 which showed significant negative SCA effects. The same pattern was observed for the number of days to 50 percent ripe pod, with the exception of Danilla×IT92KD-357-35, IT92KD-357-3×IT97K-499-35 and TVU7778×IT97K-499-35 which showed significant negative SCA effect under well-watered and TVU7778× IT97K-499-35 showing significant negative effect under both conditions.

With respect to the number of pods per plant, positive SCA effect was observed in all the hybrids under well-watered conditions except, Danilla×IT92KD-357-35, Danila× TVU7778, Danilla×IT98K-491-4, IT92KD-357-35×TVU7778, and IT93K-432-1×IT97K-499-35. However, under water-stressed condition, only IT92KD-357-35×TVU7778, IT92KD-357-35× IT98K-205-8, and IT93K-432-1×IT97K-499-35 had negative SCA effect. For the number of seeds per pod, only Danilla×IT92KD-357-35, and IT92KD-357-35×IT97K-499-35 had negative SCA effect under well-watered condition, while under water-stressed, Danilla×IT98K-205-8, and IT92KD-357-35×IT98K-205-8, had negative SCA effect.

100 seeds weight, under well-watered condition showed positive SCA effect for all the hybrids except Danilla×IT92KD-357-35, Danila×TVU7778, and IT92KD-357-35×TVU7778. Under water-stressed, Danila×TVU7778, Danilla×IT98K-205-8, IT92KD-357-35× IT98K-205-8, and TVU7778×IT97K-499-35 had negative SCA effect. Only Danilla×IT92KD-357-35, Danila×TVU7778, IT92KD-357-35×IT97K-499-35 IT92KD-357-35×IT91K-513 and IT97K-499-35× IT98K-205-8, had negative SCA effect for total seeds weight under well-watered condition, while under water-stressed Danilla×IT92KD-357-35, Danila×TVU7778, Danilla×IT98K-205-8, IT92KD-357-35×IT98K-205-8, and IT93K-432-1×IT97K-499-35 had negative SCA effect for total seed weight.

For pod length under well-watered condition, all hybrids had positive SCA effect except Danilla×IT92KD-357-35 while water-stressed condition, all the hybrids were positive except Danilla×IT98K-205-8 and IT92KD-357-35×TVU7778.

As for the number of seeds per pod, 9 and 6 hybrids showed positive RCA effects under water-stressed and well-watered conditions respectively. Fifteen hybrids were observed for a positive RCA effect for 100SW under water-stressed, while only eight hybrids were observed for a positive RCA effect under well-watered conditions. The positive RCA had effect of 6 and 7 hybrids under well-watered and water-stressed conditions. For both conditions, 16 hybrids for pod lengths were found to be the best individual combiners for this trait, whereas 12 and 8 hybrids were observed for strong, important RCA effects for well-watered and water-stressed respectively.

Table 5. Specific combining ability effect for different agronomic characteristics in cowpea under water-stressed (WS) and well-watered environments

Cross	**NDF**		**NRP**		**NPP**		**NSP**		**100SW**		**TSW**		**POL**	
	WW	**WS**	**WW**	**WS**	**WW**	**WS**	**WW**	**WS**	**WW**	**WS**	**WW**	**WS**	**WW**	**WS**
P1×P2	-11.2	7.58	-11.3	9.06	-3.85	4.34	-4.2	0.84	-2.32	3.12	-5.68	-0.96	-4.6	1.56
P1×P3	3.39	6.20	5.56	10.07	-1.66	1.88	2.78	1.23	-0.54	-2.69	-2.70	-1.98	0.61	0.91
P1×P5	9.32	23.80	13.08	31.68	12.27	7.31	1.56	5.99	5.27	14.52	11.09	9.24	3.60	10.34
P1×P6	-0.48	5.16	1.04	11.67	3.01	5.59	0.94	4.75	1.12	9.98	9.33	19.91	2.23	4.40
P1×P8	16.92	2.90	20.77	2.62	11.04	0.14	2.82	-1.59	5.69	-0.59	7.77	-4.23	5.46	-0.51
P1×P9	22.30	28.27	29.44	36.92	-1.72	0.35	5.97	4.27	9.09	9.26	5.36	6.90	7.02	6.82
P2× P3	7.45	4.83	9.93	8.22	-4.17	-1.25	2.36	3.02	-0.91	1.24	4.37	2.30	1.57	-0.39
P2× P5	8.47	25.32	12.12	35.42	1.70	8.72	2.77	6.96	4.92	11.91	3.73	14.61	5.80	9.97
P2× P6	-1.42	6.34	-2.92	10.67	0.41	1.44	-0.73	3.12	-0.17	0.13	-4.08	2.51	0.46	4.83
P2×P8	11.56	-0.25	16.06	-0.56	3.33	-4.50	3.91	-0.87	7.81	-1.74	5.03	-4.82	5.07	0.34
P2×P10	13.31	26.78	16.40	35.74	2.60	3.10	3.98	3.49	6.30	11.39	-6.26	7.77	4.00	9.07
P3× P5	11.99	12.35	14.12	14.51	11.35	8.54	4.14	1.51	3.02	2.33	5.76	1.12	4.90	4.02
P3× P6	-0.48	-0.92	-3.17	-1.89	1.30	0.55	0.93	1.72	1.42	-0.49	1.38	3.16	0.19	0.45
P3×P7	22.94	26.46	33.13	35.42	2.27	2.43	6.26	4.83	11.37	10.21	9.80	9.93	9.01	7.30
P3× P10	11.34	9.38	14.65	13.40	18.66	10.11	4.06	6.42	7.77	3.81	27.77	8.55	6.50	7.26
P4× P6	18.37	20.68	26.95	27.23	10.55	4.14	3.42	2.47	8.28	9.73	9.86	0.90	6.17	6.72
P5× P6	6.74	6.97	7.60	9.56	-3.00	-1.54	2.53	0.24	4.05	5.01	1.18	-3.76	3.80	1.63
P6× P10	15.93	16.33	21.75	23.77	9.78	4.22	4.99	6.65	8.03	1.59	11.90	10.85	7.84	5.98
P6×P8	21.67	9.86	33.38	11.62	1.37	1.28	4.37	1.44	7.76	5.53	-2.23	-0.05	8.68	2.14
P6×P9	19.02	20.93	27.05	26.98	13.19	1.61	6.91	3.89	10.05	8.16	10.53	10.99	8.96	7.47
P8 ×P10	19.19	21.69	28.36	33.17	6.50	4.94	7.36	5.81	9.98	8.18	12.38	7.37	8.52	6.42
S.E	**0.51**	**0.61**	**0.90**	**0.64**	**1.99**	**1.50**	**0.64**	**0.76**	**0.62**	**0.85**	**2.60**	**1.42**	**0.44**	**0.78**

Number of Days to 50% flowering (NDF), Number of Days to 50% ripe pods (NRP), Number of Pods, per Plant (NPP) and Number of Seeds per Plant (NSP), Pod Length (POL), 100 Seed weight (100SW) and Total Seed Weight.

Table 6. Reciprocal combining ability effects for some agronomic characteristics of cowpea crosses under water- stressed (WS) and water-watered conditions

Cross	**NDF**		**NRP**		**NPP**		**NSP**		**100SW**		**TSW**		**POL**	
	WW	**WS**	**WW**	**WS**	**WW**	**WS**	**WW**	**WS**	**WW**	**WS**	**WW**	**WS**	**WW**	**WS**
2*1	0.00	-0.28	-4.50	-1.17	-0.77	0.83	-0.17	-0.08	0.63	-0.02	-0.42	0.15	0.30	-0.22
3*1	0.00	1.33	1.83	2.50	-0.37	2.92	-0.58	-1.25	-2.50	-0.83	2.50	2.33	-1.33	-0.92
5*1	-3.83	0.17	-4.58	1.00	10.12	0.10	1.80	-0.55	0.00	-0.52	12.02	1.85	1.12	-0.42
6*1	-0.17	0.33	1.50	2.33	2.17	0.50	-0.33	0.63	0.08	-2.25	0.68	-4.17	2.08	0.50
8*1	0.00	-0.33	0.50	-0.83	0.60	1.25	0.73	0.18	0.12	-1.80	6.55	3.02	0.95	0.75
9*1	0.67	-0.17	-0.67	0.17	0.42	-0.45	1.08	1.17	-3.17	-4.63	5.08	-2.25	1.83	-0.33
3*2	-0.33	-0.39	-1.17	-0.50	1.20	1.83	0.50	0.25	-0.83	-1.75	5.83	7.58	-0.50	0.50
5*2	-1.75	3.67	-1.92	4.92	1.92	-1.50	0.58	-0.17	0.58	-3.33	-5.42	-7.50	-0.83	1.50
6*2	0.50	0.50	0.17	-1.50	-1.67	-1.73	0.60	-1.62	3.70	1.05	-2.80	-0.10	-0.18	-0.25
8*2	0.25	-0.50	1.42	-1.50	2.67	0.17	0.17	-0.75	-0.28	0.17	-5.43	-3.50	0.33	-0.25
10*2	-0.25	1.33	1.00	1.17	6.75	0.08	0.77	0.00	-0.65	-1.58	-1.73	-0.75	-0.92	-4.07
5*3	3.50	-0.17	2.33	-3.67	14.12	-2.67	1.05	0.48	-0.84	-1.05	13.12	3.65	1.27	-0.35
6*3	-1.33	-0.83	-1.83	0.50	4.05	0.22	1.73	0.05	-2.97	0.05	10.27	0.02	1.78	-0.43
7*3	1.00	1.00	5.00	1.50	-0.70	0.58	-1.50	-3.08	-1.50	-1.40	1.43	4.58	-1.83	-2.83
10*3	-0.83	0.17	-0.83	-0.67	-8.20	-4.65	0.78	-2.08	1.13	-3.25	0.40	1.52	0.15	0.05
6*4	0.67	0.00	3.33	0.17	-1.92	1.17	-0.08	-0.40	0.45	1.42	-5.23	-1.67	2.17	1.42
6*5	-1.62	-0.10	1.00	1.17	-6.67	-0.67	0.70	1.20	1.35	1.13	-4.22	0.98	0.48	0.02
10*5	-0.67	2.33	2.00	0.83	5.83	0.08	0.85	0.00	-0.08	-3.77	1.25	12.33	-0.08	-1.17
8*6	0.50	-1.72	-0.50	-4.00	-1.92	0.73	-0.58	-0.13	1.70	2.53	-0.17	-1.45	0.86	0.42
9*6	2.42	1.33	4.33	0.83	-4.22	-0.75	-0.73	-2.93	-0.57	0.13	-1.92	-1.33	-0.48	-2.47
10*8	-0.17	-0.33	1.00	-4.33	-2.17	1.08	-1.00	-1.58	0.00	0.10	-3.42	-4.92	0.50	-1.80
S.E	**0.57**	**0.68**	**0.99**	**0.71**	**2.20**	**1.66**	**0.70**	**0.84**	**0.68**	**0.94**	**2.87**	**1.57**	**0.49**	**0.86**

Number of Days to 50% flowering (NDF), Number of Days to 50% ripe pods (NRP), Number of Pods, per Plant (NPP) and Number of Seeds per Plant (NSP), Pod Length (POL), 100 Seed weight (100SW) and Total Seed Weight.

4. Discussion and Conclusion

Both additive variance (D) and dominance variance (H1) of genetic variance components suggested important for most study characteristics in well-watered and water-stressed environments, this indicates that the expression of all the characteristics is influenced by both additive and dominance gene behavior. However, additive variance was more pronounced for number of pods per plant but small for pod length under water-stressed condition. Dominance variance was more important for number of pods per plant and total seed weight under well-watered condition. In both conditions, however, there was the preponderance of the dominance gene action.

The H2/4H1 reflecting the proportion of dominance gene with positive or negative effects in parents was less than 0.25 for all characteristics under both conditions except total seed weight under WS indicating asymmetric distribution of positive and negative dominant genes in parents as suggested by (Amiri-Oghan et al., 2009). The Fr variable representing the sigh path showed positive with more than zero for all traits also indicated asymmetrical distribution of dominant and recessive alleles in parents, which also indicates that dominant alleles are more common in both conditions than recessive alleles. However, some Fr values are positive but insignificant for some traits indicating the symmetric distribution of dominant recessive genes in the parents.

The (H1 / D) 1/2 that reflects mean degree of dominance was more than one in all characteristics and ranged from 1.51 for the number of days to the first flowering to 4.36 for total seed weight both under well-watered indicating the importance of overdominance gene-action.

The values of h2 under all conditions except 100SW under both conditions and total seed weight under well-watered conditions indicating the existence of overall dominant gene effect for certain traits were important in all traits. The ratio h2 / H2 shows the varying number of genes that regulate these traits. This study suggested at least ten plant height genes in the water-stressed environment, and at least three and eight genes for terminal leaflet area and number of leaves per plant in well-watered and water-stressed environments respectively, thus revealing that their polygenic inheritance is a feature of quantitative traits. For all the traits, the environmental variable (E) was not important.

A very important genetic method for identifying successful parental combinations to grow superior hybrid populations is the combination of ability analysis (Hussain, 2009). General combination ability (GCA) tests an individual parent's average success in hybrid combinations and is related to additive gene effect. The Specific Combining abilities (SCA) tests the relative efficiency of specific combinations of hybrids and is correlated with a non-additive gene effect (Rojas and Sprague, 1952; Griffing, 1956). Genetic interactions influence both the GCA and SCA effects (Miranda et al., 1988). Identifying combinations of superior hybrids can effectively assist breeding of drought-tolerant hybrids.

Variance analysis for combining abilities revealed highly significant variations in both the cowpea parents' general combination (GCA) and specific combining ability (SCA) suggesting the importance of both additive and non-additive gene effects in their ancestry in one or both environments suggesting heterogeneous crosses. Hira Lal et al. (2009) testing the combination of quantitative trait ability in cowpea also suggested the important effects of GCA and SCA in most traits except for peduncle length and 100-seed weight. The predicted variances due to specific combination ability is higher than the general combination ability suggesting the predominance of the non-additive gene action in both environments in these traits. This also matches (Kadam et al., 2013; Bhavesh Patel et al., 2013; Selvarkumar et al., 2014), but contrasts with (Romanus et al., 2008; Carvallo et al., 2012; Ayo-Vaughan et al., 2013). The estimates of the predictability ratio less than unity in these characteristics indicate that hybrid success for these characteristics may be difficult to predict on the basis of parents' general combining ability due to the value of dominance. Thus, selection for better hybrids would have to wait for later generations. With regard to the number of days to 50 percent flowering and the number of days to 50 percent ripe pods, many parents seemed not to be favored due to high positive GCA effects under water stress, which is an indication of water deficit lateness. Significant numbers of parents were promising for a water deficit environment for other characteristics considered due to their high GCA effects, particularly Danilla and IT97K-499-35 observed in all the characteristics. This implies that in an intensive breeding program Danilla and IT97K-499-35 could be used for seed yield to exploit both additive and non-additive components of seed variation and were therefore good combiners in a water-stressed environment and could have contributed to a maximum number of favorable genes and possible allelomorphs (Ojo, 2005; Gouri Shankar et al, 2005).

The breeders' goal will be to grow a hybrid that will perform under drought stress in terms of yield. Despite their major SCA effects on the traits, large numbers of crosses were found to perform well under both conditions. Some parents appeared to be specific when cross-examining the performance of GCA and SCA results, therefore it is suggested that the selection should be based on success at both levels. This is the combination which will include parents with high GCA results. Most crosses with a major SCA effect often have at least one parent with a strong GCA effect, indicating the presence of additive material additive × additive material and additive × dominance gene activity. The hybridization of high combiners can be controlled by additive and additive × additive forms of gene action, so crosses can result in transgressive segregation for the trait involved in the advanced generation. Crosses that exhibit low GCA effects but high SCA effects suggest epistatic gene action. This may also mean that both parents contributed to the gene dispersion and genetic interaction between beneficial alleles. A partial superiority is demonstrated by crosses with a negative SCA estimate (Ojo, 2005).

In conclusion, in the analysis of the characters, additive and nonadditive gene actions were detected; however, under both circumstances, predominance of nonadditive gene action occurred. Consequently, enhancement for these traits would involve a recurrent selection procedure as a result of the prevalence dominance gene effect to allow favorable gene recombination in both conditions at later generations. IT97K-499-35 and Danilla could be used as parents with desirable genes for genetic improvement of the considered yield components in cowpea with relatively large, positive, and important GCA results. Also, TVU7778 × 89KD-288 and Danilla × IT97K499-35 proved to be the best specific combiners in this analysis for all the traits. The heritability of narrow-sense ranged from 24.0 percent for the number of pods per plant and pod length to 66.0 percent for the number of days to 50 percent for flowering under water-stressed conditions. This indicates that some of these characteristics could be improved in both situations.

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